



# New land in the Neotropics: a review of biotic community, ecosystem, and landscape transformations in the face of climate and glacier change

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## Abstract

The high tropical Andes are rapidly changing due to climate change, leading to strong biotic community, ecosystem, and landscape transformations. While a wealth of glacier, water resource, and ecosystem-related research exists, an integrated perspective on the drivers and processes of glacier, landscape, and biota dynamics is currently missing. Here, we address this gap by presenting an interdisciplinary review that analyzes past, current, and potential future evidence on climate and glacier driven changes in landscape, ecosystem and biota at different spatial scales. We first review documented glacier changes and landscape evolution over past decades to millennia and analyze projected future glacier shrinkage until 2100 for two case studies in the tropical Andes. The effects of climate and glacier change on high Andean biota are then examined from paleoecological research and comparative gradient analyses to chronosequence and diachronic studies of vegetation dynamics. Our analysis indicates major twenty-first century landscape transformations with important socioecological implications which can be grouped into (i) formation of new lakes and drying of existing lakes as glaciers recede, (ii) alteration of hydrological dynamics in glacier-fed streams and high Andean wetlands, resulting in community composition changes, (iii) upward shifts of species and formation of new communities in deglaciated forefronts, (iv) potential loss of wetland ecosystems, and (v) eventual loss of alpine

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biota. We advocate strengthening an interdisciplinary research agenda with a strong policy formulation link that enables enhanced cross-sectorial cooperation and knowledge sharing, capacity building of relevant stakeholders, and a more active participation of both government agencies and social organizations.

**Keywords** Tropical mountains · Deglaciation · Colonization · High-Andean wetlands · Primary succession · Vegetation dynamics

## Introduction

Driven by climate change, the mountain cryosphere is rapidly changing. The massive decline of mountain glaciers in the last decades is well documented worldwide (Vaughan et al. 2013; Zemp et al. 2015), and an increasing amount of studies have also modeled future glacier changes at global (Radić and Hock 2011) and regional scales (Salzmann et al. 2012; Clarke et al. 2015; Kraaijenbrink et al. 2017). Concomitant with glacial recession, high-mountain landscapes are changing through (i) the formation and growth of new lakes and wetlands, and (ii) fragmentation and desiccation of former lakes due to seasonal disconnection from glacier-fed streams (Gardelle et al. 2011; Linsbauer et al. 2016; Drenkhan et al. 2018). Glacial recession is also triggering colonization processes in the new deglaciated areas (Seimon et al. 2017; Zimmer et al. 2018) that together with warming and changing precipitation patterns due to climate change (Buytaert et al. 2011) are modifying species geographic ranges and biota composition (Seimon et al. 2017; Lamprecht et al. 2018). This is the case of the tropical Andes, a mountain range that has been identified as a global hotspot region of cryosphere change (Vuille et al. 2018), landscape transformation (Dangles et al. 2017), and enhanced vulnerability of both population (Mark 2008; Bury et al. 2011; Vuille et al. 2018) and alpine biota (Tovar et al. 2013; Ramirez-Villegas et al. 2014) to climate change. Deviation from mean annual temperatures in the tropical Andes above 3000 m above sea level (asl, from here onwards) in the last 30 years of the twentieth century has increased at a rate of approximately  $0.04\text{ }^{\circ}\text{C year}^{-1}$  (Vuille et al. 2003).

The tropical high Andean ecosystems are ideal to study the effects of climate and glacier change on the biota because 99% of all tropical glaciers are located in the Andes (Kaser 1999), strong human land-use change is absent in these highlands, and many species are close to the edge of their bioclimatic limits (Dangles et al. 2017). Extending from  $11^{\circ}\text{ N}$  to  $27^{\circ}\text{ S}$ , the high tropical Andes ( $> 3000\text{ m asl}$ ) are the longest and widest mountain region in the tropics (Fjeldså and Krabbe 1990; Clapperton and Clapperton 1993). The tropical section of the Andes spans along 4500 km in a north-south direction with a prominent precipitation and temperature gradient (Josse et al. 2011). The northern section (Venezuela, Colombia, Ecuador) experience a non-seasonal humid climate with short dry periods and well-distributed rainfall throughout the year

(Buytaert et al. 2006). In addition, glaciers are generally smaller in this region than in the south, and alpine ecosystems called páramos can provide for additional water storage, as their soils have a remarkable water retention capacity (Buytaert et al. 2011; Harden et al. 2013). The central Andean highlands, called punas (Perú, Bolivia), are characterized by a noticeable seasonal climate with a pronounced cold and dry season that spans from June to September (Rundel and Palma 2000). Annual rainfall varies from 500 to 1000 mm decreasing from east to west and north to south. Additionally, mountain glaciers in the central Andes are much larger than their northern counterparts and act as a buffer against prolonged dry seasons providing water for ecosystem processes and human uses (Vuille et al. 2008b).

Although past (paleo) glacier fluctuations and contemporary glacier recession are well studied across the tropical Andes (Jomelli et al. 2009; Rabatel et al. 2013), landscape and ecosystem change due to past and future glacier dynamics have been explored only recently. The emergence of new lakes and wetlands (Réveillet et al. 2015; Colonia et al. 2017; Schauwecker et al. 2017; Drenkhan et al. 2018), species range displacement, and colonization of deglaciated areas (Morueta-Holme et al. 2015; Moret et al. 2016), as well as ecosystem vegetation shifts and formation of new communities (Seimon et al. 2007; Seimon et al. 2017), are associated with glacier dynamics in the tropical Andes. However, there is limited empirical data and only a few studies address and interrelate the involved drivers and processes, which limits our understanding of glacier and biota dynamics.

Besides being recognized as a biodiversity hotspot (i.e., a region with high endemism and highly threatened species, sensu Myers et al. (2000); Mittermeier et al. (2011)), the tropical Andes provide key ecosystem services. Both local inhabitants and those living in downstream areas with large and growing urban populations benefit from these services (Buytaert and De Bièvre 2012; Buytaert et al. 2017; Kinouchi et al. 2019). These include water provision for domestic use, agricultural production and hydropower generation, carbon accumulation in soils and biomass, flood risk control, and recreational/cultural values to native populations (Bradley et al. 2006; Carey et al. 2017). In view of the critical role Andean ecosystems play for ecosystem service provision and the preservation of their singular biodiversity, an analytical framework that integrates cryosphere, ecosystem, and landscape transformations is highly needed.

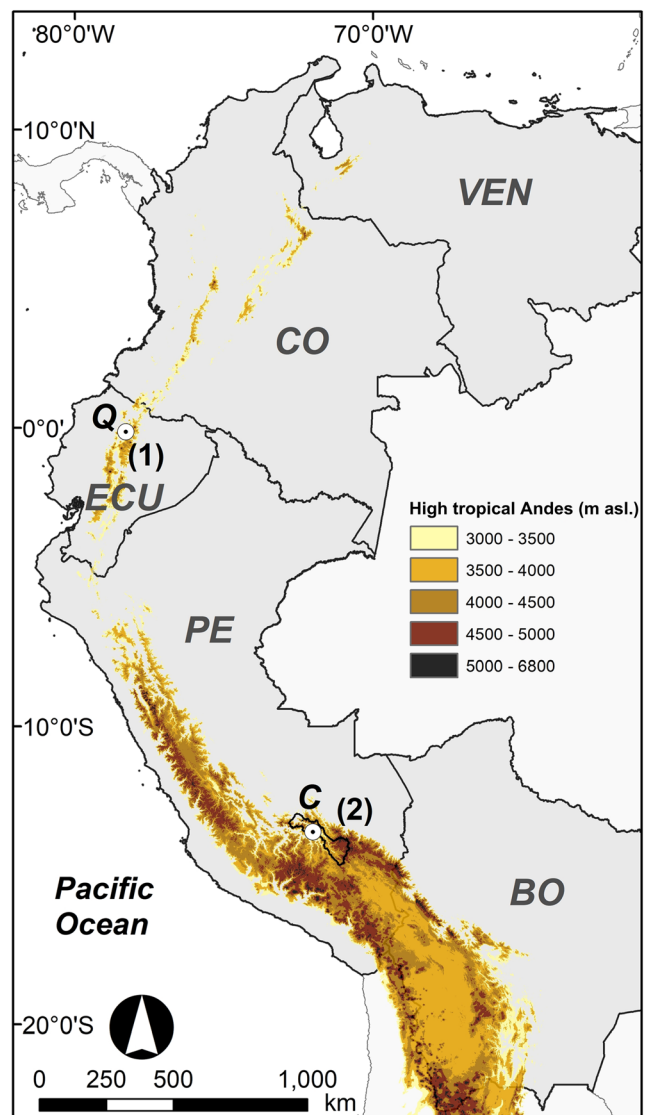
Our aim in this review is to contribute towards the development of such a framework by understanding how glacier change has interacted with biota and ecosystem changes. We adopt an interdisciplinary perspective, relating past, current and projected climate, glacier and hydrological change to transforming landscape elements (e.g., high Andean lake and wetland systems), and changes in biota composition and their spatial distribution. First, we review glacier change in the tropical Andes over a time scale of the past decades to millennia, to understand long-term landscape evolution, and then focus on potential future changes. The effect of climate and glacier change on high Andean biota is then reviewed through the lens of paleo-ecological, diachronic, and synchronic approaches, in order to develop a more integrated perspective. We complement this review by looking at two case studies in the humid inner-tropical northern Andes (Antisana volcano, 0.48° S; Fig. 1) and the seasonally dry outer-tropical central Andes (Vilcanota Cordillera, 13.77° S; Fig. 1). Additionally, the potential of initiatives, such as the GLORIA-Andes comparative network (Global Observation Research Initiative in Alpine Environments), is discussed, in order to consolidate a more integrated long-term perspective.

## Climate change impact on tropical Andean glaciers

### Climate change impact during the Quaternary

Through the Quaternary (~the last 2.5 Ma), the waxing and waning of glaciers, and the concomitant landscape change in the high Andes, has been traced by using ice core records (Thompson et al. 2005; Thompson et al. 2013) and sedimentary deposits (Baker et al. 2001; Hooghiemstra and van der Hammen 2004). Andean glacier fluctuations over the Pleistocene (~2.5 Ma–11,700 years B.P.) were coincident with the onset of global glacial-interglacial cycles, with major Andean glacial advances occurring parallel to globally cooler glacial periods. Since the global Last Glacial Maximum (LGM, c. 21,000 years B.P., Hughes and Gibbard (2015)), a more detailed understanding of changes in the tropical Andean glaciers is possible due to greater abundance of preserved features and records (Abbott et al. 2003; Valencia et al. 2018).

For example, since the maximum glacier extent during the Little Ice Age (LIA) that occurred between the mid-17th and early 18th centuries, glaciers have consistently retreated over the region. However, the exact timing of the maximum LIA glacier extent during this period depends on the mountain range, and it is only known for a limited number of well-studied locations in Bolivia (Rabatel et al. 2008; Jomelli et al. 2011), Peru (Solomina et al. 2007; Emmer 2017), Ecuador (Jomelli et al. 2009; Heine 2011), and Colombia (Ceballos et al. 2008). Research indicates that the maximum



**Fig. 1** Overview of the study region between Venezuela (VEN), Colombia (CO), Ecuador (ECU), Peru (PE) and Bolivia (BO) with a SRTM DEM overlay of the high tropical Andes (3000–6800 m asl). Indicated are the two case study areas: (1) Antisana volcano (Ecuador) southeast of Quito (Q) and (2) Cordillera Vilcanota (Vilcanota-Urubamba basis, Peru – black outline) southeast of Cusco (C)

LIA glacier extent was reached earlier in the outer tropics (Bolivia and Peru), around the mid-seventeenth century, and later in the inner tropics (Ecuador, Colombia, Venezuela), in the early eighteenth century (Jomelli et al. 2009). Paleoclimatic studies based on dating of glacier extents and simple climate-glacier models indicate that LIA temperatures were 1–2 °C cooler than present, and up to 3 °C cooler during the Holocene, depending on the region (Jomelli et al. 2011).

### Climate change impact during the last century

Glaciers in the tropical Andes are sensitive indicators, and unique visible signs, of the effects of contemporary climate

change in the region (Haerberli et al. 2007; Magrin et al. 2014). Temperatures along the western slopes of the tropical Andes have increased since the 1960s at a rate of 0.1–0.2 °C per decade, while coastal regions showed reduced warming or cooling over the past three decades (Vuille et al. 2015). Although precipitation trends are more uncertain, an increasing trend in the inner tropics and a possible decrease of precipitation in the outer and subtropical region have been described for the 1950–1994 period (Vuille et al. 2003).

Instrumental glacier observations started in the early and mid-twentieth century at some selected locations in the tropical Andes, and have continuously expanded over the past decades (Francou et al. 2000). The advent of satellite remote sensing has improved the temporal resolution and geographic coverage of the observations. The late 1970s, the mid-1990s, and the early 2000s were marked by strong glacier shrinkage phases. Since the 1970s, glaciers in the tropical Andes have lost 20 to 50% of their area (locally even more), and some have completely disappeared (Rabatel et al. 2012; Braun and Bezada 2013; Salzmann et al. 2013; Schauwecker et al. 2014; Morán-Tejeda et al. 2018). During the same period, glacier mass balances have been consistently negative, ranging from around –0.5 to –1.5 m annual water equivalent on average (Rabatel et al. 2013; Vuille et al. 2018). As such, glacier shrinkage in the tropical Andes has been more pronounced than the global average, and is consistently and robustly related to increasing temperatures (Vuille et al. 2018) and a high sensitivity to changes in air humidity (Kaser 1999).

Parallel to glacier shrinkage, new lakes have formed and existing ones have grown (see case study sections). For example, in the Vilcanota-Urubamba basin (VUB) in Peru, lakes have expanded by 16% in area and by 18% in number (84 new lakes) over the past 28 years (Drenkhan et al. 2018).

### Future climate change projections

Projections of future glacier shrinkage are relatively scarce for the tropical Andes. Some studies have used simple trend extrapolations of glacier area loss rates (Peduzzi et al. 2010). Others have applied projections of future glacier equilibrium line altitudes (ELA) and glacier thickness assessments to estimate the pace and timing of glacier extinction. In general, it is thought that glaciers below 5400 m asl and small in extent are likely to disappear in the coming decades (Rabatel et al. 2013; Rabatel et al. 2018). Freezing level heights derived from Coupled Model Intercomparison Project 5 (CMIP5) climate models illustrate the important difference of the impact of low and high greenhouse gas emission scenarios on future glacier extents in the Cordillera Blanca and Vilcanota in northern and southern Peru, respectively (Schauwecker et al. 2017). For instance, a low-emission scenario (RCP 2.6) would translate in a loss of ca. 50% of glacier extent by the end of the twenty-first century as compared to current values, and an almost

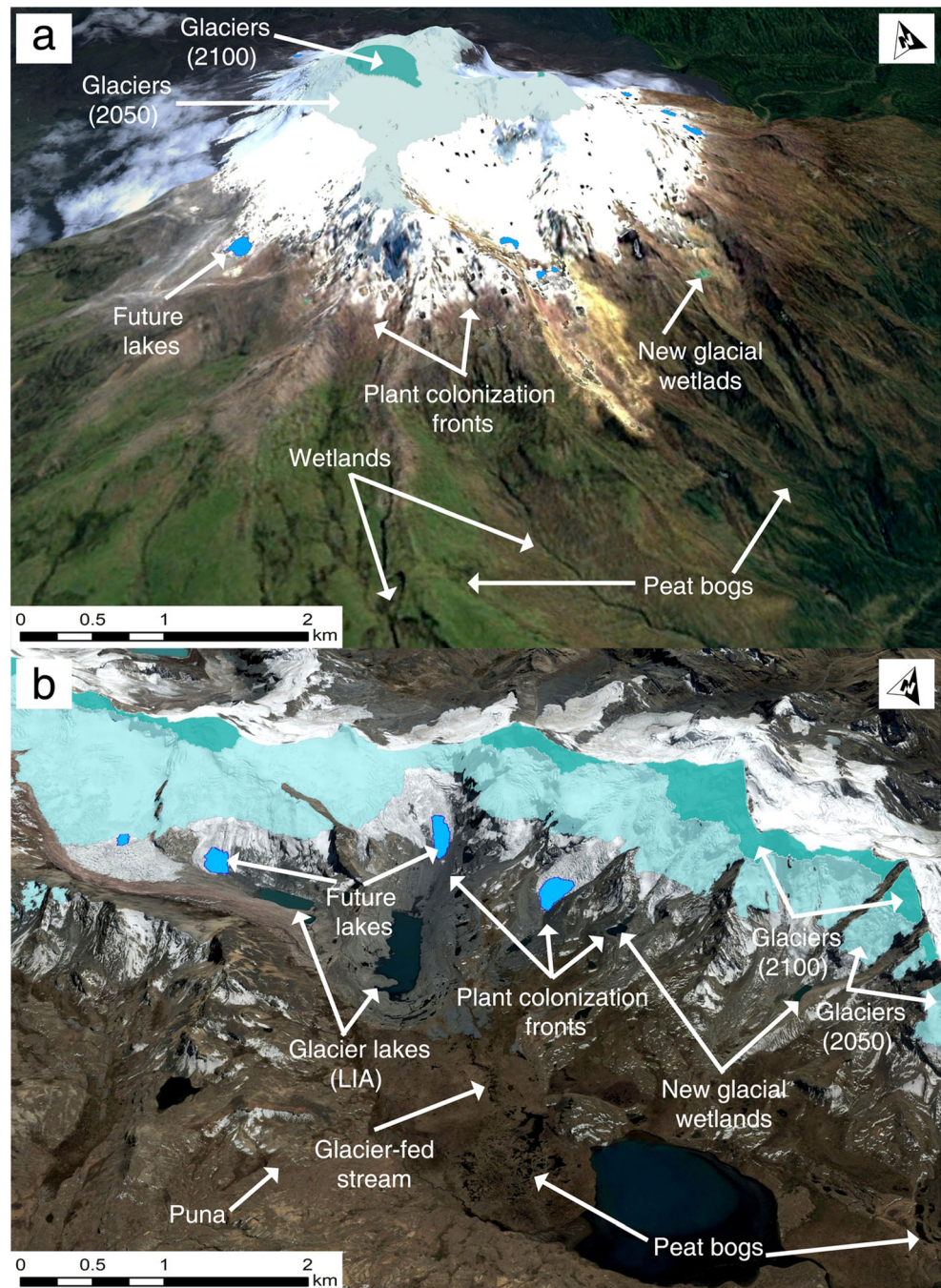
complete loss of glaciers in case of a high-emission scenario (RCP 8.5), associated with a 1–2 °C and a 5–6 °C temperature increase, respectively, above the 1976–2005 period (Schauwecker et al. 2017). Similar conclusions were reached when analyzing the potential future ELA rise for glaciers in Bolivia, Peru, and Ecuador, showing that glaciers in the inner tropics are likely to be most affected due to smaller size and lower maximum elevation (Vuille et al. 2018). Application of more sophisticated, physically based glacier models is particularly rare but available for Zongo glacier in Bolivia, indicating a projected volume loss of 40 and 89% for RCP 2.6 and RCP 8.5, respectively, by the end of the century as compared to 2000 (Réveillet et al. 2015). Frans et al. (2015) projected an ice loss of 81% for the same glacier by the end of the century, implying a dry season discharge reduction of 57%.

The decisive role of future emission pathways on the twenty-first century glacier extent could also extend to ecosystem and landscape transformations, particularly in the seasonal dry parts of the Andes (Peru and Bolivia). For instance, high-elevation wetland ecosystems critically depend on water from glacier melt during the dry season, and are expected to degrade once disconnected from water resources as glaciers vanish (see section “Integration of glacier, landscape and biotic community dynamics”).

### Case study 1: past, present, and future glacier and lake changes of Antisana (Ecuador) and Vilcanota (Peru)

Antisana (5760 m asl), located 40 km east of Ecuador’s capital, Quito, is a volcano covered by glaciers (~16 km<sup>2</sup>) extending down to about 4800 m asl (Fig. 1, Fig. 2a) (Rabatel et al. 2012). The landscapes surrounding the volcano have been shaped by both multiple nearby eruptions of neighboring volcanos, particularly between 4000 and 200 years B.P. (Hall et al. 2008; Mothes and Hall 2008), and by the last glacial period that carved deep valleys, resulting in a myriad of lakes and extensive wetlands, intermingled on a complex topography (Schubert and Clapperton 1990; Jomelli et al. 2009). Scarce vegetation cover near the snow line (>4600 m asl) on glacial moraines, and on rocky and sandy slopes, alternates with wind-dispersed species of the Asteraceae family growing in less exposed crevices and rock fissures (Sklenář et al. 2016). There is no distinct dry period, although about 70% of the annual precipitation falls between February to June, and September to November, with a total amount of 700 to 1300 mm/year along an altitudinal gradient of 3930 to 4850 m asl (Manciati et al. 2014). Antisana is also strongly affected by inter-annual climate variation related to El Niño Southern Oscillation (ENSO), with negative glacier mass balance trends during El Niño (Vuille et al. 2008a). Between 1979 and 2007, glaciers on Antisana lost 33% of their surface area, with an increased rate of loss since the early 1990s

**Fig. 2** Glacier, lake, and landscape features including potential future glacier extent (RCP 8.5 scenario, for 2050 (2031–2060) colored in cyan, for 2100 (2071–2100) colored in turquoise) and lake areas (blue polygons) for **(a)** Antisana glacier (0.48° S, 78.14° W, 5704 m asl) and **(b)** Cordillera Vilcanota (clip, 13.79° S, 71.00° W, 6384 m asl)



(Rabatel et al. 2012). The páramos and wetlands surrounding the Antisana volcano are part of an important protected area for both ecosystem conservation and services, supplying around one third of Quito’s drinking water (Vergara et al. 2009).

The Cordillera Vilcanota (CV) is located in southern Peru, some 100 km southeast of the city of Cusco and rising up to 6384 m asl (Fig. 1, Fig. 2b). With about 240 km<sup>2</sup>, it covers the second largest tropical glacier area worldwide. Climatically, the CV forms part of the outer tropics at the northwestern part of the Altiplano region, which is characterized by a distinct

dry season (May to September) and a wet season (October to April), when moisture from the Amazon basin and convective storms can generate substantial precipitation (Garreaud et al. 2003). Interannually, ENSO exerts an important role on precipitation and temperature and thus on glacier mass balance (Vuille et al. 2008a; Perry et al. 2017). Being a remote and relatively pristine region, CV represents a primary site for observation of bio-physically changing environments.

Glacier fluctuations and recession over the past millennia gave rise to landscape and ecosystem evolution. For instance, in the northwestern Ausangate area of the CV, glaciers

between 41,500 and 16,600 years B.P. reached about 8 km further downstream than modern glacier extents (Mark et al. 2002). Around 1600, probably a LIA maximum, glaciers still extended around 2 km further downstream from the modern ice limit. Ice cores collected from the Quelccaya Ice Cap indicate that the recent warming in the region is unprecedented in the last several thousand years (Thompson et al. 2006). In modern periods, the glaciers of the CV lost 48% of their extent since the 1960s (Drenkhan et al. 2018; INAIGEM 2018).

Glacier shrinkage, formation of new lakes, landscapes, and ecosystems on Antisana and in the CV will continue in the future, but the magnitude of landscape transformation and ecosystem affection will depend on the level of anthropogenic emissions. The wet season freezing line has been found to be a reasonable indicator for the lower altitude limit of tropical glaciers (Schauwecker et al. 2017). For Antisana, based on a present freezing line at 5100 m asl (Basantes-Serrano et al. 2016), CMIP5 climate models reveal a potential glacier area loss of 72% and 98% for RCP 2.6 and RCP 8.5, respectively (Fig. 2a, Table S1a). For the CV, multi-ensemble CMIP5 models indicate a median increase of the freezing line in the wet season of 230 m and 850 m for the RCP 2.6 and RCP 8.5 emission scenarios, respectively (Schauwecker et al. 2017). This translates into a glacier area reduction of 60% and 97% for RCP 2.6 and RCP 8.5, respectively, by the end of the century as compared to present values (Fig. 2b, Table S1b; Drenkhan et al. (2018)). Therefore, an important conclusion is that the high-emission scenarios imply a virtually complete loss of glaciers while low-emission pathways could preserve a substantial amount of glacier ice within this century.

As glaciers further recede in the future, new lakes can form in the next decades. Potential lake formation sites can be simulated using empirical parameterization models, calculating glacier ice thickness based on geometric characteristics and glacier flow considerations, and thus the location of topographic depressions at the glacier bed (Linsbauer et al. 2012; Colonia et al. 2017). For Antisana, a total of 10 lakes could develop under both the RCP 2.6 and RCP 8.5 scenarios until 2050, with a total area (volume) of 0.1 km<sup>2</sup> (3.5 Mm<sup>3</sup>; Fig. 3a). For the VUB, 14 (RCP 2.6) to 16 (RCP 8.5) lakes could develop until 2050 and 14 (RCP 2.6) to 20 (RCP 8.5) lakes until 2100 (Drenkhan et al. 2018), with total area (volume) of 0.9 km<sup>2</sup> (32.4 Mm<sup>3</sup>) for RCP 2.6 and 1.6 km<sup>2</sup> (41.4 Mm<sup>3</sup>) for RCP 8.5 until the end of the century (Fig. 3b).

These new lakes, fed by glacial meltwater, form new landscapes, represent new aquatic environments, and may become relevant for downstream ecosystems and human populations as glaciers further retreat. Glacier contribution to river streamflow (for VUB in headwaters of the dry season currently ~25%) is expected to be substantially reduced within the next decades and be negligible until the end of this century (~0–3% for VUB; Drenkhan et al. (2019)).

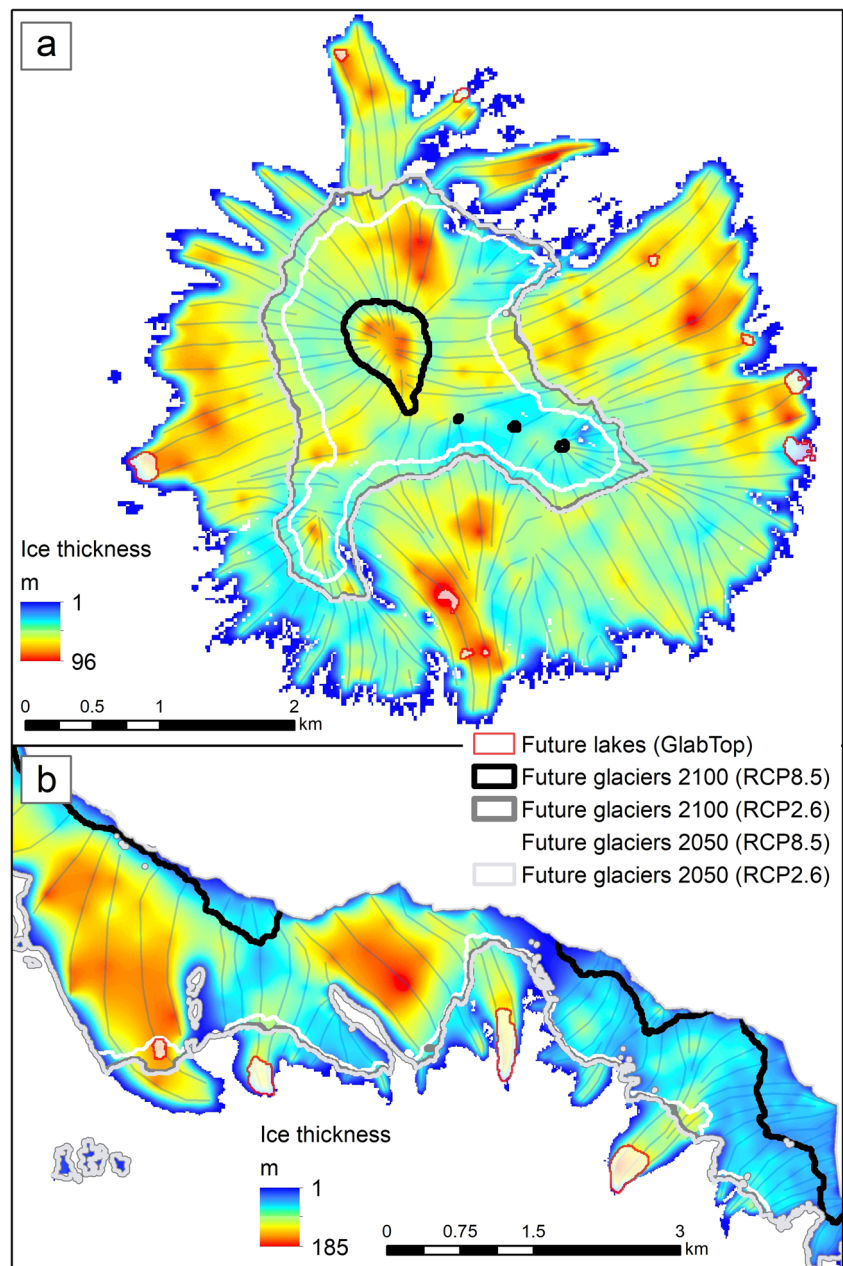
New lakes could act as potential dry season buffers for dwindling water resources, freshwater biota (Cauvy-Fraunié et al. 2015), and carbon stocks and fluxes (Hribljan et al. 2016). Additionally, ecological studies have documented vegetation shifts and species range expansions (e.g., for anuran species in the CV, Seimon et al. 2017, see section 3). However, the new lakes will not replace the water resources lost by vanishing glaciers. Furthermore, in combination with over-steepened ice, rocks and moraines, permafrost degradation, and de-buttressed slopes that can produce landslides into the lakes, downstream populations may be threatened by devastating outburst floods from these lakes (Colonia et al. 2017; Haerberli et al. 2017). In conclusion, our case studies suggest that landscapes and high Andean ecosystems will be strongly transformed with likely range shifts but also risk of extinction, as a result of twenty-first century glacier shrinkage, and hence emission pathways.

### Climate change and glacier dynamics effects on highland communities, ecosystems, and landscapes

Analyzing successional dynamics is key for interpreting the effects of global change on landscapes, ecosystems, and alpine biotas (Zimmer et al. 2018). Landscape transformation and ecosystem modifications in alpine regions can result from changes induced by (i) new environmental conditions as a result of volcanic activity or glacier retreat (primary succession); (ii) disturbances linked with mass movements or land-use change (secondary succession); and (iii) short-term climatic variability and long-term climate change (Gray et al. 1987; Walker and del Moral 2003). These changes involve different underlying mechanisms and can interact in complex ways.

Several approaches have been used to analyze landscape transformations and ecosystem change in the high tropical Andes. Paleoecological studies provide a long-term perspective, particularly on climate-vegetation links after the LGM (e.g., van der Hammen and Cleef (1986); Flantua and Hooghiemstra (2018a)). A second approach compares sites that represent different stages in the process of ecosystem development (i.e., synchronic approach or space-for-time substitution). These studies compare communities along elevation gradients (e.g., Sklenář and Balslev (2005); Suárez et al. (2015)) or use explicit chronosequences, when dates after disturbance or glacier retreat are known for different locations (Sarmiento et al. 2003; Sklenář et al. 2010; Zimmer et al. 2018). A third, less common alternative, uses multi-temporal analyses of remote images or repeated surveys of the same sites (diachronic approach), when long-term information is available (e.g., (Morueta-Holme et al. 2015; Moret et al. 2016; Dangles et al. 2017; Seimon et al. 2017)).

**Fig. 3** Ice thickness distribution and bedrock overdeepenings with potential sites for developing lakes (white polygons with red outlines) modeled with GlabTop for (a) Antisana glacier (0.48° S, 78.14° W, 5704 m asl) and (b) Cordillera Vilcanota (clip, 13.79° S, 71.00° W, 6384 m asl). Current (2016, 2017) glacier extent was computed with the Normalized Difference Snow Index (NDSI) using Sentinel-2 imagery. Future (2050/2100) glacier outline scenarios (RCP 2.6 in gray colors, RCP 8.5 in white and black) are estimated with a Freezing Level Height (FLH) approach following Schauwecker et al. 2017. For more details on the methods used here see, e.g., Drenkhan et al. 2018; Linsbauer et al. 2012; Schauwecker et al., 2017. *Note: ice thickness distribution is represented by a relative color scheme with e.g. red color representing larger depth values for Cordillera Vilcanota*



## Paleoecological studies

High-Andean landscapes underwent a series of transformation related to global glacial-interglacial cycles (van der Hammen and Cleef 1986; Felde et al. 2016). During colder global glacial periods, air temperature in the Andes was as much as 6–7 °C lower than modern (Van Der Hammen 1974; Bush et al. 2004; Cárdenas et al. 2011) and precipitation regimes varied greatly (Mosblech et al. 2012). During the LGM, the treeline descended between 1200 and 1500 m with the associated expansion of the alpine zone (Van Der Hammen 1974; Hooghiemstra and Cleef 1995; Moscol Olivera and Hooghiemstra 2010). Vegetation in plant communities occurred

together with the glacier expansion-retreat (van der Hammen and Cleef 1986; Hooghiemstra and Cleef 1995). Species range expansion-contraction on an individual level resulted in the formation-dissolution of different plant communities through time; this process of recombination over the last c. 21,000 years ultimately produced the present-day communities (Nolan et al. 2018).

The glacial-interglacial cycles likely produced a high frequency of Andean speciation events (Rangel et al. 2018), which have been linked to changes in alpine extent (Madrinán et al. 2013; Flantua et al. 2014). During glacial periods, the area occupied by alpine vegetation expanded and many of the now “isolated páramo islands” became

functionally connected (Hooghiemstra et al. 2006; Flantua and Hooghiemstra 2018b) allowing a rapid diversification from the local Neotropical alpine flora (Cleef 1979; von Hagen and Kadereit 2001; Bell and Donoghue 2005; Hughes and Eastwood 2006). These adaptive radiation events indicate the capacity of alpine plant species to colonize and adapt to the areas exposed after the contraction of glaciers. Thus, we hypothesize that above 4600 m asl, present-day high-Andean plant communities' composition is the result of the last 10,000 years of plant interactions along with environmental filtering. Today, high tropical alpine floras are dominated by a diverse array of genera from different biogeographic origins with a prevalence of puna and páramo endemics, tropical Andean alpine, and tropical montane species, which may be a reflection of the landscape dynamics and rapid diversification (Sklenář et al. 2011; Cuesta et al. [under review](#)).

Since the LGM, landscape formation and ecosystem development in the Andes varied latitudinally depending on the regional climate and glacial dynamics (Bush and Gosling 2012). Regional variation can be illustrated through case studies from a latitudinal gradient in the Andes. In Bolivia, around 18,000 years ago, a lake formed at Khomer Kotcha (4153 m asl, 17° 61.514' S; Williams et al. (2011)). Immediately post-formation, the fossil pollen record indicates the presences of *Polylepis* woodland in the area, albeit in low abundance, suggesting that these trees were able to persist locally during glacial expansion allowing for rapid post-glacial colonization. In Peru, at Laguna Chochos (3285 m asl, 7° 38.175' S), the inception of the lake indicates glacier shrinkage commenced 17,000 years ago (Bush et al. 2005). Initially, local vegetation abundance was low (low pollen concentrations) with grasses and *Dryopteris* appearing early in the local signal (after 14,400 years ago); the arrival of woodland elements in the region proceeded gradually until c. 6100 years ago, when *Polylepis* likely established locally. In Colombia at Laguna La Cocha (2780 m asl; 1° 6' N), the first sediments were deposited c. 14,000 years ago; the initial vegetation was dominated by Poaceae and Asteraceae and gradually shifted towards a woodier component over the next 2000 years (González-Carranza et al. 2012). On shorter timescales, in the Ecuadorian Andes (0° 7' N), Villota et al. (2017) reported that páramo grassland vegetation has been the main vegetation type at 3748 m asl in the last ca. 3400 years, implying that during the last three millennia, cool, and moist conditions prevailed.

### Comparative gradient analyses

Changes in vegetation structure along environmental gradients can be analyzed in terms of (a) *alpha* diversity, corresponding to species richness and composition and patterns of relative abundance *within* a given community; and (b) *beta*-diversity, which refers to changes in species composition and abundance *between* communities along environmental

gradients in a landscape (Huston 1994; Colwell 2009). The available studies of vegetation change along elevation gradients in the high Andes indicate a general decrease in *alpha* diversity of vascular plants and an increase in community turnover (i.e., *beta*-diversity) with higher elevation, which could be the combined effect of limiting abiotic conditions and recent community development since glacier retreat (Cleef 1981; Sklenář and Ramsay 2001; Sklenář and Balslev 2005; Cuesta et al. 2017). Ongoing glacier retreat combined with increased climate warming are forcing species upward migration, and are already modifying species *alpha* diversity and plant community composition along environmental gradients in the high-Andes (Seimon et al. 2017; Carilla et al. 2018). The establishment of plants seems to depend more on finding local favorable conditions associated with rocky outcrops at the highest periglacial habitat than in lower elevations (Suárez et al. 2015). Facilitation mechanisms provided by nurse-plants (i.e., cushion plants, shrubs), which can modify local conditions and provide more favorable habitat for plant colonization and establishment, also increase towards the highest periglacial areas (Anthelme et al. 2012; Cáceres et al. 2015; Anthelme et al. 2017; Hupp et al. 2017).

Further, diversity patterns in wetland ecosystems in the Bolivian Andes indicate a decrease in plant community *beta*-diversity towards higher elevations (Loza Herrera et al. 2015). Yet, in primary succession due to volcanic eruptions, zonal plant communities show the opposite trend, where *beta*-diversity and vegetation patchiness is higher towards the top of the gradient (Sklenář 2006; Suárez et al. 2015).

Comparative analyses of glacier-fed river systems in the Ecuadorian Andes have also found a decrease with elevation in the species richness of aquatic macroinvertebrates, which play a key role in organic matter decomposition and as food sources for vertebrates (Jacobsen et al. 2012; Cauvy-Fraunié et al. 2014). However, these studies found a hump-shaped relationship between richness and the percent of glacier cover/glacial flood intensity in the studied catchments (GCC). Results suggest that a complete disappearance of glaciers from catchments would result in the reduction of the local and regional diversity of macroinvertebrates, particularly because of the loss of specialists adapted to the harsh conditions of glacier-fed streams (e.g., low channel stability and temperatures, high turbidity). Further support for these conclusions has been derived from a careful experimental study in which glacier outflows were diverted, and the dynamics of the aquatic invertebrate communities monitored for four consecutive years (Cauvy-Fraunié et al. 2016).

### Synchronic chonosequence studies of vegetation dynamics

Long-fallow agriculture for the production of crops such as potatoes and cereals has been extensively practiced for



centuries in the alpine habitats of the tropical Andes, integrating agricultural technologies developed by native populations with those introduced by Europeans after the conquest (Sarmiento et al. 1993; Pestalozzi 2000). Long-fallow systems have provided a unique opportunity to study soil and vegetation regeneration during the fallow using a chronosequence approach (Sarmiento et al. 2003; Ortuño et al. 2006; Bueno et al. 2015). These studies report relatively fast vegetation regeneration rates after land abandonment (with estimates of 30 years for attaining a community structure similar to the reference ecosystem), except in semi-arid areas subjected to centuries of degradation by wheat cultivation (Sarmiento et al. 2003; Sarmiento et al. 2015). However, explicit chronosequence analyses of primary succession in glacier forefronts or after volcanic eruptions are scarce.

Zimmer et al. (2018) studied four glacier chronosequences in Bolivia and Peru above 4700 m asl spanning five dates in each site from 1975 to 2013. A consistent increase in plant richness, cover, and abundance was observed along the four chronosequences in the direction of the oldest date (1975). Wind-dispersed plants (e.g. Poaceae, Asteraceae) were over-represented at the study sites when compared to the regional flora, while plants dispersed by animals represented only 0–5% of the recorded species but with higher dispersal distances (Melcher et al. 2000). There was a clear shift in abundance from ruderal to stress-tolerant species from the youngest site (2013) towards the oldest site, which can be related with a low abundance of nurse plants during the earliest successional stages of the chronosequence. Yet, Zimmer et al. (2018) also reported that positive spatial associations of colonizing plants with superficial rocks (see also Suárez et al. (2015) and biological soil crusts were more frequent than associations with cushion and forb nurses. Hence, both dispersal limitation and a low effectiveness of nurse plants suggest that many species affected by rapid current climate change could face barriers for upward migration (i.e., migration time-lag) into recently deglaciated areas. Moreover, we hypothesize that the unprecedented warming rate in the high tropical Andes may exacerbate the dispersal filter, with new plant communities being even more dominated by anemochorous species than what has been observed along longer post-glacial chronosequences.

The other chronosequence study on glacial primary succession involves the establishment of two transects with unreplicated permanent plots between 4651 and 4725 m asl (i.e., 30 to less than 7 years) in the Santa Isabel volcano, Colombia (Cuellar 2017). Results from the baseline data indicate a successional increase in species richness and cover for lichens, mosses, and vascular plants; the latter being almost exclusively represented by wind-dispersed grasses and herbs (Poaceae and Asteraceae). The only species present in the highest plots (11 or less years of succession) were the grasses *Calamagrostis recta* and *Poa pauciflora*, which colonized these plots even before non-vascular plants.

Sklenář et al. (2010) reconstructed primary succession on the lower limit of the superpáramo (c. 3800 m asl) in lahars of the Cotopaxi volcano, Ecuador (with 130, 250, and 475 years of age). Successional dynamics also showed an increase of species richness towards the oldest lahar, although *alpha* diversity peaked at intermediate stages. Fruticose lichens were dominant on the youngest lahar, whereas foliose lichens and bryophytes peaked at intermediate stages. Finally, cushions plants, prostrate herbs, and subshrubs dominated in the oldest site. While no biological soil crusts were observed, many of the lichen species present during early-intermediate stages had N-fixing photobionts. This indicates they could play an important facilitation role, as have been observed in other volcanic primary successions, in which nitrogen usually limits productivity (Walker and del Moral 2003).

The interactions of limited nutrients and soil development require further investigation, given the extremely limited information on the processes of soil development during primary succession in the high tropical Andes. Zimmer et al. (2018) documented an increase in fine soil fractions along their studied chronosequences; yet, other key elements of ecosystem dynamics such as soil organic matter and nutrient accumulation remain to be explored. Nonetheless, based on the evidence of very low rates of soil development that characterize glacial chronosequences in other regions (e.g., He and Tang (2008); Bárcena et al. (2011); D'Amico et al. (2014)), we would expect this to be a key factor limiting the speed of vegetation colonization in tropical glacier forefronts.

Despite the limited numbers of available chronosequence studies, their findings are of outmost importance, as they could indicate future trajectories of plant community dynamics in glacier forefronts at high elevations. However, Young et al. (2017) argues that even though in the Cordillera Blanca, ecological succession is occurring on surfaces exposed by glacier recession, plant colonization is heterogeneous and subject to different biophysical constraints than glacier loss. Hence, rates of soil development or slope instability might limit upward expansion in cases of primary succession. Further, plant colonization is likely to be confronted with feedbacks from land-use dynamics that will certainly affect ecological succession, as livestock can potentially graze near the highest peaks.

### Case study 2: long-term observation of vegetation dynamics in high-Andean summits

The Global Observation Research Initiative in Alpine Environments (GLORIA) is a network for long-term biodiversity monitoring. The GLORIA-Andes, established in 2008, is the longest alpine monitoring transect across the Neotropics (4200 km), comprising 19 target zones and 75 mountain summits from Patagonia to Venezuela. It studies long-term changes in plant communities associated to soil temperature and

substrate cover patterns (Table 1). Over 1200 species of vascular and non-vascular plants have been recorded across 50 of these summits (Cuesta et al. 2017). Twelve of these summits reach elevations between 4600 and 5498 m asl, offering a unique opportunity to analyze vegetation dynamics in areas probably deglaciated after the LIA (~seventeenth century); half of these summits are located near peaks with glaciers expected to disappear in the next few decades (Vuille et al. 2008b; Thompson et al. 2011). Analyzing plant community structure in these summits can help us understand (1) the ecological and environmental filters that influence colonization at high elevations; and (2) which plant species and growth forms are colonizing these areas and how do they shape the novel communities that develop.

Environmental filters influencing plant establishment and growth in these areas include a high frequency of freezing air temperatures (mean monthly minimum temperature =  $-1.9 \pm 1.6$  °C), in combination with katabatic winds coming down from the glaciers (Almeida et al. 2013), and water and nutrient limitations due to the incipient development of an organic soil layer (entisols and inceptisols in the majority of cases). The summits are covered to a large extent by rocks and scree (associated with intense gelifraction processes, Pérez (1995)), increasing local topographic heterogeneity (Table 1). Differences in microclimate due to topographic complexity can favor the presence of species with narrow thermal niche ranges and higher thermal optima within a given area (Graae et al. 2018). The areas covered by superficial rocks and boulders create an interspersed set of microhabitats in cracks, crevices, and sheltered surfaces, which could facilitate plant colonization and effective

establishment (Suárez et al. 2015; Graae et al. 2018; Zimmer et al. 2018).

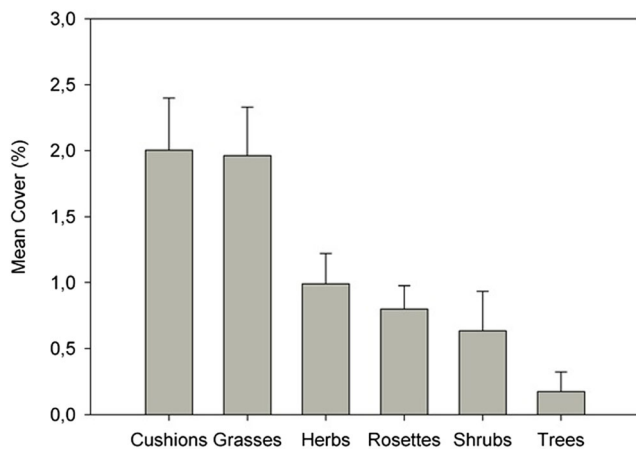
Despite the harsh conditions and low plant cover, we have recorded 135 vascular plant species in the 12 summits, of which 61 have been recorded above >5000 m asl (Table 1). The majority of these plants belong to the families Asteraceae (29%) and Poaceae (24%) (see Cuesta et al. (2017)) which mostly have adaptations to disperse by wind (anemochory) and are able to colonize periglacial areas. The dominance of anemochory contrasts with the lower relative importance of animal mediated dispersal (epizoochory or endozoochory) (Fig. S1. Supplementary Online Material), possibly due to the limited presence of animals at high elevations (Melcher et al. 2000). These patterns are consistent with the post deglaciation plant colonization processes documented through chronosequence studies in Bolivia, Peru, and Colombia (Cuellar 2017; Zimmer et al. 2018).

Cushions and grasses show the highest average cover across the 12 summits (Fig. 4). The fact that cushions constitute a dominant growth forms is interesting, as they have been shown to act as nurse-plants by facilitating the establishment and growth of other species in areas adjacent to some of these summits both in páramos (Antisana and La Culata, see Anthelme et al. 2012; Hupp et al. 2017) and punas (Sajama, Anthelme et al. 2017). Both cushions and grasses are represented by cryophilic species with narrow thermal ranges ( $14.5 \pm 5.4$  °C and  $13.1 \pm 3.4$  °C, respectively) and low thermal optima ( $5.2 \pm 2.02$  °C and  $4.6 \pm 1.4$  °C, respectively; (Cuesta et al., [under review](#))). The prevalence of these thermal niche traits suggests a high vulnerability to warming, as many of these species will be forced to migrate upwards to track their

**Table 1** Descriptive data of the 12 highest summits of the GLORIA-Andes network (Cuesta et al. (2017))

Country	Site	Summit	Elevation (m asl)	Latitude	Mean T°	Minimum T°	Quadrat species richness	Vascular plants cover (%)	Non vascular plants cover (%)	Rock cover (%)	Scree cover (%)
VEN	CPB*	MO6	4604	8.8792	2.1	0.9	10	16.7	30.45	40.87	38.65
ECU	ANT*	CGL	4936	-0.4804	0.4	-0.5	3	2.2	1	25	64
AR	CUC <sup>+</sup>	ISA	4743	-26.6257	2.3	-3.1	26	6.8	0.9	75.9	9.5
BO	SAJ <sup>+</sup>	JAS	4931	-18.1553	1	-3.1	19	4	2.5	72.9	9.7
PE	SIB <sup>+</sup>	PUM	4960	-13.835	1.8	-1.5	42	34.2	0	1.5	4.8
BO	APL <sup>+</sup>	MIT	5050	-15.0202	1.6	-1.1	12	0.9	1.1	6.1	83.9
BO	TUC <sup>+</sup>	PAT	5058	-16.2087	1.6	-1.2	4	0.3	1.6	17.9	74.4
BO	APL <sup>+</sup>	MOR	5195	-15.0148	0.9	-1.8	1	0.1	0.2	0.2	97.4
PE	SIB <sup>+</sup>	RIT	5250	-13.766	0.1	-3.1	48	18.2	42.2	64.7	2.5
PE	SIB <sup>+</sup>	ORQ	5320	-13.761	-0.2	-3.4	4	2.9	0.4	35.4	25.8
BO	TUC <sup>+</sup>	SAL	5325	-16.2373	0.6	-5.1	0	0	21.4	74.7	48
PE	SIB <sup>+</sup>	YUR	5498	-13.767	-1.4	-4.5	2	0.3	0	94.1	4.1

Cover percentage of vascular plants and other substrates is the mean of the cover in the plots present in each summit. \*stands for Páramo summits whereas + relates to Puna summits



**Fig. 4** Mean cover of plant growth forms in the 12 highest summits of the GLORIA-Andes network (Cuesta et al. 2017). Mean cover was calculated as the sum of the cover of all species of each growth form, averaged across the sixteen  $1 \times 1$  m permanent plots present in each summit. The bars represent the standard error

thermal optima, suffering range contractions due to topographically constrained upward displacement, as their distributions would be usually centered near upper mountain areas, as reported for Europe (Pauli et al. 2012).

The GLORIA-Andes network of permanent plots constitutes a unique platform for comparative studies of the dynamic responses of vegetation along the wide elevation and latitudinal gradients that characterize the Andean chain, with many sites having recently completed a first or second resampling campaign (e.g., Carilla et al. (2018)).

## Integration of glacier, landscape, and biotic community dynamics

The tropical Andes constitute a unique scenario for the study of the effects of climate and glacier change globally. They are the largest, most diverse, and populated tropical alpine region in the world (Llambí and Cuesta 2014). Additionally, the high-Andes harbors 99% of the remaining tropical glaciers in the world (Kaser 1999) with considerable regional differences. The northern section encompasses only 9% of the total remaining glacier extent, whereas the central Andes contains the remaining 91%, providing opportunities for comparative research. The combination of increased habitat heterogeneity along ample environmental gradients (Kattan et al. 2004; Hillyer and Silman 2010), increased warming rates ( $0.4$  °C/decade; Vuille et al. (2003), and unique characteristics of cold tropical climates (e.g., large daily thermal amplitudes, moderate seasonal variations; see Cuesta et al. *under review*) poses particularly challenging conditions for vegetation and soil development after glacial retreat. Moreover, the outstanding species, functional (e.g., plant growth-forms) and

ecosystem diversity of the region, could result in unique pathways of primary succession.

Climate niche models have projected an upward range displacement of tropical Andean ecosystems (Tovar et al. 2013) and species (Ramirez-Villegas et al. 2014) as a response to climate change, assuming species located at the treeline are able to colonize alpine habitats and are able to track their climatic niches (Feeley and Silman 2010; Rehm and Feeley 2015). For species restricted to high elevations, upward range displacement is followed by a contraction of their ranges as a result of the conical or diamond shape of most mountain tops (Lamprecht et al. 2018). The few cases were long-term records of species distributions in the Andes are available indicate warming-driven dynamics are already occurring, as evidenced by upward migration reported for alpine vascular plants (Morueta-Holme et al. 2015), Carabidae beetles (Moret et al. 2016), and amphibians (Seimon et al. 2007).

As tropical Andean glaciers shrink, new surface areas become exposed and landscape transformation through the development of new ecosystems (e.g., glacial ponds) and the appearance of novel plant communities can occur. In the Vilcanota range (Peru), three amphibian species have colonized newly formed ponds in a recently deglaciated corridor at 5200–5400 m asl (Seimon et al. 2017). The observed range expansion reveals dynamic landscape changes, including ongoing rapid deglaciation ( $18.4$  m/year widening of a migration corridor between retreating glaciers from 2005 to 2015), new pond formation, and changes in vegetation and amphibian habitats (from *Distichia* cushion bogs to tussock grasses). However, amphibians are dependent on cushion peat bogs, which in turn critically depend on glacial runoff, particularly during the dry season. Glacier shrinkage has been associated with the drying of some of these cushion bogs and their replacement by tussock grasses, threatening long-term persistence of these “new” amphibian community (complicated by changes in amphibian fungal disease dynamics) and revealing the complex links between glacier dynamics, vegetation succession, and animal populations dynamics (Seimon et al. 2017). Morueta-Holme et al. (2015) report an average upward shift of 675 m in the distribution of several plant species in Chimborazo glacier (Ecuador) since 1802, corresponding to an average shift per decade of 32 m. Glacier coverage has retreated from 4814 m measured by Von Humboldt (Von Humboldt 1807) to a mean location of 5270 ( $\pm 260$  m) in 2013 for the glaciers on the south and east side of the volcano (La Frenierre and Mark 2017). Between 1986 and 2013, Chimborazo experienced a 21% ( $\pm 9\%$ ) reduction in ice surface area and a 180-m increase in the mean minimum elevation of non-debris-covered ice, implying that at least the last 150 m of plants upward expansion document by Morueta-Holme et al. (2015) occurred approximately in the last 30 years.

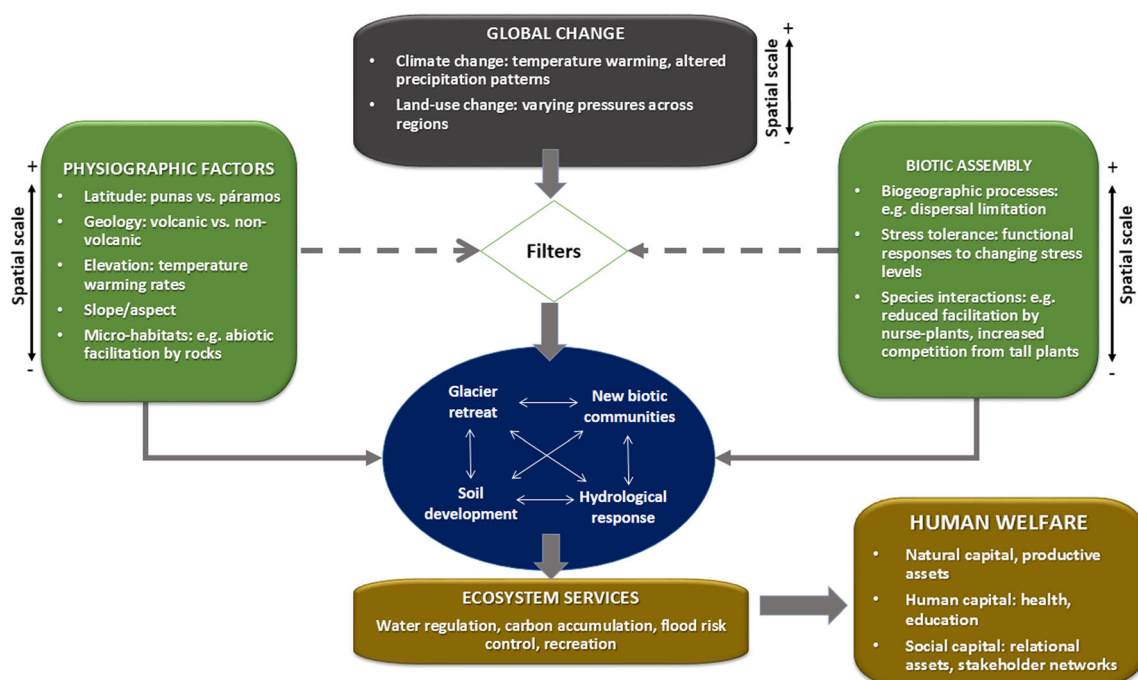
Further, warming temperatures and glacier shrinkage are creating new empty niches that could be filled by alpine species

through dispersal events (Steinbauer et al. 2018). Overall, the handful diachronic studies available indicate that under warming conditions species are being forced to migrate upwards. Two possible outcomes of species range displacement include (a) upward displacement of more warm-demanding plants that could eventually outcompete cold-adapted species, and (b) species with a distribution centered near mountain tops would be more prone to suffer range contractions due to a topographically constrained upward displacement, as documented in other mountain systems (Lamprecht et al. 2018; Steinbauer et al. 2018). However, species centered near mountain tops are likely to be the first to colonize the new available habitats on deglaciated mountain areas as they showed lower thermal optima (Cuesta et al. *under review*). The combination of both scenarios suggests the conformation of new communities with probably marked differences to present-day ones. Chronosequence studies of plant primary succession indicate that, as in other alpine areas (Davey et al. 2015; Cazzolla Gatti et al. 2018), pioneer species include lichens, mosses, grasses, and non-graminoid herbs (particularly Asteraceae), with wind-dispersed species being especially overrepresented (Suárez et al. 2015; Zimmer et al. 2018). Yet, further studies are needed to compare migration and colonization rates across the latitudinal gradient of the Andean chain. So far, the available studies suggest that colonization depends on the availability of suitable microsites, which can include abiotic features such as rocky outcrops and facilitative interactions with biological soil crusts and nurse plants. Species persistence in the new colonized

habitats will critically depend on their ability to adapt to the dynamic new communities and biotic interactions (e.g., from competitors, herbivores, pests) and landscapes evolving at the highest elevations (Fig. 5).

Some of the most prominent new landscape elements associated with glacier shrinkage are lakes that typically form in topographic depressions eroded by the glaciers (Linsbauer et al. 2012). Within the tropical Andes, high-elevation areas in Peru have been particularly exposed to glacier lake formation, a process that resulted in thousands of new lakes (Emmer et al. 2016). Notably, the majority of these lakes are small (< 1 ha) and 50% of them are located above 4600 m asl and were probably formed in the last 30–40 years. Similarly, wetlands in the Eastern Andean flank in Bolivia have increased by 300% in surface area and by 218% in wetland numbers in a 30-year period (1984–2011), mainly related to the appearance of wet grassland patches during the wetter years (Dangles et al. 2017).

A key aspect of these landscape transformations is whether these new small lakes can form a permanent ecosystem in the mid-term, particularly when glacial fed streams are gone and a prolonged dryer season is expected (Vuille et al. 2018). In the Cordillera Vilcanota (Peru), as glacier areas have decreased, 77% of the lakes connected to glacial watersheds have either remained stable or shown a roughly synchronous increase in lake area, while 42% of lakes not connected to glacial watersheds have declined in area (Hanshaw and Bookhagen 2014). Therefore, wetland connectivity seems to provide resilience to these systems. Additionally, analyzing successional vegetation



**Fig. 5** Conceptual scheme of some key physiographic and biotic factors that modulate the impacts of climate change on tropical high mountain ecosystems and their interactions with glacier dynamics at different

spatial scales (from factors operating at local to regional scales). For each factor, we provide concrete examples based on the literature review presented here

dynamics is crucial for predicting the long-term persistence of the newly formed wetlands. Cushion plants, such as *Distichia* spp., are key for regulating carbon accumulation and water retention in wetlands of the high Andes (Benavides 2014; Hribljan et al. 2016), allowing the persistence of other wetland specialist plants. However, Dangles et al. (2017) found that the increase in wetland cover mainly concerned small areas dominated by grassland species (Poaceae) instead of cushion-forming species, which requires several decades to colonize new habitats in a changing environment (Anthelme et al. 2014).

Furthermore, landscape changes can result from shifting hydrological processes and, in turn, feedbacks through altered evapotranspiration, runoff, and water storage can further influence wetlands persistence and landscape structure (Polk et al. 2017). For example, both increase and decrease in wetland areas have been documented between 1987–1999 and 1999–2000 respectively in the Cordillera Blanca, Peru (Polk 2016). Changes in flow regimes have also affected the wetland area in the upper watershed of the Santa River, Peru (Baraer et al. 2012). Here, satellite data suggest that glacier area decreased by 0.81% annually between 1990 and 2009. After an initial phase in which glacier melt resulted in increased water flows, glacier-fed streams now exhibit decreasing annual and dry season discharge. Changes in wetland area are reflecting the changes in flow, following the peak water curve, but with a clear time lag. Once the glaciers are gone, the discharge will likely be lower than today, at least during the dry season (Polk et al. 2017). The expected water shortage could have negative feedback effects on the new wetland systems; effects may include wetland fragmentation, attrition, and dissection. These modifications would likely result in associated ecological effects including loss of species adapted to or dependent on water saturated substrates and loss of soil organic carbon (see Benavides et al. (2013)).

The evidence reviewed here indicates that landscape and ecosystem dynamics of the high Andes, including glaciated areas, biotic communities, soil development, and hydrological responses, are modulated by physiographic factors (Fig. 5) that change along environmental gradients at different spatial scales, including ecosystem changes with latitude (e.g., páramos and punas), geology (i.e., from volcanic to non-volcanic regions), geomorphology (formation of extensive wetlands), elevation (e.g., increased rates of warming at high altitudes), slope/aspect, and microtopographic features (e.g., depressions and rock crevices). Additionally, the available literature suggests that understanding ecosystem dynamics requires a comprehensive analysis of the biotic mechanisms of community assembly at various scales (Lortie et al. 2004), including (i) macro biogeographic and colonization filters (e.g., dispersal limitations into high deglaciated areas); (ii) adaptive responses of different functional groups to the micro-climatic, hydrological or edaphic gradients at the site scale;

and (iii) the effects of species interactions, both positive (e.g., changes in the effectiveness of facilitation, seed dispersal or pollination at high elevations) and negative (e.g., increased effects of competition, herbivory, or pests modulated by a changing climate). Hence, both physiographic gradients and biotic processes can act as filters that modulate the effects of global change on high Andean landscapes and ecosystem dynamics, including community development in deglaciated forefronts. In turn, these processes exert a great influence on the provision of ecosystem services and ultimately, changes in human welfare for Andean populations (Fig. 5).

## Conclusions: future challenges and opportunities

In this review, we related observed and projected changes in climate, with the documented glaciological, hydrological, and biotic responses of high tropical Andean ecosystems and landscapes. We explored the links between global change (i.e., interactions between climate and land-use change) and their modulation by physiographic and biotic assembly processes that operate at different spatial scales, highlighting examples of the main processes that can operate at each scale (Fig. 5). We propose that an explicit analysis of the synergies and interactions between these abiotic and biotic modulating process could contribute to the development of an analytical integrated framework and interdisciplinary research agenda.

Overall, the documented evidence (e.g., Dangles et al. (2017)) and future scenarios of glacier shrinkage (e.g., Drenkhan et al. (2018)) indicate that in areas with important glacier cover, glacier loss can significantly modify the landscape through (i) formation of new lakes together with the fragmentation and drying/attrition of former lakes; (ii) alteration of hydrological dynamics in glacier-fed streams and high Andean wetlands, leading to vegetation modification and changes in community composition and species interactions (e.g., on aquatic macroinvertebrates); (iii) species colonization of new deglaciated areas along with species upward migration; (iv) shifts in the balance between diverse cushion-dominated peat bogs and drier grass-dominated wetlands; and (v) eventual loss of alpine biota adapted to waterlogged conditions.

Glacier shrinkage, landscape transformation, and ecosystem modifications in the Andes can in turn affect critical ecosystem services for a large number of rural and urban population centers (Mark et al. 2017), including water provision and streamflow regulation (Mark 2008), increased risks of flooding or lake outbursts, degradation of grazing grounds for domestic cattle (particularly Andean camelids, Duchicela et al. (2019)), and loss of carbon accumulation capacity in soils (Benavides et al. 2013). Furthermore, the combined effect of climate change and land-use stressors on Andean

wetlands has the potential to reduce soil water regulation capacity, increase soil erosion, and increase organic matter decomposition (Buytaert et al. 2011; Urbina and Benavides 2015; Hribljan et al. 2016). The resulting changes to these ecosystem functions could threaten the carbon stability of high Andean wetlands, transforming them from a long-term sink to sources.

The ecological and social implications of the observed and projected changes are diverse and complex due to the fact that coupled biophysical and social dimensions mediate and amplify these risks (Bury et al. 2011). Assessing the social risks related to glacier loss and landscape transformations requires deciphering the magnitude and diversity of these changes over space and time, and exploring how such changes interact with dynamic social relations and processes (Mark et al. 2017). Thus, observed and projected changes need to be further addressed, requiring more integrated approaches from earth-sciences fields such as climatology, glaciology, hydrology, edaphology, different branches of ecology (from paleoecology to ecophysiology and landscape ecology), and notably, important contributions from and engagement with social sciences and local stakeholders.

Important knowledge gaps could be addressed, and critical ecological thresholds identified, to support the decision-making processes, by comparative multi-scale studies across the Andes, linking glacier retreat dynamics to its consequences on biodiversity and ecosystem processes (e.g., the carbon and water balance), combined with different land-use trajectories. Further research efforts are specially needed to understand (i) the links between changes in landscape structure and ecosystem distribution in regions affected by climate and glacier change (e.g., glacier-wetland-grassland interactions); (ii) the processes of soil development in deglaciated forefronts (e.g., permanent plots along glacier chronosequences); and (iii) the impacts of landscape and ecosystem change on ecosystem services provision for rural livelihoods and Andean cities.

All of this call for integrating research efforts across the region. Existing disciplinary observational networks such as the GLORIA-Andes network and World Glacier Monitoring Service need to be maintained, but could be complemented by integrated observatories such as currently proposed under the GEO (Group of Earth Observation) Global Network for Observation and Information in Mountain Environments (GEO-GNOME). In our view, this constitutes an exciting challenge to develop a more comprehensive understanding of the complex feedbacks between climate change, glacier dynamics, biodiversity, ecosystem services, and socio-economic development across the tropical Andes. An improved understanding of the described linkages will be a key contribution to conserving and managing these dynamic landscapes and designing better strategies for adaptation to climate change. Sustained long-term research programs require a more effective integration with the decision-making process

(Lindenmayer et al. 2013). An effective research agenda, with a strong policy formulation link, needs to be supported by (i) an enabling environment capable to strengthening information sharing platforms; (ii) enhanced cooperation among research centers; (iii) capacity building of relevant stakeholders, and (iv) active participation of government agencies and social organizations in all phases of the research/monitoring cycle (e.g., see IDEAM et al. (2018)).

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