

Glacial-fed and páramo lake ecosystems in the tropical high Andes

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Abstract The effects of climate change in the tropical Andes are predicted to be devastating. While changes altering hydrology are already occurring, our knowledge of high-altitude lentic ecosystems is limited. Therefore, we carried out a survey of 16 small (0.06–7.1 ha) and shallow (≤ 6.5 m) fishless lakes, above the treeline in the Ecuadorian Andes (≤ 3863 m). Our objectives were (a) to provide baseline data of representative lakes for future monitoring and research and (b) to identify environmental variables driving taxon richness and plankton biomass. We hypothesised that both would decline along

the altitudinal gradient. A range of geographical, physical and chemical data and samples of phytoplankton, zooplankton and benthic macrofauna were collected. We found that the lakes are cold, oligotrophic and have a low plankton diversity and biomass. We were able to show that altitude, depth, water chemistry and inflow of glacial meltwater are the most important variables controlling the lake biota. Furthermore, we identified two distinct types of lakes: highly turbid due to glacial runoff and clear watered lakes. These may represent different stages of lake development from newly formed, ultraoligotrophic pro-glacial lakes to oligotrophic páramo lakes.

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Introduction

The Andes in South America have a large density of tropical high-altitude (> 3800 m a.s.l.) lakes (Löffler, 1968) and are one of the most strongly affected places by climate change (Rabatel et al., 2013). The region's glaciers, which supply water to downstream ecosystems, are highly sensitive to the increasing temperatures, and thus glacial retreat may lead to large-scale hydrological changes (Buytaert et al., 2006). Initially, the number and size of pro-glacial lakes will likely increase (Carrivick & Tweed, 2013), but ultimately

the volume of meltwater inflow is expected to decrease, reducing niche heterogeneity both within lakes (Hylander et al., 2011) and at the landscape level (Jacobsen et al., 2012; Cauvy-Fraunié et al., 2015). Additionally, the warming may lead to the terrestrial vegetation belt shifting to higher altitudes allowing for the expansion of agriculture and cattle-raising (Buytaert et al., 2006), which will increase the amount of allochthonously derived organic matter and nutrient input to mountain waterbodies.

Above the treeline (ca. 3800 m a.s.l.), in the Northern Andes the dominant ecosystem is the páramo grassland, where the local climate is characterised by the lack of seasonal changes, low mean air temperature, large diel temperature variation and frequent winds (Buytaert et al., 2011). As a result, páramo lakes are cold polymictic without stable stratification, and the water transparency is low due to humic substances from the surrounding soil and vegetation (Aguilera et al., 2013). The perennial snowline (ca. 5000 m a.s.l.) sets the upper limit to the páramo, above which the landscape turns barren with scarce vegetation supplying little allochthonous organic matter to the waterbodies (Buytaert et al., 2011). Most Andean lakes are of glacial origin and many are still in contact with a glacier that provides cold and turbid meltwater from year-round glacier ablation, which has a strong influence on the high-altitude lake biota (Sommaruga, 2015).

Ecuador has 4% of the world's tropical glaciers (Rabatel et al., 2013) and shallow lakes with glacial origin are abundant in the country. In addition, many lakes lie in protected areas, which provide an opportunity to study high-altitude lentic ecosystems under near-natural conditions. Water extraction, recreational activities and agricultural use by indigenous communities are, however, often allowed. In fact, glaciers and the páramo region are the main water sources for many cities in the Andes (Buytaert et al., 2006). Thus, climate change could have an indirect but devastating impact on human populations and the downstream ecosystems, as it can bring about the disappearance of the glaciers by the end of the century (Rabatel et al., 2013). In light of the predicted climatic changes and their likely impact on tropical high-altitude lakes, it is crucial to enhance our knowledge of the state and function of these lakes. This will allow for the interpretation of data from future assessments and the implementation of appropriate management

strategies. However, comprehensive limnological studies including physical, chemical and biotic parameters of lakes in this region are currently lacking.

Therefore, the objectives of this study were twofold: (a) to characterise shallow, high-altitude lakes in the tropical Ecuadorian Andes with respect to the abiotic and biotic conditions, providing baseline data for future monitoring and research, and (b) to identify important environmental variables driving communities and species richness. High-altitude lakes in this region have no native fish fauna (Knapp et al., 2001); hence only fishless lakes were included. In general, we expected the lakes to be oligotrophic with low pelagic diversity and biomass of phyto- and zooplankton, as well as to have a low taxon richness of the benthic macrofauna. Based on visual observation during sampling, lakes displayed variation in their physical characteristics. Thus, we expected to find distinct lake types that significantly differ in their physical and chemical characteristics, and that these differences would be reflected in their biological attributes and community composition. Glacial meltwater has generally a limiting effect on the biomass and diversity of lake organisms (Sommaruga, 2015). As most Andean lakes are of glacial origin, the time since the lakes stopped receiving glacial meltwater decreases along the elevational gradient. Therefore, we hypothesised that biomass and taxon richness decline with increasing altitude. This would imply that the ongoing and predicted changes in climate will lead to significant changes within these ecosystems.

Materials and methods

Study area

The study involved 16 lakes located in the Ecuadorian Andes (Fig. 1). Lake selection was based on accessibility, comparability (size, depth and altitude) and the lack of fish. The absence of fish was confirmed by local knowledge and observations on site. Visually different types, clear and highly turbid, were included. All lakes were small (0.06–7.1 ha) and shallow (max. depth \leq 6.5 m), but permanent. They were located in five protected areas within the altitude range of 3863 and 5083 m a.s.l. (A1). Thus, all lakes lay above the treeline either in the páramo belt or even higher, where the vegetation cover was sparse. Five lakes had a

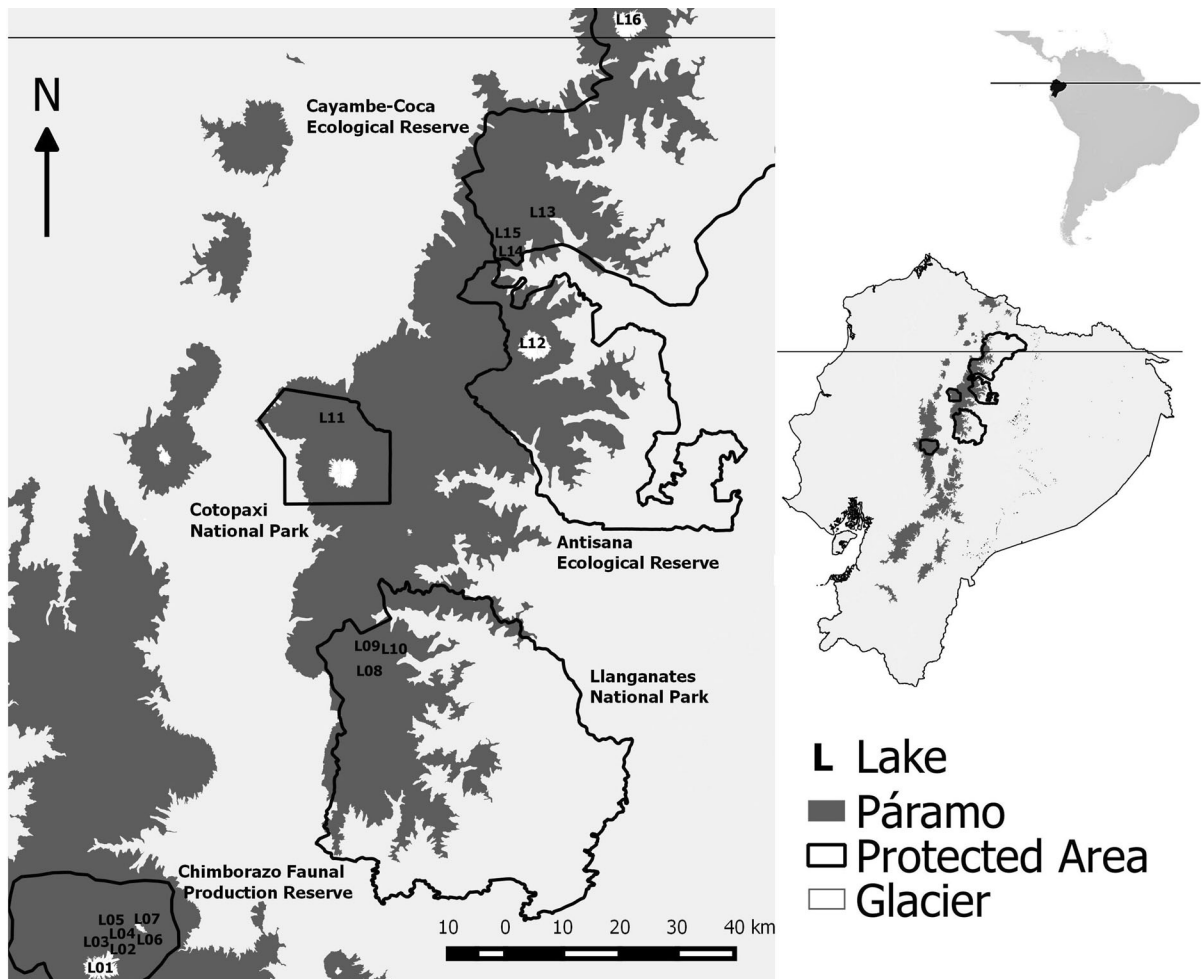


Fig. 1 Location map of the 16 lakes in Ecuador ($00^{\circ} 00' 54''\text{N}$ – $00^{\circ} 59' 11''\text{S}$, $78^{\circ} 00' 28''\text{W}$ – $78^{\circ} 50' 11''\text{W}$)

glacier within their catchment and received direct inflow of glacial meltwater. Sampling was carried out between November and January during 2014–2015 and 2015–2016, and sample processing was done within the next 1–2 months.

Field measurements and data collection

Site coordinates and altitude were obtained using the mobile phone application Motion X-GPS. The following measurements were taken on site as close to the centre as possible using a small rubber boat: Secchi depth using a white disc ($\phi = 22$ cm), pH (EcoTestr pH2), turbidity (Eutech TN100), oxygen saturation at 0.1 m and 3.0 m depths or at the bottom (YSI 55) calibrated at sea level and values later corrected for

altitude. Mean and maximum depths were determined via random recording (10–20 measurements per lake) using a digital echo-sounder (Hondex PS7). Surface (0.1 m) and bottom (3.0 m or bottom) temperatures, and conductivity (at 0.1 m, corrected for 25°C) were measured using a YSI 30 conductivity meter. To obtain a measure for grazing activity by wildlife and domestic animals, the number of animal droppings was counted in three 30-m-long and 4-m-wide strips perpendicular to the shoreline. The droppings were identified and the number of piles was recorded, except for rabbit droppings, which was assessed on a scale of 1–3. The distribution of droppings was expressed as a percentage of the total amount.

Lake water for chemical analyses was collected from the pelagic at 1 m depth as close to the centre as

possible. Known volumes of water (0.25–1 l) for chlorophyll *a* and particulate organic matter (POM) were filtered in situ through Whatman GF/C filters, which were folded and wrapped in aluminium foil. Duplicate samples were taken. A subsample from the GF/C filtered water was stored for coloured dissolved organic matter (CDOM) analysis. Three top-sediment core samples were collected for benthic chlorophyll content using a cutoff syringe ($\phi = 2.8$ cm). The top 0.5 cm was transferred to airtight plastic bags. Water samples for nutrient analysis were added to sterile plastic tubes. Pebbles, approx. 10 pieces of 1–2 cm length, were collected in the littoral zone at 5–20 cm for epilithic chlorophyll analysis. All samples were kept in dark and frozen until further processing.

Phytoplankton and crustacean zooplankton qualitative samples were collected using plankton nets of 20 and 200 μm mesh size, respectively. The nets were dragged 5–6 times from the centre towards the shore and the concentrated material was transferred to a vial. Lake water (250 ml) from the pelagic was collected at approx. 1 m depth for the phytoplankton quantitative analysis. A known volume of water (between 5 and 10 l) was poured through a 200 μm mesh net and the retained crustacean zooplankton transferred into a vial. All plankton samples were preserved using Lugol's solution (approx. 1 ml per 50 ml sample) and stored in cold and dark conditions. Benthic macroinvertebrates were collected with a D-net via stratified sampling based on substratum, taking one sample from each substrate (2-min sweeping per sample). Organisms were identified on location to the lowest possible taxonomic level and abundances were estimated on a scale from 1 to 4 (i.e. present, common, abundant and dominant). Representative individuals were preserved in 70% ethanol and taken to the laboratory to verify on-site identification.

The presence of macrophytes was assessed visually from the shore and from the boat, and the coverage in the littoral zone was ranked on a scale from 1 to 4 (i.e. present, common, abundant and dominant). The dominant macrophytes were only identified to the genus level.

Laboratory procedures

CDOM samples were filtered through Whatman GF/F filters and the absorbance at 440 nm was recorded with a spectrophotometer (Thermo Spectronic Heλios

β). Values were converted to Hazen Unit (HU, Pt l^{-1}) following Cuthbert and del Giorgio (1992). POM filters were dried overnight at 105°C, then weighed when cooled, followed by 3 h of burning at 550°C, and re-weighed after cooling. Sediment core samples were sucked dry through GF/C filters using a suction pump. Chlorophyll *a* extraction and measurement was carried out following Jespersen and Christoffersen (1987) for pelagic water ($\mu\text{g l}^{-1}$), surface sediment (mg cm^{-2}) and pebble surface ($\mu\text{g cm}^{-2}$). Filters containing phytoplankton, drained sediment samples and pebbles were covered with 96% ethanol and kept in dark at room temperature overnight. The extracts were filtered through GF/C filters, the total volume of ethanol was recorded and the absorbance at 665 and 750 nm was measured using a spectrophotometer (Shimadzu UV160A). The surface area of the pebbles was calculated according to Graham et al. (1988). The nutrient analysis was carried out using persulfate digestion following Koroleff (1970) for total phosphorus (TP) and Solórzano and Sharp (1980) for total nitrogen (TN). Water samples were placed in the autoclave for 30 min at 120°C with added potassium peroxydisulphate solution. TN ($\mu\text{g l}^{-1}$) was measured in an ALPKEM AutoAnalyzer and TP ($\mu\text{g l}^{-1}$) was determined by measuring absorbance at 882 nm in a spectrophotometer (Shimadzu UV160A).

Zooplankton samples were processed using an Olympus SZX12 stereo (7–90× magnification) and a BH2 light microscope. Specimen was identified and counted in each quantitative sample and the dimensions of 10 individuals per taxon were measured. The dry weight of individuals was calculated using standard length–weight regression following Hansen et al. (1992) and multiplied by the density to get the total zooplankton biomass ($\text{DW } \mu\text{g l}^{-1}$). Phytoplankton samples were processed using an Olympus IMT/2 inverted microscope (100–400× magnification). Qualitative samples were used to determine taxon richness. Identification was done to the lowest possible taxonomic level. The number of individuals in the dominating phytoplankton taxa (i.e. those making up approx. 95% of the sample) were counted in sedimentation chambers along random transects following Lawton et al. (1999) and Utermöhl (1958). The dimensions of 10 individuals per taxa were measured and their volume estimated from known geometric forms. In case of major size differences within taxa, individuals were divided into cell size classes. For

each taxon, the biovolume was calculated and the total biovolume ($\text{mm}^3 \text{ l}^{-1}$) for each sample was determined by adding the biovolumes of all taxa.

Data analysis

GIS analysis was carried out in ArcGIS (ESRI, USA). Lakes and glaciers were digitised using orthophotographs provided by the Instituto Geográfico Militar del Ecuador (IGM) and Google Earth images obtained from Google Earth Pro (v.7.1.5.157). Catchment delineation was carried out using the Hydrology toolset and Digital Elevation Model retrieved from the ASTER Global DEM dataset (v.2) via the Global Data Explorer, followed by manual correction using orthophotographs, personal observations and Google Earth images. Lake surface area, perimeter, catchment area and the area of the glacial cover within the catchment were calculated. The shortest, Euclidean distance between the lakes and glacier terminal was measured manually. The age of the lakes was estimated using historical aerial photographs provided by IGM. The oldest available photograph was from 1962 and thus the estimation for lakes formed before this year was not possible.

The environmental variables were analysed using PRIMER analytical software (v6, PRIMER-E Ltd, Plymouth, UK). Principal Component Analysis (PCA) using Euclidean distance was carried out on the log ($x + 1$)-transformed and normalised dataset including temperature, conductivity, pH, oxygen saturation, turbidity, Secchi depth, TP, TN, altitude, mean depth, surface area, perimeter length, catchment size, percentage glacial cover in catchment and distance from glacier. Variables with missing data were excluded (e.g. POM, CDOM). Using the results of the PCA and Cluster analyses, the lakes were grouped and the variables responsible for most of the variation on the PC1 and PC2 axes were identified. Similarly, PCA was carried out on 4 biotic variables (pelagic chlorophyll *a*, zooplankton biomass, number of phytoplankton and of benthic macroinvertebrate taxa). The means of environmental and biological variables were then compared between the groups using data analysis software R. The Shapiro–Wilk test was used to test for normality, followed by Bartlett’s test for normally distributed and Levene’s test for non-normally distributed data to test for homoscedasticity. The independent *t* test and the independent *t* test of unequal

variances were applied on parametric data, and the Mann–Whitney *U* test was used on non-parametric data.

Species composition analysis was carried out in Primer (v6) on the benthic macroinvertebrate data (Clarke & Warwick, 1994). The mean of the abundance scores (1–4) of each taxa was taken over all the subsamples in each lake. Non-metric Multi-Dimensional Scaling (NMDS) and Cluster analysis using Bray–Curtis distance were carried out to show how lakes group based on taxon composition. Additionally, multiple linear regression analysis in R was used to identify the abiotic factors responsible for the variation in the biotic variables (zooplankton biomass, pelagic chlorophyll, and phytoplankton and macrofauna diversity). Model selection was based on AIC scores.

Results

PCA of environmental variables

We collected physical, chemical and biological data from 16 lakes located above the treeline in the Ecuadorian Andes, five of which had a glacier in their catchment. As two groups of lakes appeared visually distinguishable, we tested if this grouping is supported by the measured environmental parameters. Principle component analysis (PCA) was carried out to assess similarities between lakes and to identify any grouping.

The first two PCA axes explained 61% of the total variation in the abiotic data (Fig. 2). The PC1 axis accounted for 39% of the total variance and was positively associated with temperature and distance from the glacier terminal, and negatively with percentage glacial cover of the catchment, altitude and turbidity. The PC2 axis accounted for 22% of the total variance. There was a positive association with Secchi depth and a negative association with pH and catchment area. The PCA plot and Cluster analysis showed a grouping of the lakes, which aligned with the grouping based on whether the lakes received glacial meltwater inflow or not. The first group consisted of the lakes with direct glacial influence (L01–L03, L12 and L16) and low vegetation coverage in the catchment. The second group comprised lakes that had no glacial inflow (L04–L11, L13–L15) and located in the

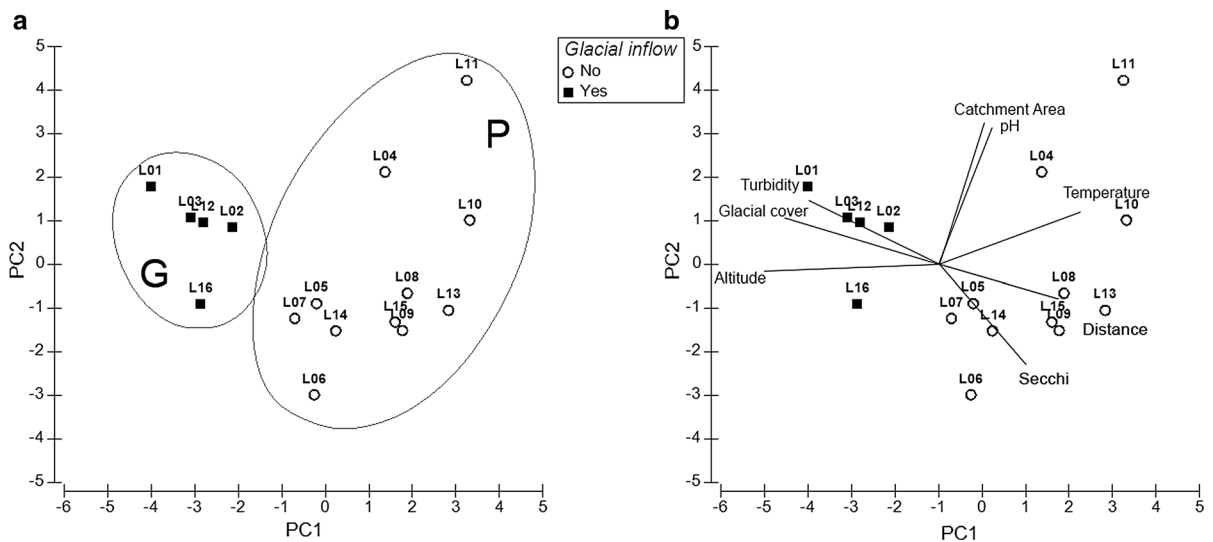


Fig. 2 Two-dimensional principal component analysis (PCA) ordination based on the 15 transformed ($\log(x + 1)$) and normalised environmental variables of the 16 high-altitude lakes from the Ecuadorian Andes. **a** PCA superimposed with grouping from the Cluster analysis with lines delineating the

páramo landscape. Hereafter the groups are referred to as 'glacial' and 'páramo', respectively. The statistics of the measured geographical, physical, chemical and biological variables for the two groups are summarised in Table 1.

Environmental variables

The pair-wise comparison of the environmental variables showed significant differences between the glacial and páramo lakes (Table 1). The glacial lakes were located at higher altitudes ($\bar{x} = 4840$ m, $W = 0$, $P < 0.001$), closer to the glaciers ($\bar{x} = 0.3$ km, $t = -3.7411$, $df = 10.01$, $P < 0.01$) and a significant portion of their catchment was covered by a glacier ($\bar{x} = 68\%$, $t = 8.59$, $df = 4$, $P < 0.001$). They were characterised by low temperature ($\bar{x} = 5.3^\circ\text{C}$, $W = 7$, $P < 0.05$), low Secchi depth ($\bar{x} = 36$ cm, $t = 3.56$, $df = 10.87$, $P < 0.01$), low TN:TP ratio ($\bar{x} = 4$, $t = 8.88$, $df = 11.41$, $P < 0.001$) and high turbidity ($\bar{x} = 173$ NTU, $W = 1.5$, $P < 0.01$). In contrast, the páramo lakes were found at lower altitudes ($\bar{x} = 4,218$ m), farther from glaciers ($\bar{x} = 14.3$ km) and had no glacier in their catchment. They were characterised by higher water temperature ($\bar{x} = 9.4^\circ\text{C}$), higher TN:TP ratio ($\bar{x} = 50$) and higher

different types of lakes: *G* glacial, *P* páramo. **b** The strength and the direction of the 8 most significant variables responsible for the variation in the environmental data (PC1 = 39% and PC2 = 22%)

Secchi depth ($\bar{x} = 221$ cm) and lower turbidity ($\bar{x} = 8$ NTU).

Biological variables

The top-sediment chlorophyll *a* content ($\bar{x} = 8.8 \mu\text{g cm}^{-2}$, $W = 6$, $P < 0.05$), zooplankton density ($\bar{x} = 42$ ind. l^{-1} , $W = 0$, $P < 0.01$) and zooplankton biomass ($\bar{x} = 121 \mu\text{g l}^{-1}$, $W = 55$, $P < 0.01$) of the páramo lakes were significantly higher than those of the glacial lakes ($\bar{x} = 2 \mu\text{g cm}^{-2}$, $\bar{x} = 0$ ind. l^{-1} and $\bar{x} = 0 \mu\text{g l}^{-1}$, respectively) (Table 1). The pelagic and epilithic chlorophyll *a* contents and the phytoplankton biovolume of páramo lakes also tended to be higher, although not significant ($P > 0.05$). The separation of lakes into the two categories was thus reflected in the biotic attributes. It was further supported by the PCA carried out on the biotic variables. The only difference was that L06 and L07 showed a closer association with glacial lakes than with the rest of the páramo lakes (A2).

Community composition

The total number of phytoplankton taxa identified in this study was 99 genera (A3). Páramo lakes had a

Table 1 Summary of statistics for the biotic and abiotic variables of the two types of high Andean lakes with significant differences and CV [Coefficient of Variation] (páramo $n = 11$, glacial $n = 5$; CDOM [Coloured Dissolved Organic Matter] páramo $n = 10$, glacial $n = 3$; POM [Particulate OrganicMatter] páramo $n = 7$, glacial $n = 3$; Sediment chl-*a* páramo $n = 10$, glacial $n = 4$; Epilithic chl-*a* páramo $n = 4$, glacial $n = 5$; Age páramo = 2, glacial = 5 and the rest of the páramo lakes are older, but the exact age is unknown)

	Páramo			Glacial		
	Range	Mean	CV (%)	Range	Mean	CV (%)
Geographical parameters						
Altitude (m a.s.l.)	3863–4619	4218	7	4729–5083	4840***	3
Surface area (ha)	0.21–7.10	1.91	121	0.06–2.20	0.84	105
Perimeter length (km)	0.18–1.35	0.52	70	0.10–0.65	0.49	50
Catchment area (ha)	5.6–713.4	109.4	194	66.2–169.7	127.2	35
without glacier ^a				7–79	39.4	94
Watershed: Lake surface area ^a	9–126	45	81	77–1103	413	101
without glacier ^a				19–197	79	
Glacial cover in catchment (%)	0	0	–	53–93	68***	27
Distance from glacier (km)	0.53–31.05	14.31**	87	0.09–0.55	0.30	63
Age (years) ^a	58 \leq	–	–	12–33	25	–
Physical parameters						
Mean depth (m)	0.40–3.20	1.82	61	0.60–5.32	2.69	79
Temperature (°C)	4.1–12.1	9.4*	32	3.3–7.1	5.3	31
Conductivity ($\mu\text{Si cm}^{-1}$)	10–107	34	87	6–25	15	50
Turbidity (NTU)	0–50	8	186	19–356	173**	87
Secchi depth (m)	0.42–5.50	2.21**	76	0.12–0.70	0.36	67
Oxygen saturation (%)	104–161	124	16	102–142	120	13
CDOM (mg Pt l^{-1}) ^a	12–201	63	92	17–222	98	112
Chemical parameters						
pH	5.6–9.1	–	–	5.1–8.5	–	–
Total phosphorus (TP; $\mu\text{g l}^{-1}$)	0–54	20	89	12–420	158	102
Total nitrogen (TN; $\mu\text{g l}^{-1}$)	27–868	414	69	30–395	142	109
TN:TP ^a	28–81	50***	31	1–11	4	101
Biological parameters^a						
POM (mg l^{-1}) ^a	1.8–8.4	4.1	61	2.7–5.8	3.9	42
Pelagic chlorophyll <i>a</i> ($\mu\text{g l}^{-1}$)	0.3–9.5	2.1	133	0.3–2.7	1.1	90
Sediment chlorophyll <i>a</i> ($\mu\text{g cm}^{-2}$)	1.0–33.2	8.8*	104	0.4–6.8	2	139
Epilithic chlorophyll <i>a</i> ($\mu\text{g cm}^{-2}$)	0.4–7.4	2.3	150	0.1–1.1	0.5	87
Phytoplankton biovolume ($\text{mm}^3 \text{l}^{-1}$)	2×10^{-2} –4	1	134	0.4×10^{-1}	1×10^{-1}	145
Zooplankton density (No l^{-1})	0–265	40**	194	0	0	149
Zooplankton biomass ($\mu\text{g DW l}^{-1}$)	0–462	121**	115	0	0	162
Number of phytoplankton taxa	12–45	30***	38	13–24	18	22
Number of benthic macrofauna taxa	4–11	8***	26	1–5	3	58

* Significant at the 0.05 probability level

** Significant at the 0.01 probability level

*** Significant at the 0.001 probability level

^aNot included in the PCA on the environmental variables

significantly higher number of taxa ($\bar{x} = 30$) than the glacial lakes ($\bar{x} = 18$, $t = -3.13$, $df = 13.57$, $P < 0.01$) and the composition differed as well (Fig. 3). The glacial lakes, L02 and L03, were dominated by cryptophytes and dinoflagellates with chrysophytes and cyanobacteria present. The other 3 glacial lake samples contained too few number of cells to be quantified. The páramo lakes had a diverse phytoplankton composition. Chlorophytes, dinoflagellates and euglenids dominated, and cryptophytes, chrysophytes, cyanobacteria and diatoms also contributed to the biovolume, along with a portion of ‘Other’ phytoplankton (i.e. phytoplankton that could not be identified or phytoplankton groups that individually made small contribution to the total biovolume).

The zooplankton identified belonged to three orders: Cladocera, Cyclopoida and Calanoida (Table 2a). Only two of the five glacial lakes had zooplankton in their quantitative samples with biomass composed of *Boeckella occidentalis* Marsh, 1906 and other calanoid copepods. The páramo lakes had a more diverse zooplankton composition dominated by a *Daphnia* complex (*Daphnia pulicaria*

Forbes, 1893, *Daphnia pulex* Leydig, 1860 and *Daphnia schoedleri* Sars, 1862) and *B. occidentalis*. The lower lying páramo lakes had higher biomass of daphnids, while lakes at higher altitude had more calanoids (Fig. 4c). While the density was below our detection limit (0.1 No l^{-1}) in the quantitative samples of three glacial lakes (L03, L12 and L16), the qualitative samples contained *Eurycercus* sp., *Daphnia* sp. and *Bosmina longirostris* (O. F. Müller, 1776).

In total, 20 benthic macroinvertebrate taxa were identified. The number of taxa in the páramo lakes ($\bar{x} = 8$) was significantly higher than that in the glacial lakes ($\bar{x} = 3$, $t = -5.3$, $df = 14$, $P < 0.001$). Hirudinea and Lumbriculidae were among the most abundant taxa in páramo lakes along with *Hyalella* and Chironomidae, while Nematoda and Chironomidae dominated in the glacial lakes (Table 2b). The multi-dimensional scaling plot of species composition showed an alternative grouping: L06 separated from the rest of the páramo lakes; L02 and L03 separated from the other glacial lakes and L07 and L02 grouped closely together (A4).

Macrophytes were present in almost all páramo lakes, but absent from most glacial lakes (A1). The coverage by macrophytes in the littoral zone, in relation to other substrate types, ranged from present to common. Only in one lake macrophytes dominated the littoral zone. One set of páramo lakes (L04, L08–L10 and L13) had a more developed aquatic plant community including *Myriophyllum*, Characea, Lilaepsis, Isoetes, *Callitriche*, *Potamogeton* and *Ranunculus*. The other set of páramo lakes had only small-growth plants: L05 and L15 contained Isoetes and *Crassula*, while L06 and L07 had only mosses.

There was no sign of terrestrial grazers in the area around the glacial lakes, while droppings of various animals were recorded around each of the páramo lakes. The native, small-bodied animals, such as duck (16%), alpaca (3%), rabbit (5%), tapir (1%) or deer (1%), were recorded less frequently, than larger, non-native grazers such as cattle (54%) and vicuña (19%). The distribution of grazers varied among areas. Domestic cattle were abundant in the Llanganates National Park, vicuñas were common in the Chimborazo Faunal Production Reserve and at the rest of the study sites only native animals were present.

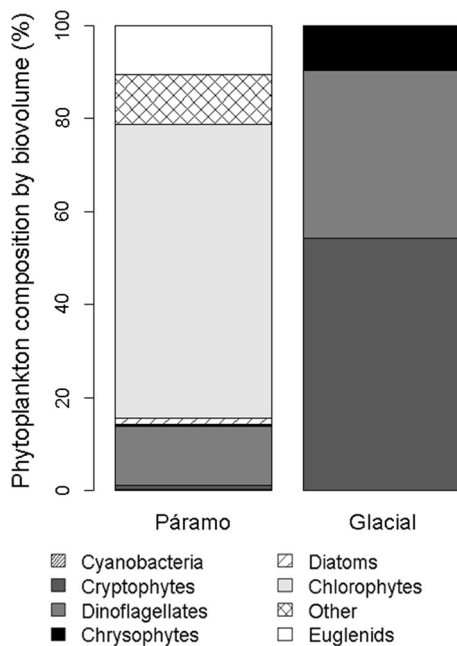


Fig. 3 Percentage contribution of major phytoplankton groups to the pelagic biovolume in the different types of shallow, high-altitude lakes in the Ecuadorian Andes (páramo $n = 11$, glacial $n = 5$)

Table 2 (a) Zooplankton composition with mean biomass and mean density values and (b) the benthic macroinvertebrate composition with the mean abundance values from lakes in the Ecuadorian high Andes (páramo $n = 11$, glacial $n = 5$)

	Páramo		Glacial	
	Biomass $\mu\text{g DW l}^{-1}$	Density No l^{-1}	Biomass $\mu\text{g DW l}^{-1}$	Density No l^{-1}
(a) Crustacean zooplankton				
Calanoida				
Calanoida indet.	30	27	1×10^{-2}	4×10^{-2}
<i>Boeckella occidentalis</i>	33	8	6×10^2	2×10^{-2}
Cyclopoida				
Cyclopoida indet.	6×10^{-2}	5×10^{-2}		
<i>Cyclops/Metacyclops</i>	1	3×10^{-1}		
Cladocera				
<i>Bosmina longirostris</i>	8×10^2	7×10^{-1}	a	a
<i>Chydorus sphaericus</i>	4×10^{-1}	3×10^{-1}		
<i>Daphnia</i> sp.	55	4	a	a
<i>Eurycercus</i> sp.			a	a
	Páramo		Glacial	
(b) Benthic macroinvertebrates (mean abundance score on a scale 1–4)				
Non-insect				
Bivalvia	0.43			
Hirudinea	1.47			
<i>Hyalella</i>	2.57			
Hydracarina	1.20			
Nematoda	0.57		0.80	
Lumbriculidae	1.30		0.60	
Oligochaeta indet	0.30		0.40	
Ostracoda	0.88			
Planariidae	0.23			
Insect				
Dytiscidae	0.06			
Coleoptera indet	0.10			
Corixidae	1.13			
Limnephilidae	0.40		0.40	
Trichoptera indet	0.05			
Orthoclaadiinae	0.20		0.60	
Podonominae	0.07			
Chironominae sp 1	0.50			
Chironominae sp 2	0.90		0.80	
Muscidae			0.40	

^aFound only in qualitative, net samples

Relationship between environmental and biological variables

The relationship between altitude and nutrient content was negative but weak for TN and positive but weak

for TP. The molar ratio of TN:TP, however, did show a strong, linear relationship with altitude (Adj. $R^2 = 0.44$, $F_{1,13} = 12.2$, $P < 0.01$), i.e. as altitude increases, the ratio decreases (Fig. 4a).

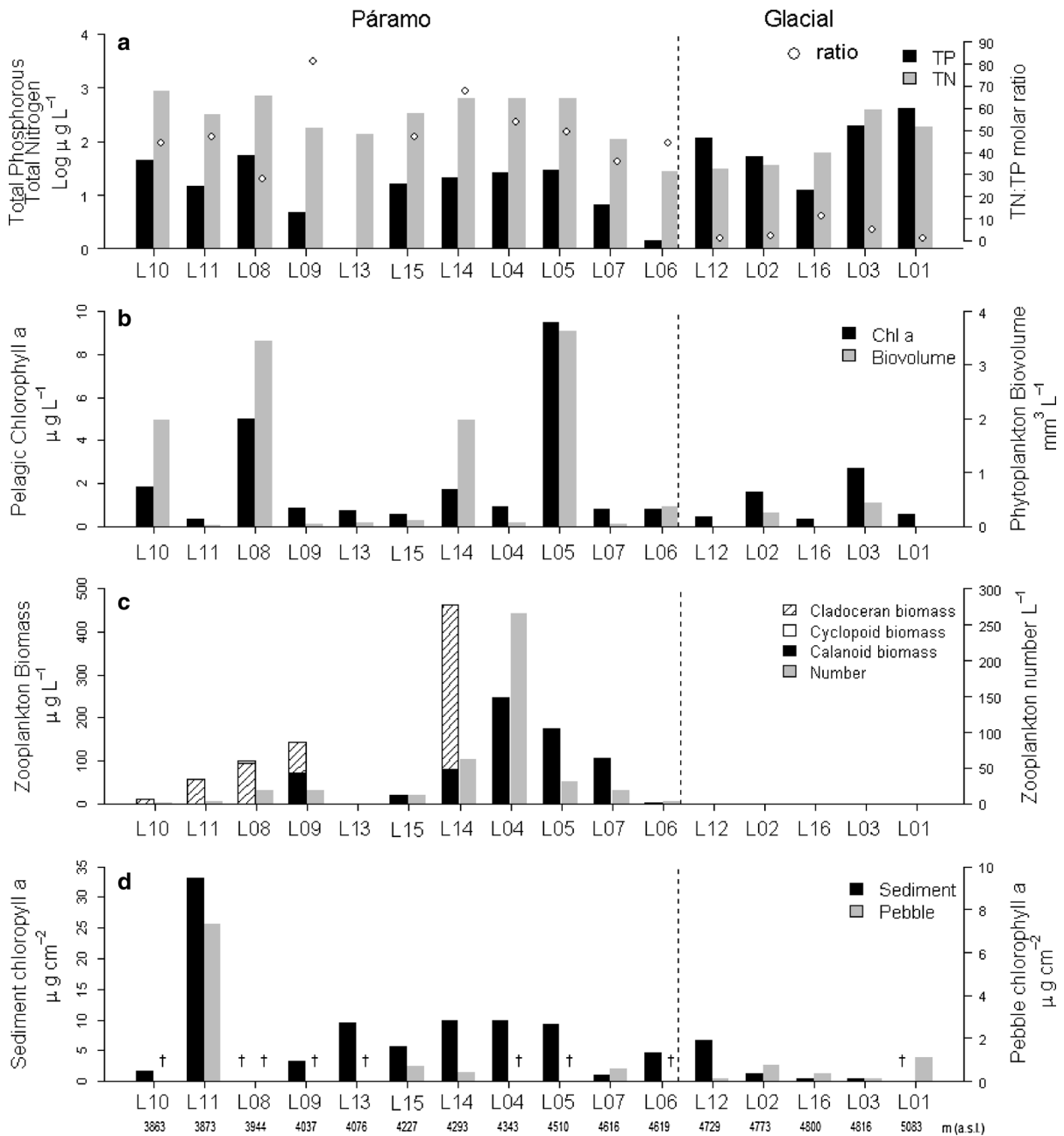


Fig. 4 Nutrient content and biological attributes of 16 shallow, high-altitude lakes in order of increasing altitude (3863–5083 m a.s.l.) from the Ecuadorian Andes († missing data)

Pelagic and sediment chlorophyll concentration and zooplankton biomass did not vary significantly with altitude (Fig. 4b, d). The only measured abiotic variable that explained some variation (Adj. $R^2 = 0.22$) in the pelagic chlorophyll *a* data was total nitrogen ($F_{1,14} = 5.1$, $P < 0.05$). The number of

phytoplankton genera significantly decreased with altitude and increased with conductivity ($F_{1,13} = 12.77$, $P < 0.001$), accounting for 61% of the variation (Adj. $R^2 = 0.61$). Zooplankton biomass had a significant positive, linear relationship with TN and a negative, linear relationship with mean depth

with interaction between the two variables ($F_{3,12} = 7.36$, $P < 0.01$) explaining 56% (Adj. $R^2 = 0.56$) of the variation. The number of benthic macroinvertebrate taxa significantly increased with temperature and \log_{10} distance from the glacier terminal and decreased with altitude ($F_{5,10} = 22.09$, $P < 0.001$). The model selected based on Akaike information criterion (AIC) scores included the interaction terms of altitude with temperature and altitude with \log_{10} distance, and it explained 88% of the variation (Adj. $R^2 = 0.88$).

Discussion

Our results bring further support to the previous but few descriptions of pristine tropical high-altitude lakes as being cold oligo- and ultraoligotrophic waterbodies (e.g. Steinitz-Kannan, 1979). The phytoplankton and zooplankton biomass and taxon diversity are generally low and comparable to alpine lakes in temperate regions (reviewed in Laybourn-Parry & Bell, 2012), African mountain lakes (Eggermont et al., 2007) and Arctic oligotrophic lakes (reviewed in Lizotte, 2008 and Rautio et al., 2008). Besides these general features, the lakes in this study could be divided into two distinct groups: páramo and glacial.

The cold and highly turbid glacial lakes are harsh environments, under which only the most tolerant phytoplankton groups can be found, such as cryptophytes, dinoflagellates and chrysophytes. In contrast, the páramo lakes have a higher number of phytoplankton taxa and are dominated by chlorophytes. The higher diversity is related to lower elevation and higher conductivity, which is likely driven by catchment characteristics (Nöges, 2009). Glacial lakes have typically very sparsely vegetated catchments due to the presence of glaciers, frozen soil and dry, epilithic surfaces, which limits processes leading to nutrient supply. Contrary to our expectation, the phytoplankton biomass did not differ significantly between the two lake types and could not be strongly linked to any measured abiotic variable.

Despite the similarity between glacial and páramo lakes in food availability for secondary production, the latter had markedly higher crustacean zooplankton density and biomass. This could be because zooplankton is limited by density-independent factors, such as low temperature or high turbidity in the glacial lakes,

due to differences in the palatability of food items or due to the inference of glacial flour particles with Cladoceran zooplankton feeding. In the case of the páramo lakes, lake depth and total nitrogen content are also important. The shallower lakes with higher nitrogen content have higher zooplankton biomass. The zooplankton composition in the lowest lying páramo lakes is dominated by the cosmopolitan cladoceran species *Daphnia pulex* and *D. pulicaria*. As altitude increases, copepods, mainly calanoids, become more dominant. The most abundant copepod species in the glacial lakes is *Boeckella occidentalis*, which is common in high-altitude lakes in Ecuador (Torres & Rylander, 2006) and throughout South America (Menu-Marque et al., 2000). Cladocerans are often absent from highly turbid waters, because the particle size of their food spectrum overlaps with that of the glacial flour. Therefore, under low phytoplankton density and high glacial flour load, non-selective filter feeders like daphnids will ingest large quantities of particles with low nutritional value and therefore do not thrive. In contrast, copepods, which have a more efficient and targeted feeding strategy and a wider range of food items, may be less affected (Koenings et al., 1990). Despite this, we found cladocerans in the glacial lakes, but only in insignificant numbers.

The benthic macrofauna of the páramo lakes is characterised by *Hyalella*, a common South American genus (Väinölä et al., 2008), Hirudinea, chironomids, which are common at high altitudes all over the world (e.g. Jacobsen, 2008; Čiamporová-Zat'ovičová et al., 2010) and other aquatic insects. The abundance of macroinvertebrates is low in these lakes, while they are almost absent from the glacial lakes. Due to the high altitude and the close proximity to glaciers, the lake water is cold and turbid, which limits taxon diversity, similar to glacier-fed streams (Jacobsen et al., 2010; Kuhn et al., 2011). Furthermore, the littoral zone of páramo lakes is more heterogeneous and has some macrophytes, and the benthic primary producer biomass is higher providing more niches, protection and food.

Macrophytes are an integral part of high-altitude lake ecosystems, where they can provide nursing habitats for invertebrates and likely also function as protection from the high UV radiation for all aquatic fauna. In this study, we found that glacial lakes have almost no macrophyte development, while various taxa were present in the páramo lakes. Clearly, the

glacial lakes being unstable and with low transparency is not a suitable habitat for macrophytes to establish.

Overall, it seems that taxon diversity in lakes in the Ecuadorian Andes does decline along the altitudinal gradient following general patterns described in other parts of the World (Huss et al., 2017) and is supporting our hypothesis. On the other hand, as a large portion of the variation in the data remains unexplained, other factors, for example, colonisation and succession rates, may also play a role. The two youngest páramo lakes (L06 and L07), which ceased to receive melt-water relatively recently, i.e. approx. 58 yrs ago, have the physical and chemical characteristics of páramo lakes, but their biological attributes are more similar to glacial lakes. Thus, these lakes might represent a transition phase between glacial and páramo lakes along a gradient of decreasing glacial influence and altitude.

Considering the predicted impacts of climate change, this transition between lake types has implications for the future state of these ecosystems (Peter & Sommaruga, 2017). Firstly, as the climate warms, the influence of glaciers will decrease markedly both on the function of individual lake ecosystems and on the landscape level. Similar changes in community composition and structure in response to decreasing glacial influence and increasing temperatures have been observed in temperate (Khamis et al., 2014; Sommaruga, 2015) and Arctic glacier lakes (Smol et al., 2005), as well as tropical glacier-fed streams (Jacobsen et al., 2012; Cauvy-Fraunié et al., 2015). Furthermore, Michelutti et al. (2016) found that páramo lakes are becoming thermally stratified due to the rising temperature and the declining wind velocity, which in turn results in a shift in the species composition and the biological structure (Michelutti et al., 2015). Finally, changing climate will likely bring about an expansion of terrestrial vegetation, which may provide more grazing sites and thus allow for more intensive cattle grazing in the region (Jampel, 2016). Nitrate leaching to freshwater bodies has been linked to increased grazing activity (Di & Cameron, 2002) with the highest rate from domestic cattle (Hoogendoorn et al., 2011). We could not link grazing activity to nutrient input to the lakes. However, we found higher density of droppings from introduced grazers, such as cattle and vicuñas, compared to native species. Additionally, these animals are bigger and occur in herds; therefore, it is likely that they increase

nutrient transport across the landscape when they come to the lakes to drink. Given that the phytoplankton and zooplankton biomass did show a small response to increasing total nitrogen and the lakes are oligotrophic, their trophic status and community composition might change in response to increasing nutrient inputs in the future.

This study provides an insight to the physical, chemical and biological features of a range of high-altitude lakes in the tropical Andes, and a glimpse into the likely near-future evolution of glacial lakes that climate change is expected to trigger. However, research effort should be increased to cover a larger spatial and temporal scale, and further empirical studies are required to understand the trophic interactions, biodiversity patterns and nutrient cycling in these ecosystems. Furthermore, monitoring the lakes and time series measurements of the biological response coupled with local climatic data are crucial for predicting the future changes as climate change advances.

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