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Frontiers in páramo water resources research: A multidisciplinary assessment

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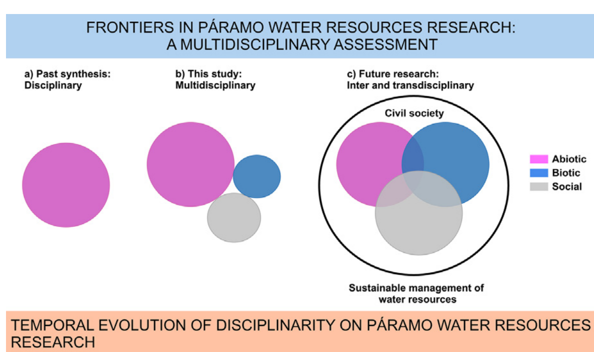
HIGHLIGHTS

- Multidisciplinary literature review of 147 studies on páramo water resources research
- Abiotic studies dominate (59 %), rather than biotic (18 %) and social studies (23 %)
- Most abiotic studies have been carried out in the humid páramo of southern Ecuador
- Few biotic studies directly assessed in-stream metabolic and nutrient cycling processes
- Social studies assessed the implementation of water funds and payment for ecosystem services

GRAPHICAL ABSTRACT



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ABSTRACT

Interdisciplinary knowledge is necessary to achieve sustainable management of natural resources. However, research is still often developed in an exclusively disciplinary manner, hampering the capacity to holistically address environmental issues. This study focuses on páramo, a group of high-elevation ecosystems situated around ~3000 to

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~5000 m a.s.l. in the Andes from western Venezuela and northern Colombia through Ecuador down to northern Peru, and in the highlands of Panama and Costa Rica in Central America. Páramo is a social-ecological system that has been inhabited and shaped by human activity since ~10,000 years BP. This system is highly valued for the water-related ecosystem services provided to millions of people because it forms the headwaters of major rivers in the Andean-Amazon region, including the Amazon River. We present a multidisciplinary assessment of peer-reviewed research on the abiotic (physical and chemical), biotic (ecological and ecophysiological), and social-political aspects and elements of páramo water resources. A total of 147 publications were evaluated through a systematic literature review process. We found that thematically 58, 19, and 23 % of the analyzed studies are related to the abiotic, biotic, and social-political aspects of páramo water resources, respectively. Geographically, most publications were developed in Ecuador (71 % of the synthesized publications). From 2010 onwards, the understanding of hydrological processes including precipitation and fog dynamics, evapotranspiration, soil water transport, and runoff generation improved, particularly for the humid páramo of southern Ecuador. Investigations on the chemical quality of water generated by páramo are rare, providing little empirical support to the widespread belief that páramo environments generate water of high quality. Most ecological studies examined the coupling between páramo terrestrial and aquatic environments, but few directly assessed in-stream metabolic and nutrient cycling processes. Studies focused on the connection between ecophysiological and ecohydrological processes influencing páramo water balance are still scarce and mainly related to the dominant vegetation in the Andean páramo, i.e., tussock grass (*pajonal*). Social-political studies addressed páramo governance and the implementation and significance of water funds and payment for hydrological services. Studies directly addressing water use, access, and governance in páramo communities remain limited. Importantly, we found only a few interdisciplinary studies combining methodologies from at least two disciplines of different nature despite their value in supporting decision-making. We expect this multidisciplinary synthesis to become a milestone to foster interdisciplinary and transdisciplinary dialogue among individuals and entities involved in and committed to the sustainable management of páramo natural resources. Finally, we also highlight key frontiers in páramo water resources research, which in our view need to be addressed in the coming years/decades to achieve this goal.

Contents

1. Introduction

Mountainous areas worldwide provide important hydrological ecosystem services that sustain the social and economic development of surrounding and downstream populations (Immerzeel et al., 2020; Viviroli et al., 2007). In the tropical Andes and Central America, a group of ecosystems – known as páramo (Hofstede and Llambí, 2020) – are situated above the tree line (at ~3000 m a.s.l.) and below the glaciers (where these are present; at ~5000 m a.s.l.). Páramo landscapes are molded by volcanic and glacial and periglacial activity (Luteyn, 1992; Smith and Cleef, 1988), as well as by human activity (White, 2013). Given the high elevation location and biophysical characteristics of páramo, its water resources support and regulate the water supply for domestic, industrial, agricultural, and recreational use, as well as for hydropower energy generation (Buytaert et al., 2006a; Célleri and Feyen, 2009). At the same time, rapid diversification rates of organisms that occupy this environment in response to unique and extreme hydrometeorological conditions make páramo the fastest-evolving biodiversity hotspot in the world (Madriñán et al., 2013).

While its hydrologic ecosystem services create a large social basis for páramo conservation and sustainable management, other uses of páramo – including extensive animal husbandry, large-scale agriculture (mostly potatoes), mineral extraction, and afforestation with exotic species – affect its capacity to provide hydrological benefits for the wider society (Mosquera et al., 2022). As a social-ecological system (Berkes and Folke, 1998; Cortés-Duque and Sarmiento Pinzón, 2013; Crespo, 2012; Hofstede, 2001a), it is thus crucial to understand how páramo abiotic and biotic elements and processes influence hydrological services. It is also important to assess how those services influence and are affected by communities and water users within and beyond páramo boundaries. An improved understanding of the physical, chemical, ecological, and social-political dynamics and interactions of this system can help in formulating strategies and policies aimed at securing the sustainable management of páramo water resources.

Biophysically, páramo is characterized by open vegetation consisting of tussock-forming grasses, small herbs, xerophytic shrubs, cushion-forming plants, and several unique life forms such as giant caulescent rosettes (Cuatrecasas, 1958; Luteyn, 1999). Within this open landscape, there are also small trees and occasional patches of woodlands, mainly within the genus *Polylepis* (Bader et al., 2007; Sevink and Hofstede, 2014; Vargas and Zuluaga, 1986). Abrupt changes in fog and dew, radiation, temperature, atmospheric demand, and soil moisture availability throughout the day influence páramo ecological and biological processes (Azócar and Rada, 2006; Hedberg and Hedberg, 1979; Lauer, 1981; Monasterio and Sarmiento, 1991).

Socially, páramo has been used by people ever since the early days of human occupation of the South American continent (10,000 years BP; Bruhns, 2003; Lavallée, 2000; Salazar, 1985). As a result, it has been shaped by the coexistence of cultural and natural diversity, particularly by the cyclic occurrence of human-induced fire to increase resource productivity (White, 2013). While widespread and intensive fire is reported to reduce páramo biodiversity (Verweij, 1995), small-scale farming and low to intermediate levels of burning may add to landscape biological diversity (Bremer et al., 2019; Keating, 2007; Maldonado and De Bièvre, 2011). Páramo also remains central to the culture and livelihoods of many local and Indigenous communities and farmers who rely on it for agriculture, grazing, and water supply (Hofstede, 2001b; Manosalvas et al., 2021). It also provides important cultural ecosystem services, including spiritual value, which contribute to the well-being of local communities (Farley and Bremer, 2017).

Early European naturalists in the 19th century such as Alexander von Humboldt recognized the singularity and ecological importance of páramo (e.g., Humboldt and Bonpland, 1807). Although the diversity, structure, and ecology of páramo vegetation were studied in detail since then and with more emphasis throughout the 20th century (e.g., Acosta-Solís, 1984; Cuatrecasas, 1958; Monasterio, 1980; Van der Hammen and Cleef, 1986), institutional research on páramo water resources was only carried out in the last three decades. A synthesis of the status of hydrological research was conducted in 2006 (Buytaert et al., 2006a), providing a baseline description of strictly biophysical (e.g., vegetation, soils, topography) and hydrometeorological (climate, precipitation, and streamflow) features of páramo. The authors highlighted several knowledge gaps, related to the lack of measurements for different compartments of the hydrological cycle and/or the low quality and short monitoring periods of the available data. In response to this, studies focused on the investigation of páramo hydrology increased during the last decade (Correa et al., 2020; Mosquera et al., 2022). In addition, information regarding the chemical quality of water generated by páramo streams and rivers also improved (e.g., González-Martínez et al., 2019; Pesántez et al., 2018; Riveros-Iregui et al., 2018). Despite these dispersed efforts, an integrated synthesis of páramo hydrology and its relation to water quality and ecosystem processes is still lacking.

Recently, the feedback and interactions between terrestrial and aquatic environments influencing the flow regulation of páramo have been investigated. Initial studies focused on evaluating metabolism (e.g., Carrillo-Rojas et al., 2019; Minaya et al., 2016b) and nutrient transport and cycling (e.g., Schneider et al., 2020; Whitmore et al., 2021). Few ecohydrological investigations have been devoted to understand the role of vegetation on páramo water balance (e.g., Ochoa-Sánchez et al., 2018, 2020; Suqui et al., 2021), as well as their influence on soil hydraulic properties. However, investigations on the influence of in-stream ecological processes and vegetation ecophysiological function on páramo flow generation and regulation remain scarce (Aparecido et al., 2018).

More recently, research on the social and political dimensions of páramo water resources complemented earlier biophysical and ecological investigations (e.g., Hofstede et al., 2014; Manosalvas et al., 2021; Sarmiento et al., 2017). As a result of the increased understanding of the role of páramo in water supply and elevated attention to environmental justice concerns (Manosalvas et al., 2021), researchers increasingly perceive páramo as a cultural landscape and social-ecological system long used and shaped by people (Denevan, 1992; Hess, 1990; Hofstede, 2001b; Keating, 2007). Thus, research on the social dimensions of páramo includes substantial work on the role of water funds and the outcomes of payment for ecosystem services programs mainly targeting páramo grasslands (e.g., Farley et al., 2011; Joslin, 2020a).

Although the understanding of the abiotic, biotic, and social-political aspects and elements of páramo water resources substantially improved in the last two decades, the information is still dispersed and disconnected from political platforms targeted to manage natural resources. This situation not only limits the capacity to guide decision-making and develop policies based on scientific evidence, but also the dissemination of generalized findings at a regional scale. Therefore, the overarching objective of this study is to synthesize and evaluate the status of knowledge regarding the water resources of the Andean and Central American páramo as an important provider of hydrological ecosystem services. This study not only contributes to improved information available for decision-making, but it also identifies frontiers in research that need to be considered to achieve sustainable management of páramo water resources.

2. Methods: literature search and synthesis

The literature review was conducted following the Guidelines for Systematic Reviews in Environmental Management (Collaboration for Environmental Evidence, 2013). First, we defined a list of search terms in English and Spanish related to the abiotic, biotic, and social elements and aspects of páramo water resources. The search terms were grouped into three main categories: (1) ecosystem (e.g., páramo, tropical alpine, high Andean), (2) aquatic environment (e.g., water, freshwater, aquatic), and (3) abiotic (e.g., precipitation, evaporation, streamflow), biotic (e.g., ecohydrology, metabolism, nutrient cycling), and social (e.g., payment for ecosystem services, governance, social impact) elements and aspects, and local and global change stressors (e.g., grazing, agriculture, forestation). The search terms in each category are listed in a text file as Supplementary Material. The Boolean operator

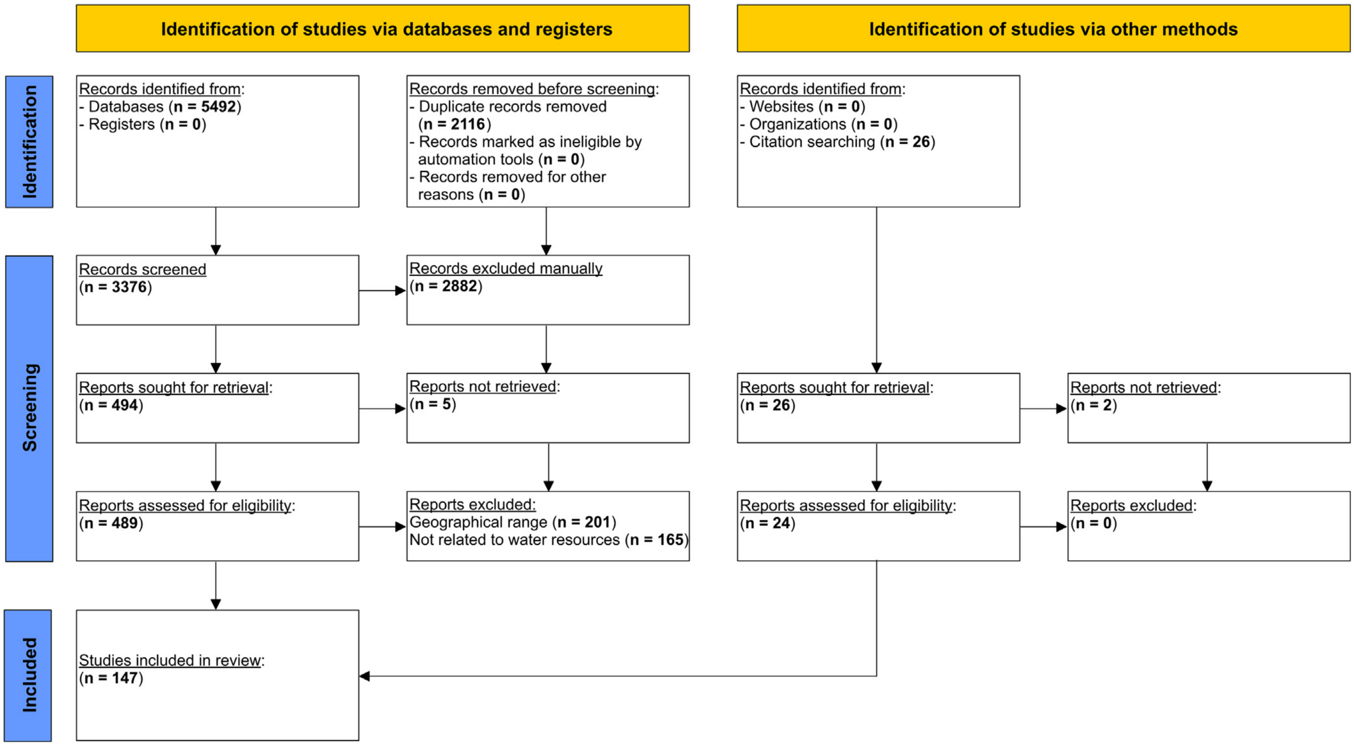

Fig. 1. Preferred Reporting Items for Systematic Reviews and Meta-Analyses flow chart (PRISMA 2020) of the systematic literature review (Page et al., 2021).

"AND" was used among the terms in each category and the Boolean operator "OR" to connect the terms among categories 1–3. The terms were searched in the title, abstract, and keywords of articles and books indexed in Scopus, the Web of Science, Ovid, and SciELO databases on June 22, 2021. We built a database of papers related to research on páramo water resources after careful review of the title, abstract, and/or the whole content of the articles retrieved from the systematic literature search. Additionally, we examined citations included in the originally selected references that were deemed relevant. A few papers published beyond the date of review were included in the database since their preprints were available online during the literature revision phase; they only account for a minimal proportion of the synthesized literature (2 %; $n = 3$). The search procedure is presented as a "Preferred Reporting Items for Systematic Reviews and Meta-Analyses" (PRISMA 2020) flow diagram (Fig. 1; Page et al., 2021). The search procedure yielded a total of 147 published studies related to the abiotic, biotic, and social elements and aspects of the Central American and Andean páramo water resources. The list of selected publications is presented as Supplementary Material. We only included peer-review scientific literature to avoid potential subjectivity and uncertainty arising from the information presented in gray literature and technical reports that may be locally disseminated. The compiled literature was carefully examined by the research team to extract relevant information to develop a multidisciplinary synthesis of knowledge regarding páramo water resources.

3. Geographic and thematic distribution of scientific information

Páramo covers an area of approximately 24,300 km^2 extending across western Venezuela, Colombia, Ecuador, and northern Peru (11° North to 8° South; Peyre et al., 2021), with a small extension (about 250 km^2) in Costa Rica and Panama (Buytaert et al., 2006a; Luteyn, 1999). The spatial distribution of páramo in Central and South America and the sites where research related to water resources has been conducted are shown in Fig. 2. According to Peyre et al. (2021), Ecuador possesses the largest area of páramo (11,421 km^2) representing 46.5 % of the total páramo land, followed by Colombia with a comparable extension (10,450 km^2; 42.5 % of páramo). While in Ecuador páramo forms large, connected extensions across the two branches of the Andean mountain range, in Colombia páramo is scattered over the three branches of the Andes and in the Sierra Nevada de Santa Marta. Smaller páramo patches are present in northwest Venezuela (1944 km^2) and northern Peru (486 km^2), corresponding respectively to 7.9 % and 2.0 % of the total páramo land. Small patches of páramo also occur in Costa Rica (229 km^2) and Panama (38 km^2), representing 0.9 % and 0.2 % of the total páramo area.

More than half of the published studies on páramo water resources are related to abiotic aspects and elements (59 %, $n = 86$; Fig. 3a), while a lower number of publications are related to biotic (18 %, $n = 27$) and social (23 %, $n = 34$) components. The majority of studies have been carried out in Ecuador both when considering the total number of studies (71 %), and when categorizing them into abiotic (77 %), biotic (56 %), and social (66 %) ones (Fig. 3b). Research in Colombia accounts for a fifth of all published studies (21 %); most of those studies focused on biotic (36 %) and social (31 %) aspects, while a minority of studies are related to abiotic aspects (12 %). A much lower proportion of studies originated in Venezuela (4 %), Costa Rica (3 %), and Peru (1 %). In general, <5 % of the publications per category were conducted in these countries, except for Venezuela which accounted for 8 % of the publications on the biotic aspects of páramo water resources (Fig. 3b). We did not find any study conducted in Panama.

3.1. Development of páramo water resources research

Scientific investigation on páramo natural resources increased considerably since the mid-20th century. While research in Colombia and Venezuela focused mainly on plant biodiversity (e.g., Cleef, 1981; Cuatrecasas, 1958; Van der Hammen and Cleef, 1986) and ecological functioning (e.g., Goldstein et al., 1984; Monasterio, 1980; Rada et al., 1987), respectively; the most prominent orientation of páramo research in Ecuador was on hydrology. The surge of hydrological research in Ecuadorian páramo can be explained by the strong water-related debate in that country during the 1990s, which inspired ecosystem-water-development-related studies (Baud, 2012; Boelens et al., 2012) and thus explains the dominance of studies on páramo water resources research in that country (Figs. 2 and 3b).

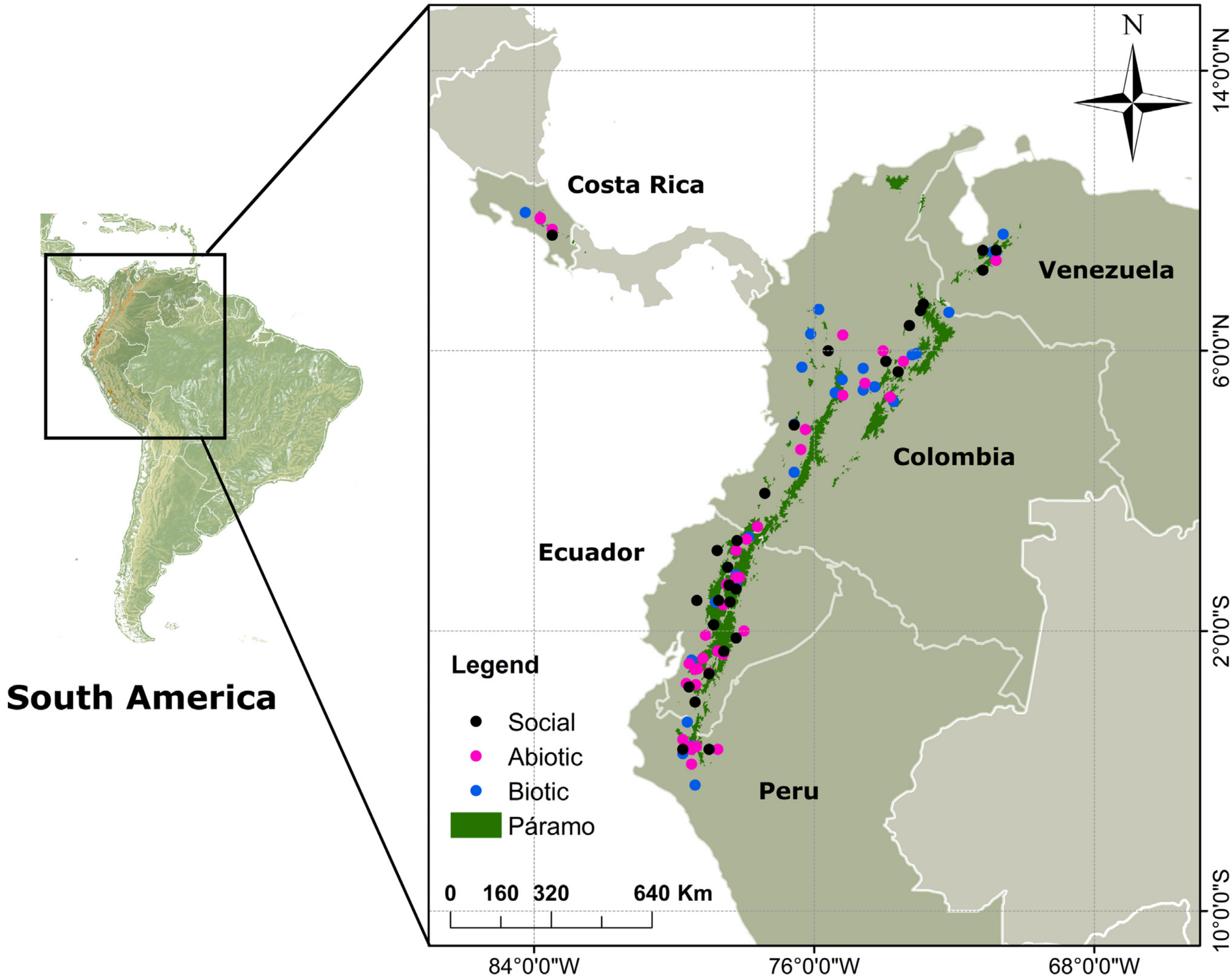

Fig. 2. Geographical extent of páramo in Central America (Costa Rica and Panama) and the tropical Andes in South America (from northwest Venezuela to northern Peru). The inset shows a map of the region with respect to Central and South America. The symbols in the map indicate sites where research on the abiotic, biotic, and social elements and aspects of páramo water resources have been investigated.

In this context, it is worth noting how the implementation of two long-term ecohydrological observatories, Zhurucay (7.5 km^2) and Quinuas (300 km^2; Mosquera et al., 2016a), managed by researchers at the University of Cuenca resulted in a dominance of páramo hydrological studies in southern Ecuador (Fig. 2). Continuous monitoring of ecohydrological information at those observatories since 2011 led to the creation of graduate programs at the Master of Science and Doctoral levels from 2015 onwards. These programs resulted in a steady generation of knowledge on páramo hydrology (Fig. 4). Further, the strong increase of research during the last decade and collaborative programs between Andean countries, such as IMHEA (Célleri et al., 2010), yielded highly relevant hydrological publications at the integrated Andean páramo level. In Costa Rica, the Chirripó Hydrological Research site established in 2015 is the only observatory situated above the tree timberline in the Central American páramo (Esquivel-Hernández et al., 2021).

4. Hydrological processes and variables influencing páramo flow generation and regulation

Water yield and flow regulation are two of the most important ecosystem services provided by páramo (Buytaert et al., 2006a; Correa et al., 2020; Mosquera et al., 2015). Since those services are highly dependent on the water balance of páramo catchments, quantifying inputs, storages, and outflows of water is paramount to understand páramo hydrology. In this section we present information regarding hydrological processes and variables influencing the water balance of páramo catchments.

4.1. Precipitation

Páramo precipitation is characterized by a large spatial variability across Central America and the tropical Andes (Buytaert et al., 2006a). Large discrepancies in precipitation amount and dynamics between ground measurements and remote sensing products (satellite data and climate models) in páramo regions hinder the capacity to utilize the latter in studies at scales necessary to understand the ecosystem's hydrological function (González-Zeas et al., 2019; Ochoa et al., 2016). Therefore, this section presents information from precipitation ground measurements documented in the literature from Central America to the tropical Andes, highlighting hydroclimatological processes influencing the spatial variability of páramo precipitation.

In Costa Rica, rainfall has an unimodal regime (i.e., one seasonal peak) with ~85 % of precipitation falling between May and November and a well-established dry season lasting from December to April (Kappelle and Horn, 2016). Average annual rainfall can vary widely between 1000 and ~ 2500 mm in the slopes facing the Caribbean Sea (Herrera, 1986, 2005). This variation is mainly due to the influence of mountain ranges and the seasonal migration of the Intertropical Convergence Zone (ITCZ; Kappelle and Horn, 2016). During an extreme El Niño Southern Oscillation

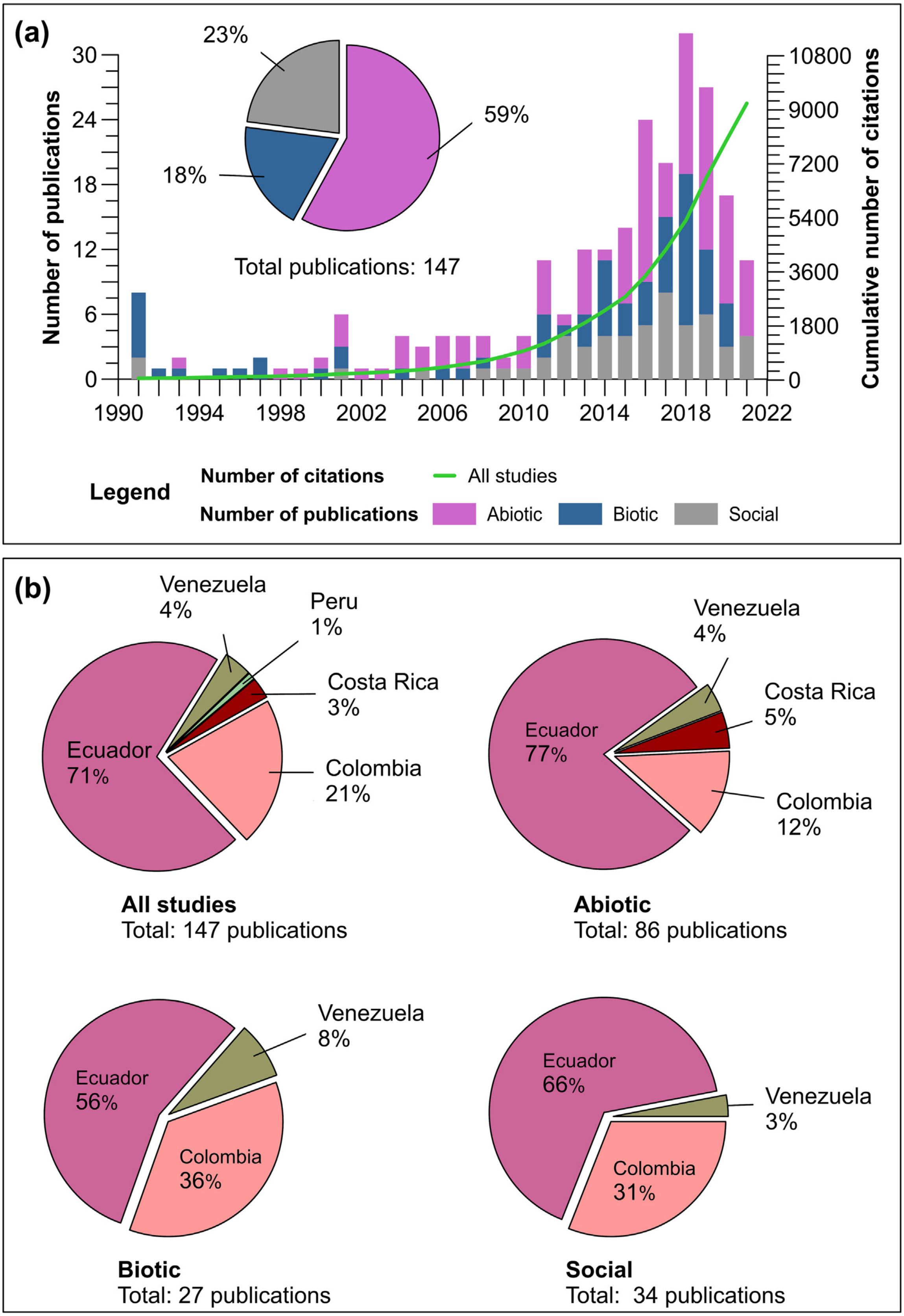

Fig. 3. Synthesis of published literature on the abiotic, biotic, and social elements and aspects of páramo water resources. (a) Bars show the temporal evolution of the publication of all consulted studies ($n = 147$) and for each category, the line depicts the cumulative number of citations of all studies, and the pie charts show the proportion of publications for each category. (b) The pie charts show the percentage of research articles developed in each páramo country in total and for each category. No scientific literature was identified for Panama.

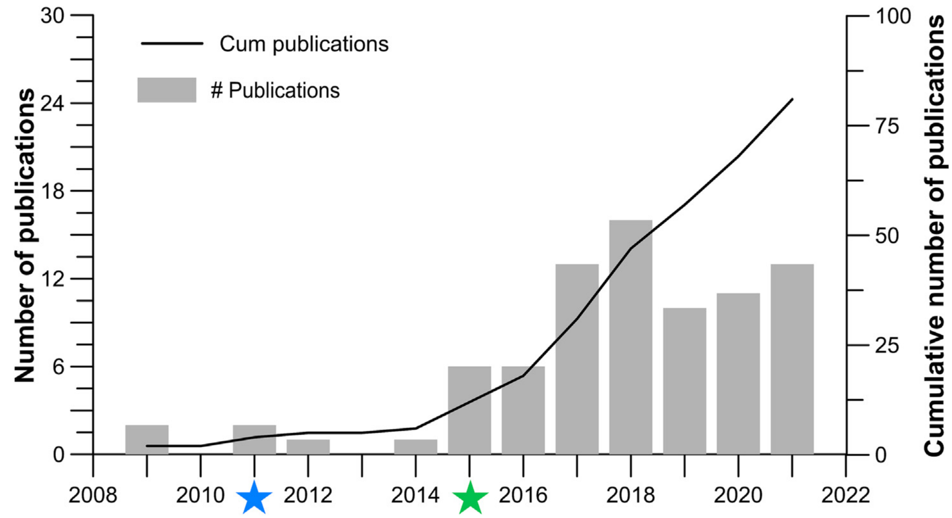

Fig. 4. Individual (gray bars) and cumulative (Cum; black line) number of peer-reviewed scientific publications on páramo water resources developed by researchers from the Department of Water Resources and Environmental Sciences (iDRHICA) of the University of Cuenca since 2009. The blue star indicates the establishment of the Zhurucay Ecohydrological Observatory in the páramo highlands of southern Ecuador (2011), and the green star shows the start of the Doctoral Program in Water Resources lead by faculty staff of iDRHICA (2015).

(ENSO) event (2015–2016), a study showed that north-east trade winds transported moisture from the Caribbean Sea to the Central American páramo of the Costa Rican highlands (Esquivel-Hernández et al., 2019). This atmospheric process causes the formation of convective rainfall associated with the ITCZ during wetter seasons and orographic precipitation during drier ones. In Venezuela, a unimodal rainfall regime was reported for the páramo of Mixteque (Sierra Nevada de Merida) presenting a mean annual precipitation of 1013 mm during the period 2009–2016 (Rodríguez-Morales et al., 2019).

In Colombia, in the páramo of the Claro River Basin, situated on the west flank of the central Cordillera, mean annual rainfall was 1400 mm during the period 1981–2003 (Ruiz et al., 2008). More recently, wide spatial variability of mean annual rainfall between páramo areas in the central and eastern Cordilleras was reported for the period 2009–2015. Two sites in the central Cordillera presented mean annual rainfall of 970 and 1478 mm with unimodal and bimodal (i.e., two seasonal peaks) regimes, respectively. A site in the eastern Cordillera reached annual rainfall of 3098 mm with a unimodal regime (Cárdenas et al., 2017). A regional study in the Magdalena-Cauca River basin, that includes páramo areas in the three branches of the Andes in northern Colombia, showed that precipitation formation is influenced by complex interactions between the recycling of local moisture and the influence of terrestrial moisture sources mainly stemming from the Orinoco and northern Amazon basins (Escobar et al., 2022). These interactions are principally influenced by the dynamic of the ITCZ, likely explaining the high spatial variability of rainfall in páramo areas across the Colombian Andes.

In Ecuador, high spatial variability of precipitation was also found among páramo sites. Mean annual precipitation in the páramo of northern Ecuador near Antisana volcano was 778.5 mm over the period 2014 to 2020 (Lahuatte et al., 2022). In southern Ecuador, páramo precipitation has been characterized in detail, finding mean annual precipitation amounts between 1000 and 1300 mm with unimodal and bimodal regimes depending on the study site (Buytaert et al., 2006b; Célleri et al., 2007; Padrón et al., 2020). In this region, frequent drizzle added up to 30 % to total annual rainfall during the period 2011–2014 (Padrón et al., 2015). Precipitation in the páramo of southern Ecuador is mainly influenced by the ITCZ (Vuille et al., 2000) and formed by recycled atmospheric moisture stemming from the Amazon rainforest east of the Andean cordillera (Esquivel-Hernández et al., 2019; Zhiña et al., 2022).

Despite the claimed influence of fog in the climate and water balance of páramo, this hydrological feature is still understudied with a handful of exceptions in southern Ecuador and central Colombia. Occult precipitation, being the result of a combination of drizzle and fog, added 7 to 28 % to total annual rainfall in Colombian páramo (Cárdenas et al., 2017). These authors reported large spatial variability among different páramo areas and within sites at each páramo. They attributed the differences to multiple causes such as meteorological conditions, orientation, and altitudinal and topographical differences. So far, only one study in the same region assessed the influence of fog-only events in páramo precipitation (Berrones et al., 2021). These authors found that fog primarily occurs early in the morning and at night, and that fog water content can be up to 22 % of annual precipitation (i.e., 340 mm in a 12-month period during 2017–2018). However, studies of fog interception in Colombian and Ecuadorian páramo dominated by small-height tussock grasses suggest that it does not reach the soil and thus does not contribute to streamflow (Berrones et al., 2022; Tobón and Gil Morales, 2007).

4.2. Evapotranspiration

Evaporation from the land surface (i.e., excluding water bodies), interception loss from vegetation canopy, and transpiration from vegetation – which combined form the evapotranspiration term of the water balance – account for a large proportion of the global water cycle (Good et al., 2015). Nevertheless, those components of páramo water balance remained poorly studied until half a decade ago.

In Colombia, the maximum canopy interception capacity (i.e., the maximum amount of water that can be stored in the vegetation canopy) was measured for three different vegetation types: tussock grasslands (*pajonal*; *Calamagrostis effussa*), bamboo shrub (*chuscal*; *Chusquea tessellata*), and stem rosettes (*frailejón*; *Espeletia uribei and Espeletia killipii*) at an elevation between 3616 and 4150 m a.s.l. (Valencia-Leguizamón et al., 2017). These authors found that the last two vegetation types had a higher maximum interception capacity (2.8 and 2.5 mm, respectively) than tussock grasslands (1 mm). Canopy interception loss by tussock grass was measured at a humid páramo site in South Ecuador (3765 m a.s.l.) during rainfall events. High percentages of canopy interception loss (80 to 100 %) were found during precipitation events of low intensity, indicating a tussock grass maximum canopy interception capacity of 2 mm.

Actual (or real) evapotranspiration (i.e., the amount of water that is effectively evaporated from the soil surface and transpired by vegetation) from páramo tussock grasslands (*Calamagrostis intermedia*) was directly measured for the first time in southern Ecuador (3765 m a.s.l.). The daily average of this water flux is 1.7 mm day^{-1}, varying between 1.6 mm day^{-1} during wet months and 2.0 mm day^{-1} during relatively dry months. It accounts for up to 50 % of total annual rainfall (Carrillo-Rojas et al., 2019; Ochoa-Sánchez et al., 2019, 2020). Tussock grasslands' actual evapotranspiration is primarily controlled by net radiation and is mainly composed of canopy interception loss (evaporation of water from the vegetation canopy) rather than transpiration (Ochoa-Sánchez et al., 2020). Not surprisingly, evapotranspiration in páramo catchments increases as the areal extent of tussock grass increases (Mosquera et al., 2015).

Considering the difficulties of measuring actual evapotranspiration in mountainous areas, several studies in páramo regions have estimated potential evapotranspiration (i.e., the demand or maximum amount of water that would evaporate if there was unlimited water available in the ground surface). Potential evapotranspiration can be relatively easily estimated by using measurements of frequently monitored meteorological variables (e.g., air temperature and humidity, wind speed, and solar radiation) and transformed to actual evapotranspiration using a crop coefficient (i.e., the relationship between the actual evapotranspiration for a specific vegetation type and potential evapotranspiration under the same conditions and in that same microclimate). There are several studies that report the potential evapotranspiration of páramo vegetation, mainly of tussock grasslands in Ecuador. Sklenář et al. (2015) identified average potential evapotranspiration values varying between 1.4 and 2.1 mm day^{-1} for grasslands in the Antisana volcano reserve in northern Ecuador during the period 2007–2010. In a páramo site located in southern Ecuador, where the vegetation is mainly dominated by tussock grass and small shrubs, average potential evapotranspiration values of 2.4 mm day^{-1} were estimated, ranging between 0.8 and 4.2 mm day^{-1} during the period 2010–2012 (Iñiguez et al., 2016). These values coincide with those determined at two other sites mainly covered by tussock grass in southern Ecuador, where average values of potential evapotranspiration were 1.9 and 2.0 mm day^{-1} during the period 2011–2013 (Córdova et al., 2015). It is important to note that although the number of studies on potential evapotranspiration have increased in recent years, there is only one investigation in which crop coefficient was estimated. Carrillo-Rojas et al. (2019) reported a crop coefficient of 0.9 for the tussock grasslands of southern Ecuador using the global standard method suggested by the FAO in its Irrigation and Drainage Paper No. 56 (Allen et al., 1998) for the calculation of potential evapotranspiration.

To our knowledge, only one study has assessed evapotranspiration in degraded páramo. High rates of evapotranspiration (annual mean of 61 % of total precipitation) were found in the páramo of Gavidia in Venezuela (3200–4000 m a.s.l.) in agricultural plots scarcely covered by herbs (*Rumex acetosella* and *Lachemilla moritziana*; Sarmiento, 2000).

Despite a large number of lakes – including tarns and small ponds – being prevalent in Central American and Andean páramo as a result of their geomorphological characteristics shaped by past glaciation (e.g., Umaña et al., 1999; Van Colen et al., 2017; Zapata et al., 2021), the hydrological features of these open water bodies remain currently understudied. The first insights into lakes' evaporation show that in the páramo of Chirripó, Costa Rica (3490–3520 m a.s.l.) the annual ratio of evaporation to inflow is low (2–18 %) in comparison to other tropical lakes (24–60 %; Esquivel-Hernández et al., 2018).

4.3. Infiltration

Once precipitation reaches the ground surface, the infiltration capacity of the soil is responsible for the redistribution of precipitated water through surface and subsurface flow paths (Hillel, 2004), influencing the water regulation capacity of páramo catchments. Even though the water infiltration capacity of soils varies across the humid páramo of southwestern Colombia and northern Ecuador (Benavides et al., 2018; Poulenard et al., 2001), it is generally higher (varying between 20 and 80 mm hr^{-1}) than the usually low intensity of páramo rainfall (<10 mm hr^{-1}; Padrón et al., 2020). Vegetation cover has also been shown to influence the water infiltration capacity of volcanic ash soils (Andosols) in páramo. In one study, soils under shrubs and *Polylepis* forests presented considerably higher infiltration rates (>1000 mm hr^{-1}) than grasslands (Suárez et al., 2013). High infiltration reduces the occurrence of surface runoff and facilitates the entrance and recharge of water into the soil, enhancing the dominance of subsurface flow paths (Correa et al., 2017; Mosquera et al., 2016b).

Regarding the effects of changes in land use, intensive land use practices produce detrimental effects on infiltration. Frequent burning (every 1–3 years), tillage, intensive cattle grazing on non-native grass (*Pennisetum clandestinum*), managed shrubland (various bush species used as live fences and livestock fodder), and complete removal of ground vegetation substantially decrease infiltration rates (up to 10-fold) compared to native vegetation cover (Benavides et al., 2018; Poulenard et al., 2001; Suárez et al., 2013). These effects demonstrate unfavorable consequences of land use or cover change on the infiltration of páramo soils (Mosquera et al., 2022).

4.4. Soil water dynamics and storage

The amount of water stored in and released from soils is an essential component of páramo water balance (Buytaert et al., 2006a; Mosquera et al., 2016b). Despite this, only a few studies examined the spatial and temporal dynamics of soil water movement in undisturbed páramo soils. One study investigated how water flows through thin (<1 m depth) volcanic ash páramo soils (Andosols) at a hillslope covered by tussock grass vegetation in the highlands of south Ecuador (Mosquera et al., 2020a). The study demonstrated that although Andosols have high water content throughout the year, percolation (or vertical movement of water) is the dominant flow path in these soils. This was observed despite the formation of a perched (saturated) water layer in the organic-rich andic horizon of the soil below the root zone. These findings exemplify the "sponge-like" behavior of volcanic ash soils in the south Ecuadorian páramo. This behavior is explained by the high organic matter content and fine texture (i.e., a dominance of clay and loam particles) of the Andosols (Buytaert et al., 2006a; Mosquera et al., 2020b) that favors water retention, and their porous structure and high saturated hydraulic conductivity (Buytaert et al., 2006c) in relation to the typically low intensity of rainfall in the region that facilitate percolation (Mosquera et al., 2020a). At the same experimental hillslope, lateral flow was mainly restricted to thin (<few centimeters) transition zones between soil layers with marked differences in hydraulic conductivity (e.g., the transitions between the rooted and unrooted layers of the andic horizon of the soil, and between the soil mineral horizon and the underlying bedrock with very low permeability). Undisturbed Andosols in the Andean páramo highlands of south Ecuador also re-wet to saturation faster (2–3 months) than lowland mineral soils (8 months) following drought periods (Iñiguez et al., 2016). This hydrological behavior mainly results from the high organic matter in the andic horizon of the Andosols, highlighting their capacity to quickly recover soil moisture after droughts.

Other investigations focused on assessing the impacts of land cover and land use change on soil water content, storage, and dynamics, particularly in the páramo of southern Ecuador. In that region, several studies consistently demonstrated that afforestation with pine plantations significantly decreases soil water content (up to 50–60 %) due to increased evapotranspiration and saturated hydraulic conductivity compared to native vegetation cover (i.e., tussock grasses, shrubs, *Polylepis* forests; Farley et al., 2004; Harden et al., 2013; Hofstede et al., 2002; Marín et al., 2018; Mosquera et al., 2022; Patiño et al., 2021). These observations indicate that pine afforestation should be discouraged in conserved páramo areas to ensure their capacity to support water yield and maintain regulation services (Mosquera et al., 2022).

On the contrary, studies on cultivation – mainly with potatoes – and intensive sheep and cattle grazing have shown contrasting effects on soil water content and storage, varying from strong reductions (e.g., Daza Torres et al., 2014; Marín et al., 2018; Patiño et al., 2021; Podwojewski et al., 2002) to no change or even a slight increase (e.g., Buytaert et al., 2005; Harden et al., 2013; Marín et al., 2018). These differences are likely related to soil type, hydrometeorological conditions, and antecedent and recent land management, including burning, tilling, and trampling activities, as well as the number of animals grazing the land (Marín et al., 2018; Podwojewski et al., 2002). Based on the considerable variability of the impacts of these activities, past investigations advise to avoid generalizing the impacts of cultivation and grazing among study sites, and to consider the aforementioned factors when planning for soil and water management strategies in páramo areas (Marín et al., 2018; Mosquera et al., 2022). Montenegro-Díaz et al. (2019) investigated the effects of extensive grazing on soil water dynamics and the impact of the removal of tussock grasses on the water content of undisturbed Andosols. They reported that although a slight change in soil water dynamics was observed due to reduced canopy interception loss and transpiration in the intervened plot, no significant changes in mean soil water content were found. These observations suggest that the hydrophysical properties of the soil are not affected when only vegetation is removed, as long as the soil structure is not affected.

4.5. Streamflow

4.5.1. Streamflow dynamics

Early hydrological assessments in páramo catchments were aimed at defining the dynamics of streamflow response to precipitation, particularly in southern Ecuador. In this region, undisturbed páramo catchments with thin soils (<1 m depth) underlain by bedrock with very low permeability, maintained a high water yield (or capacity to generate streamflow) as evidenced by high runoff coefficients (the ratio between streamflow and precipitation). These coefficients frequently range between 50 and 70 % at annual time scale (Buytaert et al., 2007; Crespo et al., 2010, 2011; Guzmán et al., 2015; Mosquera et al., 2015; Ochoa-Tocachi et al., 2016); and coefficients up to 90 % have been reported during rainstorm events (Correa et al., 2016). The high water yield is explained by the sustained input of low intensity precipitation and high air humidity throughout the year that reduces evapotranspiration (Córdova et al., 2015; Padrón et al., 2015) in combination with the high infiltration and water retention capacity of páramo soils in the region (Buytaert et al., 2005, 2006a; Mosquera et al., 2020a). A similar water yield was reported for a páramo catchment in northern Peru (runoff coefficient of 66 %; Ochoa-Tocachi et al., 2016).

Páramo catchments in Venezuela (Rodríguez-Morales et al., 2013, 2019) and northern Ecuador (Ochoa-Tocachi et al., 2016) have shown lower water yield (runoff coefficient varying between 28 and 37 %) than those in the humid páramo of southern Ecuador. These observations can be attributed to two factors. First, the drier and more seasonal climatological conditions in the Venezuelan páramo highlands (Rodríguez-Morales et al., 2019) and in the northern and central Andes of Ecuador (Torres and Proaño, 2018), as compared to the year-round humid conditions found in southern Ecuador. Second, the different pedological (e.g., deep soils presenting a coarse texture and/or low organic matter content) and geological (e.g., highly fractured and permeable bedrock favoring deep percolation) characteristics of the catchments (Ochoa-Tocachi et al., 2016; Rodríguez-Morales et al., 2019) compared to the southern Ecuadorian region. Such differing characteristics difficult the capacity to quantity all subsurface flow components (e.g., percolation and groundwater flow) of the catchments and to assess their water balance.

High baseflow during dry periods suggests that undisturbed páramo catchments in southern Ecuador and northern Peru have a high streamflow regulation capacity (Buytaert et al., 2007; Crespo et al., 2011; Mosquera et al., 2015; Ochoa-Tocachi et al., 2016). This capacity is favored by the same local climate, soil, and geological conditions influencing the catchments' high water yield. Even though no information on this issue exists for páramo catchments in other regions with different climatological (e.g., seasonally dry), pedological (e.g., several meters deep coarse-textured soils or non-volcanic soils), and geological (e.g., highly permeable fractured bedrock) conditions, a differing streamflow regulation capacity can be expected. For instance, other grassland-wetland dominated catchments in seasonally dry environments and highly fractured bedrock across the tropical Andes exhibit a substantially lower streamflow regulation capacity than the humid páramo of south Ecuador (Ochoa-Tocachi et al., 2016). Even though it is generally assumed that páramo catchments across the tropical Andes present a high water yield and regulation capacity (Buytaert et al., 2006a; Correa et al., 2020), the identified differences along the region indicate that local climate, soil, and geological features need to be considered in water quantity assessments.

Investigations in southern Ecuador examined the impact of land use and cover change on the dynamics of streamflow. Several studies revealed that pine afforestation negatively affects water yield and flow regulation of catchments by reducing high, moderate, and low flows (Buytaert et al., 2007; Crespo et al., 2010, 2011; Ochoa-Tocachi et al., 2016). This behavior responds to augmented canopy interception loss and transpiration of trees relative to the dominant páramo vegetation (tussock grasses, cushion plants, and shrubs). These effects not only reduce water yield up to a 50 %, but also diminish the water regulation capacity as evidenced by a reduction in baseflow. Even though potato cultivation did not substantially reduce the water yield of páramo catchments (i.e., runoff coefficient decreases by ~10–20 %), it tends to produce higher and faster peak flows and lower baseflow, reducing the water regulation capacity of the ecosystem (Buytaert et al., 2004, 2006d, 2007; Crespo et al., 2010, 2011; Ochoa-Tocachi et al., 2016). These effects have been attributed to the formation of furrows and ditches used in agriculture that cause faster drainage of water to streams and reduce soil water storage (Buytaert et al., 2007; Crespo et al., 2010).

The impacts of grazing on streamflow generation and regulation are less evident. While the direction of change depends principally on animal density that can cause a decrease in vegetation cover and soil compaction (Hofstede, 1995a), the magnitude of change is mainly related to catchment physiographic features and soil properties (Ochoa-Tocachi et al., 2016). Findings in the south Ecuadorian Andes indicate that extensive grazing, i.e., low animal density per unit area (reported values range between 0.5 and 3 cattle heads per hectare), does not cause significant changes in water yield and flow regulation (Crespo et al., 2010, 2011). The effects of intensive grazing (including a high density of cattle that graze freely on the land and are not stabled) have not been studied in páramo. Nevertheless, field observations suggest that this impact can cause a strong reduction of vegetation cover and soil compaction, which in turn can increase the flashiness in streamflow response after rainfall events (i.e., increased water yield) and reduce the amount of water that is stored in the catchment (i.e., decreased flow regulation; Ochoa-Tocachi et al., 2016).

Evaluations of environmental change (i.e., climate change and population growth) on páramo water yield and its impacts on the water supply to human settlements downstream are scarce. A decrease in water resource availability due to changes in land use from páramo to agricultural land was reported in northern Ecuador using a hydrological modeling approach (Espinosa and Rivera, 2016). Despite the large uncertainties of climate change predictions in the tropical Andes (Buytaert et al., 2010), investigations agree that human activities (i.e., reduction of páramo land cover at the expense of the expansion of the agricultural frontier due to population growth) are likely to produce larger water yield reductions than changes in precipitation and temperature patterns (Buytaert and De Bièvre, 2012; Flores-López et al., 2016). Changes in land cover/use are in turn predicted to diminish water supply in high-Andean cities such as Bogota, Quito, and Piura.

4.5.2. Mechanistic understanding of streamflow generation

Given that streamflow generation and regulation depend on how different water sources contribute to streamflow over time, interest in defining surface and subsurface water flow paths has increased in páramo scholarship in the last decade. The most extensive mechanistic (process-based) understanding of streamflow generation in páramo to date has been developed at a nested system of eight heavily instrumented and monitored experimental headwater catchments (0.2–7.5 km^2) situated in the southern Ecuadorian highlands in the Zhurucay Ecohydrological Observatory (Mosquera et al., 2016a). In this region, soils of volcanic origin are shallow (up to 1–2 m depth), the shallow underlying bedrock layer up to 20 m depth from the ground surface is fractured, and the bedrock below has a very low permeability. A summary of hydrological and hydrogeochemical observations and key findings from 12 studies carried out at the observatory are shown in Fig. 5. At Zhurucay, early investigations dealt with identifying how catchment physiographic characteristics (e.g., vegetation, topography, soil type and spatial distribution, and geology) influence streamflow generation and regulation (Mosquera et al., 2015). These authors found that while water yield (runoff coefficient) and the generation of moderate and high flows were controlled by the areal extent of páramo wetlands (the combination of organic-rich, peat-type, Histosol soils and cushion plant vegetation), the generation of baseflow was influenced by topography.

At the same study site, the use of environmental tracers (isotopic and geochemical data) allowed the characterization of surface and subsurface water flow paths, the mean transit time or age (i.e., the time elapsed since water molecules enter a hydrological system as precipitation until they leave it at an outlet; McGuire and McDonnell, 2006) of soil and stream water, and the water storage capacity of catchments at Zhurucay. The characterization of isotopic signals indicated that although wetlands covered only 20 % of the areal extent of the catchment, they are the main source of water contributing to streamflow throughout the year (Mosquera et al., 2012, 2016b; Fig. 5b). Hillslopes, covering the remaining 80 % of the area, in turn, play a key role in recharging the Andean wetlands during dry periods (Mosquera et al., 2016b). The utilization of geochemical information (dissolved nutrients and metals) allowed quantifying the contribution of different water sources (i.e., precipitation, hillslopes, riparian wetlands, and springs) to streamflow generation during different flow conditions (Correa et al., 2017, 2019). These investigations confirmed that Histosols are the main source of stream water during both baseflow and rainstorm events (Fig. 5c), contributing 50–60 % of total streamflow. At Zhurucay, it was also demonstrated that hillslopes are hydrologically connected to the stream network during rainstorm events, contributing up to 40 % to streamflow (Correa et al., 2019; Fig. 5d).

At the Zhurucay catchments, spring water or flow emerges to the surface from water stored in the shallow fractured bedrock near the ground surface (up to 20 m depth) that maintains a high phreatic level due to the sustained input of rainfall year-round. As a result, spring water also contributes to streamflow, particularly during periods of low flow (Correa et al., 2017; Mosquera et al., 2015). The importance of shallow subsurface flow from soils and the fractured bedrock near the ground surface in streamflow generation is supported by the relatively young ages of soil and stream water in the Zhurucay catchments, which vary between 2 and 9 months (Lazo et al., 2019; Mosquera et al., 2016c), as compared to much longer water ages found in other hydrological systems dominated by the contribution of deeper subsurface layers that present water age of the order of several years to decades (e.g., Cartwright and Morgenstern, 2015; Ma and

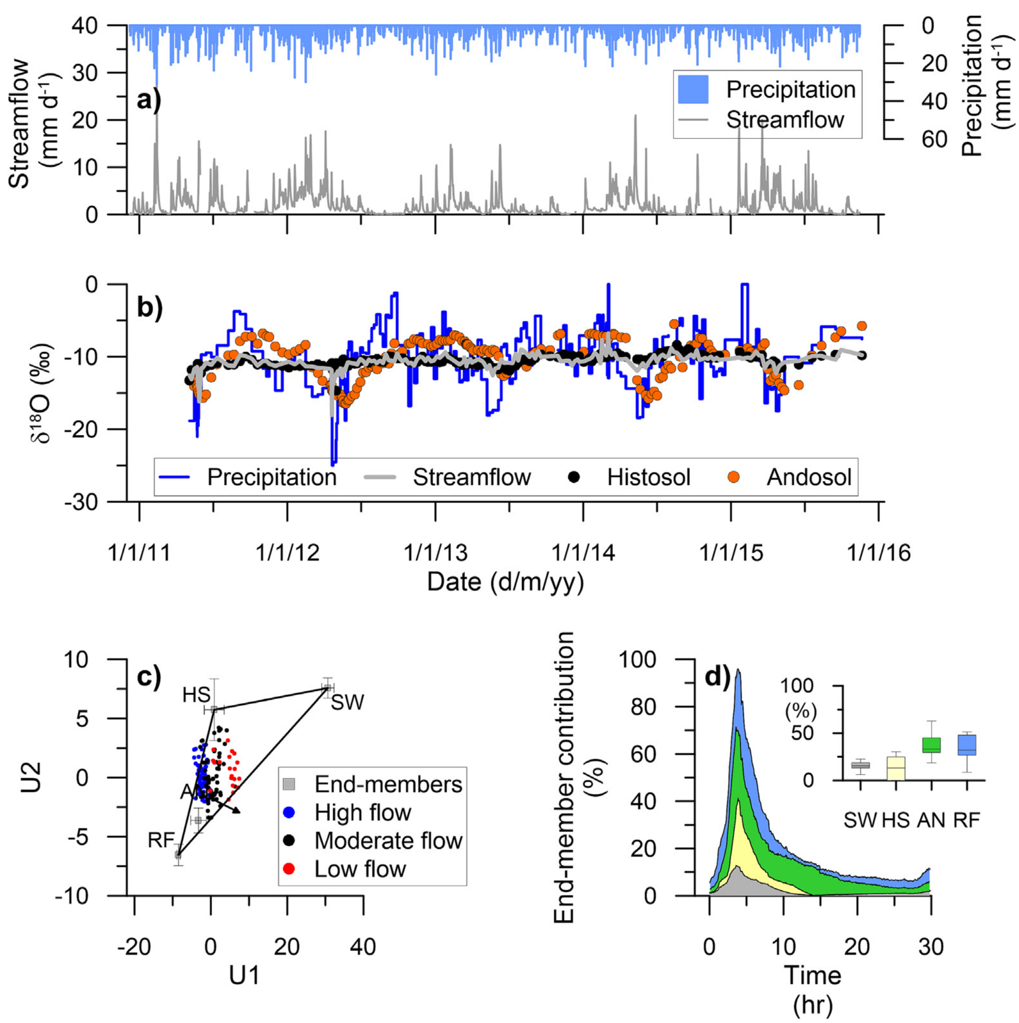

Fig. 5. Hydrological and hydrogeochemical observations and key findings of selected runoff generation studies carried out at a nested system of experimental páramo catchments situated in the Zhurucay Ecohydrological Observatory (ZEO), southern Ecuador (3400–3900 m a.s.l.; Mosquera et al., 2016a). (a) Daily precipitation (P) and unit area streamflow (Q); (b) $\delta^{18}O$ isotopic composition in P, Q, hillslope (Andosol) and riparian (Histosol) soils for the period May 2011–December 2016; (c) subspaces (U1 and U2) from end-member (geographical sources) mixing modeling; and (d) hydrograph separation with end-member contributions during a rainstorm event monitored between 1 and 2 March 2014 (inset boxplot shows the percentage of end-member contributions). In subplots (c) and (d): RF, rainfall; AN, Andosols; HS, Histosols; SW, spring water. Subplot (c) reproduced from Correa et al. (2017) and subplot (d) reproduced from Correa et al. (2019) with permission of Elsevier.

Yamanaka, 2016). The water storage capacity of the Zhurucay catchments varies between 300 and 600 mm, representing about a third to a half of annual precipitation (Lazo et al., 2019). Water stored in riparian wetlands mainly composed of Histosol soils in those catchments represents the majority of this water storage and are therefore the most important water reservoir of the catchments. Altogether, these findings emphasize 1) the relevance of wetlands in páramo for streamflow generation and flow regulation, despite their small areal extent across the observatory, and 2) that subsurface water transport through the shallow soils are dominant streamflow generation mechanisms in the south Ecuadorian páramo.

The aforementioned conceptual hydrological framework was recently assessed at another experimental catchment in southern Ecuador with similar vegetation, soil, and geological characteristics to those found at Zhurucay, but with a larger drainage area (21.7 km^2) and influenced by the presence of lakes (Ramón et al., 2021). Interestingly, wetlands were found to contribute an even higher proportion of water to streamflow formation despite their smaller areal extent (only 7.7 % of catchment area) in comparison to Zhurucay (20 %). On the contrary, lakes covering 5 % of the catchment were not found to be a main water source to streamflow as believed until now by local stakeholders and water managers in the region (Telecommunications, Drinking Water, and Sewage Company of the City of Cuenca ETAPA-EP, personal communication). Even though the streamflow regulation capacity of lakes might be important in small páramo catchments, these findings suggest that their water level fluctuations (in response to frequent precipitation inputs) and storage capacity are not sufficient to influence water yield in larger catchments. These findings stress the importance of obtaining an improved process-based understanding of hydrological processes to correctly define where management and conservation efforts should be targeted. For example, the conservation of Andean wetlands for sustaining the availability of water for downstream users in south Ecuador should be prioritized.

Even though process-based understanding of streamflow generation in other páramo regions is scarce, the few available studies have shown marked differences in relation to the well-understood hydrology in the south Ecuadorian páramo. It has been recently shown that percolation is an important water transport mechanism in a headwater catchment (0.68 km^2) influenced by recent volcanism, i.e., thick volcanic soils (up to 27 m depth) and fractured bedrock, in northern Ecuador (Lahuatte et al., 2022). The combination of low annual precipitation inputs (<800 mm yr^{-1}), marked climate seasonality, and the high permeability of the soil and bedrock allowing water to percolate down through the subsurface (Lahuatte et al., 2022), likely explain the aforementioned low water yield of páramo in northern Ecuador (Lahuatte et al., 2022; Ochoa-Tocachi et al., 2016). These findings are in line with the reported relevance of groundwater flow in streamflow generation in catchments possessing fractured young volcanic bedrock in north and central Ecuador (Favier et al., 2010; Saberi et al., 2019).

Investigations in glacierized-páramo catchments in north and central Ecuador demonstrated the significance of glacier melt contributions to streamflow generation. Such contributions represented 20 % of stormflow in a 15.2 km^2 catchment with a 15 % glacier area on Antisana volcano during a dry season rainfall event (Minaya et al., 2016b), and between 20 and 60 % at day-time hours in a 7.5 km^2 catchment with 34 % glacierized area on Chimborazo volcano (Saberi et al., 2019). These findings raise concerns in páramo regions dependent on glaciers for streamflow generation, as increased temperature in the tropical Andes is leading to their disappearance (e.g., Mark et al., 2017; Thompson et al., 2011). Altogether, water quantity studies emphasize the diversity of water sources and pathways water can take to streams depending on local climatological, geomorphological, pedological, and geological conditions.

5. Chemical water quality

Supplying high quality water for human consumption is a key goal to achieving the sustainable development of nations (Alcamo, 2019; Germann and Langergrabe, 2022). To date, there is a widespread belief by the scientific community (Buytaert et al., 2006a; Célleri and Feyen, 2009; Correa et al., 2020 and references therein) and civil society (e.g., ETAPA-EP personal communication) that conserved páramo headwaters produce water of sufficiently high chemical quality to supply urban and rural population drinking water needs. Surprisingly, this aspect of páramo water resources has not been assessed in past synthesis studies. This section focuses on the chemical quality; here specifically referred to dissolved substances including nutrients, metals, and contaminants in water originated from páramo catchments.

The first scientific investigation dealing with páramo water quality was carried out at Antisana volcano in northern Ecuador (Williams et al., 2001). During dry climate conditions, these authors reported significant differences in the concentration of inorganic and organic species of C, N, and P between stream water and wetlands. Riveros-Iregui et al. (2018) compared the nutrient concentrations in stream water during a dry period in undisturbed and disturbed (a mixture of pastures and potato cultivation) páramo sites situated near Bogota, Colombia. The undisturbed sites showed generally higher concentrations of DOC, NO_3, and PO_{4-} compared to the impacted sites, although no statistically significant differences between the sties were observed. Differences in concentrations could be attributed to changes in the physical and chemical properties of soils caused by human activities, which alter the complexation of nutrients and metals observed in undisturbed páramo areas, and therefore favor their release from the soil into the stream (Buytaert et al., 2006c; Pesántez et al., 2018, 2021).

More recently, high temporal resolution monitoring of water quality parameters (samples collected every 4-hr during 16 months in 2017–2019) in a headwater catchment in southern Ecuador indicated that high DOC loads are exported to streams during rainstorm events. The production of organic compounds, and of DOC in particular (Pesántez et al., 2021; Ramón et al., 2021), results from the accumulation of high amounts of C in soils (Buytaert et al., 2006a). This occurs especially in wetlands (Hribljan et al., 2016) which are often hydrologically connected to streams (Mosquera et al., 2016b). Although DOC does not represent a direct threat to human health, chlorine disinfection (the most commonly applied method for drinkable water treatment across all páramo countries) of organic-rich water could result in the potential production of carcinogenic byproducts such as trihalomethanes (Hsu et al., 2001; WHO, 2017).

Water in contact with bedrock and soils originated from volcanic material dissolves major and trace elements. Such elements subsequently leach out to streams and influence their chemical water quality (Ma et al., 2019; Paula et al., 2020; Rodriguez-Espinosa et al., 2015). Considering the key role volcanism plays in shaping landscapes in several regions across the Andean páramo, the monitoring of water quality parameters, and of heavy metals which in elevated concentration can endanger human health (e.g., Achene et al., 2010; Briffa et al., 2020; Malandrino et al., 2015; Vigneri et al., 2017), should be a requirement for companies in charge of domestic water supply in such regions. Despite this, our literature search yielded only one study that investigated the concentration of dissolved metals in conserved páramo streams. Using a spatially distributed synoptic sampling strategy during a 4-day campaign in the dry season, Riveros-Iregui et al. (2018) reported a relatively low spatial variability of stream water metal concentrations (Al, Cd, Fe, and K) in an undisturbed páramo catchment located in central Colombia. Stream water in undisturbed páramo catchments of southern Ecuador presents dissolved metals associated with health problems (e.g., Al, Cu; Correa et al., 2019; Pesántez et al., 2021) at concentrations above permissible limits for drinking water and the preservation of aquatic life according to the Ecuadorian (Ministerio del Ambiente del Ecuador, 2015), United States (U.S. Environmental Protection Agency, 2022), and World Health Organization (WHO, and Water, Sanitation and Health Team, 2004) water quality standards.

For instance, water quantity and quality data collected at sub-daily temporal frequency shows that during rainfall events the concentrations of Al regularly exceed the permissible limits for the survival of aquatic biodiversity, and even those for human water consumption a few times throughout the year during high intensity rainfall events at an undisturbed catchment within the Zhurucay Ecohydrological Observatory (Fig. 6). These observations highlight the importance of carrying out chemical water quality assessments that include the analysis of dissolved nutrients and metals, particularly those related to health issues (e.g., Cd, Fe, Mn, Pb) in páramo streams due to the significant presence of organometallic complexes in soils (Buytaert et al., 2005), which can be released to streams, particularly during rainfall events (Fig. 6). Such evaluations should be conducted during variable flow conditions (from low to high flows) as different solutes are preferentially mobilized during wet and dry hydrological events in páramo catchments (Arízaga-Idrovo et al., 2022; Correa et al., 2019; Pesántez et al., 2018, 2021). Additionally, it is important to mention that their exportation to stream water could be exacerbated due to changes in climate (Pesántez et al., 2018) as expected increased temperature in the highlands of the tropical Andes could cause an increase DOC mobilization from soils (Buytaert et al., 2009, 2010).

Although several páramo areas in the Andean region are affected by anthropogenic activities, only a few evaluations of the impacts of such practices on the chemical quality of stream water exist. The presence of pesticides (malathion, difenoconazole, tebuconazole, and chlorothalonil) has been reported in an onion-producing region in Colombia (Mojica and Guerrero, 2013). Grazing and potato cultivation have shown to increase stream water concentrations of Al, Cd, Fe, and K during the dry season in relation to undisturbed páramo in central Colombia (Riveros-Iregui et al., 2018). Water downstream of a coal mining area in the east Andean Cordillera of Colombia presented higher concentrations of Fe, Mn, Pb, and Zn than those observed upstream of the mining site. Downstream concentrations of the aforementioned elements were above national permissible limits for drinking water, and just below those for agricultural purposes (González-Martínez et al., 2019). The main sources of contamination were mining outlets and wastewater discharge from urban centers. However, the proportional contribution of contamination originated from cocaine production and agriculture is yet to be quantified. Another study in southwestern Colombia showed significantly higher concentrations of As in stream water downstream of a gold mining area in relation to those in undisturbed areas (Alonso et al., 2020). It is worth noting that although at early stages of contamination processes páramo soils can help buffer the export of metals to streams due to their high metal accumulation capacity, they could become a potential contamination source if their redox potential is affected by contamination (González-Martínez et al., 2019). The latter risk can be exacerbated by the strong acidity of páramo soils, which facilitates the mobility of metals and pesticides (González-Martínez et al., 2019; Mojica and Guerrero, 2013).

6. Ecological and ecohydrological processes mediating páramo water supply

6.1. Biogeochemistry of páramo water resources

The study of biotic aspects of water resources across the terrestrial-aquatic interface is one of the major thrusts in the rapidly growing field of biogeosciences (Richter et al., 2018). Considering the interplay among climate, recent volcanism, extremely rich soil carbon stores, and complex topography in páramo regions, it is important to assess how metabolic regimes and biogeochemical processes influence the system's water and nutrient cycles (Bernhardt et al., 2018). Here, we summarize the limited biogeochemical knowledge across the terrestrial-aquatic interface in páramo.

6.1.1. Nutrient cycling

Three general factors arise as potential controls of nutrient content and dynamics in páramo streams: catchment geomorphology, riparian vegetation, and land use change. Catchment geomorphology of páramo streams can be broadly classified according to drainage type into three main categories, i.e., glacial, peatland, and upslope (or hillslope). These drainage types differentially affect the amount of nutrients delivered to páramo streams. In a páramo region of the Antisana volcano area in northern Ecuador, for example, glacier-fed lakes and streams had lower N loading than lakes and streams originating in upslope soils, which in turn were likely limited by P as suggested by their higher N:P ratios (Barta et al., 2018). This can be explained by low organic matter in high-elevation glacier-fed lakes and the strong fixation of P that characterizes young volcanic soils (Arnalds and Stahr, 2004; Wada, 1985) typically found in upland páramo soils in northern Ecuador. In the same region, a stream draining upland soils had higher soluble reactive P (SRP: 263 μg L^{-1}), but much lower DOC (0.4 mg L^{-1}) than a stream draining a peatland (SRP below detection limits; DOC: 23 mg L^{-1}; Williams et al., 2001). Furthermore, geomorphology – including catchment slope and surface water extent – also plays an important role in gas exchange from the water to the atmosphere (CO_2, CH_4) and from the atmosphere to the water column (O_2; Whitmore et al., 2021). These patterns suggest that coupling landscape geomorphology, drainage

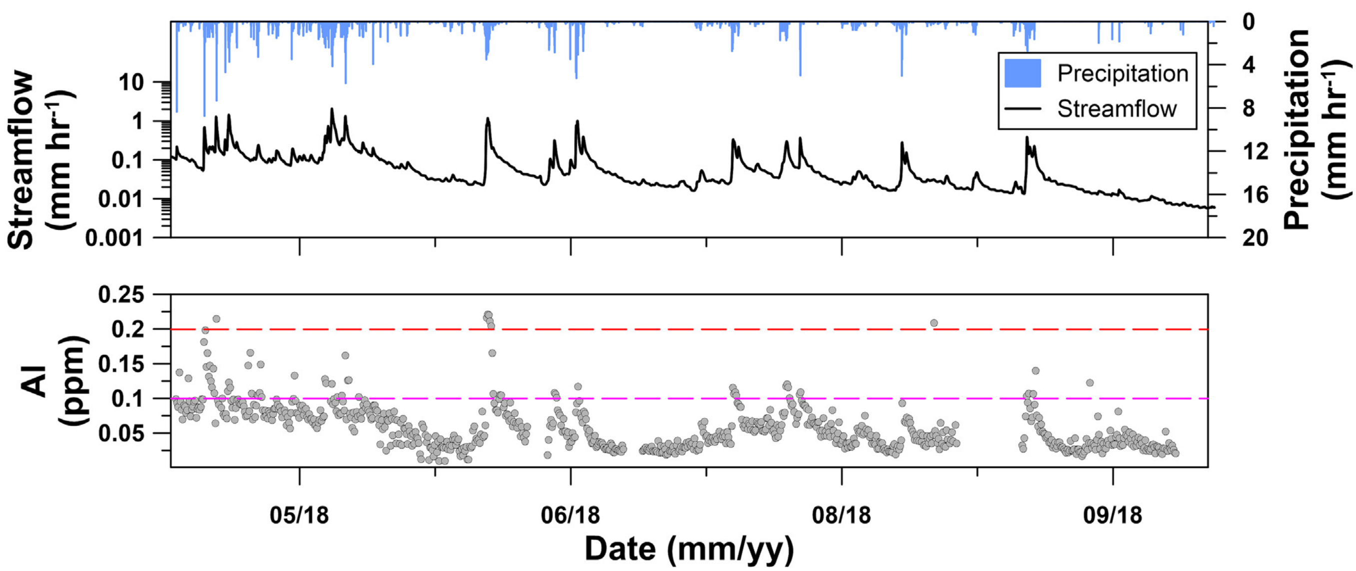

Fig. 6. High-frequency time series of a) precipitation and streamflow (hourly) and b) aluminum (Al) (every 6 h) data in a páramo headwater catchment (3.28 km^2) within the Zhurucay Ecohydrological Observatory in Southern Ecuador. The purple and red horizontal dashed lines in b) represent the permissible limits for the preservation of aquatic life and drinking water, respectively, according to the Ecuadorian, United States Environmental Protection Agency, and World Health Organization water quality standards.

network organization, gas transfer velocities, and biogeochemical transformations under variable hydraulic regimes may provide a conceptual framework for upscaling nutrient transformation and stream metabolism across the complex topography that characterizes high-Andean landscapes.

Riparian vegetation plays a crucial role in mediating organic matter loads, light penetration, and other resources that may influence stream biogeochemistry. In general, páramo is considered an open environment and, as such, streams in these landscapes should tend towards autochthonous (algal-based) food webs. Supporting this idea, a study along an altitudinal gradient (1260 to 4045 m a.s.l.) in the northeastern Ecuadorian Andes showed that stream invertebrates in the highest altitudes (i.e., páramo) were primarily supported by autochthonous food sources, as compared to insects from montane forest streams at lower altitudes, which were primarily supported by allochthonous materials (Atkinson et al., 2018).

Not surprisingly, land use change can alter nutrient inputs into páramo streams. In central Ecuador, for example, Gauthier et al. (2013) showed that stream sections downstream from páramo areas transformed to cattle pastures had higher total N concentrations (239 to 318 μg L^{-1}) than corresponding upstream undisturbed sections (182 to 220 μg L^{-1}). Agriculture has similarly been shown to increase nutrient inputs in stream ecosystems. At páramo sites in Colombia, for instance, land plots turned into potato fields had higher N and P concentrations than non-native pastures (Gauthier et al., 2013). This was explained by higher soluble nutrient content in agricultural soils because of fertilization and drying of soils leading to increased nutrient mobilization (Hofstede, 1995a; Otero et al., 2011; Podwojewski et al., 2002). In addition, research on factors influencing soil water DOC concentrations under different land use in a southern Ecuadorian páramo showed that native (*Polylepis reticulata*) forest produced the highest DOC concentrations followed by pastures, tussock grass, and pine plantations (Pesántez et al., 2018). These authors also found that land use change and soil moisture were the most influential variables explaining DOC leaching from soils, whereas climatological variables (including precipitation and evapotranspiration) were of less importance.

6.1.2. Metabolism

Due to the low air temperature, high air humidity, and high soil moisture content that characterizes high-elevation páramo sites, metabolic processes occur at slower rates than at lower-elevation ecosystems presenting warmer temperatures. This assessment is based on growth rates of plant communities, decomposition of organic matter, turnover of aquatic biota, and high accumulation of organic matter and dead material above and belowground. The high build-up of biomass is important for soil protection, carbon storage, and water regulation (Buytaert et al., 2006a; Mosquera et al., 2015). Understanding the interactions among organic carbon loads, allochthonous vs. autochthonous substrates, and the role of rapidly changing water residence times is critical for the characterization of ecosystem metabolism in páramo watersheds.

Measurements of CO_2 ecosystem balance in a conserved páramo grassland in southern Ecuador (3765 m a.s.l.) yielded a mean productivity value of 1.17 kgC m^{-2} yr^{-1} (Carrillo-Rojas et al., 2019), whereas ecosystem modeling approaches used in northern Ecuadorian páramo sites between 4000 and 4600 m a.s.l. reported productivity values varying from 1.20 to 1.44 kgC m^{-2} yr^{-1} (Minaya et al., 2016a). In contrast, plant yield methods in grassland páramo sites of southern Ecuador (3700–4000 m a.s.l.) resulted in mean aboveground productivity values between 0.08 and 0.14 kgC m^{-2} yr^{-1} (Ramsay and Oxley, 2001). Even though these studies suggest that primary productivity in upland páramo sites can be influenced by elevation, vegetation type, and land use; it is worth noting that the use of different estimation methods hampers the capacity for direct comparison among sites. In general, productivity tends to decrease with increasing elevation, but might also be constrained by the accumulation of necromass in tussock grasses (Ramsay and Oxley, 2001), or by P limitation, especially in soils developed on volcanic ash (Hofstede, 1995b).

Respiration estimates for a conserved páramo grassland (3300–3600 m a.s.l.) vary between 1.73 and 3.68 kgC m^{-2} yr^{-1} (Cardozo-G and Schnetter, 1976; Peña-Quemba et al., 2016), and between 3.77 and 4.20 kgC m^{-2} yr^{-1} for a páramo area that was transformed into potato fields and pastures (Peña-Quemba et al., 2016). Increased soil temperature due to the removal of vegetation cover for cultivation or the reduction in the height of pastures due to grazing is likely to favor the decomposition of soil organic matter, explaining the higher respiration rates in disturbed páramo areas. The latter in turn can result in an enhanced release of CO_2 stored in the soil to the atmosphere (Peña-Quemba et al., 2016).

The only available measurement of respiration and its balance with primary productivity in conserved páramo grasslands was reported in a study carried out in southern Ecuador (3765 m a.s.l.) by Carrillo-Rojas et al. (2019). In this study, the average respiration rate was 1.27 kgC m^{-2} yr^{-1}, which, compared with a mean primary productivity of 1.17 kgC m^{-2} yr^{-1}, resulted in an annual net loss of 0.10 kgC m^{-2}. Although the authors concluded that undisturbed páramo grasslands can be a source of greenhouse gases, the findings cannot be generalized given the limited spatial and temporal coverage of the study. Nevertheless, these results suggest that páramo grasslands could lose their soil organic carbon reserves even in undisturbed conditions, directly influencing aquatic processes (Buytaert et al., 2011).

6.2. Ecophysiological-ecohydrological interactions and feedbacks in páramo vegetation

Plant ecophysiological processes influence hydrology at ecosystem to watershed scales in ways that are mediated by differences in plant species' physiological, anatomical, and morphological traits and adaptive strategies (Asbjornsen et al., 2011; Wright et al., 2017). Species belonging to the same functional group typically share a set of fundamental traits that influence water movement along the soil-plant-atmosphere continuum (Rada et al., 2019), and contribute to regulating the water cycle (Leimer et al., 2014; Lin et al., 2019; Mitchell et al., 2016). In this section, we summarize knowledge on plant ecophysiological characteristics related to páramo ecohydrology of four dominant functional groups: tussock grasses, cushion plants, rosettes, and trees.

Grasslands dominated by tussock grass frequently comprise the most common plant community in páramo, covering up to 90 % of the land area (Llambi et al., 2013; Mosquera et al., 2015). A recent study by Ochoa-Sánchez et al. (2020) used an eddy-covariance approach to assess landscape-scale patterns in tussock grass (*Calamagrostis intermedia*) evapotranspiration in a south Ecuadorian wet páramo. Their findings suggest that overall evapotranspiration was low (average of 1.7 mm day^{-1}) due to strong energy limitation. Net radiation was the primary factor controlling this water balance component, followed by wind speed, aerodynamic resistance, and surface resistance. Interestingly, canopy interception loss contributed more to evapotranspiration than transpiration, highlighting the constraints of the low evaporative demand and solar radiation on plant productivity.

Cushion plants characterized by hemispherical to mat-like growth forms occurring at the ground surface enhance the accumulation of peat in páramo wetlands (Mosquera et al., 2015). Cushion plants' high rates of carbon accumulation are largely attributed to their high root biomass productivity and turnover rates (Suárez et al., 2021). The presence of aerenchyma on their roots allows cushions to access oxygen and maintain physiological functions despite saturated conditions (Fritz et al., 2011). The water storage capacity of páramo catchments was shown to increase directly with the areal proportion of wetlands formed by the association of cushion plant vegetation and underlying organic-rich (Histosol) soil (Lazo et al., 2019). These observations underscore the important ecohydrological role of cushion plants via their impact on promoting carbon accumulation, catchment water storage, and flow regulation (Mosquera et al., 2016b).

While the ecophysiology of the rosette functional group has been widely studied in páramo (e.g., Rada et al., 2012; Sandoval et al., 2019; Sklenář et al., 2010), we found only one study that specifically assessed the relationship between rosette ecophysiology and páramo hydrological functioning. Cárdenas et al. (2018) carried out a study in a Colombian páramo involving measurements of sap flow in 8 individuals of the giant rosettes *Espeletia* *occidentalis* and *E. hartwegiana* over 6 months. The results obtained during a few sunny days confirm that temperature, solar irradiance, and relative humidity explain 76 % of sap velocity, while transpiration was not limited by soil moisture content. Transpiration and sap flow rates decreased markedly later in the day on sunny days as a protection strategy against strong irradiance. Nighttime transpiration allowed for the refilling of the inner water reservoirs in the pith and leaves, providing buffering capacity to withstand unfavorable conditions. The authors estimated that on a sunny day, mature *Espeletia* plants transpire around 1 L of water. After extrapolating transpiration during the dry, sunny season to the entire watershed, the authors estimated that transpiration by this páramo vegetation represents about 21 % of streamflow, in an ecosystem with a 60 % water yield.

While trees are relatively scarce in páramo landscapes, scattered patches of woodlands occur, many of these dominated by species of the genus *Polylepis* (Hensen et al., 2012; Jameson and Ramsay, 2007). *Polylepis* species adapt to páramo's extremes in temperature and solar radiation by the ability to upregulate photosynthesis quickly in response to short periods of favorable climatic conditions and maintain high photosynthetic efficiency (Rada et al., 1996). A study on effective precipitation in a *Polylepis reticulata* forest catchment in southern Ecuador indicated that mean annual throughfall was 773.2 mm (59 % of gross precipitation), and showed a decreasing trend with increasing leaf area index and canopy density (Suqui et al., 2021).

7. Social and political dimensions influencing páramo water management, governance, and ecosystem services provision

In addition to providing important hydrologic ecosystem services (Buytaert et al., 2006a; Célleri and Feyen, 2009; Hofstede, 2001a), páramo is often central to rural livelihoods (Manosalvas et al., 2021) and ceremonial activities of cultural value (Farley and Bremer, 2017). Balancing the various uses and values of páramo is a key challenge for local and regional management and it is well-recognized that successful conservation efforts will involve local communities, protect local and Indigenous peoples' rights, and incorporate sustainable local livelihoods as a way of reciprocity between páramo inhabitants and water users downstream. In this context, we classified the social-political páramo studies as follows: 1) páramo management and governance, 2) assessment of ecosystem services, and 3) compensation for ecosystem services.

7.1. Páramo management and governance

The reviewed papers on páramo management and governance with direct implications for water resources were subclassified into the following, often overlapping, categories: 1) páramo land use and management, 2) collaboration between civil society organizations, and 3) political ecology assessments.

7.1.1. Páramo land use and management

Recognizing the important role of páramo for local livelihoods and regional water supplies, in one of the first social-ecological studies of páramo, Hess (1990) presented a conceptual model of Andean land use systems to stimulate interdisciplinary discussion about páramo production systems. More recently, several studies evaluated how contemporary land tenure and governance influence páramo land use and management with implications for páramo ecology and hydrology. For instance, López-Sandoval and Maldonado (2019) examined how communal land tenure systems in Ecuadorian páramo areas influenced agricultural frontier expansion, grazing practices, and land use rules. Similarly, Acevedo and Correa (2019) analyzed collective action mechanisms emerging against mining in the páramo of Santander, Colombia. Other articles focused on the technical aspects of management and sustainable livelihoods in páramo landscapes including alpacas and agrotourism as a means to protect páramo water resources (Verano and Villamizar, 2017; White and Maldonado, 1991).

A single study focused explicitly on management activities of water user associations in high-elevation ecosystems (Leroy, 2019). Using interviews with farmers and strategic actors in water user associations in Colombia and Venezuela, the authors concluded that adaptation actions, including wetland restoration and investment in efficient irrigation technologies, are driven both by perceptions of climate change (e.g., less and more extreme precipitation) as well as socio-economic drivers of water scarcity (e.g., increases in cultivation area). Taking a broader national focus, Garcia and Leal (2019) analyzed how the Colombian government developed legislation for the legal protection of páramo, but concluded that it has not meant much in terms of actual conservation actions.

7.1.2. Collaboration between civil society organizations

Given the importance of páramo for biodiversity, water supply, and local livelihoods, there have been substantial NGO initiatives in páramo communities. Several projects were led by environmental NGOs in the early 2000s to develop participatory management plans in rural and Indigenous communities. These included Proyecto Páramo in Ecuador (Mena-Vásconez et al., 2001) and Proyecto Páramo Andino in Venezuela, Colombia, Ecuador, and Peru (Crespo, 2012). While the core objective of these efforts focused on the conservation of biodiversity and protection of páramo for hydrologic services, community participation was encouraged in plan design and implementation (see Crespo, 2012; Mena Vásconez et al., 2011).

Other articles analyzed strategies for more effective collaboration among government, NGOs, and páramo communities. For example, Robineau et al. (2010) used spatial-temporal analysis of farming activities and interviews to demonstrate how improved understanding of farming systems in the páramo of Rabanal (Colombia) can foster mutual collaboration between local communities and environmental groups and results in the conservation of páramo biodiversity and water resources. Focused on government-community relations, Avellaneda-Torres et al. (2015) conducted a literature review and analyzed alternative solutions to conflicts over water resources between environmental authorities and páramo communities. They recommended four strategies: funding of community management plans, development and implementation of agroecological models, rescue of biocultural memory, and changes in agrarian structure. Similarly, Iñiguez et al. (2013) used rapid ethnographic methods to assess the feasibility of governing a proposed Ramsar wetland in Ecuador across multiple communities and jurisdictions, including páramo. The authors concluded that attention to land tenure conflicts and institutional frameworks is critical in the design of sustainable collaborative governance strategies.

7.1.3. Political ecology assessments

There has been a recent increase in scientific articles focused on páramo management and water resources from a political ecology perspective (*sensu* Bassett and Peimer, 2015). The articles found in this review drew on various theoretical frameworks from political ecology and related fields to analyze how structural conditions, community agency, and power relations at multiple scales influence the management of páramo and its natural resources, including water. Several studies within the realm of political ecology focused specifically on the construction of "hydrosocial territories" defined as "the contested imaginary and socio-environmental materialization of a spatially bound multi-scalar network in which humans, water flows, ecological relations, hydraulic infrastructure, financial means, legal-administrative arrangements, and cultural institutions and practices are interactively defined, aligned, and mobilized through epistemological belief systems, political hierarchies, and naturalizing discourses" (Boelens et al., 2016, p.2). Using mixed methods such as participatory action research, hydrosocial network analysis, and literature review, Duarte-Abadía and Boelens (2016) and Osejo and Ungar (2017) assessed power dimensions of páramo hydrosocial governance and resource use conflicts in Santurbán, Colombia. Also drawing on hydrosocial territories, Manosalvas et al. (2021) used qualitative and participatory methods to illuminate the agency of Indigenous and rural communities in decolonizing processes which facilitate their own forms of development and water management in north-central Ecuador.

Other political ecology studies used mixed methods to describe resistance to mining and other extractive industries in San Isidro, Ecuador (Partridge, 2016), Santurbán, Colombia (Parra-Romero and Gitahy, 2017), and in the de Pisba páramo, Colombia (López Rojas, 2018). Using ethnographic methods, Pinel et al. (2018) pointed to the need for increased contributions from political geographers to better understand the relationships and motivations of local actors in engagement with "boundary-spanning regional strategies" in southern Ecuador. Betancur-Alarcón and Krause (2020) used interviews and policy analysis to demonstrate how the shift in power occurring from the Colombian Peace Agreement and the retraction of the Colombian Revolutionary Armed Forces (FARC) reinforced unequal access to land and water in the páramo of the Cauca Valley, Colombia.

7.2. Assessment of ecosystem services

Several studies reported that land cover change to agriculture or tree plantations and climate change cause a negative effect on páramo provision and regulation of ecosystem services (e.g., Hofstede et al., 2002; Marín et al., 2018; Mosquera et al., 2022; Patiño et al., 2021; Podwojewski et al., 2002). Farley and Bremer (2017) linked community perceptions of páramo ecosystem services with measured ecological outcomes resulting from afforestation and fire suppression incentivized by payment for ecosystem services programs. They concluded that there are areas of agreement and disagreement between available ecological data and local perceptions of how land use change might affect valued páramo ecosystem services. For instance, while most participants thought that pine plantations decrease water supply, in line with available ecological data, some expected increased streamflow. In a related study on páramo stakeholder perceptions, Quiroz et al. (2018) conducted interviews with landowners, local government representatives, foresters, and nature conservationists, and found that while landowners generally perceived pine plantations to increase páramo water regulation, the other groups perceived a decrease in water regulation with afforestation.

7.3. Compensation for ecosystem services

Given the recognition of páramo for water regulation, it became a hotspot for the development of payment for ecosystem services programs over the last several decades, particularly in Ecuador.[1] These include the national scale Socio Bosque program financed by the government, including a Páramo chapter, as well as local and provincial water funds in which governmental groups, civil society, and private entity actors finance interventions of páramo conservation and restoration (Bremer et al., 2016; Farley et al., 2011). While these programs can be considered part of a wider body of watershed payments or payment for ecosystem services, resistance to any term which could be perceived as alluding to water privatization led to either calling the programs conservation incentives (as in the case of Socio Bosque; Farley et al., 2011), or using non-monetary incentives (as in water funds; Kauffman, 2014).

In a review of the social and ecological goals of payment for ecosystem services programs in Ecuador using interviews and surveys with program managers, Farley et al. (2011) found nine programs, including two national-scale (Socio Bosque focused on water, carbon, biodiversity, and livelihoods; and PROFAFOR centered on carbon sequestration) and seven local or regional programs targeted on water. The authors concluded that these programs have the potential to contribute to local development goals, but that social metrics, particularly related to poverty alleviation, are lacking. They also found that programs were supporting a mix of protected areas and "working landscapes" (where urban and rural, agricultural patches are combined). Using a similar approach, Bremer et al. (2016) reviewed the structure, goals, and monitoring of water funds within the Latin American Water Funds partnership. They found seven water funds in the Andean region, all of which worked in páramo (three in Ecuador and three in Colombia) or puna (one in Peru). Kauffman (2014) described the evolution and adaptation of water funds to varying political and cultural contexts since the first program launched in Ecuador (i.e., Quito's Water Fund for Water Protection; Fondo Ambiental para la Protección de Agua, hereafter referred to as FONAG). According to this author, water funds are innovative in providing financing for watershed conservation in countries like Ecuador where there is resistance to privatizing water.

There have been several efforts to evaluate the outcomes and nature of both Socio Bosque programs and water funds. Since its establishment in 2009, the first set of studies used interviews with the Socio Bosque community and individual participants to assess the motivations for participation (Bremer et al., 2014a) and perceived social outcomes (Bremer et al., 2014b). The authors found that the program successfully attracted participation among rural farmers and communities. At the same time, issues related to land tenure, low levels of trust in government institutions, and social and financial constraints often made the program more accessible and desirable to larger and slightly wealthier landowners (Bremer et al., 2014b). They also found that potential livelihood outcomes varied among communities that organized around protecting their páramo prior to the program providing the most promising opportunities for both conservation and livelihood gains; while some small, rural farmers experienced the greatest tradeoffs in livelihood losses with agreed land use changes (Bremer et al., 2014b). Overall, with the exception of the smallest farmer participants who were often simultaneously subject to legal restrictions on their land use, the authors found that the program largely functioned as a "reward for conservation", rather than as a trigger for major changes in land management (Bremer et al., 2014a, 2014b).

Another line of research conducted surveys with community leaders and households to evaluate how participation in the páramo chapter of Socio Bosque influenced the governance of communal lands (Hayes et al., 2015; Hayes and Murtinho, 2018; Murtinho and Hayes, 2017). Hayes et al. (2015) found that most communities strengthened their land use rules since participation in the program, and that poorer communities were more likely to implement a rule change compared with wealthier ones. In a follow-up study, Hayes et al. (2017) further reported that communal governance and payment for ecosystem services influenced conservation outcomes in páramo. Focusing on a subset of participating communities, Hayes and Murtinho (2018) demonstrated the key role of community governance in the equitable distribution of benefits in the program, finding that members of well-organized communities were more likely to perceive positive benefits of the program than less organized communities. In line with Bremer et al. (2014a), Murtinho and Hayes (2017) found discordance between individual and communal decisions to participate in the program. They reported that individual landholders were less likely to participate in the program than communal groups.

A set of publications derived from a doctoral dissertation evaluated FONAG through a political ecology lens and a mix of ethnography and archival research. Joslin and Jepson (2018) argued that the water fund represents a process of urban market actors and NGO alliances, creating "non-state territorialization" associated with ecosystem service conservation. Joslin (2019) used ethnographies from three participant communities to assess FONAG's narrative of success. Joslin (2020a, 2020b) analyzed the role of FONAG community páramo park guards as intermediaries in the program as well as a discourse analysis of how the program is discussed more broadly (focused on water benefits) versus how the guards of the community park present the programs to their rural communities (focused on the relational and environmental benefits of protection). The author claimed that despite varying discourses and efforts, FONAG positions within the realm of neoliberal conservation (Joslin, 2020b).

Rodríguez de Francisco and Boelens (2014, 2016) also focused on páramo and payment for hydrologic services using a political ecological lens related to power and territory in the Ecuadorian highlands. These authors argued that such payments are not neutral development tools acting in cultural voids, but items constructed by market- or environmentalist-oriented networks with definite perspectives, values, and interests that interact with the unequal power structures within the societies where the policies are introduced. Rodríguez de Francisco and Boelens (2016) analyzed how depoliticized payment for hydrologic

[1] The Ecuadorian Ministry of Environment and Water (MAAE) established in 2008 the Socio Bosque Program to conserve forests and páramos through economic incentives to individual or collective owners. The condition is that they voluntarily commit to their conservation and protection and to follow-up protocols under a 20-year agreement and with a maximum payment of US $ 30/ha per year. To enter, communities and individuals must have the property title (https://sociobosque.ambiente.gob.ec/).

services initiatives create a new type of hydrosocial territory, in which the control of resources is deeply reshaped via repatterning and commoditizing the relationship between water providers (upstream) and consumers (downstream).

8. Frontiers in páramo water resources research

Based on the assessment and synthesis of scientific knowledge regarding the abiotic, biotic, and social-political aspects of páramo water resources, we identified key research frontiers in páramo scholarship. Addressing such frontiers is a key step toward improving the management, governance, and conservation of páramo natural resources, as well as to achieve a sustainable availability of clean water for supplying the needs of rural and urban centers while maintaining the integrity of terrestrial and aquatic páramo environments.

8.1. Frontier 1: diversity in páramo hydrological processes and streamflow generation mechanisms

The complex topography of the Andean and Central America mountain ranges cause a high spatial variability in climatological, geomorphological, pedological, and geological conditions along páramo. These conditions in turn result in a diversity of hydrological behavior in páramo regions that needs to be assessed and accounted for in future studies to improve water resource management. Ground measurements of precipitation are still needed in the páramo of Venezuela and Peru. The influence of fog in soil water dynamics and the water balance of páramo catchments remains poorly studied across the Central America and Andean páramo. No quantifications of actual and potential evapotranspiration and their partition into different components exist for most páramo vegetation forms, except for tussock grasslands of southern Ecuador. Similarly, evapotranspiration studies on degraded and restored páramo areas are scarce. Studies of evaporation from open water bodies are also lacking, except for a lake province in Costa Rica.

Surface and subsurface flow studies are still scarce for seasonally dry and glacierized páramo regions, and for areas presenting non-volcanic soils and permeable bedrock. Research on infiltration in regions with non-volcanic soils, as well as for vegetation types other than tussock grasses are still nonexistent. Subsurface water movement in non-volcanic and organic-rich (peat-type or Histosol) páramo soils are lacking. Mechanistic understanding of rainfall-runoff processes in páramo catchments is generally unknown across páramo, except in southern Ecuador. The role of lakes in water yield and flow regulation also remains understudied across páramo. Notably, although Andean wetlands likely play a key hydrological role as main sources of streamflow generation and regulation, their hydrology is still poorly understood throughout the Central and South American páramo.

Apart from pine afforestation, the impacts of other exotic (e.g., *Cupressus* and *Eucalyptus*) and native (e.g., *Polylepis*) plantations on soil water dynamics and storage as well as on flow generation and regulation have not been investigated in the Andean páramo region. This also includes possible (positive or negative) impacts of plantations on the hydrology of revegetation practices as part of ecosystem restoration. The influence of other changes in land use including fire, intensive cattle grazing, and agriculture on hydrological processes and catchment rainfall-runoff processes is still limited and often times inconclusive or not detailed enough to be translated into management recommendations. Experiments on how soil water dynamic and storage would react under extreme meteorological conditions such as droughts are also lacking, and would be of tremendous value for evaluating the impacts of climate change on páramo soil and catchment hydrology. Assessments of the effects of restoration on páramo hydrological function are also missing.

8.2. Frontier 2: generation of empirical evidence of páramo chemical water quality

Very few chemical water quality studies in streams, springs, and lakes exist in the literature, making this an important knowledge gap in páramo water resources research. Water quality investigations of toxic elements like heavy metals, pesticides, and persistent organic compounds in areas impacted by anthropogenic changes including mineral extraction, burning, intensive agriculture, grazing, and urbanization are still very scarce across the Andean páramo. In Central America, the traditional conception that protected ecosystems like páramo are risk-free of pollution effects limits the monitoring of water quality parameters. The production of potentially harmful byproducts due to the chlorination process of organic-rich water originated from páramo catchments has not been investigated. Therefore, a major step to improve environmental management in the Andean and Central American páramo requires the implementation of systematic monitoring of water quantity and quality.

8.3. Frontier 3: implications of ecological and ecophysiological processes on páramo water supply

More information is required to understand biogeochemical processes in páramo aquatic environments. Investigating the interplay among landscape geomorphology, drainage network organization, and gas transfer velocities will permit upscaling nutrient transformation and stream metabolism in páramo streams. In situ and laboratory experiments are needed to quantify reactivity rates of organic carbon across different hydrological conditions (wet versus dry periods) and altitudinal gradients, the degradation of dissolved organic matter under dark and light settings, the diel to annual dynamics of ecosystem metabolism, and the general controls on diel oxygen curves in páramo wetlands, lakes, and streams. Although variation in the physiognomy, phenology, and litter quality of vegetation has important implications for aquatic biogeochemical processes, their influence on the cycling of nutrients in páramo streams have not yet been characterized. Improved understanding of these biogeochemical processes and interactions will help to identify their influence on streamflow water quality. It is also necessary to examine how climate change may further modify reactivity rates of dissolved nutrients, and as a result, the availability, export, and cycling of elements such as C, N, and P. New knowledge from examining these processes will allow assessing how changes in nutrient availability and export may in turn affect aquatic biota.

Very few studies have examined the relationship between plant physiological processes and páramo hydrology. A major knowledge gap is understanding how fog-vegetation interactions affect the hydrologic cycle (via additional precipitation inputs due to canopy fog interception) and the distribution and persistence of different plant species (via fog-dependent physiological processes). Another research topic deserving greater attention is to understand water use patterns of páramo vegetation and plant functional types in relation to environmental controls. Emphasis should also be placed on combining different methods (e.g., flux towers, modeling, remote sensing) to scaling plant-level physiological measurements to derive estimates of evapotranspiration at the ecosystem to watershed scales. The potential of different páramo vegetation types to adapt and survive under future climate conditions should be experimentally assessed through the investigation of their potential to adapt and survive during extreme dry and wet events. Another critical knowledge gap is understanding how potential shifts in species or functional group composition may affect plant water use dynamics, fog-vegetation interactions, and soil water storage capacity due to changes in climate and/or land use.

8.4. Frontier 4: social-ecological resilience of páramo water resources

There is a need for future research on water management, governance, conflicts, and power relations in páramo communities and in the broader páramo regions. In many areas, water boards (locally known as *juntas de agua*) represent the principal authority for community water management, but these have received little to no attention from the research sector. There is also a great need for research on social-ecological resilience to climate change within páramo communities. Future work could link climate and hydrologic monitoring and modeling to assess access, use, and governance of water. Climate impacts could also be usefully studied in the context of environmental, social, and political change which affects páramo social-ecological systems. Given that water conflicts may escalate with climate

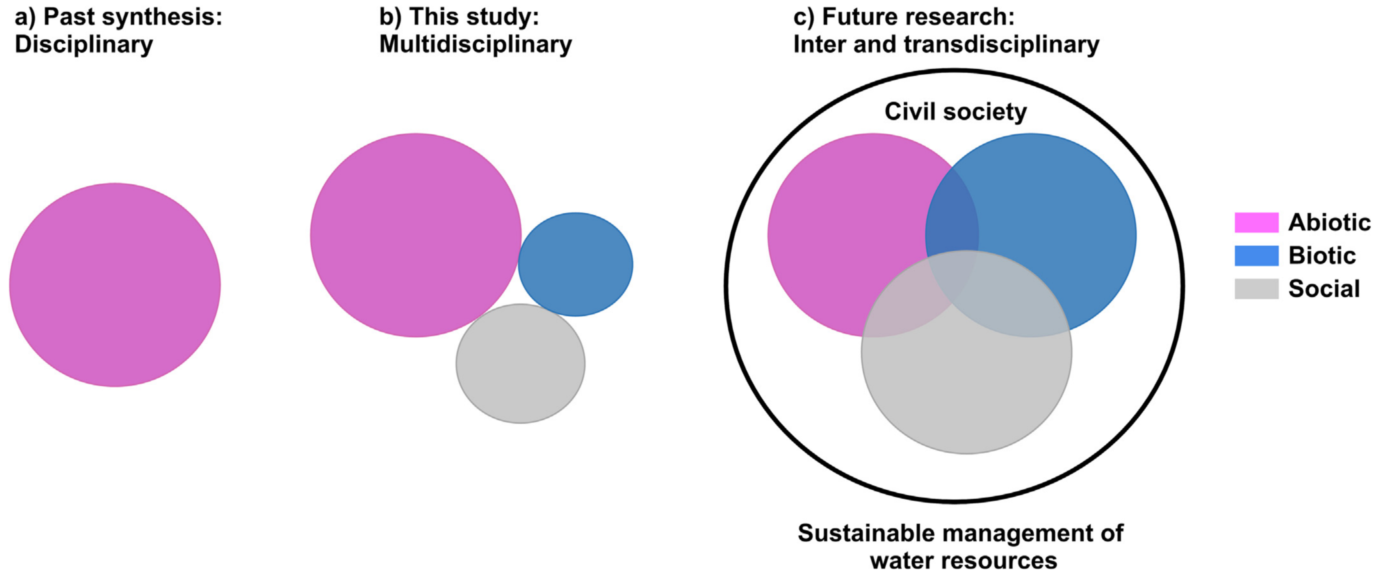

Fig. 7. Temporal evolution of disciplinarity on páramo water resources research. a) Past: disciplinary studies focused exclusively on water quantity (cf., Buytaert et al., 2006a; Correa et al., 2020); b) Present: multidisciplinary synthesis study showing a dominance of abiotic (water quantity and quality) studies (59 % of the revised scientific articles) and a small proportion of biotic (ecological and ecophysiological) and social-political investigations (18 and 23 % of the 147 revised scientific articles, respectively; this study); and c) Future: interdisciplinary (the combination of at least two disciplines of different nature) and transdisciplinary research accounting for societal needs and including the participation of local livelihoods to achieve sustainable management of páramo water resources.

change, strategies to manage conflict are expected to emerge and it would be worthy to investigate them. Importantly, the ecosystem services provided by páramo in Central America have received very little attention, pointing to an important potential research area. It is worth noting that no examples of social studies on páramo conducted by researchers from local communities exist. Co-producing research agendas between researchers and local communities provides an important opportunity to establish a dialogue with local and indigenous systems of knowledge. Research led by community members could support such dialogue.

8.5. Frontier 5: moving beyond disciplinarity on páramo water resources research

Despite the potential of interdisciplinary approaches – here defined as the combination of methodologies from at least two disciplines of different nature (i.e., abiotic, biotic, or social) –, or even transdisciplinary approaches that combine these divisions in innovative ways, our assessment depicts that the vast majority of páramo water studies have a disciplinary focus (Fig. 7a-b). We found only a few exceptions in which social and economic evaluations were combined with abiotic and biotic measurements or modeling approaches (e.g., Espinosa and Rivera, 2016; Farley and Bremer, 2017). An important benefit of integrating different dimensions of páramo water resources is to achieve an improved capacity to ask and answer questions related to ecosystem management and decision-making. Through greater collaboration among researchers from various disciplines as well as with communities and other managers, there is enormous potential for research programs to better address the pressing challenges facing páramo communities and broader society (Fig. 7c).

We see immense potential for hydrosocial modeling (e.g., Carey et al., 2014; Mark et al., 2017) in páramo, which links changes in i) land use, management, and governance; ii) ecological function; iii) hydrologic services (e.g., water quality and flow regulation); and iv) multiple dimensions of human well-being. To understand such complexity, academicians are looking beyond disciplinary research toward integrated interdisciplinary and transdisciplinary methods and approaches (Vogel et al., 2015). However, a major critique of hydrosocial logical models (among water resources, biota, and human society) is that they fail in being predictive due to the great heterogeneity of human behavior. This limitation could be addressed by complementing modeling approaches with hydrosocial research that comes from critical geography and produces rich narratives about their case studies. This way, positivist currents that believe their research is done in a "vacuum" can combine with more constructivist perspectives and add important variables, such as power, across all relations between society and nature, in detailed physical-biological conditions (Wesselink et al., 2017).

A truly integrated, holistic approach can help to improve the multidimensional valuation of ecosystem services provided by páramo water resources, assess their vulnerability to changes in land use and climate, and provide a diverse knowledge base for wise stewardship of the landscape (e.g., Jaeger et al., 2019; Motschmann et al., 2022). In this sense, we expect that this multidisciplinary synthesis can serve as a starting point to guide future investigations (Fig. 7) based on the proposed frontiers in páramo water resources research, as well as to motivate páramo scientific community to work in an interdisciplinary and transdisciplinary manner.

CRediT authorship contribution statement

Conceptualization and Methodology: G.M.M.; Formal analysis and Literature Review: G.M.M., R.H., L.L.B., H.A., A.C.-H., R.C., R.M., F.M., P.M.-V., P.M.-D., A.O.-S., J.P., D.A.R.-I., E.S.; Investigation: G.M.M., R.H., L.L.B., H.A., A.C.-H., R.C., P.C., R.M., P.M.-V., P.M.-D., A.O.-S., J.P., D.A.R.-I., E.S.; Funding acquisition, Project administration, and Resources: G.M.M.; Visualization: G.M.M., P.M.-D., J.P.; Writing - original draft: G.M.M., R.H., L.L.B., H.A., A.C.-H., R.C., R.M., P.M.-V., A.O.-S., J.P., D.A.R.-I., E.S.; Writing - review & editing: all authors. All authors have read and agreed to the published version of the manuscript.

Data availability

Data will be made available on request.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: G.M.M. reports financial support was provided by CONDESAN, the Mountain Research Initiative (MRI), and the University of Zurich.

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Appendix A. Supplementary data

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