

## REVIEW ARTICLE

# Ecohydrological drivers of Neotropical vegetation in montane ecosystems

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## Abstract

Montane ecosystems are known for their high numbers of endemic species, unique climate conditions, and wide variety of ecosystem services such as water supply and carbon storage. Although many ecohydrological and climatic studies of montane environments have been carried out in temperate and boreal regions, few have been done in Neotropical regions. Hence, the objective of this review is to synthesize the existing literature on the main factors (biotic and abiotic) that influence vegetation distribution, functional traits, and ecohydrological processes and feedbacks in tropical montane ecosystems and to identify key knowledge gaps. Most of the literature used includes work conducted in Neotropical montane rainforests, cloud forests, and grass/scrublands (e.g., *páramos*, *punas*, and *campos de altitude/rupestres*). Fog is a major climatic attribute in tropical montane habitats. We found that fog regimes (frequency and intensity of fog events) influence both water inputs (i.e., canopy interception and foliar water uptake) and outputs (evapotranspiration) and represent an important driver of local species composition, dominance of plant functional types, and ecological functioning. The stability and conservation of tropical montane ecosystems depends on such ecohydrological fluxes, which are sensitive to increases in air temperature and changing precipitation and fog regimes. Furthermore, to better inform effective conservation and restoration strategies, more work is needed to elucidate how key ecohydrological processes are affected by land use conversion to agriculture and pasture lands, as human activities influence the water budgets in Neotropical montane watersheds not only at regional-scales but also globally.

## KEYWORDS

cloud forest, ecophysiology, ecosystem services, fog, grasslands, montane rain forest, water and carbon budgets

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## 1 | INTRODUCTION

Tropical mountain regions are known for their rich species diversity and high endemism (Myers, Mittermeier, Mittermeier, da Fonseca, & Kent, 2000). These regions provide many ecosystem services, such as the maintenance of water quality and water supply, protection against soil erosion, and carbon storage (Bruijnzeel, Mulligan, & Scatena, 2011; Dias, Grosjean, & Graumlich, 2003; Nogués-Bravo, Araújo, Errea, & Martínez-Rica, 2007; Spracklen & Righelato, 2014). Their influence is not limited to their geographical boundaries but extends to the surrounding lowlands, shaping watershed scale hydrologic, and climatic regimes (Dias et al., 2003; Nogués-Bravo et al., 2007).

To date, previous efforts aimed at synthesizing the ecohydrology of tropical montane ecosystems have generally focused on the global extent of all montane ecosystems (e.g., Beniston, 2003) or exclusively on tropical montane forested ecosystems (e.g., Hamilton, Juvik, & Scatena, 1995). Comparative syntheses including tropical montane grassland and shrubland ecosystems (above treeline) are lacking in such studies, despite their recognized role in providing key hydrological services (Dias et al., 2003; Nogués-Bravo et al., 2007). Tropical montane ecosystems are considered especially susceptible to global climatic changes and land use conversion (Dias et al., 2003; Wright et al., 2017), and consequently, ecohydrological processes on tropical mountains may exhibit a greater magnitude and faster rates of change in response to changes in environmental conditions than lower altitude forests (Gibbs et al., 2010). Moreover, global warming rates have been shown to be especially pronounced at higher elevations, which could potentially accelerate the rate of change in hydrological regimes and biodiversity in tropical montane ecosystems (Pepin et al., 2015).

Vegetation removal or conversion to other land uses may also alter ecohydrological processes in tropical montane ecosystems through decreases or increases in evapotranspiration (ET), changes in throughfall and soil moisture dynamics, variations in water input from fog, and altered infiltration and run-off response (Foster, 2001; Oliveira, Christoffersen, et al., 2014). Further, land use change often causes changes in soils hydro-physical properties (e.g., hydraulic conductivity and pore space size and distribution), which can alter nutrient turnover time and organic matter decomposition rate (Leon & Osorio, 2014). Combined, these impacts may affect the provisioning (e.g., water supply) and regulation (e.g., flood mitigation) of hydrological ecosystem services (Hamel et al., 2017; Foster, 2001; Ponette-Gonzalez, Weathers, & Curran, 2009). Developing countries, including most Neotropical countries, are experiencing the highest rates of land use change globally (Gibbs et al., 2010).

The high sensitivity of tropical montane ecosystems to both climatic and anthropogenic changes has already resulted in significant modifications of their ecohydrological processes, including ET, streamflow, infiltration, and run-off (Wohl et al., 2012). Consequently, the need to enhance scientific understanding of the ecohydrological consequences of land use and climate change on tropical mountains as a basis developing effective strategies for mitigating their effects on ecosystem services is especially urgent. To this end, we conducted a comparative synthesis of the ecohydrological drivers of vegetation distribution, vegetation–water interactions, and ecohydrological

feedback mechanisms for the dominant Neotropical montane forests and grass/scrublands ecosystems. Specifically, we address the following questions: (a) How do edaphic, climatic, and hydrological characteristics of tropical montane landscapes affect the distribution and functional traits of vegetation? (b) How do plant traits and physiological functioning feedback to influence the ecohydrology of Neotropical montane ecosystems? (c) What are the possible effects of land use and climate change on Neotropical montane vegetation and their hydrological functioning? To address these questions, we searched through nearly 200 studies from the existing literature, using the following key terms: montane vegetation, ecology, geology, meteorology, anthropogenic processes, TMRF, TMCF, *campos rupestres*, *campos de altitude*, *páramos*, and *punas*; and any approximate or related terms to ecohydrology and ecophysiology.

## 2 | EDAPHIC, CLIMATIC, AND HYDROLOGICAL CONTROLS ON THE DISTRIBUTION AND FUNCTIONAL TRAITS OF NEOTROPICAL MONTANE ECOSYSTEMS

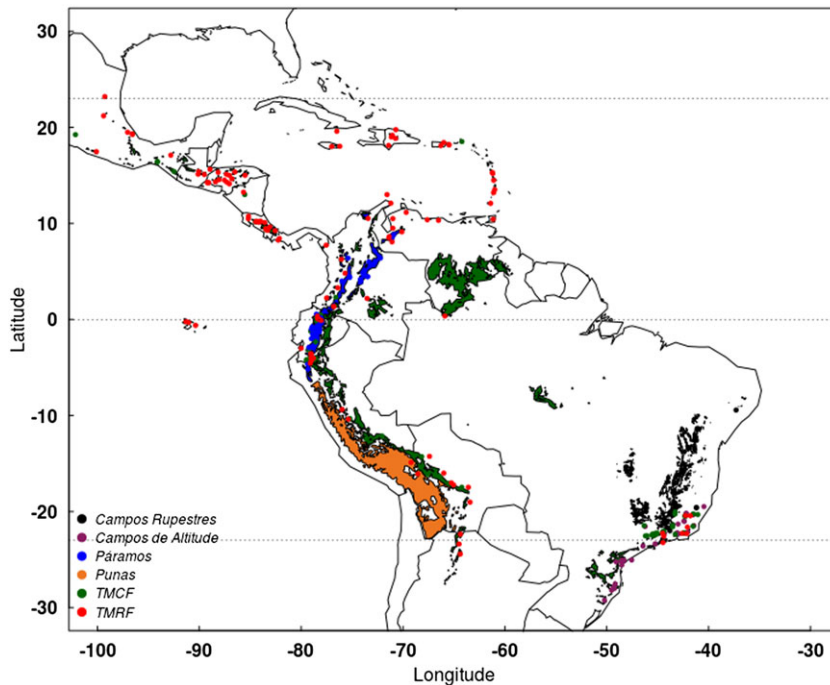
In the Neotropics, where mountain regions extend above 6,000 m.a.s.l., elevation is a main driver of environmental conditions and variability, which gives rise to many different types of vegetation with distinct traits and functionalities (Figures 1, 2). Increasing elevation is associated with a decline in atmospheric pressure, temperature, ET, and photon flux density, and an increase in cloudiness, ultraviolet B (UV-B) radiation (Letts & Mulligan, 2005), relative humidity, and annual rainfall (Gerald, Schawe, & Bach, 2008; Hamilton et al., 1995; Table 1). Neotropical montane ecosystems can be broadly distributed into two major groups: (a) forest ecosystems, including tropical montane rainforests (TMRFs) and tropical montane cloud forests (TMCFs), and (b) grassland and scrubland ecosystems, including *páramos*, *punas*, “*campos de altitude*” (altitudinal grasslands), and “*campos rupestres*” (rock outcrop grasslands/scrublands or mountaintop grasslands). However, the specific combination of factors leading to a particular vegetation type is poorly defined for tropical montane systems. Moreover, the high degree of altitudinal and climatic overlap (Table 1) among these ecosystems underscores the need for better delineation of the environmental determinants of their establishment and persistence. In this section, we synthesize the current understanding of the distinct climatic, edaphic, and hydrological characteristics that influence the species distribution and the functional traits of each of these tropical montane ecosystems.

### 2.1 | Tropical montane forests

Relative to temperate montane forests, tropical montane forested ecosystems have a more constant temperature and higher relative humidity, even during the “dry season,” which typically is less pronounced ( $>100 \text{ mm month}^{-1}$  is typical for dry periods). TMRFs and TMCFs are particularly distinct from lowland tropical forests in regard to their carbon and water budgets. For example, Gotsch, Asbjornsen, and Goldsmith (2016) found that microclimatic factors (e.g., energy-limitation) of high altitude forests suppressed photosynthetic rates,



**FIGURE 1** Examples of Neotropical montane ecosystems. (a–b) Transitional premontane–montane tropical rainforest in Costa Rica (San Isidro de Peñas Blancas–Texas A&M University Soltis Center) at ~600 m.a.s.l.; (c–d) tropical montane cloud forest in Brazil (RPPN Alto-Montana, Itamonte, Brazil) at 1400–2400 m.a.s.l.; (e–f) páramos grasslands in Ecuador (Zhuruca River Ecohydrological Observatory, San Fernando, Ecuador) at 3400–3900 m.a.s.l.; (g–h) campos rupestres in Brazil (Serra do Cipó National Park, Minas Gerais, Brazil) at 1200 m.a.s.l.; (i–j) campos de altitude in Brazil (Campos do Jordão National Park, Campos do Jordão, São Paulo, Brazil) above 1500 m.a.s.l. Photo credits: a—Georgianne Moore; b—Luiza Aparecido; c & d—Patrícia Pompeu; e—Giovanny Mosquera; f—Ximena Palomque; g & h—Grazielle Teodoro; i & j—Hans Lambers



**FIGURE 2** Map of the geographic distribution of the described Neotropical montane ecosystems. These include tropical montane cloud forest (TCMF), tropical montane rain forest (TMRF), páramos, punas, campos de altitude, and campos rupestres. Dots represent research field sites referenced by geographic coordinates collected in the literature based on the montane ecosystem's classification and each Neotropical country's parks and reserves focusing on their altitude, vegetation, and climatic conditions to distinguish the montane ecosystem type. The data points used and links to these references are available as Supporting Information. Additionally, the full coloured areas represent entire biomes delineated through polygon shapefiles—geospatial vector data format for geographic information system (GIS)—processed using R software with the mapproj package (Bivand & Lewin-Koh, 2017). Shapefiles were obtained from previously published studies (Mulligan, 2010; Silveira et al., 2016) and from the ArcGIS site, when available ([www.arcgis.com](http://www.arcgis.com)) (Supporting information)

**TABLE 1** General vegetation and climate characteristics of tropical mountainous ecosystems in the Neotropics

Vegetation type		Altitude (m.a.s.l)	Precipitation (mm year <sup>-1</sup> )	Seasonality (n° dry months)
Forest	Tropical montane rain forest (TMRF)	700–2,500	3,000–8,000	5–6 <sup>a</sup>
	Tropical montane cloud Forest (TCMF)	800–3,500	2,000–3,500	0–3 <sup>a</sup>
Grassland/Scrublands	<i>Campo rupestre</i>	900–2,100	1,100–1,800	5–6 <sup>b</sup>
	<i>Campo de altitude</i>	1,800–2,900	1,500–3,000	1–3
	<i>Páramos</i>	3,000–4,500	700–3,000	2–5 <sup>c</sup>
	<i>Punas</i>	3,200–5,000	1,000–2,000	6–8 <sup>b</sup>

<sup>a</sup>Dry season characterized by lower precipitation rates, but rarely below 100 mm month<sup>-1</sup>.

<sup>b</sup>In the driest months, part of these ecosystems can have no precipitation.

<sup>c</sup>Depending on the location, the precipitation regime may be unimodal or bimodal, but in general, yearly seasonality is low.

which resulted in a lower net productivity and transpiration but higher water use efficiency than lowland forests. Meanwhile, TMRFs are characterized by high precipitation inputs (3,000–8,000 mm year<sup>-1</sup>) with negligible fog contributions (Holdridge, 1967), whereas TCMFs receive between 800 and 3,400 mm year<sup>-1</sup> and are frequently covered in clouds or mist (Jarvis & Mulligan, 2011). The persistent fog typical of TCMFs and associated wet and cool climate distinguishes them from other terrestrial ecosystems (Jarvis & Mulligan, 2011; Still, Foster, & Schneider, 1999).

Comparing the soil of different montane forests, TMRFs soils generally have higher nutrient availability than those of TCMFs, especially phosphorous (P) and nitrogen (N) (Graefe, Hertel, & Leuschner, 2010; Wilcke, Yasin, Valarezo, & Zech, 2001). This is due to lower temperatures and higher soil water saturation with elevation that decreases mineralization rates (Gerald, 2008). Some studies showed declining nutrient availability and increase in acidity as elevation increases (Bücker et al., 2010; Homeier, Breckle, Gunter, Rollenbeck, & Leuschner, 2010; Wilcke et al., 2008; Wilcke, Yasin, Abramowski, Valarezo, & Zech, 2002), which results in a decrease of soil microbial activity and, thus, organic material decomposition rates (Brujnzeel et al., 2011). This slow organic matter decomposition in montane

forests promotes an inverse relationship between P levels in the litter and soil (i.e., the higher the P levels in litter, the lower the P levels in soils; Turner, 2004). The development of the organic horizon of TMRFs soils, which is substantially thicker than in TCMFs, provides more favourable conditions for plant growth<sup>1</sup> (Wilcke et al., 2002), whereas a large proportion of total nutrients is retained in the litter (Wilcke et al., 2001). Moreover, the combination of climatic conditions and faster nutrient cycling results in a higher primary productivity and plant biodiversity in TMRFs compared to TCMFs (Clark, Hurtado, & Saatchi, 2015).

The vegetation in TMRFs is mostly composed of evergreen tree species (Moore, 2008), which vary greatly across regions. A notable feature of both TMRFs and TCMFs is the abundance of co-occurring plant functional types (e.g., trees, palms, epiphytes, ferns, and herbaceous understory plants), with dicot trees comprising up to 80% of the forest stand (Lieberman, Lieberman, Peralta, & Hartshorn, 1996). Epiphytes are more common at the altitudes where fog is frequent and provides an important water source (Grubb, 1974; Grubb & Whitmore, 1966). As altitude increases, hemiepiphytes become more abundant and lianas less abundant (Hernandez, Dezzio, Sanoja, Salazar, & Castellanos, 2012; Jimenez-Castillo & Lusk, 2013; Vazquez

& Givnish, 1998), whereas palms and lianas are more abundant in warmer TMRFs, where conditions are similar to those of their preferred lowland and premontane microclimates (Lieberman et al., 1996). It is also notable that tropical conifers, although rare because of climatic and edaphic restrictions, are found in some TMRFs in Brazil (*Podocarpus* sp., *Araucaria* sp.; Longhi et al., 2009), Chile, and Argentina (*Araucaria* sp.; Reis, Ladio, & Peroni, 2014), which can provide important ecohydrological functions. For example, *Araucaria* sp. provides shade to understory and midstory plants while still allowing a large amount of water to reach the soil and the intercanopy atmosphere through weak interception and stemflow (Thomaz & Antoneli, 2015) and has an important role in increasing soil nutrients through large litter inputs (Thomaz, 2007).

The transition between TMRFs and TMCFs is mainly determined by atmospheric and soil humidity levels, as well as the frequency and intensity of fog (Bruijnzeel, Kapelle, Mulligan, & Scatena, 2010; Grubb & Whitmore, 1966; Jarvis & Mulligan, 2011; Mulligan, 2010). However, because of the highly variable environmental and topographical conditions on tropical mountains, there is no exact altitudinal transition between these two ecosystems (Table 1; Richter, 2008). Moreover, because of the great diversity of plant functional types and their dependence on local climatic conditions, it is not possible to categorize these ecosystems on the basis of plant species occurrence alone, and often structural characteristics are used to delineate vegetation distribution and functional traits. For example, in the transition from TMRF to TMCF ecosystems, there are significant changes in forest structure, including shorter and more multitemmed trees, declining presence of buttressed roots (Grubb, 1977; Leuschner, Moser, Bertsch, Röderstein, & Hertel, 2007; Lieberman et al., 1996; Richter, 2008; Soethe, Lehmann, & Engels, 2008; Wilcke et al., 2008), increasing root-shoot ratio (Leuschner et al., 2007) and root longevity (Graefe, Hertel, & Leuschner, 2008), and thicker and more coriaceous leaves (Grubb, 1977). These leaf adaptations not only provide protection from strong winds and high radiation but also help drain water from their leaf surface, which is important because high leaf wetness caused by persistent fog or rain can suppress plant gas exchange (Aparecido, Miller, Cahill, & Moore, 2017). Other leaf adaptive traits that help maintain gas exchange in high-altitude plants include trichomes, water repellency (Aparecido et al., 2017; Holder, 2007; Rosado, Oliveira, & Aidar, 2010), and drip-tips (leaf drainage; Goldsmith et al., 2016; Malhado et al., 2012). Additionally, some species can take advantage of these leaf wetness events by absorbing water directly through their leaves, which can alleviate the effects of periodic moisture stress on plant functioning (Eller, Lima, & Oliveira, 2013; Goldsmith, Matzke, & Dawson, 2013; Gotsch et al., 2014; Hietz, 2010).

The underlying drivers that alter vegetation structure along the transition from TMRFs to TMCFs with increasing altitude have been explored in great detail (Clark et al., 2015; Girardin et al., 2014; Hager & Dohrenbusch, 2011; Homeier et al., 2010; Kessler, 2001; Lieberman et al., 1996; Martin, Fahey, & Sherman, 2010; Prada & Stevenson, 2016; Sanchez, Pedroni, Eisenlohr, & Oliveira-Filho, 2013; Vazquez & Givnish, 1998; Veneklaas & van Ek, 1990). Yet much uncertainty remains (Foster, 2001) and generalities are challenging to make (Bruijnzeel et al., 2011). Several hypotheses put forth have emphasized the role of changing microclimate conditions with increasing elevation.

For example, TMCFs have more acidic soils with low fertility, due to low decomposition and mineralization rates under wet and cold conditions (Bruijnzeel & Veneklaas, 1998), and lower energy inputs due to persistent fog and cloud, resulting in lower transpiration (T) and photosynthetic activity (Bruijnzeel & Veneklaas, 1998; Stadtmüller, 1987). TMCFs also are more prone to anoxic conditions due to soil saturation, which inhibits root respiration (Bruijnzeel & Proctor, 1995; Bruijnzeel & Veneklaas, 1998; Weaver, Byer, & Bruck, 1973). Other associated factors that differentiate TMRFs and TMCFs include greater soil toxicity with elevation due to higher aluminium saturation and lower pH (Hafkenscheid, 2000), strong winds, which can cause physiological desiccation (Bruijnzeel & Veneklaas, 1998); and high UV-B, which requires that plants maintain high levels of protective phenolic compounds in leaves. High UV-B may have detrimental effects on photosynthesis, stomatal opening, root cell division, and ion uptake (Bruijnzeel & Veneklaas, 1998; Foster, 2001), which further affects vegetation structure.

## 2.2 | Grassland/scrubland montane ecosystems

Neotropical montane grasslands and scrublands include the Andean *páramos* and *punas*, which are grasslands dominated by megaphytic Asteraceae species (e.g., giant rosette plants) (Díaz, Péfaur, & Durant, 1997; Figure 1e–j), and the Brazilian *campos rupestres* and *campos de altitude*, which are dominated by small sclerophyllous trees and shrubs interspersed in a matrix of grasses and sedges (Oliveira et al., 2016). In this section, we further describe how the combination of elevation, latitude, and local climate interact to influence the distribution of these vegetation types, plant functional traits, and the transition between forest and grassland ecosystems.

*Páramo* ecosystems lie above the tree line and below the perpetual snow line, at altitudes ranging from about 3,000 to 4,500 m.a.s.l. (Baruch, 1984). They are found mainly in the northern Andes of Venezuela, Colombia, Ecuador, and Peru, and to a lesser extent in Central America (Nicaragua, Costa Rica, and Panama). They cover approximately 35,000 km<sup>2</sup> (Madriñán, Cortés, & Richardson, 2013) between latitudes 11°N and 8°S (Frantzen & Bouman, 1989).

Due to the high elevation, the *páramo* climate is typically cold and humid throughout the year, with frequent night frosts, strong winds, intense solar radiation, and high relative humidity, ranging between 70% and 90% (Buytaert, Cuesta-Camacho, & Tobon, 2011; Córdova, Carrilo-Rojas, Crespo, Wilcox, Céleri, 2015; Luteyn, 1999). Mean annual temperatures vary between 2 and 10 °C, decreasing with altitude, whereas diurnal temperature fluctuations are especially extreme, often varying by 20 °C (van der Hammen & Hooghiemstra, 2000). Climate and precipitation regimes vary depending on the geographical location of a particular *páramo* region with respect to (a) the position of the Intertropical Convergence Zone (Vuille, Bradley, & Keimig, 2000); (b) regional circulation patterns such as the El Niño Southern Oscillation (Martínez et al., 2011); (c) the north-easterly Caribbean trade winds (Lauer, 1979); and (d) the Humboldt Current (Jørgensen et al., 2011). Precipitation in the *páramo* is characterized by frequent rainfall, mainly in the form of drizzle (long duration, low intensity) (Padrón, Wilcox, Crespo, & Céleri, 2015). Annual rainfall amounts depend on the geographical location, with patterns that are difficult

to generalize due to the complex topography of the Andean mountain barrier and the influence of water vapour stemming from both the Pacific Ocean and the Amazon basin (Garreaud, 2009; Vuille et al., 2000). As a result, annual precipitation is highly variable (Luteyn, 1992) and can reach values as low as 500 mm (e.g., the dry *páramos* of Central Ecuador and Venezuela) and as high as >3,000 mm (e.g., the outer slopes in the Colombian western and eastern Cordillera; Buytaert et al., 2011). Although fog is common in the *páramo*, with an estimated contribution of up to 35% of additional water inputs in an Ecuadorian TMRP-*páramo* transition zone (Bendix, Rollenbeck, Richter, Fabian, & Emck, 2008; Rollenbeck, Bendix, & Fabian, 2011), detailed studies on the relative importance of fog to total water inputs and water balance are still lacking.

Geologically, the *páramo* is of relatively recent origin and consists of U-shaped valleys formed by glacial activity (Coltorti & Ollier, 2000; Schubert, 1980). The main soil types are Histosols and Andosols (Buytaert, Deckers, & Wyseure, 2005), originated from the accumulation of organic matter and volcanic ash from past volcanic activity combined with low temperatures and high environmental humidity (Podwojewski, Poulénard, Zambrana, & Hofstede, 2002; Poulénard, Michel, Bartoli, Portal, & Podwojewski, 2004). Because of their high organic matter content (Buytaert, Wyseure, De Bièvre, & Deckers, 2005) and porous structure with low bulk density, these soils are humic and acidic with high water-storage capacity (up to 90% volume; Buytaert, Deckers, & Wyseure, 2006).

The *páramo* vegetation consists of a combination of species that have adapted to the ecosystem's extreme climatic conditions, including grasses, evergreen herbs, shrubs, rosette plants, and scattered dwarf forests (Cleef, Rangel-Churio, & Salamanca-Villegas, 1983; Frantzen & Bouman, 1989). Grasslands are the dominant cover type (>70%), composed of tussock grasses (commonly in the genera *Calamagrostis*, *Festuca*, and *Stipa*) and various species of the Cyperaceae family. Most of the remaining land area is wetlands, composed of cushion plants (such as *Plantago rigida* Kunth, *Xenophyllum humile* (Kunth) V.A. Kunk, and *Azorella* spp.; Ramsay & Oxley, 1997; Sklenar & Jorgensen, 1999). The dominant tree species in the *páramo* are in the genus *Polylepis* (Rosaceae), distributed primarily as small patches near the lower elevation *páramo* boundary (~3,000–3,200 m a.s.l.) and as scattered individuals along the entire *páramo* elevation range (Hensen et al., 2012) and comprising a relatively small proportion of the landscape (<5%, [Mosquera, Lazo, Celleri, Wilcox, & Crespo, 2015]). Although the ecology and plant diversity of the *páramos* have been studied in detail, the ecophysiological traits related to different plant species' hydraulic functions and their feedbacks and interactions with the hydrologic regime at the catchment scale remain poorly investigated. For example, although the capacity of plants to absorb fog water through their leaves as a mechanism to alleviate moisture stress has been widely documented across diverse ecosystems (Goldsmith et al., 2013), the capacity for foliar water uptake (FWU) among *páramo* species is not known. Additionally, the role of different *páramo* vegetation types in influencing the water balance via processes such as canopy cloud water interception (e.g., Holwerda et al., 2010), transpiration (e.g., Alvarado-Barrientos, Holwerda, Asbjornsen, Dawson, & Bruijnzeel, 2014), and hydraulic redistribution (Oliveira, Eller, Bittencourt, & Mulligan, 2014) represents another important knowledge gap.

*Puna* grasslands, categorized as the drier version of the *páramo*, are found at altitudes between 3,200–5,000 m a.s.l. throughout Peru, Bolivia, Chile, and Argentina (Nicholson, 2011). Their position on the opposite side of the eastern orographic chain from the Amazon basin explains the markedly lower precipitation (Sarmiento, 1986). Peruvian *punas* are the most humid (1,000–2,000 mm year<sup>-1</sup>), whereas Chilean-Argentinian *punas* are desertic (<100 mm year<sup>-1</sup>). The *puna* of the southern Andes is particularly arid and cold, with a long, intense dry season (e.g., in Bolivian *punas* winter temperatures reach -30 °C and rainfall is ~300 mm year<sup>-1</sup>; Mani, 1968, Sarmiento, 1986). Relative humidity ranges between 35% and 65% throughout the year (Mani, 1968; Nicholson, 2011). In contrast to the *páramos*, where approximately 70% of annual rainfall occurs in the rainy season, the drier *punas* are much more seasonal, concentrating up to 90% in rainy season (Sarmiento, 1986) and experiencing less frequent fog and snow (Nicholson, 2011). Dry *puna* winters last between 6 and 8 months (Nicholson, 2011), which combined with relatively low cloud cover (~20% during the summer and 50% during winter), result in higher annual insolation rates and more extreme temperature fluctuations compared to *páramo*. Average annual temperatures range between 9 and 11 °C, with frequent night-time frosts and daytime temperatures increasing sharply (up to 30 °C) on sunny, dry days.

*Puna* vegetation is dominated by open grasslands with scattered patches of dwarf forest (Becerra & Bittencourt, 2007). The *puna* vegetation is further classified along a decreasing moisture gradient as: humid *puna*, arid *puna*, thorn *puna*, succulent *puna*, and desert *puna* (Mani, 1968). Similar to the *páramos*, the vegetation in *puna* consists of a combination of species adapted to the ecosystem's extreme climatic conditions. The vegetation is dominated by tussock-like grasses (Poaceae; e.g., *Poa*, *Festuca*) and sedge (Cyperaceae) species, although scattered shrubs of Asteraceae (e.g., *Baccharis*), Solanaceae (e.g., *Fabiana*), and dwarf trees (*Polylepis*) are also found (Baied & Wheeler, 1993). However, these vegetation groups have shown to be dependent on local water and thermal stresses (Bonaventura, Tecchi, & Vignale, 1995; Lambrinos, Kleier, & Rundel, 2006). In contrast to the cushion plants that dominate *páramos* wetlands, in a Chilean *puna*, Lambrinos et al. (2006) observed that cushion live forms were most abundant on xeric, rocky sites with low water retention and high solar radiation. On these xeric sites, cushion plants' large water storage capacity was valuable to maintain metabolic functioning during hot, dry days, as well as moderating extreme diurnal temperature fluxes by keeping the cells warm and turgid to withstand night-time frosts (Kleier, 2001). Shrubs and grasses growing on these sites with more favourable soil conditions (i.e., deep soils with few rocks and higher water and nutrient availability) did not express specialized adaptive traits for moisture stress. However, they were physiologically adapted to rapidly upregulate gas exchange processes in response to occasional pulses of favourable temperature and solar radiation conditions throughout the day. To better understand patterns of landscape distribution and to predict *puna* vegetation response to future climatic change, additional adaptive traits for coping with environmental extremes should be elucidated.

*Campes de altitude*, found in south-eastern Brazil (Figures 1, 2) between 1,800 and 2,900 m.a.s.l. and geographically distributed along the mountain chains of the Serra do Mar and Serra da Mantiqueira, are

cool-humid, mountaintop grasslands, and shrublands, underlain by igneous and metamorphic substrates (Safford, 2007). The cool-humid climate of *campos de altitude* is dominated by subtropical and temperate influences (Safford, 1999). Precipitation ranges between 1,500–3,000 mm year<sup>-1</sup>, increasing with elevation due to an orographic effect, and is seasonally distributed, with the rainy season typically occurring between November and March and the dry season (reaching <50 mm month<sup>-1</sup> in some areas) between June and August (Safford, 1999). Average annual temperature ranges between 12 and 18 °C, depending on altitude. Frost events occur during the winter in some areas, such as Itatiaia National Park at 2,200 m.a.s.l., where frost occurs ~56 days per year (Safford, 1999). *Campos de altitude* soils are characterized as having shallow soils with significant horizontal and vertical variation, ranging from clayey to rocky outcrops, and varying greatly according to local-scale topographic features such as well-drained slopes or poorly drained bogs (Oliveira, Costa, Azevedo, Camargo, & Larach, 1983). The *campos de altitude* mountain chains are ancient landscapes, with a long history of erosion; consequently, they occur at lower elevations than the younger Andean mountains of western South America (Safford, 1999; Safford, 2007), where *páramo* occur.

In the *campos de altitude*, the environmental filters that most strongly influence vegetation establishment include frequent frost, high solar radiation, shallow soils, and dry conditions (Scarano, 2009), resulting in a dominance of phanerophytes, hemicryptophytes, and geophytes (Safford, 1999). In general, vegetation distribution is controlled by local topography, the drainage network, and the distribution of soil types (Safford, 2007). Nurse plants, which are able to colonize the rocky surfaces with especially harsh environments, play a critical role in facilitating the establishment and persistence of other species (Scarano, 2002; Scarano, 2009). Information about distinct plant traits and functioning of the Brazilian *campos de altitude* is relatively scarce. The *campos de altitude* that occur adjacent to cloud forests can also benefit from occasional fog, with additional cloud water inputs potentially compensating for dry season moisture deficits (Eller, Lima, & Oliveira, 2016; Safford, 1999).

*Campos rupestres* are montane grasslands and scrublands characterized by a mosaic of fire-prone vegetation and rocky outcrops of quartzite, sandstone, or ironstone substrate, occurring between 900 m and 2,050 m.a.s.l., primarily along the “Espinhaço” mountain range in eastern Brazil (Silveira et al., 2016). Including a few sparse, disconnected locations, the total estimated area of *campos rupestres* is 66,447 km<sup>2</sup>, with much of their original area replaced by anthropogenic activities, such as agriculture (Fernandes, Barbosa, Negreiros, & Paglia, 2014). In contrast to *páramo* and *campos de altitude*, the climatic regime in the *campos rupestres* is more strongly seasonal, with a marked dry season occurring in May–September. Along the Espinhaço Range, latitudinal differences account for decreasing total rainfall towards the north and decreasing mean monthly temperatures towards the south (Silveira et al., 2016). The average precipitation is 1,461 ± 308 mm year<sup>-1</sup>, and monthly temperatures vary from 16.0 ± 2.1 °C in winter to 21.2 ± 1.5 °C in summer (wet season; Silveira et al., 2016). Fog can occur in *campos rupestres*, but there are no data quantifying its relative contribution to the local water balance or to the vegetation physiology. Soils in *campos rupestres* are relatively old,

poorly developed, extremely leached, nutrient-impoverished (mainly in phosphorus and cations), and consequently, strongly influenced by the acid, chemically poor parent materials (Oliveira et al., 2015; Silveira et al., 2016).

Similar to the other grasslands, *campo rupestres* are dominated by grasses, sedges, herbs, rosettes, and shrubs, especially from the Asteraceae, Cyperaceae, Eriocaulaceae, Poaceae, and Velloziaceae families (Le Stradic, Buisson, & Fernandes, 2015). Vegetation growth is strongly influenced by water availability and soil properties. During the dry season, the shallow soils dry out and vapour pressure deficit increases, creating more stressful conditions for plant growth and survival (Oliveira et al., 2016) and favouring perennial plants with very slow growth rates. *Campos rupestres* show the greatest degree of seasonality in precipitation among tropical montane ecosystems and, in this environment, plants use a wide range of strategies to cope with drought (Oliveira et al., 2016). These plants have morphological and physiological adaptations to improve water and nutrient acquisition, including drought-tolerant, drought-avoiding, and desiccation-tolerant strategies (Castro, Silveira, Marcato, & Lemos-Filho, 2017; Jacobi, Carmo, Vincent, & Stehmann, 2007; Oliveira et al., 2016; Porembski & Barthlott, 2000; Vitarelli, Riina, Cassino, & Meira, 2016). Drought-tolerant species in *campos rupestres* deal with drought by maintaining metabolism and cell turgor through regulatory mechanisms, such as strong stomata control over water loss. Drought-avoiding plants typically have deep or dimorphic root systems that enable them to access deep and stable water sources, or phenological strategies such as drought-deciduousness (Brum, Teodoro, Abrahão, & Oliveira, 2017). Desiccation-tolerant plants enter an apparent anabiosis state resulting in a desiccated appearance. *Campos rupestres* are particularly a centre of diversity for desiccation-tolerant vascular plants, also known as resurrection or poikilohydric plants, which are able to equilibrate their water content with that of dry air during water-limiting conditions (Alcantara et al., 2015; Gaff & Oliver, 2013; Porembski & Barthlott, 2000).

*Campos rupestres* support one of the highest levels of plant biodiversity on Earth. For instance, about 1,590 species were recorded in a 200 km<sup>2</sup> area (Giulietti, Menezes, Pirani, Meguro, & Wanderley, 1987). Species distribution in *campos rupestres* is also shaped in part by fire (Bush et al., 2015; Safford, 2007), which could be critical to maintain plant diversity and the distinct plant community characteristics of these systems. Fires are mainly caused by lightning strikes at the transition between dry to rainy season and, hence, are closely coupled with the carbon and hydrological balance due to the large accumulation of dry fuel loads (Oliveira et al., 2016).

### 3 | ECOHYDROLOGICAL FEEDBACK MECHANISMS: HOW DO VEGETATION CHARACTERISTICS INFLUENCE HYDROLOGICAL PROCESSES IN NEOTROPICAL MOUNTAINS?

Across diverse ecosystems, plant species exhibit unique adaptive traits and functions that reflect a close coupling with the climatic conditions under which they have evolved (Foster, 2001; Jarvis & Mulligan, 2011;

Oliveira, Eller, et al., 2014). Because of this close coupling, Neotropical montane ecosystems not only respond to changing climatic conditions but also influence the local and regional climate through the interactions and feedbacks between vegetation and hydrology, including soil water infiltration and storage capacity, ET, plant water storage, and fog-plant interactions. In this section, we discuss each of these ecohydrological processes in relation to the unique characteristics of each Neotropical montane ecosystem, and the larger scale implications for water balance and watershed hydrology.

### 3.1 | Soil water infiltration and storage capacity

Differences in soil, vegetation, and climate are associated in multiple ways with differences in hydrological processes along altitudinal gradients. Neotropical montane ecosystems are located at the headwaters of watersheds that are the primary water supply to major population centres within lower lying regions (Dias et al., 2003; Pinto, Mello, Owens, Norton, & Curi, 2015; Soares et al., 2012), including the Amazon river that alone delivers 18% of all fresh water to oceans globally (Subramaniam et al., 2007). Consequently, vegetation-climate interactions and feedbacks play a critical role in determining soil water inputs and storage capacity, especially by maintaining good soil-water transmissivity (i.e., the extent to which soil can transmit water through its entire saturated thickness). Such transmissivity, in turn, facilitates water recharge to groundwater aquifers, which further helps regulate discharge (Pinto et al., 2015; Soares et al., 2012). For example, closed-canopy forests such as TMRFs and TMCs, typically maintain relatively high soil infiltration capacity, low run-off, high stemflow, and high soil moisture recharge, which combined, contribute to large total water inputs into the soil (Figure 4—Bruijnzeel et al., 2011, Bruijnzeel et al., 2011; Motzer, Munz, Kupperts, Schmitt, & Anhof, 2005; Teale et al., 2014).

In all four grassland and scrubland environments discussed here, the soils tend to have high water storage capacity (Figure 4), associated with vegetation with dense roots to maintain soil stability. Consequently, in both Neotropical montane forests and grasslands, maintaining high soil-water transmissivity and storage represents an important ecohydrological function of the natural vegetation, which in turn, helps regulate the hydrological cycle, control erosion, and maintain high water quality at watershed scales (Foster, 2001). Changes in vegetation type and abundance in many tropical montane ecosystems, often linked to changes in soil properties, could lead to negative consequences for water resource availability (Asdak, Jarvis, Van Gardingen, & Fraser, 1998; García-Coll, 2002).

For example, in the northern Andean páramos, water balance is largely determined by the marked topography-soil-vegetation conditions of the landscape (Mosquera et al., 2015). Andosols with low bulk densities ( $\sim 0.40 \text{ g cm}^{-3}$ ) and high water retention capacities at saturation ( $\sim 0.70 \text{ cm}^3 \text{ cm}^{-3}$ ), mainly found in steep hillslopes with grassland vegetation, control the ecosystem's water regulation capacity (i.e., year-round sustainability of streamflow) via downslope subsurface drainage of water through these soils' porous matrix towards the soils at the valley bottoms. Relative to Andosols, Histosols have even lower bulk densities ( $< 0.3 \text{ g cm}^{-3}$ ) and higher water retention capacities at saturation ( $> 0.80 \text{ cm}^3 \text{ cm}^{-3}$ ) and are mainly found in wetland

areas (at valley bottoms and flat hilltops) dominated by cushion plants that contribute to the high water storage capacity of the páramo (Mosquera, Celleri, et al., 2016; Mosquera, Segura, et al., 2016).

### 3.2 | Evapotranspiration

In Neotropical montane environments, ET rates decrease with altitude in response to increasing cloud and fog cover, lower air temperatures, higher relative humidity, low incidence of net radiation, and high leaf wetness (Aparecido, Miller, Cahill, & Moore, 2016). In TMRFs, where precipitation rates are almost twofold greater than lowland tropical forests, ET and T are lower (between 800 and 1,300  $\text{mm year}^{-1}$ , respectively), with T being equivalent to 30–50% of ET (Bruijnzeel et al., 2011; Good, Moore, & Miralles, 2017). In TMCs, which are cooler and wetter than TMRFs, the fraction of transpiration is usually lower (Bruijnzeel et al., 2011). In low-altitude forests (premontane and lowland forests), T can exceed 1,000  $\text{mm year}^{-1}$  and the T/ET ratio can be over 50%. Consequently, transpiration from lowlands and premontane forests usually contributes more to the water balance compared to evaporation, because roots are able to tap into groundwater and soil-water reservoirs in addition to higher vapour pressure deficits, making the proportion of T in the overall ET flux very high (Gotsch et al., 2016; Jasechko et al., 2013).

In altitudinal grasslands, such as the ones found in the Mantiqueira mountains of Brazil, the mean annual potential ET of a TMC region is about 2.3  $\text{mm day}^{-1}$  higher ( $\sim 1,670 \text{ mm year}^{-1}$ ) than at the adjacent *campos de altitude* ( $\sim 850 \text{ mm year}^{-1}$ ; Eller, Burgess, & Oliveira, 2015). In the *campos de altitudes* located in the Itatiaia National Park, ET is  $660.9 \pm 51.3 \text{ mm year}^{-1}$ . In this system, the lowest ET rates occur during the hot and rainy season (average of 119.6 mm), from December to February, when precipitation input is high (1,147 mm; Aximoff, Alves, & Rodrigues, 2014). The lower ET of *campos de altitude* plays a major role in sustaining the higher soil water storage and associated springs in these ecosystems. Estimated ET in wet páramo watersheds in southern Ecuador ( $510 \pm 49 \text{ mm yr}^{-1}$ ) is similar to that of *campos de altitude* (Mosquera et al., 2015). Relatively low ET rates, combined with almost daily rainfall (mostly in the form of drizzle [Padrón et al., 2015]) and high water infiltration and retention capacity (Buytaert et al., 2006) of the páramo soils, leads to high water storage capacity (Mosquera et al., 2015).

### 3.3 | Vegetation water storage

Although plant species with specialized aboveground structures for water retention can be found in lower altitude TMRFs (Hietz, 2010; Holscher, Kohler, van Dijk, & Bruijnzeel, 2004), the number and importance of these adaptive strategies is apparently much higher in TMCs (Veneklaas & van Ek, 1990). For example, epiphytes (bromeliads, mosses, and lichens), which are especially abundant in TMCs, intercept and uptake substantial amounts of water (Holwerda et al., 2010; Muñoz-Villers et al., 2012; Van Stan & Pypker, 2015; Veneklaas & van Ek, 1990). During the wet season, bryophytic epiphytes are able to store, on average, up to 300% of their dry weight as water (Holscher et al., 2004; Kohler, Tobon, Frumau, & Bruijnzeel, 2007; Stanton et al., 2014), whereas other type of epiphytes are able to store water in



succulent tissues coupled with thicker cuticles that inhibit water loss (Gotsch et al., 2015). Holscher et al. (2004) found that epiphytes contributed 6% of total canopy interception at a TMRF, with TMCFs likely to exhibit greater canopy fog interception due to a greater epiphyte abundance and fog immersion frequency. Quantifying interception by epiphytes in these ecosystems is challenging due to little knowledge of the rates in which water is taken up and lost under varying field conditions and specific epiphytic functional traits (Veneklaas & van Ek, 1990). Although water storage is vital for epiphytic growth and microclimate conditions (Stanton et al., 2014), some studies warn that potential interception among certain epiphytic functional groups (e.g., bryophytes) may result in less water and solutes reaching the forest floor during dry seasons, thus less water available for the host plants (Fleischbein et al., 2005; Ponette-Gonzalez et al., 2009; Van Stan & Pypker, 2015).

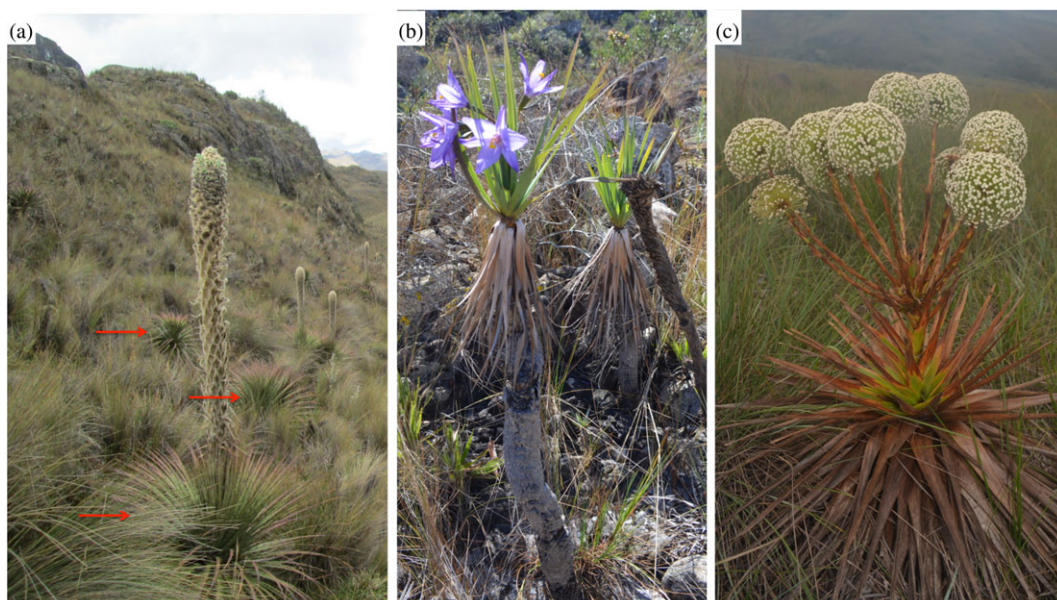
In many Neotropical grassland and scrubland mountain ecosystems, rosettes are a prevalent life form (Figure 3). For example, *Espeletia* rosettes are an important genus in *páramos* (Asteraceae, Figure 3), rosettes from the families Asteraceae and Bromeliaceae are common in *campos de altitude*, and rosettes in the Velloziaceae (Figure 3), Eriocaulaceae, Asteraceae families occur in *campos rupestres*. Their presence provides useful insights about ecohydrological drivers that favour grasslands and shrublands over forests. The manner in which the leaves are arranged in a terminal rosette is very important to the plant's physiological functioning, influencing its water and carbon acquisition capacity (Monasterio & Sarmiento, 1991). Rosettes and other herbaceous plants intercept and channel rainfall, essentially acting as funnels or channels that collect and direct significant proportions of total rainfall towards the layer of dead leaves. Water then flows through this layer to reach the base of the trunk, where a thick layer of roots with mycorrhizae associations are concentrated, facilitating rapid uptake of water and solutes (Monasterio & Sarmiento, 1991; Perez & Frangi, 2000). Similarly, *Vellozia* spp. and *Croton* spp., which occur in

*campos rupestres*, are able to collect water through stems and adventitious roots (Oliveira, Dawson, & Burgess, 2005) and via FWU (Vitarelli et al., 2016). Hence, all these mechanisms can be very important to the water balance in *páramos* (e.g., *Espeletia*; Monasterio & Sarmiento, 1991) and in *campos rupestres* (e.g., *Vellozia* [Oliveira et al., 2005; Alcantara et al., 2015]), which are strongly affected by extreme diurnal and seasonal fluctuations in soil moisture availability and atmospheric demand.

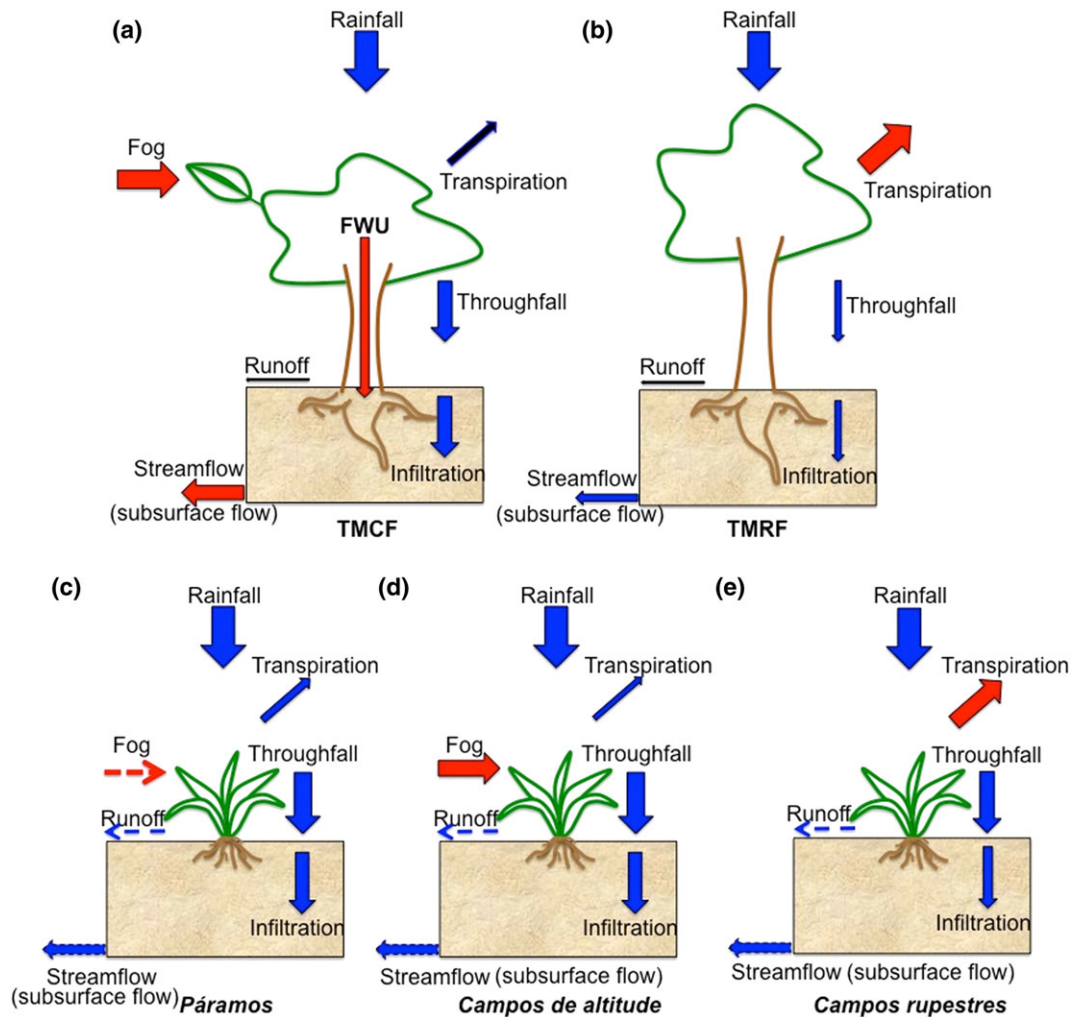
### 3.4 | Fog-vegetation interactions

As mentioned previously, fog plays an important role in the hydrology and productivity of tropical montane ecosystems (Céleri & Feyen, 2008; Goldsmith et al., 2013; Figure 4) and is considered a strong indicator of changes in plant diversity and functioning among different ecosystems. Not only does fog act as an extra water input (Muñoz-Villers et al., 2012) but it also limits water loss driven by high evaporative demand and solar radiation intensities, which are especially important during dry periods in seasonal cloud forests (Eller et al., 2013; Gotsch et al., 2015; Oliveira, Eller, et al., 2014). Combined with the lower transpiration rates and higher canopy fog interception in TMCFs compared with TMRFs (Gotsch et al., 2016), these additional water inputs contribute to groundwater recharge and the regional streamflow (i.e., 9% from fog deposition in a *puna* grassland; Clark et al., 2014) and enhance throughfall through “fog drip” (i.e., intercepted water running off the canopy leaves; Figure 4—Foster, 2001; Oliveira et al., 2014).

Plant species in TMCFs tend to exhibit more prominent and diverse strategies for benefiting from leaf wetness compared to in TMRFs. For example, cuticle properties that promote water repellency can vary widely among species and, as a result, can be highly sensitive to environmental change (Oliveira, Eller, et al., 2014). The greater amount of additional fog input in TMCFs compared to TMRFs (Figure 4) may also contribute to a higher occurrence of sap flow



**FIGURE 3** Rosettes as an example of convergence of plant life forms in Neotropical grass/scrublands: (a) *páramos* in Ecuador—*Espeletia* sp. (Asteraceae); (b) and (c) *campos rupestres* in Brazil—*Vellozia* sp. (Velloziaceae) and Eriocaulaceae sp. (Eriocaulaceae). Photo credits: a—Ximena Palomeque; b & c—Grazielle Teodoro



**FIGURE 4** Representation of the main hydrological processes in the described Neotropical montane ecosystems: (a) tropical montane cloud forest (TMCF); (b) tropical montane rain forest (TMRF); (c) páramos; (d) *campos de altitude*; and (e) *campos rupestres*. The size of the arrows qualitatively indicates the relative magnitude among water fluxes for each ecosystem (i.e., rainfall, fog, throughfall, infiltration, transpiration, and streamflow [subsurface flow]). Different arrow colours indicate the main differences between (a) TMCF versus TMRF and (b) páramos versus *campos de altitude* versus *campos rupestres*. Red arrows indicate higher flux values and marked differences between the ecosystems, whereas blue arrows indicate no significant differences in fluxes. The brown boxes represent the soil in each ecosystem. In TMCFs (a) and *campos de altitude* (d), there is an additional fog water input flux. We hypothesize that this flux enhances positively the vegetation water balance of TMCFs through fog dripping, foliar water uptake, and reduced transpiration rates. Although fog is persistent in the Páramos, its contribution to the ecosystem's water balance remains unknown dashed blue line in c. *Puna* ecosystem is not represented due to scarcity of data in terms of the magnitude of its water fluxes. Modified from Foster (2001)

reversal, leading to greater amounts of FWU (Eller et al., 2015; Goldsmith et al., 2013). Indeed, FWU has been shown to contribute to 9% of the water lost through transpiration during dry seasons (Gotsch et al., 2014). Hence, fog can be an important source of water for some plants that do not have a very strong stomata control and could reach hydraulic thresholds that might damage their hydraulic pathways (Eller et al., 2016). Thus, some species are able to redistribute water taken in via their leaves or through roots and soil promoting tissue hydration, which enables and optimizes physiological processes during drier seasons (Eller et al., 2015). Although TMRFs would benefit most from FWU due to its reduced soil water availability compared to TMCF, Goldsmith et al. (2013) argue that less frequent fog events most likely lead to fewer plant species developing this specialized trait. Additionally, the higher abundance of epiphytes capable of performing FWU in TMCFs is much higher, which consequently will result in a

larger water source (e.g., 37–100% recovery from dry season transpiration; Hager & Dohrenbusch, 2011) for these ecosystems.

Taking in consideration the importance of foliar uptake of fog water, we would assume that this feature would be especially prevalent in altitudinal grassland species; however, there are no known studies that have documented FWU in tropical grassland and shrubland ecosystems. As cited previously, plants that occur at those altitudes and conditions (e.g., cold, windy, high solar radiation incidence, and precipitation input) have adapted various traits to collect and store precipitation water. Buytaert et al. (2011) gathered that fog frequency, constant cloud cover, and high relative humidity suppresses transpiration, whereas low temperatures reduce overall ET. Additionally, the drainage of fog water through the soil has shown to be a significant contributor to highland streamflow (Clark et al., 2014); although less vegetated (or less specialized), shallow soil sites have resulted in an increase of run-off (Buytaert, Iñiguez, & Bièvre, 2007).

## 4 | PREDICTIONS AND IMPLICATIONS: THREATS FROM LAND USE AND CLIMATE CHANGE

Tropical mountain ecosystems worldwide are highly vulnerable to climatic and land use changes because of their limited and discontinuous geographical distribution, restricted altitudinal range, adaptation to unique climatic conditions, and large numbers of endemic species (Assis & Mattos, 2016). As a result, they are likely to be the first regions on the planet affected by such changes (Spehn, Liberman, & Korner, 2006), and thus, can be considered as “early indicators” of climate change. The vulnerability of montane ecosystems can be mainly attributed to their dependence on distinct biotic and abiotic factors that are not always present in lowland forests, such as (a) reliance on fog events as a water source, which increases with altitude; (b) adaptation to lower temperatures and vapour pressure deficit (i.e., higher susceptibility of plants to cavitation); and (c) limited nutrient availability that might exacerbate with increase of run-off and reduction of microbial activity. Below, we further discuss these three factors in the context of increase of land cover change in the Neotropics and global trends of a changing climate.

Although Neotropical mountains are relatively less affected by agricultural practices than their surrounding lowlands, they are highly impacted by other land use conversion practices such as deforestation, road construction, fire, invasion of nonnative species, and mining activities (Bubb, May, Miles, & Sayer, 2004). However, activities that occur in lowland forests also have an indirect effect on montane ecosystems. Extensive deforestation in lower altitudes (from lowland to TMRFs) not only reduces rainfall locally, due to reduced rain recycling (Pielke et al., 2007), but also result in lower moisture outputs to higher altitudes, which leads to lower fog frequency (Lawton, 1984).

Anthropogenic practices can also affect soil and stream water chemistry (Bücker, Crespo, Frede, & Breuer, 2011), increase surface run-off, and reduce soil water retention capacity, leading to more frequent flood events (Céleri & Feyen, 2008). For instance, expansion of road systems and degraded pastures, croplands, and mining fields in mountain ecosystems can cause slope instability, which increase the frequency of landslides. Landslides cause loss of nutrient and soil horizons, reduced infiltration, and lower water storage capacities (Restrepo et al., 2009). Although increases in run-off associated with anthropogenic activities might enhance water supplies to nearby streams and springs, this effect is only temporary. When rainfall ceases, these streams face reduced flows during dry periods leading to less water availability to flora, fauna, and local populations. Additionally, larger floods alter sediment regimes. Higher rainfall areas such as TMRFs are likely to experience the largest ecohydrological changes associated with anthropogenic activity.

In altitudinal grassland ecosystems, however, land use change, which mainly involves livestock grazing, periodic natural and/or manmade fires, agriculture, reforestation, fish farming, mining, and mineral extraction, have resulted in other drastic types of soil degradation (Luteyn, 2005). Over the last 100 years, these ecosystems have undergone large-scale and often extreme landscape transformations into agricultural lands and human settlements (IUFRO, 2000), which

fragmented and isolated the remnant *páramos*, making them more vulnerable to climatic changes (Buytaert, Sevnik, & Cuesta, 2014). Compaction due to livestock grazing and loss of vegetative cover promotes drying of the soils, which irreversibly reduces their pore space and water-holding capacity (Poulenard, Podwojewski, & Herbillon, 2003). Such disturbances can also cause soils to become crusted and hydrophobic, dramatically reducing their normally high water retention and regulation capacity (Poulenard, Podwojewski, Janeau, & Collinet, 2001). *Campos rupestres* and *campos de altitude* are greatly threatened as well, mainly by natural resource exploitation, especially, mining in the past for gold and diamonds, and more recently for iron (Assis & Mattos, 2016). Reduced soil water retention is likely to increase vulnerability of these ecosystems to climate change.

Although deforestation can be the major culprit for microclimatic changes and ecosystem degradation, the intensification of global warming (i.e., climate change) has shown to exacerbate these effects in montane ecosystems. Climate change scenarios for mountain regions predict an increase in surface temperatures and changes in precipitation regimes, in which extreme events (i.e., drought, fire, frost, and storms) may become more frequent and of greater magnitude (IPCC, 2014). Along with the documented upward migration of plant and animal species, tree mortality in Neotropical forests has increased due to recurring drought events and associated wildfires (Sherman, Martin, Fahey, & Degloria, 2008). Given the low frequency of fire in all but the driest tropical montane ecosystems and poor adaptations to drought in the wetter sites, these ecosystems are particularly vulnerable to more extreme fire and drought-related mortality (Asbjornsen, Velázquez-Rosas, García-Soriano, & Gallardo-Hernández, 2005; Oliveras et al., 2013).

Soil water availability and atmospheric vapour pressure deficit are considered the main environmental drivers that influence plant responses to drought, especially regulating plant gas exchange (Cernusak, Aranda, Marshall, & Winter, 2007). In the case of mountain species, evidence suggests that gas exchange is reduced in response to drought events (Brum et al., 2017; Damour, Simonneau, Cochard, & Urban, 2010; Eller et al., 2015). Montane plants acclimated to less extreme climate conditions are at risk to exceed cavitation thresholds under future drought conditions (Damour et al., 2010; Schuld et al., 2011) and experience irreversible cavitation, which consequently leads to significant reduction in transpiration rates, productivity and, ultimately, mortality (Bonal, Burban, Stahl, Wagner, & Herault, 2016; McDowell et al., 2008).

Furthermore, climatic models indicate substantial reduction in fog frequency in mountain regions. As stated previously, montane vegetation at every altitudinal belt are dependent on fog events to some extent. However, among the mountain ecosystems studied, TCMF might suffer more intensely from the reductions in fog quantity and frequency. The vulnerability of TCMF under climate change scenarios has been predicted by Ponce-Reyes et al. (2012) that estimated a 68% loss of climatically suitable habitat for Mexican cloud forests by 2080, making it one of the most vulnerable ecosystems in the world to short-term climate change impacts. These climatic models also suggest that climate change has brought about a reduction in low-altitude cloud formation in TCMFs (Foster, 2001; Still et al., 1999). Reduced cloud cover not only reduces vegetation composition, but precipitation

and fog frequency are lower and surface evaporation is higher, which results in decreased streamflow (Bruijnzeel & Scatena, 2011).

At the plant level, studies have shown that reduction in fog frequency can lead to plant tissue desiccation, which might ultimately result in mortality and associated lower canopy interception rates and storage capacities (Foster, 2001). Increased plant mortality in these ecosystems will ultimately result in long-term microclimatic changes that will affect the succession rates (due to slower growth rates as altitude increases) and plant composition (e.g., more fast growing plant species, such as grasses, than trees and shrubs; in addition to more adapted invasive species Ammond and Litton (2011)). Potentially cascading effects of such microclimatic changes from less fog and vegetation cover include higher radiation incidence, higher vapour pressure deficits, and higher temperatures (air and leaf), which can intensify the drought condition and, consequently, can further increase plant mortality Malhi and Wright (2004).

Additionally, as climate change leads to temperature increases worldwide and longer recovery times (especially for the tropics; Schwalm et al., 2017), mountain ecosystems are likely to continue “migrating” upwards. This effect could lead to disappearance of some tropical montane ecosystems as they are often located at the top of mountain ranges (Bubb et al., 2004; Still et al., 1999); while also favouring the introduction of highly resource-competitive, invasive plant species that will likely suppress local plant communities (Foster, 2001). The combination of microclimatic changes induced by climate change and land use conversions also increases the susceptibility of these ecosystems to the invasion of exotic plant species, which may use significantly larger amounts of water than their native counterparts (Cavaleri, Ostertag, Cordell, & Sack, 2014), further altering the ecohydrologic processes in these ecosystems.

Altered hydrologic cycles associated with ecosystem degradation in montane systems can also indirectly affect the ecosystem functioning of lower altitude forests, and urban areas that rely on a constant supply of water. Hence, about a more mechanistic understanding of soil–plant–water interactions, these ecosystems is vital to predict and, especially, to mitigate the effects of climate and land use change in Neotropical montane ecosystems and preserve their unique biodiversity and ecosystem services.

## 5 | CONCLUDING REMARKS

We highlight the interactions that operate within the soil–vegetation–atmosphere continuum unique to Neotropical montane ecosystems, whose feedbacks can lead to dramatic effects on the water supply to lower altitudes (soils and streams), prolonged droughts, and an increase in natural disasters, such as landslides and wildfires that ultimately change the biodiversity of these ecosystems. The need is therefore urgent for further study of the existing plant species and how they function individually and as a community, and for experiments to evaluate the ecohydrological and physiological resiliency of these ecosystems (e.g., soil water recharge capability at various elevations affected by plant coverage). In particular, knowing the primary determinants of each plant community structure and function is paramount to predict how these ecosystems will shift under future climate scenarios. Experiments and observations that cover

broad altitudinal gradients, especially those that span plant types, altitudinal gradients, and climates, would greatly improve our understanding of Neotropical montane ecosystems. Such studies would provide the accurate scientific information that is critical for developing better management and conservation strategies to help sustain these tropical montane regions and their valuable ecosystem services.

Finally, it is worth noting that although the ecosystem services provided by mountainous systems worldwide are well recognized, our current inadequate knowledge of these regions is largely because of the difficulty of conducting research in such remote and often inhospitable locations. Although this study contributes to our understanding of how plant and ecosystem functioning is differentiated among the various types of tropical montane ecosystems, more work is needed to fully identify the mechanisms that determine the development of *páramos*, *punas*, *campos rupestres*, and *campos de altitude* vegetation communities and their interface with forested ecosystems at lower altitudes. We especially need to further describe the contribution of fog to plants metabolism and water balance and plant strategies to cope with the climatic conditions in order to preserve them in the future. Such knowledge is essential to develop models that can help predict how global change drivers will ultimately affect the ecohydro-physiological functioning in these important ecosystems.

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## SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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