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Novel plant communities after glacial retreat in Colombia: (many) losses and (few) gains

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“Wise men say, only fools rush in” UB40

Abstract

Early plant primary succession in recently deglaciated terrains is a good indicator of the species losses and gains that affect novel alpine plant communities migrating under the pressure of climate warming. In the tropical alpine -páramo- region of the northern Andes, home to the world's greatest alpine phytodiversity, forced primary succession will condition the conservation of many species. Using post-glacial chronosequence between the little ice age and present below the Conejeras glacier (Colombia) as a space-for-time substitution approach, we sought to determine how time since deglaciation affects the composition, the biogeographic origin and the growth form distribution of novel tropical alpine plant communities. Using an array of multivariate techniques and the Dirichlet model, we assessed relationships among plant communities and with environmental factors. Communities established in less than 169 years lacked a number of characteristic and endemic species usually found in the national park Los Nevados, such as *Calamagrostis effusa*, *Senecio isabelis* and *Espeletia hartwegiana*. Moreover, these communities have been colonized by non-native species, e.g., *Rumex acetosella*. Upright shrubs and large tussock grasses, characteristic of the alpine tropics, established slowly because they required highly organic, slow-developing soils. Taxa of tropical biogeographic origin were under-represented early after deglaciation in comparison with temperate taxa. These results suggest the existence of a strong climatic debt for some native species, tropical growth forms and taxa of tropical origin, which may translate into significant taxonomic and functional losses whereas the few observed gains concern the establishment of non-native species.

Key-words: biogeographic origins, climatic debt, growth forms, Los Nevados national park, post-glacial chronosequence, tropical alpine

INTRODUCTION

The environmental constraints applied by arctic and alpine environments on plants at the boundaries of life are severe and multiple (Crawford 2008). However, they do not turn necessarily into stress since plants have evolved and developed major adaptations to increase their fitness in this type of ecosystem (Larcher 1987; Körner 2003). With sufficient time available, these species are capable of coping with the effects of natural climatic oscillations through adaptations and migrations, both altitudinal and latitudinal, as proven by the presence of the same taxa in alpine environments of different continents, at different latitudes (e.g., *Cerastium*; Scheen et al. 2004 and *Draba*; Jordon-Thaden et al. 2013). However, the Anthropocene era poses a difficult challenge for alpine plants: to adapt to rapidly changing climate and land use or to migrate within an exceptionally short period of time (Lenoir and Svenning 2015).

Among the options available to alpine populations at the limits of life in order not to disappear because of global warming, upward migration is the most common scenario (e.g., Steinbauer et al. 2018; Peyre et al. 2020). Indeed, despite having local migration options, e.g., benefiting of microclimatic refuges proposed by rocks or nurse plants (Anthelme et al. 2014a) the majority of alpine plants are expected to extend their distribution upward, seeking newly available climatic niches, whereas their bottom distribution is negatively affected by thermophilization and competition with species migrating from lower vegetation belts (Lenoir and Svenning 2015).

An increasing body of literature evidences a climatic debt, as a result of a significant lag between the pace at which the climate warms and the velocity of plants' upward migration (Kuussaari et al. 2009; Gaüzère et al. 2017). For mountain plant species this lag has been split into three types: dispersal lag, establishment lag and extinction lag (Alexander et al. 2018). In the upper alpine zone, where upward migration is assimilated to a primary succession on mostly abiotic terrains (Walker and Del Moral 2003), this lag has been associated with dispersal limitation (dispersal lag) and a deficit in positive interactions between plants (establishment lag; Zimmer et al. 2018; Llambí et al. 2021). Nevertheless, the very slow development of alpine soils, especially the slow enrichment in organic matter (Khedim et al. 2021) means that, even if plants are capable of reaching upward sites, they may not be able to establish because of the lack of organic matter (establishment lag). As a consequence, novel alpine communities at higher elevations are expected to be different from the initial species pool they come from due to (1) the loss of species of the initial pool unable to disperse or establish in novel, deglaciated terrains within a few decades and (2) the intrusion of species that were initially not part of the alpine community but are better adapted to rapid changes (Le Roux and McGeoch 2008; Peyre et al. 2020). Still, the ecology of páramo plant communities, i.e., the higher tropical alpine belt, close to glaciers, is understudied in comparison with its alpine counterparts outside the tropics (Anthelme and Lavergne 2018). Identifying species' losses and gains is a topical challenge given the high pace of climate warming in this region, which belongs to one of the major hotspots of vascular plant biodiversity in the world: the Tropical Andes (Mittermeier et al. 2011; Peyre 2021).

From a functional viewpoint, the few studies examining the first decades of plant primary succession after glacial retreat in the alpine tropics evidenced significant changes in species strategies (e.g., from opportunistic to stress tolerant; Zimmer et al. 2018; Rosero et al. 2021) and in growth forms (Llambí et al. 2021). This said, the absence of pronounced seasonality and seasonal snowpack as well as the decreasing precipitation at higher elevations in tropical alpine environments have been suggested to result in different functional trait values in the tropics and in temperate-arctic environments (Cruz-Maldonado et al. 2021). The presence of growth forms like large stem/basal rosettes and upright shrubs and the relatively high abundance/diversity of cushion-forming species and large tussock grasses in comparison with similar ecosystems at higher latitudes illustrate these differences (Hedberg and Hedberg 1979; Aubert et al. 2014). Some of these tropical alpine growth forms of the Northern Andes are dependent on the presence of highly organic, temporarily water-saturated soils, especially in depressions and relatively flat areas, e.g., some species of the giant stem rosette *Espeletia* (Valencia et al. 2020) and the cushion-forming *Distichia muscoides* that forms peatlands (Benavides et al. 2013). Still, the development of such organic soils is particularly slow, even if possibly accelerated with the effects of warming (Benavides et al. 2013; Llambí et al. 2021). Consequently, we expect that the first decades after glacial retreat may not provide adequate soil conditions for the establishment of the tropical alpine growth forms that are the most dependent on highly organic soils.

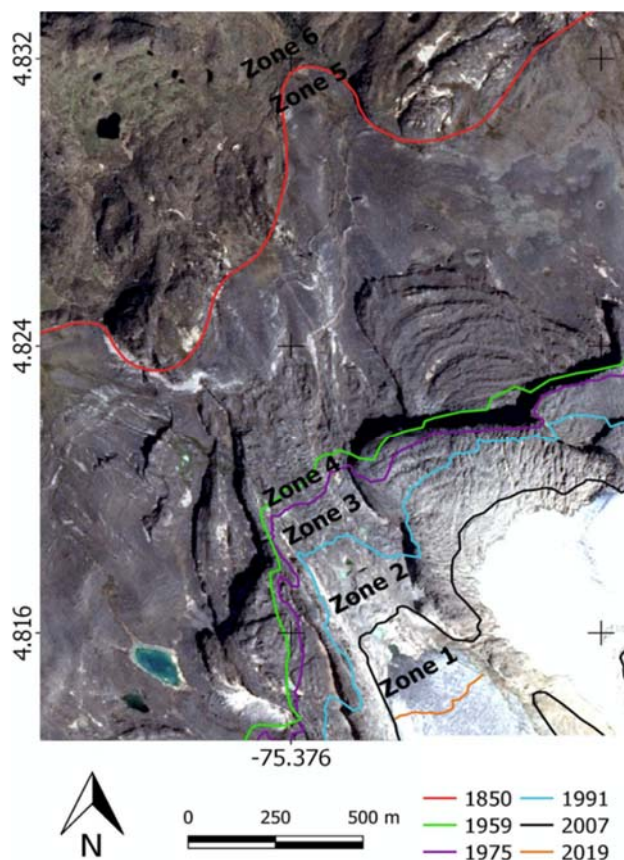
Another potential driver of primary succession specific to the páramos is their location at a biogeographic crossroad between temperate, tropical and endemic trends. Indeed, in this region, taxa may originate from temperate environments (Holarctic species from the North and Austral-Antarctic species from the South) or from tropical environments, including originating in the tropical páramo itself (Sklenář et al. 2011; Anthelme and Peyre 2020). The biogeographic origin of taxa has been observed to influence their elevational distribution in the páramo with, e.g., Holarctic genera becoming more abundant and páramo endemics becoming less abundant at higher elevations (Sklenář & Balslev 2007). Taxa of temperate origin may be pre-adapted to alpine environments, which would make them potentially more efficient for colonizing recently deglaciated terrains than their tropical counterparts, which first diversified in warm, moist environments (Sklenář et al. 2011; Gehrke 2018; Peyre et al. in press; but see Nürk et al. 2018). From this viewpoint, we might expect a deficit in species of tropical biogeographic origin during early primary succession.

As a space-for-time substitution approach, the study of plant primary succession along post-glacial chronosequences is a complementary approach to long-term monitoring (e.g., GLORIA project: Pauli et al. 2005). It provides the foundation to assess future trajectories of alpine plant communities and ecosystems (Matthews 1992; Walker et al. 2010). This approach has been used frequently and successfully in arctic and temperate alpine regions, on a time step between the Little Ice Age and today, showing a global pattern of increasing biodiversity along with time since glacial retreat (Cauvy-Fraunié and Dangles 2019). The use of chronosequences on shorter time scales, since the acceleration of global warming about 60 years ago, is likely to provide us with valuable information on the capacities of (tropical) alpine plant communities to adapt to abrupt environmental changes at the boundaries of life (Cannone et al. 2008; Anthelme et al. 2021).

We examined plant primary succession in the most phytodiverse alpine region, worldwide: the north-Andean páramos. In this region, and more generally in the tropical Andes, this approach, which requires close collaboration between glaciologists and ecologists, has been used very little so far, in the Central Andes (Zimmer et al. 2018), Ecuador (Anthelme et al. 2021; Rosero et al. 2021), and Venezuela (Llambi et al. 2021). Succession was studied along the best-documented post-glacial chronosequence in Colombia, at the foot of glacier Conejeras, located at the slopes of the Santa Isabel volcano (Ceballos et al. 2006; Rabatel et al. 2018). We focused on six periods: four distributed between 0 and 60 years of deglaciation, within the timeframe of the acceleration of global warming, and two others above and below the frontal moraine of the Little Ice Age (hereafter termed LIA, 169 and nearly 7000 years of deglaciation, respectively; Fig. 1). We aimed at determining to what extent species composition, growth forms and biogeographic origins are distributed along the chronosequence, along with environmental parameters. Our specific objectives were to test to what extent the high velocity of warming, represented by rapid deglaciation, affect positively or negatively the spatial distribution of (1) the plant communities adapted to the vicinity of glaciers, (2) the growth forms characteristics of the alpine tropics, and (3) the proportion of taxa of tropical vs. temperate origins. We tested three specific hypotheses:

- (1) Novel plant communities in the recently deglaciated terrain under study are impoverished by the absence of a number of species present in the initial pool, locally (not constrained by time since deglaciation) and enriched by species absent from the initial pool.
- (2) The growth forms that require highly organic soils may see their colonization pace slowed down by the establishment lag between the speed of global warming and the slowness of soil formation (climatic debt).
- (3) Taxa of temperate biogeographic origin may establish better than taxa of tropical origin recently after deglaciation because they are better pre-adapted to the climate of alpine environments.

Fig. 1 Post-glacial chronosequence of the rapidly retreating Conejeras glacier, divided into six deglaciation zones, from 2019 to ~7000 years BP (below the LIA moraine in red: zone 6)



2. MATERIAL AND METHODS

2.1. Study area and study site

In Colombia, the northern part of the tropical Andes divides into three main mountain systems: the western, central and eastern cordilleras, above whose treeline the páramo -the local alpine zone- occupies 1% of the national, terrestrial territory (Peyre et al. 2021). The Colombian páramo is highly fragmented and consists of a sky island system above 3000-4000 m a.s.l. (Anthelme et al. 2014b; Sklenář et al. 2014; Peyre et al. 2021). The vegetation of the Colombian páramo is under the influence of harsh environmental conditions that reduce the diversity of ecological niches for plant species. These include very low minimum temperatures each night, very high daily temperature ranges and heterogeneous, generally nutrient-poor soils (Luteyn 1999; Körner 2003). The vegetation also faces disturbances related to frequent freeze/thaw cycles and generally steep surfaces. The páramos are also subject to constraints characteristic of tropical alpine environments, such as low annual seasonality, lack of seasonal snow cover, reduced annual precipitation at higher elevations and higher UV radiation (Körner 2003; Buytaert et al. 2011; Vuille et al. 2018). Four glacier complexes, located in the Central and the Eastern cordilleras, remain in Colombia, which are about to disappear within decades because of the effects of accelerating climate warming (Rabatel et al. 2018).

The selected study area is the National Park of Los Nevados, located in the Cordillera Central of Colombia and which harbors three of the few remaining glaciers in Colombia (Rabatel et al. 2018). Our study site is the páramo located on the western side of the Volcan Santa Isabel (4965 m) between 4312 and 4716 m a.s.l. (Supplementary Material 1), within the area deglaciated between the LIA and current time below the Conejeras Glacier, approximately 25 km south-east of the city of Manizales (4° 49' 12.9324" N 75° 22' 33.2112" W). Mean annual temperature at the foot of the glacier reaches 1.3°C with very little seasonal variation (see also our data in the next section) whereas annual precipitations reach 1025 mm. During the dry season (December-January and June-August) monthly precipitations reach 75 mm per month, whereas it can exceed 150 mm during the rest of the year (wet season; Morán-Tejeda et al. 2018).

Here, the plant communities belong the midpáramo and the superpáramo vegetation belts (*sensu* Luteyn et al. 1999), which corresponds to the alpine belt in temperate environments. Lower elevations are represented by the upper zonal midpáramo represented by bunch grasslands with the large tussocks *Calamagrostis recta* (Kunth) Trin. ex Steud. and *C. effusa* (Kunth) Steud, the upright shrub *Diplostephium schultzii* Wedd. and the stem rosette *Espeletia hartwegiana* Cuatrec. At the higher elevations of the superpáramo the vegetation cover is patchy and scarce, represented by various species including the erect herbs *Agrostis foliata* Hook.f. and *Cerastium floccosum* Benth and the acaulescent rosette *Draba* spp. and *Erigeron chionophilus* Wedd. (Salamanca et al. 2003). The sampled site does not include the superpáramo blue grasslands, located between the two above-described communities and characterized by *Festuca breviaristata* Pilg. and *Agrostis araucana* Phil. The páramo of Los Nevados harbors the endemic angiosperms *Senecio isabelis* S. Díaz, *Draba pennel-hazenii* O.E.Schulz and *Lupinus ruizensis* C.P.Sm., and the endemic hummingbird *Oxygogon stuebelii* Meyer.

The Conejeras glacier has undergone two significant mass growth during the Holocene, one 7400-6050 years ago during a climate anomaly and a more recent one during the LIA, around 1850 in Colombia (Thouret et al. 1997; Florez 2003). In 1850, the Santa Isabel ice cap had an area of 27.8 km². It decreased to 10.8 km² in 1976. Since the acceleration of global warming in the 1960's, the ice cap has further decreased to only 1 km² in 2016, of which less than 0.2 km² is represented by the Conejeras glacier. In 2020, the glacier has been split into two fragments (Supplementary Material 2) and it is expected to disappear in the coming years (Rabatel et al., 2018).

We delimited a precise post-glacial chronosequence focused on the time scale of the acceleration of global warming (since the 60's) and including the LIA moraine. For this purpose, we extracted the glacier limits in 1959, 1975, 1991, 2007 and 2019 using the available aerial photographs at the Agustin Codazzi Geographical Institute. The photographs were georeferenced and the glacier's limited manually created on QGIS (URL: <http://qgis.osgeo.org>). To compare the recently deglaciated zones with that before and after the LIA (approx. 1850 AD) we used the LIA delimitation, provided by the Institute of Hydrology, Meteorology and Environmental Studies (IDEAM). The resulting chronosequences had six deglaciation zones: 2007-2019 (zone 1), 1991-2007 (zone 2), 1975-1991 (zone 3), 1959-1975 (zone 4), ~1850 (zone 5, just above the LIA moraine) and ~7000 years before present (zone 6, just below the LIA moraine; Fig. 1; Supplementary Material 1). The use of glacial advances to date the onset of primary succession in the different areas was considered relevant because they represent the last major disturbances, with the last locally observed lava flow dating to 5800 years BP and not affecting the glacier-affected area. (Kuhry 1988).

Zones 1, 2, 3 and 4 represented recent deglaciation at the time of the acceleration of warming; they were located at similar elevation. Twelve temperature loggers (HOBO Pendant® 8K data logger), two at each zone, were used to described temperature conditions along the chronosequence. They were installed 5 cm below the ground between 22 June 2018 and 12 July 2018 and they recorded temperature every 10 minutes. Data in zones 1-2-3-4 showed that daily minimum and maximum soil temperature increased with time since glacier retreat (e.g., between 0.67°C in zone 1 and 1.24°C in zone 4 for minimum temperature; Supplementary Material 5). Zone 5 and zone 6 represented older zones constrained (5) or not (6) by the presence of a glacier at the time of the LIA. They were located at the same elevation, only separated by the frontal moraine of the little ice age (Supplementary Material 1). Daily minimum temperature was higher in zone 6 (4.31°C vs. 3.75°C in zone 5) whereas daily maximum temperature was higher in zone 5 (10.45°C vs. 8.43°C in zone 6; Supplementary Material 5). The elevational difference between zones 1-2-3-4 and zones 5-6 approximates 350 m, a parameter that might explain part of the variation in our biotic and abiotic measurements along the chronosequence.

2.2. Sampling design and data collection

To sample a representative area of each zone, we haphazardly selected 15 squared vegetation plots of 4 m² after estimating that this surface was representative of the species richness, locally (see the species-area relationship curve built on plots of 4, 2, 1 and 0.25m² in size and showing no strong species enrichment beyond 4m²; in Supplementary Material 3). The minimum distance between plots was 30 m and each plot should contain at least one vascular species, to avoid plots devoid of vegetation in the recently deglaciated zones, which would have weakened statistical analyses. As a result, the species richness in these zones might

be slightly overestimated, which is not of significant concern given the objectives and the hypotheses of the study. Five plots in each zone were selected in hydromorphic areas (presence of water as a periodic stream or a pond) as this habitat was frequently observed in the sampling. Areas dominated by flagstones were avoided as being extreme constraints for plant colonization. More generally, we avoided sampling plots with extreme topography, not representative of each zone, to reduce the effects of the topography variable, which was not part of the original hypotheses. The sampling resulted in 90 plots distributed into six zones that includes superpáramo communities (Z1, 2, 3, 4) and the upper bunchgrass mi páramo (Z5 and Z6).

Fig. 2 Nine growth forms observed along the post-glacial chronosequence, with examples. A: acaulescent rosette (*Hypochaeris sessiliflora*); B: basal rosette (*Lupinus alopecuroides*); C: cushion (*Plantago rigida*); D: erect herb (*Senecio latiflorus*); E: large tussock (*Calamagrostis effusa*); F: prostrate herb (*Geranium sibbaldioides*); G: prostrate shrub (*Pernettya prostrata*); H: stem rosette (*Espeletia hartwegiana*); I: upright shrub (*Diplostegium schultzi*). Photographs of all species available at: <https://identify.plantnet.org/fr/groups/19892283922>



At each plot, we made the list of the vascular species by provisionally identifying them on the field and by collecting two specimens of each species for definitive identification at the herbarium of the University Los Andes where all samples were kept (Collecting permit AUR 007-19; see the full list in Supplementary Material 4 and photographs of species in the web/mobile application Plantnet: <https://identify.plantnet.org/fr/groups/19892283922>). Species names refer to the World Flora Online (<http://www.worldfloraonline.org>; access 28/11/2021). We visually estimated the relative cover of each species at soil surface, as well as the relative cover of biological soil crust (BSC), rock and bare soil, using a grid of 10*10 cm. We also measured slope degree and exposition with a clinometer (Sunnto Tandem). Plants

were grouped into nine growth forms inspired by the classifications by Hedberg and Hedberg (1979) and Ramsay and Oxley (1997): acaulescent rosette (AR), basal rosette (BR), cushion (CU), erect herb (EH), prostrate herb (PH), prostrate shrub (PS), stem rosette (SR), large tussock (LT) and upright shrub (US; Fig. 2). BR were large rosette-like species with a basal leaf rosette and a large inflorescence that can exceed one meter were grouped into this growth form. SR was represented with only one species: *E. hartwegiana*. PH and PS had essentially a horizontal structure aboveground. LT took into account the species with a diameter generally exceeding 1m in mature individuals. Species were grouped into CU as soon as they had a dense, hemispheric shape, providing a singular microenvironment. Species were also grouped into biogeographical origins -temperate, tropical and cosmopolite- following the classification of Sklenář et al. (2011) at the genus level, which means each species was grouped into the biogeographical origin of its genus. This was done to test to what extent the biogeographic origin of species conditions their establishment success during primary succession (Supplementary Material 4).

To measure changes in the abiotic environments and make correlations with biotic data, soil samples were extracted in ten of the plots selected in each zone, between 0 and 30 cm belowground (or less when unavailable), after removing the organic litter (recognizable pieces of plants) when present. Each sample was a combination of five subsamples collected at the corners and the center of each plot (total: approximately 500g). Soils were brought to the Environmental Engineering laboratory of the Los Andes University (Bogota, Colombia) for measurements of pH and soil organic matter content (SOM; %) following the protocol of Jaramillo (2002). In addition, at each plot we measured the soil water content (SWC; %) with vertical probes reaching 7.5 cm belowground (Fieldscout TDR-100; SWC at each plot was the average value of five measurements made at the corners and at the center). Soil and SWC collections were made during two days of stable climatic conditions without significant precipitations. Soil and SWC were measured within this time period. Averaging the two values in each zone showed that minimum temperature increased monotonously between zone 1 (0.67°C) and zone 6 (4.31°C; Supplementary Material 5). Mean temperature also increased between zone 1 (1.78) and zone 6 (6.21) but reached a maximum value in zone 5 (6.70°C).

2.3. Data analysis

To test hypothesis 1, changes in plant communities along the chronosequence were assessed with a partition around medoids (PAM) clustering analysis, which establishes clusters, or groups, of sampling units (i.e., vegetation plots) with similar variable values (i.e., species) and distribution (i.e., relative cover) (Kaufman and Rousseeuw 2009). We carried out the PAM analysis on a Bray Curtis distance matrix of our plot data with partitions increasing cluster numbers between 1 and 60 and 100 iterations each (package "cluster"). We used the within sum of squares (wss) metric to establish the best partition to divide the dataset. Each resulting cluster, revolving around a plot-defined medoid, was therefore assimilated as a plant community that we described by its characteristic flora. To do so, we calculated the Indval index to establish the probability for a species to be preferentially found in a cluster in comparison to other clusters (R package *indicpecies*). To consider a species characteristic of a specific group, we put a 0.5 threshold for the IndVal value and ensured that it was substantially less represented in other groups (min 30% less). We refrained from using the term "diagnostic" to qualify the characteristic species because of the local scale of our analysis, however, we discussed our results relating them to broader scale studies on the páramo vegetation and its characteristic species (e.g., Salamanca et al. 2003; Peyre et al. 2018).

To test hypothesis 2, changes in growth forms along the chronosequence and their correlation with environmental variables were evaluated with a principal component analysis on a matrix crossing plots with the relative cover of growth forms (eight variables) and integrating the variables pH, SOM, SWC and BSC (four environmental variables; R package *Factoextra*). Lacking values of SOM and SWC (five plots out of 15 in each zone) were filled with average values at each zone. Additionally, linear regressions were used to test the correlations between the cover of each growth and the relative content of soil organic matter.

To test hypothesis 3, the relationship between the biogeographic origin of taxa and time since deglaciation was evaluated by comparing the relative species richness of temperate, tropical and cosmopolite origins, in each plot and compared between zones. First, we calculated origin frequency within the plot data and rescaled these frequencies on a 0-1 interval. Then, we conducted a Dirichlet regression on the rescaled frequency data in function of the "zone" variable, using the mean age value of each zone: (6, 20,

36, 52, 169 and 7000 years; Supplementary Material 6). We used the alternative parametrization, which is often privileged for ecological data (R package DirichletReg; Maier 2014; Douma and Weedon 2019). Finally, we used the Akaike information criterion (AIC) to indicate model performance and predicted frequency values for each origin category along the chronosequence. The data and predicted values were plotted altogether to visually compare changes in plant community composition in term of temperate, tropical and cosmopolitan frequencies along the chronosequence.

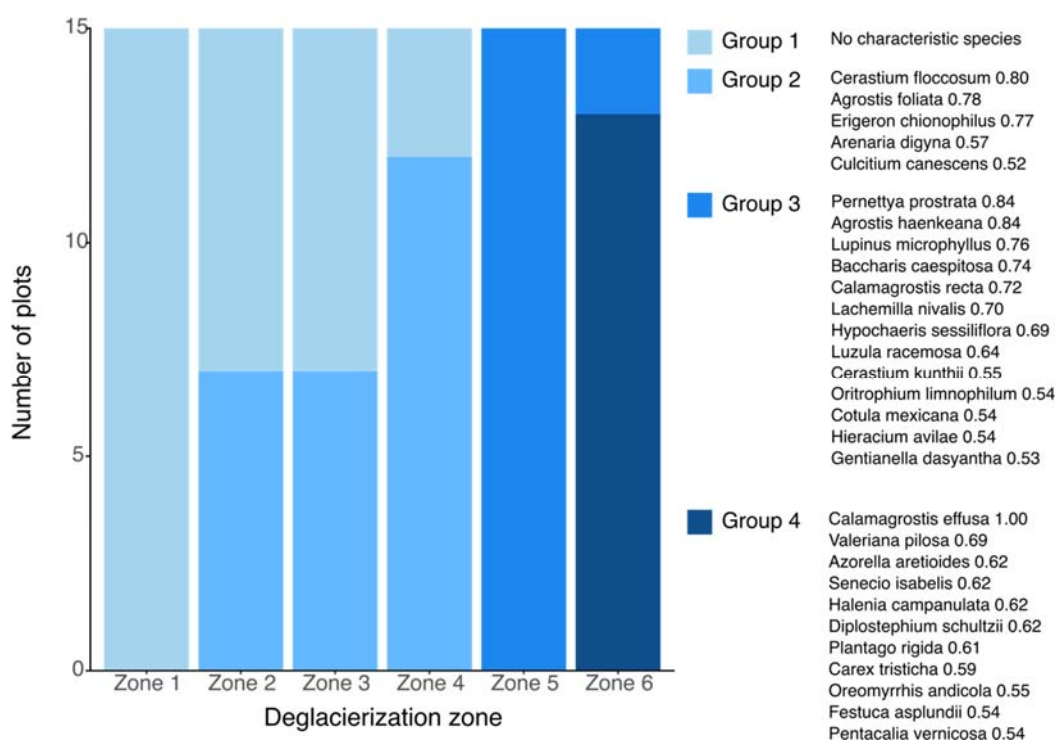
3. RESULTS

3.1. Species composition along the chronosequence

A total of 68 vascular species were recorded in the plots along the chronosequence, representing eight growth forms (Fig. 2; Supplementary Material 4). 46 species were of temperate origin, 21 species of tropical origin and one species of cosmopolitan origin (*Eryngium humile*). *Espeletia hartwegiana*, *Calamagrostis effusa* and *Senecio isabelis* were present only in Z6, below the LIA, among others. The non-native *Rumex acetosella* (Z1, 5, 6), *Bromus lanatus* and *Taraxacum officinale* (Z6) were also present in the sampling.

Based on the total within sum of squares, the PAM analysis identified four cluster partitions of species along the chronosequence (Fig. 3). Group 1 comprised 100% of the plots in Z1 and was present in Z2, Z3 and Z4. It had no characteristic species. Group 2 was present in Z2, Z3 and included the majority of the plots of Z4 (12). It was characterized by four early-colonizing species: the erect herbs *Cerastium floccosum* and *Agrostis foliata* (IndVal: 0.80 and 0.78, respectively) and the acaulescent rosette *Erigeron chionophilus* (Asteraceae; 0.77). Group 3 gathered all the plots of zone 5 and two plots in Z6. It was characterized by 13 species, notably the prostrate shrubs *Pernettya prostrata* and *Baccharis caespitosa* (0.84 and 0.74, respectively) the erect herbs *Agrostis haenkeana* and *Cerastium kunthii*, as well as the prostrate herbs *Lupinus microphyllus* and *Lachemilla nivalis* (0.84, 0.54, 0.76 and 0.70). Group 4 was present only in Z6. It was characterized by 11 species, among which the large tussock grasses *Calamagrostis effusa* and *Festuca asplundii* (1.00 and 0.54), the upright shrubs *Diplostephium Schultzii* and *Pentacalia vernicosa* (0.62 and 0.54) and the endemic basal rosette *Senecio isabelis* (0.62).

Fig. 3 Distribution of four plant communities in each of the deglaciation zones, as a result of the PAM clustering analysis



3.2. Growth forms

Regarding soil parameters, the PCA's axis 1 represented a gradient of time since glacial retreat from the right to the left where mineral, inorganic soils with high abundance of biological soil crust in recently deglaciated terrains were gradually replaced by organic soils with higher water content and a more acidic pH (Fig. 4). Axis 2 separated mainly plots of Z5, in the lower part of axis 2, and plots of Z6, in the upper part of axis 2 and associated with highly organic soils.

Along axis 1, all growth forms were associated with the older deglaciation zones on the left of the graph. The growth forms erect herb, prostrate herb, prostrate shrub and, to a lesser extent, cushion were located preferentially in Z5, 169 years after deglaciation. In contrast, the growth forms large tussock, upright shrub and, to a lesser extent, stem rosette were preferentially observed in Z6, in areas deglaciated approximately ~7000 years ago.

The relative cover of the two most characteristic growth forms of Z6, large tussock and upright shrub, was positively correlated, linearly, with SOM ($R^2 = 0.61$ and 0.42 , respectively; Fig. 5).

Fig. 4 PCA biplot combining plot (symbols, N = 90), grouped by zone (color) with centroids represented as larger symbols, with growth forms (black, regular) and environmental variables (rock, pH, biological soil crust -BSC-, soil water content -SWC- and soil organic matter -SOM; gray, italic). Variables in black with decreasing length according to their contribution. Full names of growth forms available in Fig. 2

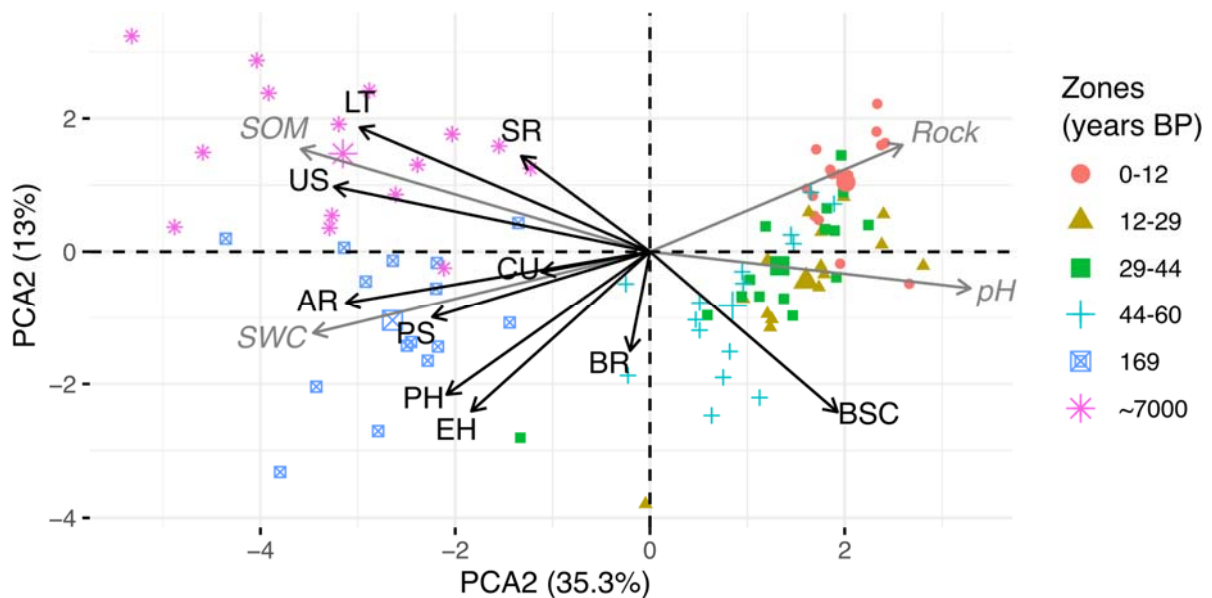
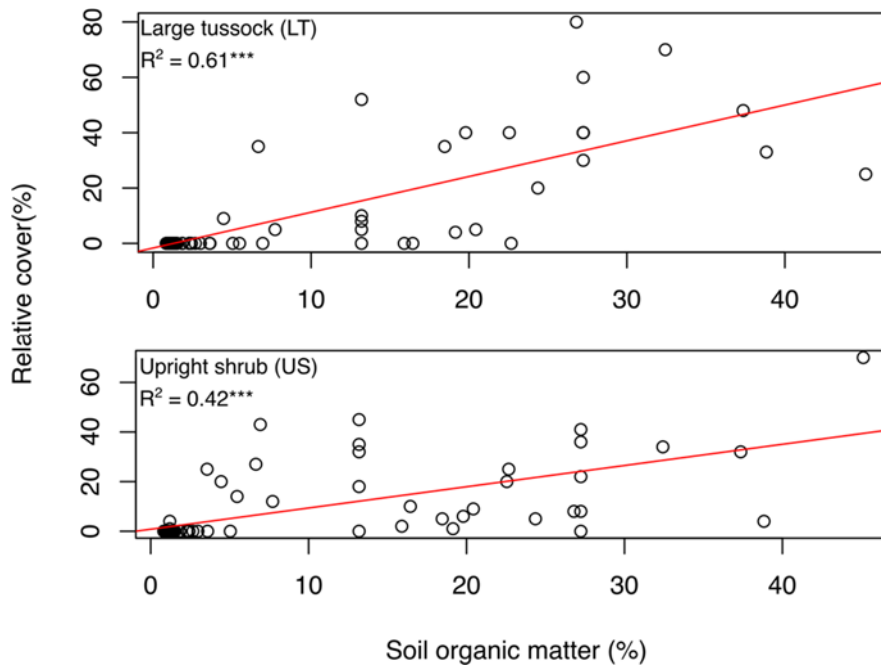


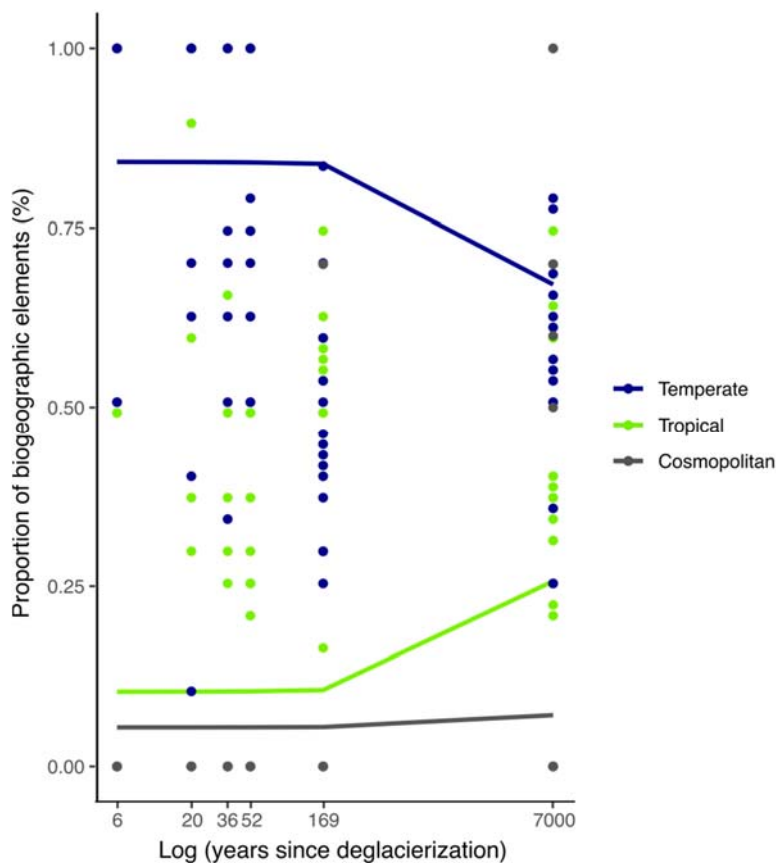
Fig. 5 Relations between the percentage of soil organic matter and the relative cover of the two most characteristic growth forms of zone 6: large tussock and upright shrub. (Red lines: significant linear regressions. SR: regression not applicable because too few values different from 0



3.3. Biogeographic origin

The Dirichlet model (Precision estimate: 1.5668; p-value: $<2e-16$; AIC: -731.7; Supplementary Material 6) predicted a relative increase of the temperate element and a relative decrease of the tropical element along the chronosequence (Fig. 6). In fact, 91% of the recorded species in Z1 plots were of temperate origin on average, while the remaining 8% were of tropical origin (Supplementary Material 4). In Z6, temperate species accounted for 72% of the sampled flora on average, while tropical species encompassed 22% and cosmopolitan species 6%. Temperate species were generally diverse in all zones, across plant families and growth forms. In contrast, tropical species were overall less represented and reached the highest elevations by the means of few species only, such as *Belloa kunthiana* and *Xenophyllum humile* (Asteraceae). The frequency trends observed were, in addition, variable among the three categories: tropical species decreased more rapidly than temperate species increased. Finally, cosmopolitan species were little represented, and followed a more linear decreasing trend along the chronosequence.

Fig. 6 Compositional changes at the biogeographic origin level along the chronosequence. Progressive changes in frequency of temperate, tropical and cosmopolitan species from the vegetation plot data and Dirichlet regression results with age of deglaciation



4. DISCUSSION

Collaborations between glaciologists and ecologists allow the use of a powerful space-for-time substitution approach: post-glacial chronosequences (Matthews 1992). Applied here to the highly phytodiverse páramo, it provides valuable insights on the climatic debt endured by plant communities during primary succession after rapid deglaciation, which will itself affect provisional, regulation and cultural ecosystem services in downstream areas (Luckman et al. 2008). We used this method to test to what extent the novel tropical alpine communities establishing after the retreat of glaciers differ from initial communities in terms of species, growth forms and biogeographic origins. However, it is to be noted that, despite our sampling efforts to reduce their effects, the parameters local topography, elevation and geomorphology can still explain a significant part of the observed variations.

4.1. Novel plant communities after deglaciation

Comparing novel plant communities that established less than 169 years ago with the (super)páramo communities described locally in the literature (Salamanca et al. 2003; Peyre et al. 2018) is a relevant way to determine how time constrains the establishment of tropical alpine communities after deglaciation. The fact that, above the LIA moraine, the first colonizing species *Agrostis foliata*, *Cerastium floccosum*, *Culcitium canescens*, *Erigeron chionophilus*, (group 2), *Baccharis caespitosa*, *Hypochaeris sessiliflora*, *Lachemilla nivalis*, *Luzula racemosa* (group 3), were characteristic species both in our sampling and in the above-cited works shows, to some extent, that the novel communities establishing after deglaciation develop common features with pre-existing communities. In contrast, the absence above the LIA moraine of *Calamagrostis effusa* (characteristic of the upper bunchgrass páramo; Salamanca et al. 2003), *Draba pennell-hazenii* (superpáramo endemic of the Central Cordillera) and *Senecio isabelis* (endemic of the páramo of los Nevados) reveals significant losses in the novel communities established less than 169 years ago in comparison with the initial species pool.

In parallel, the presence of *Rumex acetosella*, a non-native species from Europe, in the most recently deglaciated zone of the sampling is a flagship example of the rapid establishment of a few, novel species in

the tropical alpine communities. *R. acetosella* has been shown to be one of the most efficient invaders of tropical alpine communities in the tropical high Andes, with negative, competitive effects on native species (Llambí et al. 2018; 2020). Its presence shortly after deglaciation underlines its high capacity to rapidly colonize disturbed areas and contribute generating non-analogous tropical alpine communities. As well, the presence of the non-native *Bromus lanatus* in Z5 confirm the capacity for exotic plants to colonize alpine environments (see also Cavieres 2020). It should be noted, however, that *R. acetosella* was not observed along recent chronosequences in Ecuador and Venezuela (Anthelme et al. 2021; Llambí et al. 2021), although being frequently observed in these regions (Cuesta et al. 2017). These latter chronosequences are far less visited by tourists than the Colombian chronosequence under study (pers. obs.). The relationship tourism-invasive plants may thus deserve a focus in further investigations of this type.

Accordingly, from a taxonomical viewpoint and partially in line with hypothesis 1, the novel tropical alpine communities established in less than 169 years are not the same as the initial plant communities observed in the same superpáramo but not constrained by time (see also Losapio et al. 2021). Whereas species losses include characteristic, endemic and iconic species, whose absence may be detrimental to the completeness of the community, the few species gains concern only non-native species, with potential detrimental effects on the community organization. Further research on the species that are not able to colonize the chronosequence are needed, especially if they are present or absent at similar elevation but outside the chronosequence, in order to evaluate more precisely their future distribution in relation with their incapacity to rapidly colonize deglaciated areas.

From a methodological viewpoint, it is to be noted that the elevational difference between zone 4 and zone 5 might explain in part the variations found, underlining the potential limitation of using this specific chronosequence. However, the gradual changes observed in soil temperature plant community assembly along the chronosequence (see Supplementary Material 5 and Fig. 4) suggests that this parameter is not of major influence on our data.

4.2. Establishment lag for tropical alpine growth forms

Primary succession after rapid deglaciation generates differential colonization velocities among growth forms, primarily because of a dispersal lag, giving priority to wind-dispersed species (Alexander et al. 2018; Zimmer et al. 2018). The fact that the growth forms upright shrub and large tussock, known as characteristic of tropical alpine regions (Hedberg and Hedberg 1979; Rada et al. 2019), were found preferentially before the LIA and were observed in plots with higher soil organic matter content indicates, apart from dispersal constraints, that tropical alpine growth forms may be less able than more generalist growth forms to perform a rapid succession after deglaciation. Despite insufficient presence of the growth form stem rosette in our sampled plots to provide a significant statistical test, we expect that this tropical alpine growth form might as well require high levels of soil organic matter to develop (see also Urbina and Benavides 2015).

Organic soil formation in the tropical high Andes during primary succession is a very slow process, which requires thousands of years (Benavides et al. 2013; Khedim et al. 2021). Our data suggest that the soils above the LIA moraine (169 years and less) were not sufficiently developed to allow the frequent presence of dependent growth forms to establish themselves despite having the capacity to disperse easily from individuals located on the other side of the moraine (see also Llambí et al. 2021). Accordingly, in line with hypothesis 2, there would be a long-term constraint for plant establishment (establishment lag; Alexander et al. 2018) and this constraint would be growth form-specific, in accordance with results observed in nearby Ecuador (Sklenář et al. 2021). It may be exacerbated by the fact that these large, tropical alpine growth forms have been shown to increase the content in soil organic matter, and associated reduction in pH (see also Llambí et al. 2021), thus facilitating potentially the establishment of species requiring this type of habitat (Mora et al 2018; Llambí et al. 2020). Further soil analyses along chronosequences are expected to add consistence to this exploratory result.

It should be remembered, however, that in addition to the effect of soil on plant establishment, other environmental parameters influence the success of colonization of new alpine plant communities in the tropics. These include variations in dispersal abilities, cold and drought tolerance/avoidance, and the presence or absence of nurse plants to mitigate the effects of extreme local climatic conditions (Squeo et al. 1991; Zimmer et al. 2018; Rada et al. 2019).

4.3. Biogeography influences the establishment success

Taxa of tropical origin were under-represented compared to temperate species at the beginning of the succession and this imbalance was progressively corrected along the chronosequence. It shows that the first group may face a greater climatic debt than temperate species along the Conejeras chronosequence. This interpretation is consistent with biogeographic analyses showing that temperate alpine taxa, genetically pre-adapted to alpine climates, are better candidates for the colonization of tropical alpine environments after deglaciation (Sklenář et al. 2011; Gehrke 2018; Cruz-Maldonado et al. 2021). Our results moreover support previous observations that the temperate vs. tropical element ratio increases from the midpáramo to the superpáramo belt, recorded from 50/50 to 70/30 for Ecuador (Sklenář et al. 2011), even though our numbers suggest a more drastic drop for tropical taxa in Colombia. Additional records will help generalize the pattern and identify if historical factors, such as past corridors with Central America, help explaining the ratio difference along the latitudinal gradient. In fact, a recent study on the climatic refugia of páramo plant species at the regional scale has shown that tropical taxa likely found more refugia in the southern and central páramos of Peru and Ecuador, while taxa of temperate origin showed more diverse refugia patterns throughout the region, with an important refugium in the vicinity of the Nevados National Park (Peyre et al. in press).

Finally, the absence of *Espeletia hartwegiana* and *Diplostephium schultzii* above the limit of the LIA may explain (1) because of their tropical origin, which would make them less tolerant to elevation stress (see absence of *Espeletia* spp. in the highest peaks of the long-term observatories GLORIA in the northern Andes; Cuesta et al. 2017) and (2) because they develop large, tropical alpine growth forms that require highly organic soils (see section 4.2. and Fig. 2). For these reasons, *E. hartwegiana* and *D. schultzii*, two species iconic of the páramo of Los Nevados, can be considered as sentinel species when studying the effects of warming on the future distribution of tropical alpine plant communities.

5. Conclusion

According to the Colombian chronosequence, the primary succession initiated by the rapid retreat of the Conejeras glacier, consecutive to rapid warming, generates novel plant communities that differ from initial tropical alpine communities in terms of species and growth form composition and in terms of biogeographic origins. Especially, the establishment lag generated by the slow enrichment of soil organic matter seems to affect negatively and preferentially (1) characteristic, endemic and iconic species, (2) the tropical growth forms upright shrub and large tussock, and (3) taxa of tropical biogeographic origin. Therefore, and if we assume that the chronosequence used is a pertinent space-for-time substitution, the novel plant communities, which represent the future of the tropical alpine communities, could face substantial taxonomic and functional losses because of an exacerbated climatic debt. In return, they receive only a few, questionable quantitative gains, through the establishment of non-native species in the novel plant communities. This is illustrated by a picture taken in November 2021 where the first vascular species to colonize the glacier forefront, one year after glacial retreat, is *Poa annua* L., a non-native species (pers. obs.; SI2).

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Statements and declaration

Conflict of Interests/Competing Interests

The authors declare that they have no conflict of interest/competing interests.

Ethical approval

Anthelme F., Carrasquer I., Ceballos J. L., Peyre G. 2022. Novel plant communities after glacial retreat in Colombia: (many) losses and (few) gains. *Alpine Botany*, online. Doi : <https://doi.org/10.1007/s00035-022-00282-1>

This study does not involve research on human participants or animals.

Informed consent

Informed consent was obtained from all individual participants included in the study

Data availability statement All relevant data may be accessible via the VegAndes database upon request. Photographs of the species taken into consideration in the analysis are available at <https://identify.plantnet.org/fr/groups/19892283922>

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Additional supporting information in the online version of this article (see „Supplementary Material”) **contains the following:** ESM_1: description of the deglaciation zones, ESM_2 – Photograph of the glacier forefront, ESM_3: Species-area relationship, ESM_4: Species list and species characteristics, ESM_5: Temperature at each zone. ESM_6: Details of the Dirichlet regression presented in Fig. 6