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Review Article

Progress in understanding the hydrology of high-elevation Andean grasslands under changing land use

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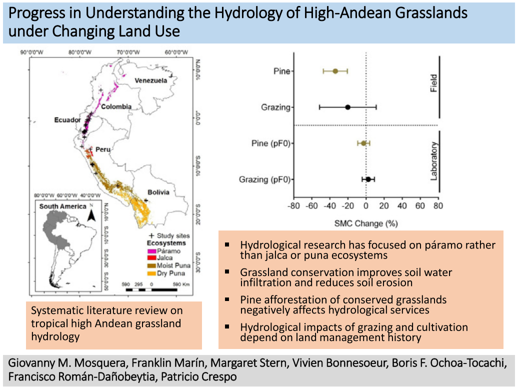
HIGHLIGHTS

- Systematic literature review on tropical high Andean grassland hydrology
- Hydrological research has focused on páramo rather than jalca or puna ecosystems.
- Grassland conservation improves soil water infiltration and reduces soil erosion.
- Pine afforestation of conserved grasslands negatively affects hydrological services.
- Hydrological impacts of grazing and cultivation depend on land management history.

GRAPHICAL ABSTRACT


Progress in Understanding the Hydrology of High-Andean Grasslands under Changing Land Use

Systematic literature review on tropical high Andean grassland hydrology

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ABSTRACT

High-elevation grasslands worldwide provide essential hydrological services including water provision, flow regulation, and erosion control. Despite their importance, hydrological research of grasslands in montane regions is usually scarce and disperse, limiting the capacity to improve water resource management. We present a systematic literature review of the hydrological function of high Andean grasslands under conserved, degraded, and restored conditions in ecosystems situated above the tree line in the tropical Andes (páramos, punas, and jalcas). Most hydrological research on these grasslands has been developed in páramos (92%), especially in Ecuador, while research in punas is scarce (6%) despite being the largest grassland extent in the region. For páramos, published literature highlights the importance of conserving grasslands to facilitate water infiltration to soils, which in turn reduces erosive processes. Water-vegetation relations for conserved páramos are well understood, indicating that about 50% of water inputs return to the atmosphere via evapotranspiration, but knowledge about hydrological functions of conserved punas and jalcas is virtually non-existent. Under changing land use, afforestation of grassland ecosystems with exotic tree species, especially pines, reduces soil water storage as well as water yield and flow regulation capacity. Impacts of grazing and agriculture on the hydrological function of páramo grasslands strongly depend on historical land management and current land use practices and are not

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generalizable. Short-term restoration studies indicate that more than two years are necessary to recover the hydrological function of degraded grasslands, therefore medium and long-term studies are required to determine efficient restoration periods. These knowledge gaps limit the ability to extrapolate and regionalize findings. Future directions aimed to fill them are proposed, and methods successfully used to investigate the hydrology of high Andean grasslands are highlighted. This research not only enlightens what is known about the hydrology of high Andean grasslands, but also seeks to guide future hydrological evaluations to fill identified geographical and topical knowledge gaps precluding improved management of water resources in the tropical Andes.

Contents

1. Introduction

High-elevation ecosystems provide essential water-related services to surrounding and downstream areas (Immerzeel et al., 2020; Viviroli et al., 2020). Tussock grasslands are found at the highest and longest mountain ranges of the planet – the Himalayas, Andes, Alps, the Tibetan Plateau, and the Ural and Altai mountains – where they form the dominant vegetation in many montane ecosystems above tree-line (Dixon et al., 2014). These grasslands represent an important ecological resource contributing to the provision of hydrological services including water yield, flow regulation, and erosion control, and they play a crucial role in supplying the water needs of millions of people worldwide (Pomeroy et al., 2015). Nonetheless, there is still a tendency to associate hydrological benefits solely to forests and forestation, whereas the hydrological role of high-elevation grasslands is generally marginalized (Aide et al., 2013; Bonnesoeur et al., 2019; Calder, 2007; Farley et al., 2005; Garcia-Chevesich et al., 2017; Jones et al., 2017). Hence, understanding the hydrological functioning of high-elevation grasslands and how they are influenced by land use change is critical to secure a sustained management of water resources in mountain regions where grasslands dominate.

In the tropical Andes, high-elevation grasslands – often dominated by tussock grass genera *Calamagrostis*, *Festuca* and *Stipa* – occur over vast areas at elevations between ~3000-5000 masl, above the tree line and below the perennial snow line, in ecosystems known as páramo, jalca, and humid and dry puna (Josse et al., 2009). Ecologically, the páramos have the most biologically and structurally diverse montane flora in the world and are an integral part of the renowned tropical Andes biodiversity hotspot (Luteyn, 1999; Young et al., 2015). Hydrologically, these grassland-dominated ecosystems collect, store and supply water for domestic, agricultural, irrigation, hydropower, and recreational needs in the region (Buytaert et al., 2006a; Correa et al., 2020; Madrigal-Martínez and Miralles i García, 2019; Rolando et al., 2017). Water originated from them is therefore of paramount importance for the socio-economic development of the Northern and Central Andean countries of Venezuela, Colombia, Ecuador, Peru, and Bolivia (Célleri and Feyen, 2009; Young et al., 2015).

Land cover change associated with agricultural land use has been occurring over thousands of years in the tropical Andean highlands (Young, 2009). Natural grasslands have been used extensively for livestock grazing and small-scale to industrial cultivation of food crops. Fires associated with those activities have been the most significant human impact on these high-elevation grassland ecosystems (White, 2013). Post-fire vegetation recovery varies according to the intensity and extent of fires and floristic composition, but tussock grasses are rarely killed by fires (Hofstede et al., 1995) and their regeneration rates appear to be relatively high (Zomer and Ramsay, 2020). Over the last 50 years, the practice of afforestation in Andean grasslands, particularly with exotic pine species, has also contributed to changes in land cover at high elevations (Farley, 2007; Marín et al., 2018; Quiroz

Dahik et al., 2019). Both government agencies and private companies promoted forestry with exotic pines on high-elevation grasslands – with questionable arguments, yet significant social acceptance – for its potential provision of numerous ecosystem services: wood production, carbon sequestration and storage, water production and regulation, and erosion control (Hofstede et al., 2002; Quiroz Dahik et al., 2019, 2021).

All these human activities lead to land use and land cover change of natural grasslands which impacts the provision of hydrological services (Célleri and Feyen, 2009; Lazo et al., 2019). However, little is known about the qualitative and quantitative nature of those impacts, nor the impacts of restoration measures to recover the hydrological functioning of high-elevation grasslands. Amid rapidly growing interest by public and private water-related utilities, water managers and environmental authorities in Andean countries to develop integrated and multi-stakeholder plans to manage watershed services and provide a reliable water supply to downstream users (e.g., Autoridad Nacional del Agua, 2020; Bremer et al., 2016; Coronel, 2019), there is immediate need for increased knowledge of the ecohydrology of high-Andean grasslands (Aparecido et al., 2018; Mosquera et al., 2016a; Wright et al., 2017). To that end, we present a systematic review of the heretofore dispersed literature on the impacts of land use change and the effects of restoration practices on the hydrology of grasslands in the tropical Andes.

A recent multicomponent bibliometric analysis (Verrall and Pickering, 2020) highlighted that even though hydrological and land use change research on high-elevation grassland vegetation has exponentially increased worldwide over the last five decades, gaps remain, including in the tropical Andes and especially in understudied ecosystems. Therefore, a synthesis and evaluation of knowledge regarding the impact of land use change on the hydrological function of Andean grasslands is highly relevant to illuminate what is known, the field methods that work best under specific conditions, and to help identify topical and geographical areas across the region where insufficient or inexistent knowledge limits the management of water resources. The synthesis is also adequate to develop an agenda that will guide hydrological research in the Andean highlands in the coming decades. To this end, the following questions were addressed through synthesis of available information:

- How does the hydrological functioning of grasslands influence the ecosystem services of water provision, flow regulation, and erosion control in the tropical Andes?
- How do land use and restoration practices implemented in tropical Andean highlands affect the hydrological functioning of the region's grasslands?

2. Methods

2.1. Literature search

Initially, a list of search terms in English and Spanish related to the provision of the hydrological services of interest (i.e., water yield, flow regulation, and soil erosion mitigation) by tropical Andean grasslands was defined. The search terms were grouped into four categories: (1) land cover (e.g., tussock grass, grassland, bunchgrass, pajonal, pastizal), (2) geographical setting (e.g., páramo, puna, jalca, Venezuela, Colombia, Ecuador, Peru, Bolivia), (3) hydrological processes (e.g., streamflow, runoff, evapotranspiration, infiltration, soil moisture), and (4) hydrological services (e.g., water yield, streamflow regulation, erosion control) and human activities (e.g., grazing, cultivation, burning, afforestation). The complete list of search terms in each category is presented in Supplementary Material. The Boolean operator "AND" was used among the terms in each category and the Boolean operator "OR" was used to connect the terms among categories 1-4. The terms were searched in the title, abstract, and keywords of articles and books indexed in the Scopus, Web of Science, Ovid, and Scielo databases on June 2, 2020. Additionally, a "citation chasing" strategy was carried out by scrutinizing and selecting relevant references included in the originally selected documents. The search procedure is presented as a PRISMA flow diagram (Fig. 1; Page et al., 2021). It yielded a total of 38 published studies related to the hydrology of grasslands in the tropical Andes (listed in Supplementary Material) and 75 others that were excluded for their geographical range outside of the tropical Andes. Additionally, eight studies on the restoration of grasslands on the Tibetan plateau will be referred to in Section 2.4.

2.2. Data extraction and analysis

The compiled literature was used to develop a qualitative assessment of the knowledge surrounding hydrological function of high-elevation grasslands in the tropical Andes. Due to scarce data for most variables of interest, a quantitative evaluation was possible only for soil moisture for which an analysis was conducted on the impacts of pine afforestation and cattle grazing on soil moisture content. To that end, publications included in the analysis reported field and laboratory data on the moisture content of soils covered by tussock grasslands to a depth of 30 cm, assumed as the greatest depth that hydraulic soil properties would be influenced by tussock grass root systems following change in land use or land cover (Marín et al., 2018). Field data included soil moisture content from in situ samples measured using properly calibrated probes. Laboratory data only considered soil moisture content at saturation as representative of the wet range of the water retention capacity of volcanic ash soils that were the dominant soils at sites in the compiled literature. These stipulations have become important due to discrepancies found between measures of soil water retention capacity made under field conditions and those using standard laboratory methods (Mosquera et al., 2020b). Relevant soil moisture content data were extracted from tables and figures. Data from figures was extracted using the Engauge Digitizerv.10.11 software (Mitchell et al., 2020).

The potential impact of land use change on field and laboratory soil moisture content was evaluated by the relative percentage change (*Cr*; Luo et al., 2010) as a measure of effect size:

$$Cr = \frac{SMC_D - SMC_C}{SMC_C} \times 100 \tag{1}$$

where SMC_D and SMC_C represent soil moisture content under disturbed and conserved conditions, respectively. Positive (negative) *Cr* values indicate an increase (reduction) in soil moisture content due to a given intervention (e.g., land use change or restoration practice). Statistical significance of changes in soil moisture content due to the evaluated interventions was assessed through the Student's *t*-test ($p\text{-}value < 0.05$) for normally distributed and homoscedastic data. For data not accomplishing these statistical assumptions, statistical significance was evaluated using the Mann-Whitney *U* test ($p\text{-}value < 0.05$).

3. Results

3.1. Geographic and thematic distribution of scientific information

The spatial distribution of high-elevation grassland ecosystems (páramos, jalcas, punas) across the tropical Andes and the sites where their hydrology has been studied is shown in Fig. 2. Although the humid and dry punas cover by far the largest area (498,095 km^2, i.e., 85% of the total area of high Andean grasslands in the region; Fig. 3a), extending from north-central Peru to western Bolivia, few studies (6%; Fig. 3b) have been conducted in these ecosystems, mainly in central Peru. Similarly, few studies have been carried out in the jalcas (19,754 km^2, 3% of the total grassland area) that are restricted to northern Peru and considered to be a type of páramo or a transitional zone between páramo and puna (Josse et al., 2009; Luteyn, 1999). Most research (92%; Fig. 3b) has been carried out in páramos extending from western Venezuela to northern Peru (66,366 km^2, corresponding to

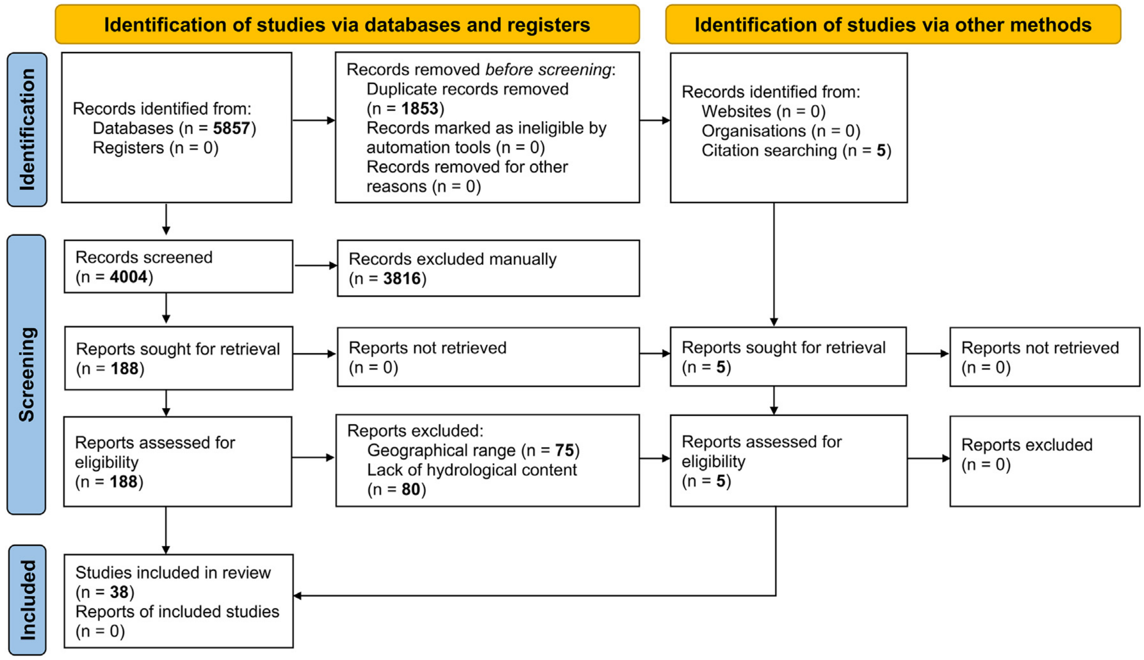

Fig. 1. PRISMA 2020 flow chart (Page et al., 2021) of the systematic literature review. A color version of this figure is available in the online version of this article.

12% of the total grassland area; Fig. 3b); note the high density (79%) of páramo study sites in Ecuador as compared to other tropical Andean countries in Fig. 2.

The hydrologic parameters most studied over all high Andean grassland ecosystems were streamflow production (29%), soil moisture (21%), evapotranspiration (15%), and infiltration (10%; Fig. 3c and Table 1). Other research topics included fog capture, peak flow, streamflow regulation, and soil erosion, which together account for 25% of the total. Most research was conducted at the catchment (53%) and plot (38%) scales, with only few conducted at the landscape scale (9%; Fig. 3d). The main research interest has been on the effects of land use or cover change on the hydrology of tropical Andean grasslands (63%) and their hydrological function under natural conditions (31%), with much less attention given to the recovery of those functions (6%; Fig. 3e).

3.2. Hydrological function of conserved grasslands in the tropical Andes

3.2.1. Water flux through soil-vegetation-atmosphere continuum

Tussock grasslands play an important role in the hydrological function of many tropical montane ecosystems where one of the main factors influencing water flux in the soil-vegetation-atmosphere continuum is evapotranspiration (ET) (Aparecido et al., 2018). These exchange dynamics not only influence the amount of precipitation (P) that infiltrates the soil, produces streamflow (Q), and recharges groundwater (GW), but also how much water returns to the atmosphere through the evaporation of intercepted water by vegetation and plant transpiration (Savenije, 2004). Due to the importance of this water balance component in the provisioning of hydrological services, it has been the focus of recent research efforts in the tropical Andes using a variety of techniques (Carrillo-Rojas et al., 2019; Ochoa-Sánchez et al., 2019).

The Eddy Covariance technique – considered the most accurate method to estimate actual ET (ET$_a$) (Aubinet et al., 2012) – was applied for the first time in Andean páramo grasslands by Carrillo-Rojas et al. (2019) who reported that this water balance component accounted for 51% of annual P (635 ± 9 mm yr^{-1} during the period 2016–2018); a lower value than the Eddy Covariance-based ET$_a$ estimates for an alpine tundra in the USA (59%; Knowles et al., 2015) and alpine meadows on the Tibetan Plateau, China (61–70%; Coners et al., 2016; Gu et al., 2008). Using the relation between ET$_a$ and the reference ET (ET$_r$), Carrillo-Rojas et al. (2019) reported crop coefficients (ET$_a$/ET$_r$) of 0.90 and 0.78 with respect to the FAO56PM (Allen et al., 1998) and ASCE-ERWI (Walter et al., 2004) ET$_r$ models, used as standard for estimating ET$_R$ by the Food and Agriculture Organization and the American Society of Civil Engineers, respectively. Eddy Covariance ground observations were further used to evaluate the accuracy of the state-of-the-art Community Land Model (CLM) version 4.0 (Lawrence et al., 2011) to simulate ET$_a$ (Carrillo-Rojas et al., 2020). Their findings indicated that despite an ~10% overestimation of ET$_a$ flux, the model produced reliable estimations of this water balance component, particularly at monthly and annual time scales. Considering the large proportion of P returning back to the atmosphere and the high crop coefficients identified, these results highlight the essential value of accurately estimating this water flux to close the water balance at the catchment and ecosystem scales (Carrillo-Rojas et al., 2016; Ochoa-Sánchez et al., 2019). They also highlight that the Eddy Covariance method, in combination with emerging modeling techniques (i.e., land surface models such as CLM; Lawrence et al., 2011), can be a reliable tool not only to estimate water losses from Andean grasslands, but also to predict changes in ET flux due to anthropic pressures and climatic effects (Carrillo-Rojas et al., 2020). The Eddy Covariance technique was also used at a páramo grassland site to assess the relative importance of different environmental factors on ET temporal variability on an event-based time scale (Ochoa-Sánchez et al., 2020). Their results indicate that ET is controlled mainly by net radiation, with wind speed, aerodynamic resistance, and surface resistance acting as secondary controllers, particularly during dry periods.

Efforts to separate the components of the ET flux into evaporation and transpiration have also been made. Ochoa-Sánchez et al. (2018) looked at water loss due to the evaporation of intercepted P (interception loss) from the long needles of tussock grasses, the dominant vegetation type on many Andean páramos, and reported a water storage capacity of 2 mm. They also found that interception loss values, as a proportion of cumulative P during rainstorm events, varied greatly: usually increasing >80% during low intensity rainstorm events, but decreasing up to 10% during high intensity rainstorm events. Given that low intensity rainfall events occur frequently on páramos (Padrón et al., 2015),

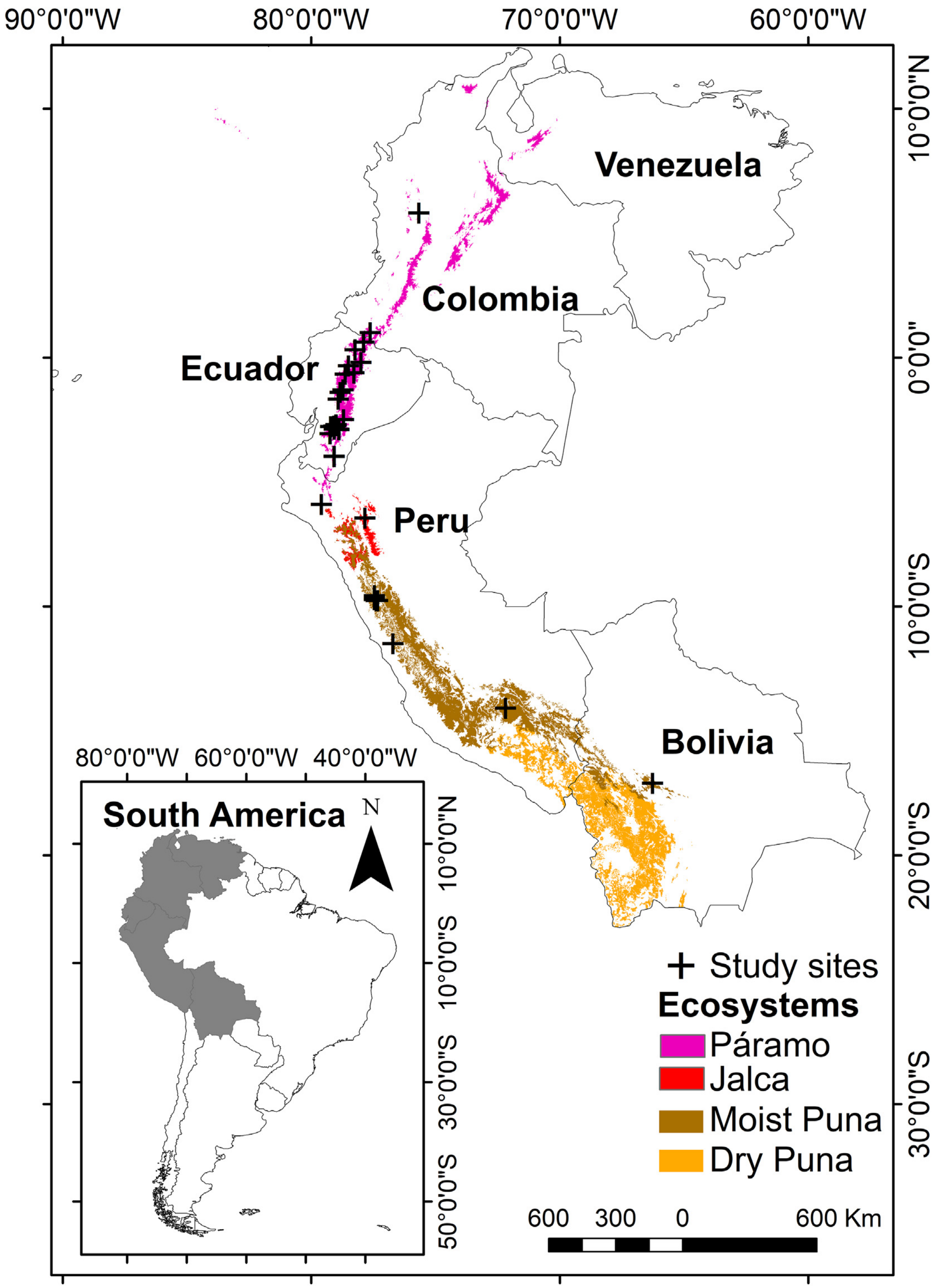

Fig. 2. Spatial distribution of the high-elevation grassland ecosystems (páramo, jalca, and moist and dry puna) in the tropical Andean countries of Venezuela, Colombia, Ecuador, Peru, and Bolivia (shown in gray in the inset map of South America). The crosses indicate study sites referred to in the systematic review of literature on the hydrology of Andean grasslands. The information required to reproduce the figure is presented as supplementary material. A color version of this figure is available in the online version of this article.

this factor may explain the high ET of tropical Andean tussock grasslands, similar to previous reports from grassland-dominated ecosystems at other latitudes (Coners et al., 2016; Gu et al., 2008; Knowles et al., 2015). At the same study site, grassland transpiration - estimated as the change in soil moisture at the rooted layer during dry periods - varied between 0.7 and 2.7 mm day^{-1} (1.5 mm day^{-1}on average) with the temporal variability primarily controlled by vapor pressure deficit and air temperature (Ochoa-Sánchez et al., 2020). Given that transpiration flux was always lower than ET even during dry periods, the authors concluded that overall transpiration accounted only for a small proportion of ET, with interception loss being the dominant water loss mechanism of the system.

Using a nested system of páramo catchments in southern Ecuador, Mosquera et al. (2015) applied the closure of the water balance approach to investigate how the spatial extent of undisturbed tussock grasslands influences ET flux across catchments. ET was estimated as

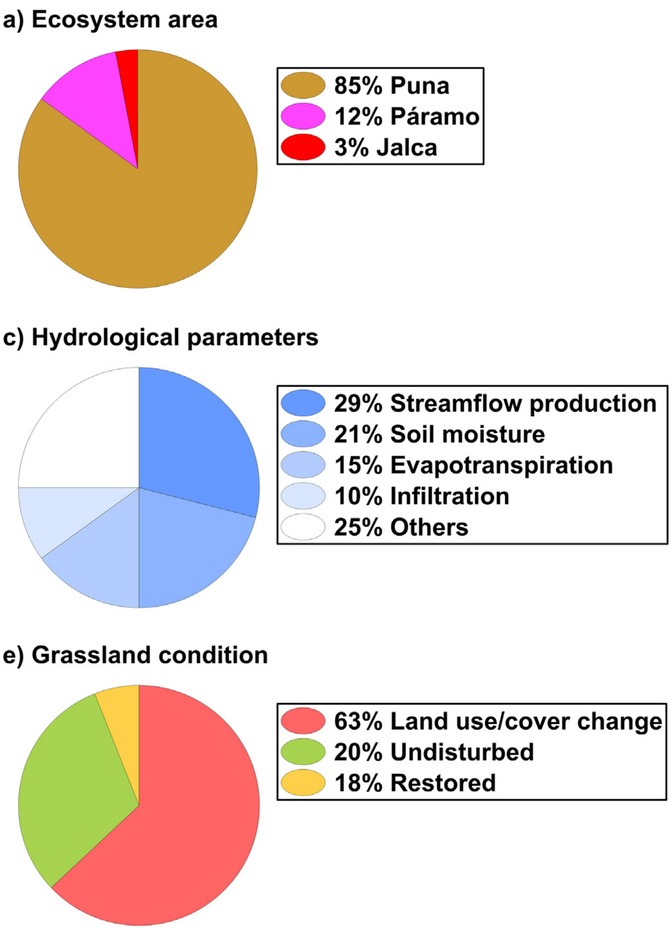

Fig. 3. Synthesis of published literature presenting data on the hydrological function of high Andean grasslands. A color version of this figure is available in the online version of this article.

Table 1
Summary of the 38 papers identified (listed in supplementary material) that analyzed hydrological components of high-elevation grasslands in the tropical Andes.

Hydrological process or service	Number of studies	Number of sites per country	Ecosystem	Spatial scale of analysis	Evaluation type[a]	References[b]
Evapotranspiration	7	Ecuador (7)	Páramo (10)	Landscape (1) Catchment (8) Plot (2)	No comparison (6) LU/LC impact (4)	[1] [2] [3] [4] [5] [6] [7]
Fog capture	2	Colombia (2)	Páramo (10)	Catchment (1) Plot (1)	No comparison (2)	[8] [9]
Streamflow production	14	Colombia (1) Ecuador (10) Peru (5) Bolivia (1)	Páramo (12) Puna (4) Jalca (1)	Catchment (17)	LU/LC impact (15) No comparison (4)	[6] [7] [10] [11] [12] [13] [14] [15] [16] [17] [18] [19] [20] [21]
Peak flow	2	Ecuador (2)	Páramo (2)	Catchment (2) Plot (1)	No comparison (1) LU/LC impact (1)	[6] [22]
Streamflow regulation	4	Ecuador (4)	Páramo (3)	Catchment (3)	No comparison (3)	[6] [10] [12] [13]
Soil infiltration	5	Colombia (1) Ecuador (4)	Páramo (5)	Plot (4) Landscape (1)	LU/LC impact (4) Restoration (2)	[23] [24] [25] [26] [27]
Soil moisture	10	Colombia (1) Ecuador (13) Peru (1)	Páramo (15)	Plot (11) Landscape (3)	No comparison (2) LU/LC impact (11) Restoration (2)	[26] [27] [28] [29] [30] [31] [32] [33] [34] [35]
Soil erosion	4	Ecuador (3) Peru (1)	Páramo (3)	Plot (3)	LU/LC impact (2) Restoration (2)	[25] [36] [37] [38]

[a] "No comparison" refers to the hydrological parameter in high-elevation Andean grasslands under natural conditions, and "LU/LC" to the impacts of land use or cover change on the parameter.

[b] References: [1] (Carrillo-Rojas et al., 2019), [2] (Carrillo-Rojas et al., 2020), [3] (Ochoa-Sánchez et al., 2018), [4], (Ochoa-Sánchez et al., 2019) [5] (Ochoa-Sánchez et al., 2020), [6] (Mosquera et al., 2015), [7] (Buytaert et al., 2006c), [8] (Tobon and Gil Morales, 2007), [9] (Cárdenas et al., 2017), [10] (Mosquera et al., 2016a), [11] (Mosquera et al., 2016b), [12] (Mosquera et al., 2012), [13] (Lazo et al., 2019), [14] (Correa et al., 2017), [15] (Correa et al., 2020), [16] (Buytaert et al., 2007), [17] (Crespo et al., 2011), [18] (Crespo et al., 2010), [19] (Ochoa-Tocachi et al., 2016a), [20] (Buytaert et al., 2006a), [21] (Ochoa-Tocachi et al., 2016b), [22] (Correa et al., 2019), [23] (Benavides et al., 2018), [24] (Suárez et al., 2013), [25] (Poulenard et al., 2001), [26] (Oscanoa and Flores, 2016), [27] (Tácuna et al., 2015), [28] (Mosquera et al., 2020a), [29] (Tenelanda-Patiño et al., 2018), [30] (Montenegro-Díaz et al., 2019), [31] (Marín et al., 2018), [32] (Buytaert et al., 2005), [33] (Farley et al., 2004), [34] (Harden et al., 2013), [35] (Oscanoa and Flores, 2019), [36] (Harden, 1988), [37] (Harden, 1993), [38] (Molina et al., 2008).

the difference between annual P and Q assuming little to no contributions of GW and small changes in internal water storage, which are valid assumptions for the study area according to Correa et al. (2017) and Lazo et al. (2019). The results showed that ET losses were positively correlated with the area of grasslands across catchments. This finding concurs with the reported interception loss of tussock grass vegetation (Ochoa-Sánchez et al., 2018), that the flux of water to the atmosphere via ET increased as grassland area increased at catchment and ecosystem scales.

Traditional techniques to estimate ET: do they work?

From a technical and methodological perspective, recent research has evaluated how well traditional instruments (e.g., tipping bucket rain gauges) and methods (e.g., water balance analysis, hydrological models) estimated ET and interception loss compared to measurements obtained with highly accurate methods and instruments. The latter include the use of laser disdrometers which obtain more precise precipitation estimates than traditional rain gauges due to their higher measurement resolution (up to 0.005 mm h^{-1}; Thies Clima, 2007) and the Eddy Covariance method (Carrillo-Rojas et al., 2019; Ochoa-Sánchez et al., 2019) to quantify P and ET_a fluxes, respectively. Results indicated that the traditionally-used tipping bucket rain gauges substantially underestimated P during rainstorm events compared to an electronic laser disdrometer (Ochoa-Sánchez et al., 2018). This is because disdrometers account for the substantial contribution of drizzle to total P of high-elevation tropical ecosystems (Aparecido et al., 2018), which rain gauges cannot measure accurately (Orellana-Alvear et al., 2017; Padrón et al., 2015).

An evaluation of methods to quantify ET_a in the grasslands of the Andean páramo found that the two evaluated hydrological models - the HBV-light model (Bergström, 1992; Bergström, 1976) and the Probability Distribution Model (Moore, 1985; Moore and Clarke, 1981) – as well as a Penman-Monteith model calibrated for the local conditions, yielded daily ET_a values similar to the reference Eddy Covariance technique (see Table 5 in Ochoa-Sánchez et al., 2019 for a list of advantages and disadvantages of each method). Even though the water balance (the most commonly used method to estimate ET in the region, e.g., Buytaert et al., 2006b, 2007; Mosquera et al., 2015), energy balance, and volumetric lysimeter methods generally provided inaccurate representations of the grasslands' ET_a variability over short time scales (sub-annual), they performed well to represent annual ET_a. This information is highly valuable for future applications across the tropical Andes where low intensity P (drizzle and fog) accounts for a significant proportion of total precipitation, and in ecosystems where knowledge about ET fluxes is scarce or inexistent (e.g., punas and jalcas).

Methods used to quantify fog

Another important factor influencing vegetation-atmosphere water fluxes in high-elevation tropical ecosystems is the occurrence and persistence of fog (Aparecido et al., 2018; Wright et al., 2017). The influence of fog on the hydrology of montane ecosystems in the tropical Andes is well known (Buytaert et al., 2006a; Célleri and Feyen, 2009; Correa et al., 2020), yet details about its role have been given little attention. Tobon and Gil Morales (2007) used an experimental approach to quantify fog capture by different types of páramo vegetation (e.g., native forest patches, grasslands, and giant *Espeletia* rosettes) in Colombia. They found that during periods of low intensity fog, no water droplets were captured regardless of vegetation type, but during moderate intensity fog events, grasslands captured more water than native forests, despite a lower leaf area index (1.17 for grasslands versus 3.14 for native forests). These results were attributed to the tendency of fog water droplets to adhere preferentially to small, exposed surfaces than to larger ones. In parallel, they compared direct vegetation measurements to indirect ones (i.e., harps and cylinders) traditionally used to quantify fog water inputs. The assessment indicated that the indirect methods measured significantly higher water amounts than the vegetation ones. This finding emphasizes the importance of using an appropriate method (i.e., fog collector device) to quantify the fog capture capacity of high Andean vegetation, research that has yet to be carried out.

The contribution of occult P (i.e., the combination of fog and drizzle) to the water balance of the páramo ecosystem in the Colombian Andes was assessed by Cárdenas et al. (2017) who found that occult P added 7 to 28% to total P depending on local environmental conditions and the geographical location. This corresponds with laser disdrometer measurements taken in an Ecuadorian páramo by Padrón et al. (2015) who found that drizzle represented 15% of total P. Past findings also indicate that direct vegetation measurements are necessary to assess Andean grasslands' fog capture capacity and its influence on water balance, given the identified overestimation by the most commonly used fog capture devices (Tobon and Gil Morales, 2007). Likewise, future experiments should carefully consider the difference between the height of the tussock grasses (often <1 m) in relation to the installation height of fog collection instruments, which is typically >1 m (e.g., Cárdenas et al., 2017), to ensure accurate measurements of fog water inputs.

3.2.2. Infiltration and soil moisture

The physical characteristics of the vegetation, particularly the distribution and density of plant roots, influence the water infiltration capacity of soils (Fischer et al., 2015; Thompson et al., 2010). This capacity and intrinsic soil properties (e.g., texture, bulk density, structure, saturated hydraulic conductivity) control the dynamics of water transport and mixing mechanisms in the subsurface (Mosquera et al., 2020a; Wang et al., 2020). Thus, knowledge about the capacity of vegetation to redistribute P to subsurface water is crucial to understand its effect on the water balance of a given hydrological system. Despite this, research is scarce on infiltration and the dynamics of soil moisture content under different land use scenarios in high-elevation tropical Andean grasslands. Here we discuss results and implications of existing studies to direct future efforts.

Most research on infiltration capacity under tussock grasslands in the tropical Andes relates to the influence of land use change on hydrophysical soil properties (e.g., Benavides et al., 2018; Patiño et al., 2021; Poulenard et al., 2001; Suárez et al., 2013). A common feature reported in those studies is the high infiltration capacity (up to 60–80 mm hr^{-1}) underlying undisturbed tussock grasses compared to the low intensity of water inputs (mainly drizzle with intensities generally <10 mm hr^{-1}) which characterizes P at high-elevations in the tropical Andes (Buytaert et al., 2006a; Orellana-Alvear et al., 2017; Padrón et al., 2015). This not only favors the dominance of subsurface water transport and mixing, but also limits the occurrence of infiltration excess overland flow (Correa et al., 2017, 2019; Crespo et al., 2011; Mosquera et al., 2012, 2016a, 2015, 2020a). Overall, the published literature highlights the importance of conserving high Andean grasslands to facilitate water infiltration to soils and subsequently recharge deeper water storage.

Previous research using periodic measurements (every few weeks to months) of soil moisture content showed that páramo soils maintained high humidity throughout the year, regardless of rainfall seasonality (Buytaert et al., 2005), but those observations did not generate a process-based understanding of vegetation-mediated water transport and mixing in the subsurface. However, more recent soil moisture content data from a densely-monitored experimental páramo hillslope covered by tussock grasses have shed light on these mechanisms: measurements taken every 5 min at the rooted layer of soils indicated a fast increase in response to rainstorm events and highly synchronized response times to reach peak soil moisture content, regardless of hillslope position. These results suggest that tussock grasslands facilitate a homogeneous infiltration capacity to the shallow, rooted layer of the soils (Mosquera et al., 2020a; Tenelanda-Patiño et al., 2018). Related results indicated that the volume and intensity of P were the main drivers of soil moisture content dynamics along the entire hillslope (Tenelanda-Patiño et al., 2018), likely due to the aforementioned higher infiltration capacity of natural tussock grasslands in comparison to the typically low intensity of P in the region that allows the latter to rapidly fill the empty pore space of soils during rainstorm events (Suárez et al., 2013). This factor, in combination with the typically high organic matter content and porosity of the Andean páramo soils, facilitates the vertical percolation of water (Mosquera et al., 2020a). Overall, these findings demonstrate that the conservation of Andean grasslands benefits the sustained input of water to the subsurface, which in combination with the intrinsic properties of the underlying volcanic ash soils (high saturated hydraulic conductivity, porosity, and water retention capacity) provide the ecosystem with a high water regulation capacity (Buytaert et al., 2006a; Correa et al., 2020; Mosquera et al., 2016a). Despite these important advances in the understanding of soil hydrology of southern Ecuadorian páramos, information is lacking from other páramos and from the puna and jalca ecosystems.

3.2.3. Streamflow generation and regulation

Streamflow generation and regulation are among the most important hydrological services provided by high-elevation ecosystems (Immerzeel et al., 2020; Viviroli et al., 2007). In the tropical Andes, the tussock grasslands that dominate landscapes above tree line are considered essential providers of these services (Buytaert et al., 2006a; Célleri and Feyen, 2009; Correa et al., 2020). However, until recently, little was known about the processes underlying Q production and regulation in these environments. The introduction of isotopic and geochemical tracers in hydrological research in the páramo, combined with hydrometeorological monitoring at different spatial scales within the same catchment (i.e., a nested monitoring scheme) and the consideration of biophysical catchment variables such as topography, geology, and the areal extent of soils and vegetation, has been key to fill these knowledge gaps. This combination of approaches has permitted researchers to understand the role of distinct landscape features (e.g., grasslands, wetlands, springs) on Q generation and how they differentially influence essential hydrological indicators such as peak flow, low flow, water yield, catchment water storage, and the age (or mean transit time) of Q.

Quantitative evaluations of the role of biophysical landscape features in the hydrology of a nested system of eight páramo catchments in southern Ecuador (Zhurucay Ecohydrological Observatory) showed that catchments having the strongest slope gradients and fractured bedrock presented higher baseflow values (Mosquera et al., 2015), shorter water ages (Mosquera et al., 2016b), and higher water storage capacity (Lazo et al., 2019) than their counterparts, highlighting the importance of topography and geology on streamflow regulation in catchments dominated by high Andean grasslands.

Further, a qualitative evaluation of the stable isotopic composition of different water sources (precipitation, grasslands, and wetlands) contributing to Q was carried out at the same study site (Correa et al., 2017, 2019; Mosquera et al., 2012, 2016a, 2016b). Results indicated that páramo soils were the major source of water contributing to discharge throughout the year (Mosquera et al., 2016a). This result was subsequently refined using geochemical tracers (electrical conductivity, metals, and nutrients) that permitted a quantification of contributions to Q by different water sources (precipitation, soil water, shallow GW) during different flow conditions (Correa et al., 2017, 2019). Using an end-member mixing model approach, these studies found that precipitation and soil water from the deeper layers of the hillslope and riparian soils were the principal components of stream water, with only small contributions from shallow GW. Therefore, the refined conceptual model indicated that hillslope soils, covered predominantly by tussock grass vegetation, are an important source of stream water, particularly during rainstorm events when riparian areas are hydrologically connected to the hillslopes at páramo sites with small or negligible GW contributions (Correa et al., 2019). These findings indicate that the high water infiltration capacity of hillslope soils covered by tussock grasslands, combined with high saturated hydraulic conductivity and porosity, provide excellent hydrological regulation capacity to these ecosystems by facilitating the downward transport of water to deeper soil layers (Mosquera et al., 2020a) and the recharge of riparian wetlands (Lazo et al., 2019; Mosquera et al., 2015). They also indicate subsurface hydrological connectivity between páramo grassland hillslopes and riparian areas during stormflow conditions (Correa et al., 2019; Ramón et al., 2021), thus providing additional evidence that Andean grasslands play an important role for providing hydrological services.

In summary, these findings emphasize the hydrological benefits provided by natural tussock grassland vegetation in Andean páramos. Importantly, the aforementioned studies also show that combining hydrometric and tracer (isotopic and geochemical) methods is an efficient approach to obtain process-based understanding of Q generation and regulation over short time periods (Mosquera et al., 2012, 2016a; Wright et al., 2017). Nevertheless, it should be noted that complementary research at more grassland sites across the high Andes is necessary, especially in the understudied punas. In páramos that present large GW contributions, it is necessary to assess and compare Q generation mechanisms under different hydrometeorological, pedological, and geological conditions.

3.3. Impacts of land use change on the hydrology of grasslands in the tropical Andes

3.3.1. Impacts of land use on evapotranspiration

Buytaert et al. (2006c) compared the crop coefficient of conserved páramo grasslands with cultivated areas to determine the effects of cultivation on ET. Their crop coefficient estimations through water balance closure assumed no influence of deep percolation and canopy interception loss, and a negligible contribution of drizzle to total P. They reported crop coefficient values of cultivated areas (0.95) that were more than double those of conserved tussock grasslands (0.42). A more recent study using the reliable Eddy Covariance method at a different páramo site reports crop coefficient values of 0.8-0.9 for conserved tussock grasslands (Carrillo-Rojas et al., 2019), similar to the previously mentioned crop coefficient value for cultivated páramo. These results put into question the veracity of assumptions made when estimating crop coefficients using the water balance approach and highlight the risks of applying this approach to study the ET flux (Ochoa-Sánchez et al., 2019). This is particularly relevant in regions where the hydrological behavior of the ecosystem is poorly understood.

3.3.2. Impacts of land use on soil infiltration

To evaluate the role of tussock grassland vegetation on infiltration capacity, Suárez et al. (2013) experimentally removed vegetation and made soil infiltration capacity measurements before and after removal, and during both wet and dry seasons. Their results show that, regardless of the season, the infiltration capacity was substantially reduced (about 8 times lower) after the grassland cover was removed. An evaluation of the potential factors controlling infiltration capacity indicates that the vegetation biomass acted as a primary control, and the soil organic matter content of the root layer showed no significant effects. These findings highlight the essential role that the tussock grasslands provide to facilitate the entrance of water into the soils and to mitigate the occurrence of soil erosion, even during extreme rainstorm events.

Precipitation simulation experiments were carried out to investigate the effects of tillage, burning, and bare fallow lands on the infiltration capacity of páramo soil overlaid by tussock grasslands in northern Ecuador (Poulenard et al., 2001). These simulations demonstrated that soils impacted by all three of these farming activities produced higher surface runoff in relation to undisturbed grasslands where 80 to 90% of P infiltrated soils. The lower infiltration capacity observed under tillage was attributed mainly to soil crusting (Nishimura et al., 1993), whereas hydrophobicity (i.e., water repellency) was the principal factor affecting the infiltration capacity on burned plots. The local Andosol soils, comprised of mature volcanic ash, have high soil organic matter such that dry conditions also caused water repellency on bare fallow lands (Clothier et al., 2000).

Benavides et al. (2018) evaluated the infiltration capacity of tussock grasslands compared to other natural land covers (i.e., shrubs and cushion plants) and land uses including potato cultivation and cattle grazing in the páramo of southwestern Colombia. These authors found that the soils under tussock grasslands had the highest infiltration capacity among all land covers, and a similar infiltration capacity to cultivated soils which they suggested may be an artifact of increased porosity and vertical water movement caused by tillage, though contrary to the aforementioned result of Nishimura et al. (1993). The high infiltration capacity of the native grassland soils may be attributed to the morphology of tussock grasses that helps protect soil structure from precipitation and wind effects. This is enhanced underground by the fibrous, dense, and uniform rooting system of tussock grasses that increases soil porosity and permeability (Hofstede et al., 1995), and thus contributes to the high infiltration capacity of underlying soils. All these findings highlight the key role of tussock grasslands for enhancing the soil infiltration capacity, which in turn influences subsurface flow and Q generation at larger scales (Correa et al., 2019; Crespo et al., 2011; Mosquera et al., 2020a).

3.3.3. Impacts of land use on soil moisture

Soil moisture content has been the most-studied hydrological variable related to the impacts of land use on the hydrology of tropical Andean grasslands (e.g., Buytaert et al., 2005; Farley et al., 2004; Marín et al., 2018; Montenegro-Díaz et al., 2019; Patiño et al., 2021). Most of these studies evaluated the impact of the most common human activities in this region – cattle grazing and pine afforestation – on soil moisture content (Buytaert et al., 2006a). The compiled data for both land use practices indicate that no effect was observed ($p\text{-}value > 0.05$) in soil moisture content at saturation: cattle grazing produced an increase of 2 ± 4% ($p\text{-}value = 0.71$) and pine afforestation showed a decrease of 2 ± 3% ($p\text{-}value = 0.43$) (Fig. 4). These results are similar to those reported for cultivation, another common human activity, at two páramo sites in southern Ecuador (Buytaert et al., 2005).

The compiled data also indicate that although the water holding capacity of páramo soils at saturation is not notably affected by these most common land use practices, afforestation with exotic pines and cattle grazing can impact the dynamics of soil moisture content under field conditions (Fig. 4). Pine afforestation produced a large and significant reduction of soil moisture, with relatively low variability among study sites (35 ± 12%; $p\text{-}value = 0.02$). This effect is explained by the presence of a large, woody, and non-uniform rooting system of the pine trees concentrated in the shallow soil layer (Farley et al., 2004; Harden et al., 2013). This factor in turn increases the rate of subsurface water movement through preferential flow paths – resulting from the longer and thicker tree root system in comparison to the fine and dense system of tussock grass roots–, thus diminishing the soil moisture content and water storage capacity of soils.

Research on the impact of cattle grazing on the hydrophysical properties of soils in high-elevation Andean ecosystems, including páramo tussock grasslands, have yielded results showing differing effects on soil properties (Benavides et al., 2018; Marín et al., 2018; Montenegro-Díaz et al., 2019). Those studies concluded that grazing impacts depend primarily on the land management history (e.g., grazing intensity and tilling activities) and that site-specific factors need to be carefully considered for evaluating those impacts (Marín et al., 2018). Although not statistically significant, the compiled dataset presented in this study depicts a similar effect (Fig. 4). Even though grazing led to a mean reduction of soil moisture content (21 ± 32%; $p\text{-}value = 0.63$), there was large variability among study sites, and soil moisture content was even observed to increase following grazing in some cases. These data corroborate the conclusions of Marín et al. (2018) that highlight the difficulty of generalizing the impacts of grazing on hydrophysical soil properties and the recommendation to evaluate the impacts of grazing on adjacent and comparable undisturbed and disturbed sites where hydrological, geomorphic, and climate conditions are similar. This, in order to reduce the possibility of attributing changes in soil properties to the effect of land use, when they could actually result from intrinsic differences in the spatial variability of soil properties across the region (e.g., Buytaert et al., 2006a, 2006b, 2006c).

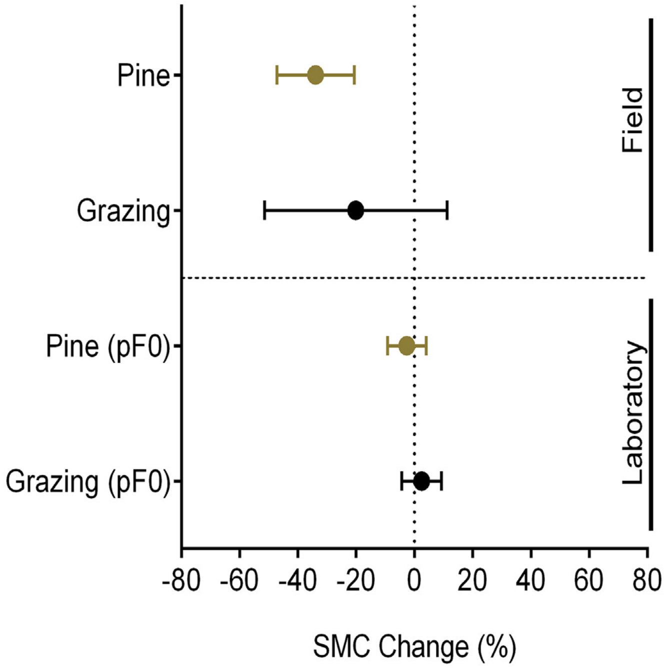

Fig. 4. Relative percentage change of the moisture content of soils to a depth of 30 cm due to pine afforestation and cattle grazing on tropical Andean grasslands. The information corresponds to soil moisture content (SMC) data obtained through field measurements (15 study sites for grazing and 4 study sites for pine afforestation) and laboratory methods (3 study sites for grazing and 6 study sites for pine afforestation) at saturation (pF0, pF is defined as the logarithm of matric potentials in cm water column). The dots represent the mean relative change (%) and the whiskers represent the standard deviation. A color version of this figure is available in the online version of this article.

In general, there is an apparent consensus regarding soil moisture content reduction due to pine afforestation (Farley et al., 2004; Harden et al., 2013; Marín et al., 2018), while the impacts of grazing are more variable and dependent on the land management history (Benavides et al., 2018; Marín et al., 2018; Montenegro-Díaz et al., 2019). Future studies, therefore, should consider such history to obtain robust results that can be used by land managers and policy makers. A similar management history dependence is likely for cultivated lands, though insufficient evidence was found for a firm conclusion on this issue.

Technical considerations for measuring hydrophysical soil properties

An evaluation of land use change on the hydrophysical properties of predominantly volcanic soils across páramo and montane forest ecosystems in southern Ecuador yielded valuable technical insights, for example, that the sampling depth and distance from the tree trunk (in pine afforested areas) may affect the assessment of hydrophysical soil properties. Marín et al. (2018) found statistically significant differences of hydrophysical soil properties measured at 0–10 and 10–25 cm depths, regardless of land cover, indicating that soil depth should be considered for a thorough evaluation of land use impacts on soil hydrological status. At afforested sites, the presence of trees did not affect hydrophysical soil properties, as measured values were not statistically different close to (75 cm) and farther from (150 cm) a tree's trunk. This suggests that the hydrophysical properties of soils in and around pine plantations are relatively homogeneous and that measurements to evaluate afforestation impact do not need to be made at a prescribed distance from trees.

3.3.4. Impacts on streamflow generation and regulation

Water resources of tropical montane ecosystems are increasingly threatened by changes in land use (Wright et al., 2017). In the tropical Andes, local and regional research efforts have consistently demonstrated high Q production and regulation capacity of high-elevation catchments that are dominated by undisturbed tussock grasslands (Buytaert et al., 2007; Crespo et al., 2011; Mosquera et al., 2015; Ochoa-Tocachi et al., 2016a, 2016b).

Some studies have assessed how the most common land use changes in the region (e.g., afforestation, grazing, and cultivation) affect these hydrological services. Research in the southern Ecuadorian highlands showed that exotic pine (*Pinus patula*) afforestation reduced the water yield (i.e., the ratio between annual Q and annual P) of a páramo catchment by 50% as compared to a catchment dominated by tussock grasslands (Buytaert et al., 2007). Similar findings of the P-Q relation were reported by Crespo et al. (2010, 2011) for the same region: páramo catchments affected by pine afforestation presented reduced water yield and low flows (baseflow). More recently, Ochoa-Tocachi et al. (2016a, 2016b) applied a paired catchment monitoring strategy at several sites across the tropical Andes in different high-elevation tussock grassland-dominated ecosystems (i.e., páramos, jalcas, and punas) to investigate the impacts of land use change on Q generation. The regional catchment comparison depicted pine afforestation as reducing water yield and the entire range of flows, especially low flows, at all study sites, irrespective of ecosystem. In general, these findings all point to afforestation's negative effects, mainly attributed to increased ET, on the water production and regulation capacity of tropical Andean catchments (Buytaert et al., 2007; Crespo et al., 2011; Ochoa-Tocachi et al., 2016a, 2016b). Higher ET rates corresponded directly with the higher leaf area index of trees compared to tussock grasses (Tobon and Gil Morales, 2007), which in turn increases interception losses. Additionally, this effect is also influenced by high water losses through higher transpiration rates of trees in comparison to those of natural tussock grasslands (Ochoa-Sánchez et al., 2020).

The impact of cattle grazing on the P-Q relation of tropical Andean catchments was studied by Crespo et al. (2010) who found no effects of grazing on water yield or different flow rates comparing two páramo catchments (grazed vs. ungrazed) in southern Ecuador. This result was attributed to the low number of animals (no more than 3 adult cows per hectare) at the grazed study site. Results from the aforementioned paired network of catchments across the tropical Andes showed a variable effect of cattle grazing on Q production and regulation (Ochoa-Tocachi et al., 2016a, 2016b). The direction and magnitude of the impact depended on both the animal density and the physiographic characteristics of the catchments, findings that are similar to the effects reported for soil moisture content of disturbed soils under grazing (Benavides et al., 2018; Marín et al., 2018; Montenegro-Díaz et al., 2019). These combined findings lead to the hypothesis that the effects of cattle grazing on Q production and regulation are closely linked to the degree of disturbance of underlying soils, and intrinsically, to the history of land disturbance and management of soil and vegetation resources. This hypothesis should be tested in the future, but meanwhile this information can be helpful for developing land management strategies in high-elevation regions of the tropical Andes.

Cultivation has also shown contrasting effects on Q production and regulation of tropical Andean catchments. Comparison studies in southern Ecuador showed no apparent effect of this land use on annual water yield but did produce an increase in peak flows, and a decrease in low flows, in catchments where potatoes were cultivated (Buytaert et al., 2007; Crespo et al., 2010). The dynamic water storage capacity was reported to be lower in a cultivated catchment than a conserved catchment at a páramo site in the same region (Buytaert et al., 2006b). These findings indicate that while cultivation did not affect the Q generation capacity of the catchments, water regulation capacity was reduced. The paired catchment comparison study across the tropical Andes showed a similar result: although cultivation might not considerably affect water yield, it reduces low flows and increases peak flows, regardless of the ecosystem (i.e., páramos and punas) (Ochoa-Tocachi et al., 2016a, 2016b). Overall, these results suggest that, like grazing, it is essential to consider land management history to determine the impacts of cultivation on Q on tropical Andean catchments.

The regional initiative for hydrological monitoring of andean ecosystems – iMHEA

The iMHEA regional network of paired-catchments across the tropical Andes has shown to be valuable for regional monitoring efforts (Célleri et al., 2010). Data generated from iMHEA have not only facilitated unravelling the differences and commonalities due to land use on Q generation and regulation processes, but also allowed regionalizing patterns of land use change (Ochoa-Tocachi et al., 2016b). Despite the generation of valuable P and Q data across the network (Ochoa-Tocachi et al., 2018), the sole use of this traditional hydrometric information is insufficient for process-based understanding about the mechanisms responsible for land-use derived P-Q relations. Therefore, iMHEA shows great potential to fill knowledge gaps through the application of tracer methods that have the potential to provide robust process-based hydrological information at different spatial and temporal scales in other high-elevation catchments across the region (e.g., Correa et al., 2017, 2019, 2020; Lazo et al., 2019; Mosquera et al., 2012, 2016a, 2016b, 2020a, 2020b).

3.3.5. Impacts on soil erosion and sedimentation

An essential role of montane ecosystems is the control and mitigation of soil erosion to decrease both the production of sediments that affect water quality and the generation of landslides (Alewell et al., 2008; Harden, 2001). Therefore, understanding how high-elevation grasslands influence these processes and how changes in land use and land cover affect the provisioning of this important ecosystem service is crucial for good management, conservation, and restoration of montane grasslands in the tropical Andes (Harden, 1988). Nonetheless, even though research on soil erosion processes and features have been investigated intensively and extensively at lower elevations in the tropical Andes (e.g., Borja et al., 2018; Harden, 1992; Molina et al., 2012; Vanacker et al., 2003; Zehetner and Miller, 2006), few studies exist at elevations above tree line.

Early work on this subject focused on evaluating the effects of cultivation on soil erosion in the Ecuadorian highlands by simulating high intensity rainstorm events to estimate soil erosion rates of conserved and degraded páramos (Harden, 1988, 1993). Results from experimental plots in central-north Ecuador showed that conserved areas with 100% cover of native tussock grasslands did not produce soil erosion, even on steep slopes. In contrast, annual soil erosion rates on degraded páramo varied between 20 and 80 t ha^{-1}, with the highest rates produced on steep, cultivated fields (Harden, 1988). Similarly, in páramo plots on the Paute watershed in southern Ecuador, the highest erosion rates were reported for overgrazed and road construction areas, while soil erosion was absent on undisturbed grasslands (Harden, 1993). Using a similar approach, Poulenard et al. (2001) studied the effects of tillage and burning on the soil erosion of young and mature volcanic ash soils in the páramos of northern Ecuador. Their findings demonstrated that both practices increased surface runoff, enhancing the effects of soil erosion. Tillage generated the reorganization of surface soil particles forming a crust layer with reduced infiltration capacity, while burning favored the creation of hydrophobic (water repellant) conditions that facilitated soil erosion. Overall, these findings indicate that soil erodibility is influenced by land use more than by soil type (Harden, 1993) and that conserving the high-elevation grasslands of the tropical Andes is crucial to decrease sediments due to soil erosion processes, given that the dense cover of tussock grasses favors the accumulation of soil organic matter and the high infiltration capacity of the soils (Zehetner and Miller, 2006). These findings are in line with those reported by Molina et al. (2008) who demonstrated the importance of conserving vegetation cover to decrease soil erosion in 37 catchments located in the highlands of southern Ecuador, particularly at sites underlain by highly erodible rocks. Importantly, the latter emphasizes the main role geology can play in soil erosion processes, although this feature has not been frequently considered in past studies.

3.4. Effects of restoration practices on hydrology

Only two studies that evaluated the impact of restoration practices on the hydrological functions of tussock grasslands in the tropical Andes were identified, despite the issue's importance. Both were carried out on high-elevation grasslands of the Cordillera Blanca in central Peru. Tácuna et al. (2015) looked at improvements of soil hydrological functions under heavily degraded grasslands due to long-term grazing following a revegetation treatment with two native grass species (*Festuca humilior* and *Calamagrostis macrophylla*) combined with the addition of organic matter (ovine urine and manure). Using a completely randomized experimental design over a 1-year period, their results showed a small increase in soil moisture content (19% to 21.8%) and infiltration capacity (0.11 to 0.14 cm min^{-1}). Applying a similar experimental approach over a 2-year period, Oscanoa and Flores (2016) evaluated the influence of soil improvement techniques (furrows and pits) on the recovery of the hydrological status of the soils under degraded grasslands. These authors also reported a small increase in soil moisture content (from 16.6% to 20.4–20.8%) and infiltration capacity (0.07 cm h^{-1} to 0.11–0.12 cm min^{-1}) by furrows and pits, concluding that recovering the hydrological function of degraded grasslands is a slow process (Oscanoa and Flores, 2016, 2019).

The paucity of data available on this topic in the tropical Andes precludes the possibility to address a key question from the soil and water management perspective in montane grassland environments (Sun et al., 2020): *What restoration period is needed to recover soil hydrological functions under degraded grasslands?*

To partially address this question, data from the Tibetan Plateau, a high mountain region where grasslands dominate the landscape (Dixon et al., 2014; Verrall and Pickering, 2020), were used to put the findings of the high-Andean grasslands into context. Data were compiled from eight Tibetan publications (Supplementary material) on the effects of restoration on soil moisture content under field conditions, considering the same assumptions as soil moisture data from high-elevation Andean grasslands (Section 2.2). As the Tibetan Plateau is characterized by a strong P seasonality during the year and large daily temperature variations (Xue et al., 2017), we assumed that the region's soil moisture data is likely to be similar to highland sites with similar climate features in the tropical Andes. The approach used to analyze Tibetan Plateau data was the same as that used to identify the effects of land use practices on soil moisture content under Andean grasslands, i.e., the relative percentage change method and the Student's t and Mann-Whitney U statistical tests.

The results of these analyses indicated that for restoration periods <5 years, the mean change in soil moisture content was not significant and almost negligible, presenting a large variability (2 ± 28%; *p-value* = 0.13; Fig. 5). However, for restoration periods >5 years, the percentage change in soil moisture content was likely to increase, albeit with large variability (36 ± 33%; *p-value* = 0.42). Though these data are from a different mountainous region, they provide a basis to explain the negligible soil moisture increase reported from the tropical Andes <2 years after restoration of degraded grasslands (Oscanoa and Flores, 2016; Tácuna et al., 2015). Sun et al. (2020) found that a 4-year grazing exclusion period using fences was optimal to promote aboveground vegetation growth on Tibetan Plateau grasslands. These authors thus recommended that restoration practices be limited to periods of 4 years. For provision of water-related ecosystem services, however, it is apparent that periods longer than 5 years are necessary to secure the recovery of the hydrological function of soils under degraded grasslands, at least on the Tibetan Plateau that has a marked seasonality.

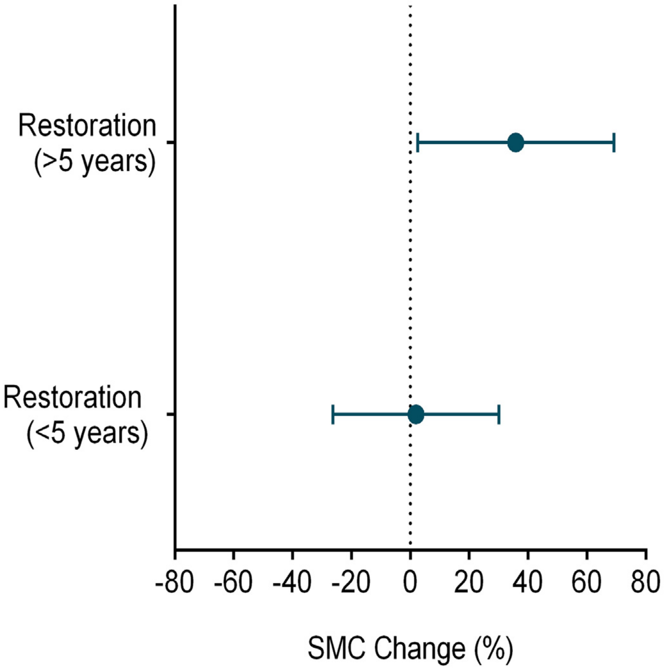

Fig. 5. Relative percentage change of the moisture content of soils to a depth of 30 cm due to the restoration of degraded high-elevation grasslands on the Tibetan Plateau. The information corresponds to soil moisture content (SMC) data obtained for restoration periods <5 years (15 study sites) and >5 years (10 study sites). The dots represent the mean relative change (%) and the whiskers represent the standard deviation. A color version of this figure is available in the online version of this article.

Though the results presented in Fig. 5 may be considered representative for land and water management on the highly seasonal dry punas and páramos of the tropical Andes, shorter periods could suffice for grassland recovery at more humid sites. Wetter environmental conditions are likely to reduce the degradation of soil organic matter and would favor not only aboveground vegetation growth, but also the recovery of soil hydrological functions.

4. Conclusions

4.1. Key findings

High-elevation grasslands are an essential resource for the provision of hydrological services in the tropical Andes. Over the last 20 years, much has been learned about their hydrological function under conserved conditions, particularly for the humid páramo ecosystem of southern Ecuador where reliable measures of actual evapotranspiration (ET_a, 51% of annual precipitation), crop coefficient (0.78–0.90), and water storage capacity (2 mm) have been obtained. These grasslands also play a key role in increasing subsurface flow due to high infiltration that in turn controls erosion processes. Additionally, they buffer streamflow in catchments and facilitate the sustained recharge of Andean wetlands when they become hydrologically connected to the stream network during rainstorm events.

Knowledge about the impacts of land use change on the hydrological behavior of high Andean grasslands has also increased, especially on Ecuadorian páramos. For example, studies on the effects of pine plantations in natural grasslands have identified negative impacts on soil water storage as well as a decrease in water yield and hydrological regulation at different spatial scales (from plot to catchment). This was attributed to increased ET of exotic pine trees in comparison to native grasslands. The hydrological impacts of cattle grazing and farming on these grasslands, however, have been studied less and are inconclusive. Grasslands that were degraded by tillage, burning, or the complete removal of vegetation cover showed a substantial reduction of water infiltration to the soils and an increase in soil loss through erosion. Impacts on soil moisture and streamflow were controversial as the available research presented contrasting results ranging from steep reductions to large increments. This suggests that land management history drives the direction and magnitude of the impacts, and that generalizations among different sites and regions should be avoided (Marín et al., 2018).

4.2. Key knowledge gaps

One critical outcome of this regional systematic analysis of literature was the identification of scarce hydrological information about the puna ecosystems in Peru and Bolivia, even though they represent the most extensive high-elevation grasslands in the tropical Andes. Similar information gaps remain for the jalca grasslands in northern Peru. Regarding páramo grasslands, it should be noted that hydrological research has been concentrated on humid páramos of southern Ecuador while hydrological data remain scarce for dry páramos and for those exhibiting recent volcanic activity. Future efforts should aim at addressing this information imbalance to broaden hydrological knowledge to regions where it remains limited and negatively affects natural resource management in the tropical Andes.

We identified important knowledge gaps related to the hydrological function of conserved high Andean grasslands. Little attention has been paid to these grasslands' role in the capture of horizontal precipitation (fog) and its influence on the water balance. The ET flux has been quantified accurately in the humid páramo of southern Ecuador but remains uncertain in other high-Andean grasslands, particularly in drier regions. Most process-based hydrological understanding of streamflow production and regulation and subsurface flow dynamics has been developed for humid páramo grasslands that present small groundwater contributions. However, little information is available for drier páramo grasslands in Colombia or Venezuela and for those with large groundwater contributions. Furthermore, the lack of information is critical in the puna and jalca ecosystems that present climatological, pedological, and geological conditions that are different from those of páramo and that could play a different hydrological role.

Major knowledge gaps remain regarding the impacts of land use change on the hydrology of high-Andean grasslands. For example, few analyses exist that quantify how ET is affected by changes in land use in any high-Andean grassland ecosystem, despite the importance of this process on water balance. The hydrological impacts of pine afforestation have been documented but forestation studies on other exotic and native tree species (e.g., *Polylepis* spp.) are lacking. Controlled and uncontrolled fires occur frequently in high Andean grasslands but their impacts on ET, infiltration, soil moisture, and streamflow production and hydrological regulation are unknown. It is crucial to study the impact of open burns over these vast Andean grassland landscapes because of the potentially large degrading hydrological effects that have been reported elsewhere in the Andes (e.g., Cingolani et al., 2020).

Restoration efforts of degraded grasslands have increased over the last decade across the tropical Andes, yet knowledge about their hydrological impacts remains unknown. In the Tibetan Plateau, it was found that restoration periods longer than five years were necessary to increase the soil moisture content of degraded alpine grasslands, thus it is not surprising that short duration (<2 years) restoration studies in high Andean grasslands did not find improved soil hydrological function. Future research to evaluate hydrological impacts of high Andean grassland restoration should consider relevant comparable findings to establish efficient monitoring strategies and appropriate evaluation timeframes.

Limited studies have described the key role that topography and geology play on water production, flow regulation, and soil erosion processes in páramo grasslands but quantitative analyses are needed for future evaluation of Andean grassland hydrology. Although we found no studies looking at the effect of seasonality and aspect on conserved, degraded, or restored grasslands, future evaluations should consider these potentially important features, particularly at locations influenced by highly seasonal hydrometeorological conditions and in the southernmost part of the tropical Andes, where solar radiation might not be equally distributed throughout the year.

Local and national environmental agencies, universities and research centers, and non-governmental organizations should consider these knowledge gaps in their research agendas to improve management, conservation, and restoration policies for high-Andean grasslands. To this end, we highlighted a variety of techniques that have been successfully applied to enlighten the hydrology of high Andean grasslands, as these findings are valuable to guide potential users towards appropriate techniques to advance understanding. Better hydrological knowledge can help safeguard upper watershed ecosystems in the high Andes and support water provision to millions of downstream users.

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Data availability statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

CRediT authorship contribution statement

Conceptualization and methodology: G.M.M., V.B., M.S., F.R.D., B.O.T.; Data curation and analysis: G.M.M., F.M.; Literature Review, G.M.M., F.M.; First draft: G.M.M., M.S.; Review and editing: G.M.M., F.M., M.S., V.B., B.O.T., F.R.D., P.C. All authors have read and agreed to the published version of the manuscript.

Declaration of competing interest

G.M.M., F.M., and P.C. developed this work as specialized consultants to the Natural Infrastructure for Water Security Project.

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Appendix A. Supplementary data

Supplementary data to reproduce the map shown in Fig. 2 of this article can be found online at https://doi.org/10.1016/j.scitotenv.2021.150112.

References

Aide, T.M., Clark, M.L., Grau, H.R., López-Carr, D., Levy, M.A., Redo, D., Bonilla-Moheno, M., Riner, G., Andrade-Núñez, M.J., Muñiz, M., 2013. Deforestation and reforestation of Latin America and the Caribbean (2001–2010). Biotropica 45, 262–271. https://doi.org/10.1111/j.1744-7429.2012.00908.x.

Alewell, C., Meusburger, K., Brodbeck, M., Bänninger, D., 2008. Methods to describe and predict soil erosion in mountain regions. Landsc. Urban Plan. 88, 46–53. https://doi.org/10.1016/j.landurbplan.2008.08.007.

Allen, R., Pereira, L., Raes, D., Smith, M., 1998. Crop Evapotranspiration-Guidelines for Computing Crop Water Requirements-FAO Irrigation and Drainage Paper 56. FAO, Rome.

Aparecido, L., Teodoro, G., Mosquera, G., Brum, M., de Barros, F., Pompeu, P., Rodas, M., Lazo, P., Muller, C., Mulligan, M., Asbjornsen, H., Moore, G., Oliveira, R., 2018. Ecohydrological drivers of neotropical vegetation in montane ecosystems. Ecohydrology 11. https://doi.org/10.1002/eco.1932.

Aubinet, M., Vesala, T., Papale, D., 2012. Eddy covariance: a practical guide to measurement and data analysis. Eddy Covariance. Springer, Dordrecht, the Netherlands https://doi.org/10.1007/978-94-007-2351-1.

Autoridad Nacional del Agua, 2020. Agua en cuencas, seguridad hídrica como política pública. Informativo sobre las acciones del PGIRH en las cuencas del pais. Proyecto Gestión Integrada de los Recursos Hidricos. Lima, Peru.

Benavides, I.F., Solarte, M.E., Pabón, V., Ordoñez, A., Beltrán, E., Rosero, S., Torres, C., 2018. The variation of infiltration rates and physical-chemical soil properties across a land cover and land use gradient in a paramo of southwestern Colombia. J. Soil Water Conserv. 73, 400–410. https://doi.org/10.2489/jswc.73.4.400.

Bergström, S., 1976. Development and Application of a Conceptual Runoff Model for Scandinavian Catchments Norrköpin, Sweden.

Bergström, S., 1992. The HBV Model -its Structure and Applications. Norrköping.

Bonnesoeur, V., Locatelli, B., Guariguata, M.R., Ochoa-Tocachi, B.F., Vanacker, V., Mao, Z., Stokes, A., Mathez-Stiefel, S.-L., 2019. Impacts of forests and forestation on hydrological services in the Andes: a systematic review. For. Ecol. Manag. 433, 569–584. https://doi.org/10.1016/J.FORECO.2018.11.033.

Borja, P., Molina, A., Govers, G., Vanacker, V., 2018. Check dams and afforestation reducing sediment mobilization in active gully systems in the andean mountains. Catena 165, 42–53. https://doi.org/10.1016/j.catena.2018.01.013.

Bremer, L.L., Vogl, A.L., De Bièvre, B., Petry, P., 2016. Bridging Theory and Practice for Hydrological Monitoring in Water Funds.

Buytaert, W., Wyseure, G., De Bièvre, B., Deckers, J., 2005. The Effect of Land-use Changes on the Hydrological Behaviour of Histic Andosols in South Ecuador, pp. 3985–3997 https://doi.org/10.1002/hyp.5867.

Buytaert, W., Célleri, R., De Bièvre, B., Cisneros, F., Wyseure, G., Deckers, J., Hofstede, R., 2006a. Human impact on the hydrology of the Andean páramos. Earth Sci. Rev. 79, 53–72. https://doi.org/10.1016/j.earscirev.2006.06.002.

Buytaert, W., Deckers, J., Wyseure, G., 2006b. Regional variability of volcanic ash soils in South Ecuador: the relation with parent material, climate and land use. Catena 70, 143–154. https://doi.org/10.1016/j.catena.2006.08.003.

Buytaert, W., Iñiguez, V., Celleri, R., De Bièvre, B., Wyseure, G., Deckers, J., 2006c. Analysis of the Water Balance of Small Páramo Catchments in South Ecuador. Springer, Netherlands, pp. 271–281 https://doi.org/10.1007/1-4020-4228-0_24.

Buytaert, W., Iñiguez, V., Bièvre, B.De, 2007. The effects of afforestation and cultivation on water yield in the andean páramo. For. Ecol. Manag. 251, 22–30. https://doi.org/10.1016/j.foreco.2007.06.035.

Calder, I.R., 2007. Forests and water-ensuring forest benefits outweigh water costs. For. Ecol. Manag. 251, 110–120. https://doi.org/10.1016/j.foreco.2007.06.015.

Cárdenas, M.F., Tobón, C., Buytaert, W., 2017. Contribution of occult precipitation to the water balance of páramo ecosystems in the colombian Andes. Hydrol. Process. 31, 4440–4449. https://doi.org/10.1002/hyp.11374.

Carrillo-Rojas, G., Silva, B., Córdova, M., Célleri, R., Bendix, J., 2016. Dynamic mapping of evapotranspiration using an energy balance-based model over an andean Páramo catchment of southern Ecuador. Remote Sens. 8, 160. https://doi.org/10.3390/rs8020160.

Carrillo-Rojas, G., Silva, B., Rollenbeck, R., Célleri, R., Bendix, J., 2019. The breathing of the andean highlands: net ecosystem exchange and evapotranspiration over the páramo of southern Ecuador. Agric. For. Meteorol. 265, 30–47. https://doi.org/10.1016/j.agrformet.2018.11.006.

Carrillo-Rojas, G., Schulz, H.M., Orellana-Alvear, J., Ochoa-Sanchez, A., Trachte, K., Celleri, R., Bendix, J., 2020. Atmosphere-surface fluxes modeling for the high Andes: the case of paramo catchments of Ecuador. Sci. Total Environ. 704. https://doi.org/10.1016/j.scitotenv.2019.135372.

Célleri, R., Feyen, J., 2009. The hydrology of tropical andean ecosystems: importance, knowledge status, and perspectives. Mt. Res. Dev. 29, 350–355. https://doi.org/10.1659/mrd.00007.

Célleri, R., Buytaert, W., De Bièvre, B., Tobón, C., Crespo, P., Molina, J., Feyen, J., 2010. Understanding the hydrology of tropical Andean ecosystems through an Andean network of basins. Status and Perspectives of Hydrology in Small Basins. IAHS Publication, Goslar-Hahnenklee, Germany, pp. 209–212.

Cingolani, A.M., Poca, M., Whitworth-Hulse, J.I., Giorgis, M.A., Vaieretti, M.V., Herrero, L., Ramos, S.N., Renison, D., 2020. Fire reduces dry season low flows in a subtropical highland of Central Argentina. J. Hydrol. 590, 125538. https://doi.org/10.1016/j.jhydrol.2020.125538.

Clothier, B.E., Vogeler, I., Magesan, G.N., 2000. The breakdown of water repellency and solute transport through a hydrophobic soil. J. Hydrol. 231–232, 255–264. https://doi.org/10.1016/S0022-1694(00)00199-2.

Coners, H., Babel, W., Willinghöfer, S., Biermann, T., Köhler, L., Seeber, E., Foken, T., Ma, Y., Yang, Y., Miehe, G., Leuschner, C., 2016. Evapotranspiration and water balance of high-elevation grassland on the tibetan plateau. J. Hydrol. 533, 557–566. https://doi.org/10.1016/J.JHYDROL.2015.12.021.

Coronel, L., 2019. The Path of Water - FONAG: Work and Lessons.

Correa, A., Windhorst, D., Tetzlaff, D., Crespo, P., Célleri, R., Feyen, J., Breuer, L., 2017. Temporal dynamics in dominant runoff sources and flow paths in the Andean Páramo. Water Resour. Res. https://doi.org/10.1002/2016WR020187.

Correa, A., Breuer, L., Crespo, P., Célleri, R., Feyen, J., Birkel, C., Silva, C., Windhorst, D., 2019. Spatially distributed hydro-chemical data with temporally high-resolution is needed to adequately assess the hydrological functioning of headwater catchments. Sci. Total Environ. 651, 1613–1626. https://doi.org/10.1016/J.SCITOTENV.2018.09.189.

Correa, A., Ochoa-Tocachi, B.F., Birkel, C., Ochoa-Sánchez, A., Zogheib, C., Tovar, C., Buytaert, W., 2020. A concerted research effort to advance the hydrological understanding of tropical páramos. Hydrol. Process., hyp.13904 https://doi.org/10.1002/hyp.13904.

Crespo, P., Célleri, R., Buytaert, W., Feyen, J., Iñiguez, V., Borja, P., De Bièvre, B., 2010. Land Use Change Impacts on the Hydrology of Wet Andean Páramo Ecosystems. IAHS-AISH Publ, pp. 71–76.

Crespo, P.J., Feyen, J., Buytaert, W., Bücker, A., Breuer, L., Frede, H.-G., Ramírez, M., 2011. Identifying controls of the rainfall–runoff response of small catchments in the tropical Andes (Ecuador). J. Hydrol. 407, 164–174. https://doi.org/10.1016/j.jhydrol.2011.07.021.

Dixon, A.P., Faber-Langendoen, D., Josse, C., Morrison, J., Loucks, C.J., 2014. Distribution mapping of world grassland types. J. Biogeogr. 41, 2003–2019. https://doi.org/10.1111/jbi.12381.

Farley, K., 2007. Grasslands to tree plantations: forest transition in the Andes of Ecuador. Ann. Assoc. Am. Geogr. 97 (4), 755–771. https://doi.org/10.1111/j.1467-8306.2007.00581.x.

Farley, K., Kelly, E., Hofstede, R., 2004. Soil organic carbon and water retention after conversion of grasslands to pine plantations in the Ecuadorian Andes. Ecosystems 7, 729–739.

Farley, K.A., Jobbagy, E.G., Jackson, R.B., 2005. Effects of afforestation on water yield: a global synthesis with implications for policy. Glob. Chang. Biol. 11, 1565–1576. https://doi.org/10.1111/j.1365-2486.2005.01011.x.

Fischer, C., Tischer, J., Roscher, C., Eisenhauer, N., Ravenek, J., Gleixner, G., Attinger, S., Jensen, B., de Kroon, H., Mommer, L., Scheu, S., Hildebrandt, A., 2015. Plant species diversity affects infiltration capacity in an experimental grassland through changes in soil properties. Plant Soil 397, 1–16. https://doi.org/10.1007/s11104-014-2373-5.

Garcia-Chevesich, P.A., Neary, D.G., Scott, D.F., Benyon, T.R., 2017. Forest management and the impact on water resources: a review of 13 countries. IHP - VIII / Technical Document No. 37. Paris, France.

Gu, S., Tang, Y., Cui, X., Du, M., Zhao, L., Li, Y., Xu, S., Zhou, H., Kato, T., Qi, P., Zhao, X., 2008. Characterizing evapotranspiration over a meadow ecosystem on the Qinghai-tibetan plateau. J. Geophys. Res. 113. https://doi.org/10.1029/2007JD009173.

Harden, C., 1988. Mesoscale estimation of soil erosion in the Rio Ambato Drainage, Ecuadorian Sierra. Mt. Res. Dev. 8, 331. https://doi.org/10.2307/3673556.

Harden, C.P., 1992. A new look at soil erosion processes on hillslopes in highland Ecuador. In: Walling, D.E., Davies, T.R., Hasholt, B. (Eds.), Erosion, Debris Flows and Environment in Mountain Regions. IAHS Publ, Chengdu, p. 85.

Harden, C.P., 1993. Land use, soil erosion, and reservoir sedimentation in an andean Drainage Basin in Ecuador. Mt. Res. Dev. 13, 177. https://doi.org/10.2307/3673635.

Harden, C.P., 2001. Soil erosion and sustainable mountain development: experiments, observations and recommendations from the Ecuadorian Andes. Mt. Res. Dev. 21, 77–83. https://doi.org/10.1659/0276-4741(2001)021[0077:SEASMD]2.0.CO;2.

Harden, C.P., Hartsig, J., Farley, K.A., Lee, J., Bremer, L.L., 2013. Effects of land-use change on water in andean paramo grassland soils. Ann. Assoc. Am. Geogr. 103, 375–384. https://doi.org/10.1080/00045608.2013.754655.

Hofstede, R.G., Mondragon Castillo, M.X., Rocha Osorio, C.M., 1995. Biomass of grazed, burned, and undisturbed Paramo grasslands, Colombia. I. Aboveground vegetation. Arct. Alp. Res. 27, 1–12. https://doi.org/10.2307/1552062.

Hofstede, R.G., Groenendijk, J.P., Coppus, R., Fehse, J.C., Sevink, I., 2002. Impact of pine plantations on soils and vegetationin the Ecuadorian high Andes. Mtn. Res. and Devel. 22 (2), 159–167. https://doi.org/10.1659/0276-4741(2002)022[0159:IOPPOS]2.0.CO;2.

Immerzeel, W.W., Lutz, A.F., Andrade, M., Bahl, A., Biemans, H., Bolch, T., Hyde, S., Brumby, S., Davies, B.J., Elmore, A.C., Emmer, A., Feng, M., Fernández, A., Haritashya, U., Kargel, J.S., Koppes, M., Kraaijenbrink, P.D.A., Kulkarni, A.V., Mayewski, P.A., Nepal, S., Pacheco, P., Painter, T.H., Pellicciotti, F., Rajaram, H., Rupper, S., Sinisalo, A., Shrestha, A.B., Viviroli, D., Wada, Y., Xiao, C., Yao, T., Baillie, J.E.M., 2020. Importance and vulnerability of the world's water towers. Nature 577, 364–369. https://doi.org/10.1038/s41586-019-1822-y.

Jones, J., Almeida, A., Cisneros, F., Iroumé, A., Jobbágy, E., Lara, A., Lima, W.de P., Little, C., Llerena, C., Silveira, L., Villegas, J.C., 2017. Forests and water in South America. Hydrol. Process. 31, 972–980. https://doi.org/10.1002/hyp.11035.

Josse, C., Cuesta, F., Navarro, G., Barrena, V., Cabrera, E., Chacón-Moreno, E., Ferreira, W., Peralvo, M., Saito, J., Tovar, A., 2009. Ecosistemas de los Andes del Norte y Centro. Bolivia, Colombia, Ecuador, Perú y Venezuela. Secretaría General de la Comunidad Andina, ECOBONA, CONDESAN, Programa BioAndes, EcoCiencia, NatureServe, Lima, Peru.

Knowles, J.F., Harpold, A.A., Cowie, R., Zeliff, M., Barnard, H.R., Burns, S.P., Blanken, P.D., Morse, J.F., Williams, M.W., 2015. The relative contributions of alpine and subalpine ecosystems to the water balance of a mountainous, headwater catchment. Hydrol. Process. 29, 4794–4808. https://doi.org/10.1002/hyp.10526.

Lawrence, D.M., Oleson, K.W., Flanner, M.G., Thornton, P.E., Swenson, S.C., Lawrence, P.J., Zeng, X., Yang, Z.-L., Levis, S., Sakaguchi, K., Bonan, G.B., Slater, A.G., 2011. Parameterization improvements and functional and structural advances in version 4 of the community land model. J. Adv. Model. Earth Syst. 3, n/a-n/a. https://doi.org/10.1029/2011ms00045.

Lazo, P.X., Mosquera, G.M., McDonnell, J.J., Crespo, P., 2019. The role of vegetation, soils, and precipitation on water storage and hydrological services in andean Páramo catchments. J. Hydrol. 572, 805–819. https://doi.org/10.1016/J.JHYDROL.2019.03.050.

Luo, Z., Wang, E., Sun, O.J., 2010. Soil carbon change and its responses to agricultural practices in australian agro-ecosystems: a review and synthesis. Geoderma 155, 211–223. https://doi.org/10.1016/j.geoderma.2009.12.012.

Luteyn, J.L., 1999. Páramos: A Checklist of Plant Diversity, Geographical Distribution, and Botanical Literature. The New York Botanical Garden Press, New York.

Madrigal-Martínez, S., Miralles i García, J.L., 2019. Land-change dynamics and ecosystem service trends across the central high-Andean Puna. Sci. Rep. 9, 1–12. https://doi.org/10.1038/s41598-019-46205-9.

Marín, F., Dahik, C., Mosquera, G., Feyen, J., Cisneros, P., Crespo, P., 2018. Changes in soil hydro-physical properties and SOM due to pine afforestation and grazing in Andean environments cannot be generalized. Forests 10, 17. https://doi.org/10.3390/f10010017.

Mitchell, M., Muftakhidinov, B., Winchen, T., 2020. Engauge Digitizer Software [WWW Document]. https://doi.org/10.5281/zenodo.3941227.

Molina, A., Govers, G., Poesen, J., Van Hemelryck, H., De Bièvre, B., Vanacker, V., 2008. Environmental factors controlling spatial variation in sediment yield in a central andean mountain area. Geomorphology 98, 176–186. https://doi.org/10.1016/J.GEOMORPH.2006.12.025.

Molina, A., Vanacker, V., Balthazar, V., Mora, D., Govers, G., 2012. Complex land cover change, water and sediment yield in a degraded Andean environment. J. Hydrol. 472–473, 25–35. https://doi.org/10.1016/j.jhydrol.2012.09.012.

Montenegro-Díaz, P., Ochoa-Sánchez, A., Célleri, R., 2019. Impact of tussock grasses removal on soil water content dynamics of a tropical mountain hillslope. Ecohydrology 12, e2146. https://doi.org/10.1002/eco.2146.

Moore, R.J., 1985. The probability-distributed principle and runoff production at point and basin scales. Hydrol. Sci. J. 30, 273–297. https://doi.org/10.1080/02626668509490989.

Moore, R.J., Clarke, R.T., 1981. A distribution function approach to rainfall runoff modeling. Water Resour. Res. 17, 1367–1382. https://doi.org/10.1029/WR017i005p01367.

Mosquera, G., Lazo, P., Cárdenas, I., Crespo, P., 2012. Identificación de las principales Fuentes de agua que aportan a la generación de escorrentía en zonas andinas de páramo húmedo: mediante el uso de los isótopos estables deuterio (d2H) y oxígeno-18 (d18O). maskana 3(2), 87–105. Maskana 3, 87–105.

Mosquera, G.M., Lazo, P.X., Célleri, R., Wilcox, B.P., Crespo, P., 2015. Runoff from tropical alpine grasslands increases with areal extent of wetlands. Catena 125, 120–128. https://doi.org/10.1016/j.catena.2014.10.010.

Mosquera, G.M., Célleri, R., Lazo, P.X., Vaché, K.B., Perakis, S.S., Crespo, P., 2016a. Combined use of isotopic and hydrometric data to conceptualize ecohydrological processes in a high-elevation tropical ecosystem. Hydrol. Process. https://doi.org/10.1002/hyp.10927.

Mosquera, G.M., Segura, C., Vaché, K.B., Windhorst, D., Breuer, L., Crespo, P., 2016b. Insights into the water mean transit time in a high-elevation tropical ecosystem. Hydrol. Earth Syst. Sci. 20, 2987–3004. https://doi.org/10.5194/hess-20-2987-2016.

Mosquera, G., Crespo, P., Breuer, L., Feyen, J., Windhorst, D., 2020a. Water transport and tracer mixing in volcanic ash soils at a tropical hillslope: a wet layered sloping sponge. Hydrol. Process. 34, 2032–2047. https://doi.org/10.1002/hyp.13733.

Mosquera, G., Marín, F., Feyen, J., Célleri, R., Breuer, L., Windhorst, D., Crespo, P., 2020b. A field, laboratory, and literature review evaluation of the water retention curve of volcanic ash soils: how well do standard laboratory methods reflect field conditions? Hydrol. Process. 35, hyp.14011. https://doi.org/10.1002/hyp.14011.

Nishimura, T., Nakano, M., Miyazaki, T., 1993. Properties of surface crusts of an andisol and their effects on soil-hydrological processes. Catena Suppl. 24, 17–28.

Ochoa-Sánchez, A., Crespo, P., Célleri, R., 2018. Quantification of rainfall interception in the high andean tussock grasslands. Ecohydrology 11, e1946. https://doi.org/10.1002/eco.1946.

Ochoa-Sánchez, A., Crespo, P., Carrillo-Rojas, G., Sucozhañay, A., Célleri, R., 2019. Actual evapotranspiration in the high andean grasslands: a comparison of measurement and estimation methods. Front. Earth Sci. 7, 55. https://doi.org/10.3389/feart.2019.00055.

Ochoa-Sánchez, A., Crespo, P., Carrillo-Rojas, G., Marín, F., Célleri, R., 2020. Unravelling evapotranspiration controls and components in tropical andean tussock grasslands. Hydrol. Process., hyp.13716 https://doi.org/10.1002/hyp.13716.

Ochoa-Tocachi, B.F., Buytaert, W., De Bièvre, B., Célleri, R., Crespo, P., Villacís, M., Llerena, C.A., Acosta, L., Villazón, M., Guallpa, M., Gil-Ríos, J., Fuentes, P., Olaya, D., Viñas, P., Rojas, G., Arias, S., 2016. Impacts of land use on the hydrological response of tropical andean catchments. Hydrol. Process. 30, 4074–4089. https://doi.org/10.1002/hyp.10980.

Ochoa-Tocachi, B.F., Buytaert, W., De Bièvre, B., 2016. Regionalization of land-use impacts on streamflow using a network of paired catchments. Water Resour. Res. 52, 6710–6729. https://doi.org/10.1002/2016WR018596.

Ochoa-Tocachi, B.F., Buytaert, W., Antiporta, J., Acosta, L., Bardales, J.D., Célleri, R., Crespo, P., Fuentes, P., Gil-Ríos, J., Guallpa, M., Llerena, C., Olaya, D., Pardo, P., Rojas, G., Villacís, M., Villazón, M., Viñas, P., De Bièvre, B., 2018. Data descriptor: high-resolution hydrometeorological data from a network of headwater catchments in the tropical Andes. Sci. Data 5, 1–16. https://doi.org/10.1038/sdata.2018.80.

Orellana-Alvear, J., Célleri, R., Rollenbeck, R., Bendix, J., 2017. Analysis of rain types and their Z-R relationships at different locations in the high Andes of southern Ecuador. J. Appl. Meteorol. Climatol. 56, 3065–3080. https://doi.org/10.1175/JAMC-D-17-0009.1.

Oscanoa, L., Flores, E., 2016. Influencia de técnicas de mejora de suelos sobre la función hídrica de pastos naturales altoandinos. Ecol. Apl. 15, 91–99.

Oscanoa, L., Flores, E., 2019. Efecto de las técnicas de mejora ecohidrológica del pastizal sobre el rendimiento hídrico de la microcuenca alto andina urpay. Ecol. Apl. 18, 1–9.

Padrón, R.S., Wilcox, B.P., Crespo, P., Célleri, R., 2015. Rainfall in the andean Páramo: new insights from high-resolution monitoring in southern Ecuador. J. Hydrometeorol. 16, 985–996. https://doi.org/10.1175/JHM-D-14-0135.1.

Page, M.J., McKenzie, J.E., Bossuyt, P.M., Boutron, I., Hoffmann, T.C., Mulrow, C.D., Shamseer, L., Tetzlaff, J.M., Akl, E.A., Brennan, S.E., Chou, R., Glanville, J., Grimshaw, J.M., Hróbjartsson, A., Lalu, M.M., Li, T., Loder, E.W., Mayo-Wilson, E., McDonald, S., McGuinness, L.A., Stewart, L.A., Thomas, J., Tricco, A.C., Welch, V.A., Whiting, P., Moher, D., 2021. The PRISMA 2020 statement: an updated guideline for reporting systematic reviews. BMJ 372. https://doi.org/10.1136/BMJ.N71.

Patiño, S., Hernández, Y., Plata, C., Domínguez, I., Daza, M., Oviedo-Ocaña, R., Buytaert, W., Ochoa-Tocachi, B.F., 2021. Influence of land use on hydro-physical soil properties of Andean páramos and its effect on streamflow buffering. Catena 202, 105227. https://doi.org/10.1016/j.catena.2021.105227.

Pomeroy, J., Bernhardt, M., Marks, D., 2015. Research network to track alpine water. Nature 521, 32. https://doi.org/10.1038/521032c.

Poulenard, J., Podwojewski, P., Janeau, J.-L., Collinet, J., 2001. Runoff and soil erosion under rainfall simulation of andisols from the ecuadorian Páramo: effect of tillage and burning. Catena 45, 185–207. https://doi.org/10.1016/S0341-8162(01)00148-5.

Quiroz Dahik, C., Marin, F., Arias, R., Crespo, P., Weber, M., Palomeque, X., Dahik, C.Q., Marín, F., Arias, R., Crespo, P., Weber, M., Palomeque, X., Quiroz Dahik, C., Marin, F., Arias, R., Crespo, P., Weber, M., Palomeque, X., 2019. Comparison of natural regeneration in natural grassland and pine plantations across an elevational gradient in the paramo ecosystem of southern Ecuador. Forests 10. https://doi.org/10.3390/f10090745.

Quiroz Dahik, C., Crespo, P., Stimm, B., Mosandl, R., Cueva, J., Hildebrandt, P., Weber, M., 2021. Impacts of pine plantations on carbon stocks of páramo sites in southern Ecuador. Carbon Balance Manag. 16, 5. https://doi.org/10.1186/s13021-021-00168-5.

Ramón, J., Correa, A., Timbe, E., Mosquera, G.M., Mora, E., Crespo, P., 2021. Do mixing models with different input requirement yield similar streamflow source contributions? Case study: a tropical montane catchment. Hydrol. Process. 35, e14209. https://doi.org/10.1002/HYP.14209.

Rolando, J.L., Turin, C., Ramírez, D.A., Mares, V., Monerris, J., Quiroz, R., 2017. Key ecosystem services and ecological intensification of agriculture in the tropical high-Andean Puna as affected by land-use and climate changes. Agric. Ecosyst. Environ. https://doi.org/10.1016/j.agee.2016.12.010.

Savenije, H.H.G., 2004. The importance of interception and why we should delete the term evapotranspiration from our vocabulary. Hydrol. Process. 18, 1507–1511. https://doi.org/10.1002/hyp.5563.

Suárez, E., Arcos, E., Moreno, C., Encalada, A.C., Maruxa, Á., Álvarez, M., 2013. Influence of vegetation types and ground cover on soil water infiltration capacity in a high-altitude páramo ecosystem. Avances 5.

Sun, J., Liu, M., Fu, B., Kemp, D., Zhao, W., Liu, G., Han, G., Wilkes, A., Lu, X., Chen, Y., Cheng, G., Zhou, T., Hou, G., Zhan, T., Peng, F., Shang, H., Xu, M., Shi, P., He, Y., Li, M., Wang, J., Tsunekawa, A., Zhou, H., Liu, Y., Li, Y., Liu, S., 2020. Reconsidering the efficiency of grazing exclusion using fences on the tibetan plateau. Sci. Bull. 65, 1405–1414. https://doi.org/10.1016/j.scib.2020.04.035.

Tácuna, R.E., Aguirre, L., Flores, E.R., 2015. Influencia de la revegetación con especies nativas y la incorporación de materia orgánica en la recuperación de pastizales degradados. Ecol. Apl. 14, 191–200.

Tenelanda-Patiño, D., Crespo-Sánchez, P., Mosquera-Rojas, G., 2018. Umbrales en la respuesta de humedad del suelo a condiciones meteorológicas en una ladera altoandina. MASKANA 9, 53–65. https://doi.org/10.18537/mskn.09.02.07.

Thies Clima, 2007. Instructions for Use: Laser Precipitation Monitor 5.4110.xx.x00 V2.2xSTD Göttingen, Germany.

Thompson, S.E., Harman, C.J., Heine, P., Katul, G.G., 2010. Vegetation-infiltration relationships across climatic and soil type gradients. J. Geophys. Res. Biogeosci. 115. https://doi.org/10.1029/2009jg001134 n/a-n/a.

Tobon, C., Gil Morales, E.G., 2007. Capacidad de interceptación de la Niebla por la vegetación de los páramos andinos. Av. en Recur. Hidráulicos 35–46.

Vanacker, V., Govers, G., Barros, S., Poesen, J., Deckers, J., 2003. The effect of short-term socio-economic and demographic change on landuse dynamics and its corresponding geomorphic response with relation to water erosion in a tropical mountainous catchment. Ecuador. Landsc. Ecol. 18, 1–15. https://doi.org/10.1023/A:1022902914221.

Verrall, B., Pickering, C.M., 2020. Alpine vegetation in the context of climate change: a global review of past research and future directions. Sci. Total Environ. https://doi.org/10.1016/j.scitotenv.2020.141344.

Viviroli, D., Dürr, H.H., Messerli, B., Meybeck, M., Weingartner, R., 2007. Mountains of the world, water towers for humanity: typology, mapping, and global significance. Water Resour. Res. 43. https://doi.org/10.1029/2006WR005653.

Viviroli, D., Kummu, M., Meybeck, M., Kallio, M., Wada, Y., 2020. Increasing dependence of lowland populations on mountain water resources. Nat. Sustain. 1–12. https://doi.org/10.1038/s41893-020-0559-9.

Walter, I.A., Allen, R.G., Elliott, R., Jensen, M.E., Itenfisu, D., Mecham, B., Howell, T.A., Snyder, R., Brown, P., Echings, S., Spofford, T., Hattendorf, M., Cuenca, R.H., Wright, J.L., Martin, D., 2004. ASCE's standardized reference evapotranspiration equation. Watershed Management and Operations Management 2000. American Society of Civil Engineers, pp. 1–11 https://doi.org/10.1061/40499(2000)126.

Wang, R., Dong, Z., Zhou, Z., Wang, N., Xue, Z., Cao, L., 2020. Effect of vegetation patchiness on the subsurface water distribution in abandoned farmland of the Loess Plateau, China. Sci. Total Environ. 746, 141416. https://doi.org/10.1016/j.scitotenv.2020.141416.

White, S., 2013. Grass páramo as hunter-gatherer landscape. The Holocene 23, 898–915. https://doi.org/10.1177/0959683612471987.

Wright, C., Kagawa-Viviani, A., Gerlein-Safdi, C., Mosquera, G.M., Poca, M., Tseng, H., Chun, K.P., 2017. Advancing ecohydrology in the changing tropics: perspectives from early career scientists. Ecohydrology 11, e1918. https://doi.org/10.1002/eco.1918.

Xue, Y., Ma, Y., Li, Q., 2017. Land–climate interaction over the Tibetan Plateau. Clim. Sci. https://doi.org/10.1093/acrefore/9780190228620.013.592.

Young, B.E., Josse, C., Stern, M., Vásconez, S., Olander, J., ... Echavarría, M., 2015. Ecosystem Profile: Tropical Andes Biodiversity Hotspot. Critical Ecosystem Partnership Fund.

Young, K.R., 2009. Andean land use and biodiversity: humanized landscapes in a time of change. Ann. Mo. Bot. Gard. 96 (3), 492–507. https://doi.org/10.3417/2008035.

Zehetner, F., Miller, W.P., 2006. Erodibility and runoff-infiltration characteristics of volcanic ash soils along an altitudinal climosequence in the ecuadorian Andes. Catena 65, 201–213. https://doi.org/10.1016/j.catena.2005.10.003.

Zomer, M.A., Ramsay, P.M., 2020. The Impact of Fire Intensity on Plant Growth Forms in High-altitude Andean Grassland. https://doi.org/10.1101/2020.04.25.061051 bioRxiv.