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Abundance and morphometry changes across the high-mountain lake-size gradient in the tropical Andes of Southern Ecuador

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Key Points:
- The tropical high-mountain lakes show power-law lake-size distributions truncated at both ends similar to those found in temperate ranges
- The marked relief limits the size of the largest lakes at high altitudes, whereas ponds are particularly prompt to a complete infilling
- Lake volume scales to lake area according to a larger coefficient than found in other lake areas of glacial origin but gentle relief

Supporting Information:
- Supporting Information S1

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Abstract The number, size, and shape of lakes are key determinants of the ecological functionality of a lake district. The lake area scaling relationships with lake number and volume enable upscaling biogeochemical processes and spatially considering organisms' metapopulation dynamics. These relationships vary regionally depending on the geomorphological context, particularly in the range of lake area <1 km^2 and mountainous regions. The Cajas Massif (Southern Ecuador) holds a tropical mountain lake district with 5955 water bodies. The number of lakes deviates from a power law relationship with the lake area at both ends of the size range; similarly to the distributions found in temperate mountain ranges. The deviation of each distribution tail does not respond to the same cause. The marked relief limits the size of the largest lakes at high altitudes, whereas ponds are prompt to a complete infilling. A bathymetry survey of 202 lakes, selected across the full-size range, revealed a volume-area scaling coefficient larger than those found for other lake areas of glacial origin but softer relief. Water renewal time is not consistently proportional to the lake area due to the volume-area variation in midsize lakes. The 85% of the water surface is in lakes $>10^4$ m^2 and 50% of the water resources are held in a few ones ($\sim$10) deeper than 18 m. Therefore, midlakes and large lakes are by far more biogeochemically relevant than ponds and shallow lakes in this tropical mountain lake district.

1. Introduction

Many ecological processes in lakes scale with size [*Fee*, 1992; *Post et al.*, 2000]. Lake-size distributions play a pivotal role from biogeochemistry to community ecology; e.g., for upscaling metabolism or emission processes to regional and global contexts or investigating species distribution and metacommunity dynamics. Based on this interest, the estimation of the number of Earth's lakes indicated that they could be power law distributed across the full-size gradient [*Downing et al.*, 2006]. In the initial data sets used, nonetheless, there was a cutoff for small lakes or were operatively underrepresented. Consideration of a broader size range has shown that small lakes deviate from the power law distribution and are less abundant than previously expected, although they still dominate inventories [*Cael and Seekell*, 2016]. Consequently, there is a current need to investigate the regional patterns of small water bodies (subkilometer scales) and unveil the geomorphological processes that may drive and constrain them.

Remote lakes, defined as those in which human activities in the catchment are not the primary drivers of their dynamics, are of interest for tracking the footprint of global change at regional and planetary scales [*Hobbs et al.*, 2010; *Catalan et al.*, 2013]. Many of these lakes are of glacial origin and located in high mountains all over the planet and Arctic and subarctic regions. They are typically relatively small [*Catalan et al.*, 2009] and thus their abundance may likely deviate from the general Earth's scaling [*Cael and Seekell*, 2016]. In the case of mountain lakes, the relieve imposes additional topographical limitations that cause deviations from lake-size distributions in flatter regions [*Seekell et al.*, 2013]. There is an increasing relevance of high-mountain lakes in the assessment of global change, including climatic [*Smol*, 2012; *O'Reilly et al.*, 2015], pollution aspects [*Grimalt et al*., 2001; *Yang et al*., 2010] and the interaction among both [*Psenner and Schmidt*, 1992]. To increase the reliability and comparability of the observations, it becomes fundamental to develop comprehensive regional mountain lake inventories and characterize the abundance-area distribution across the lake-size gradient. Recent changes in the thermal seasonal patterns in remote lakes are calling attention in the current warming situation [*Sorvari et al*., 2002; *Smol*, 2012]. Inevitably, observations are performed on a few sites. The degree by which the observations can be extended to a large number of lakes requires some regional knowledge of the lake basin morphometric scaling. Under a similar external forcing, the physical behavior of lakes depends on to the lake aspect ratio (area versus volume) [*Imberger*, 2012]. The available data on lake volume distributions are more limited than the lake area ones as the former cannot be easily inferred from remote sensing and GIS modeling as the latter. In practice, it is commonly assumed that the lake volume-area scaling does not change for lakes of similar origin. However, this assumption may not always apply, or dispersion around a general pattern may be high [*Cael et al*., 2017]. Some lakes may be on watersheds with relief, bedrocks or soils that erode more quickly than others. On the other hand, high-mountain lake districts provide excellent frameworks for the understanding of species distribution in habitats that occur discretely (that is as "islands") in a matrix of unsuitable leaving space for organisms [*de Mendoza et al*., 2017]. The metapopulation and metacommunity dynamics of the species highly depend on the abundance, density, and size structure of the habitats [*Logue et al*., 2011]. One can expect that research on this topic will increasingly take advantage of the high-mountain natural experimental setting.

There is an increasing interest in tropical high-mountain lake systems and climate change [*Michelutti et al*., 2015a]. The information about these ecosystems is sparser than for mountain lakes in temperate zones [*Catalan and Donato-Rondón*, 2016]. Particularly, there is still only a partial knowledge of the seasonal and interannual variability in the lake mixing and stratification patterns. If there is any current paradigm, this is based on a few sites of unknown representability for the whole set of lakes. A large group of tropical high-mountain lakes is situated along the Andean range in the equatorial zone (i.e., at Venezuela, Colombia, Ecuador, Peru, and Bolivia), above the tree line, between 3500 and 4500 m asl in the Paramo ecosystem [*Gunkel*, 2000; *Donato-Rondón*, 2010]. These lakes play a significant role in the hydrology of the region by regulating the availability and supply of water. Eventually, they feed both the great tributaries of the Amazon and rivers draining to the Pacific Ocean. Part of the water is used for human consumption, industry, irrigation, and electricity generation for millions of people who live in or nearby the Andean range [*Luteyn*, 1992; *Buytaert et al*., 2006]. Climate change may result in severe threats for water supply [*Bradley et al*., 2006]. Despite their relevance as ecosystems and water resources, there is little information available on the limnology of the Andean tropical lakes [*Catalan and Donato-Rondón*, 2016; *Van Colen et al*., 2017]. Some of the studies were carried out in the 1980s and 1990s [*Steinitz-Kannan et al*., 1983; *Donato-Rondón*, 2010] but knowledge on the hydrogeomorphology of these lakes is extremely scarce [*Rivera Rondon et al*., 2010].

In Ecuador, most of the high-mountain tropical lakes are situated within national protected areas, out of which, 17 areas are found entirely or partially in the Paramo mountain belt [*Steinitz-Kannan*, 1997]. Herein, the Cajas National Park (Cajas NP), located in the austral region of Ecuador, contains a large number of lentic systems, which provide drinking water to nearly the 60% of the population of Cuenca, the third largest city in Ecuador. In fact, the National Park is embedded in a large UNESCO Biosphere reserve comprising the entire Cajas Massif. In this area, geomorphological processes occurring at the last glacial period resulted in an exceptionally high density of lakes above 3400 m asl (i.e., 13 lake km^{-2}). In this study, we aim at characterizing the lake's morphometry across the full-size gradient and providing scaling relationships for the region and similar tropical high-mountain lake districts in the Andes. We performed an inventory of all the high-mountain lakes of glacial origin in the Cajas Massif and determined their area using GIS information. For a representative lake subset in the Cajas NP, we carried out a bathymetry survey to complete the morphometric characterization. We compare the relationships found with those in other alpine and lowland locations and discuss the results according to current geomorphological theories. The lake abundance and morphometric relationships derived constitute a comparative framework for current and future ecological, biogeochemical and physical research in these lakes and the basis for a more robust geographic upscaling of the processes investigated and informed management of the protected areas.

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2. Materials and Methods

2.1. The Region and Study Sites

The studied lakes are situated in the Cajas Massif by the south of Ecuador, between 3°11′26″ and 2°40′21″ South; and 79°9′09″ and 79°17′57″ West. An inventory of all the lakes and ponds of glacial origin (5955) was intended for the region, and a representative subset of them (202) was selected within the Cajas NP for a bathymetry survey (Figure 1). For the sake of brevity, we will use "lake" as the general name for water

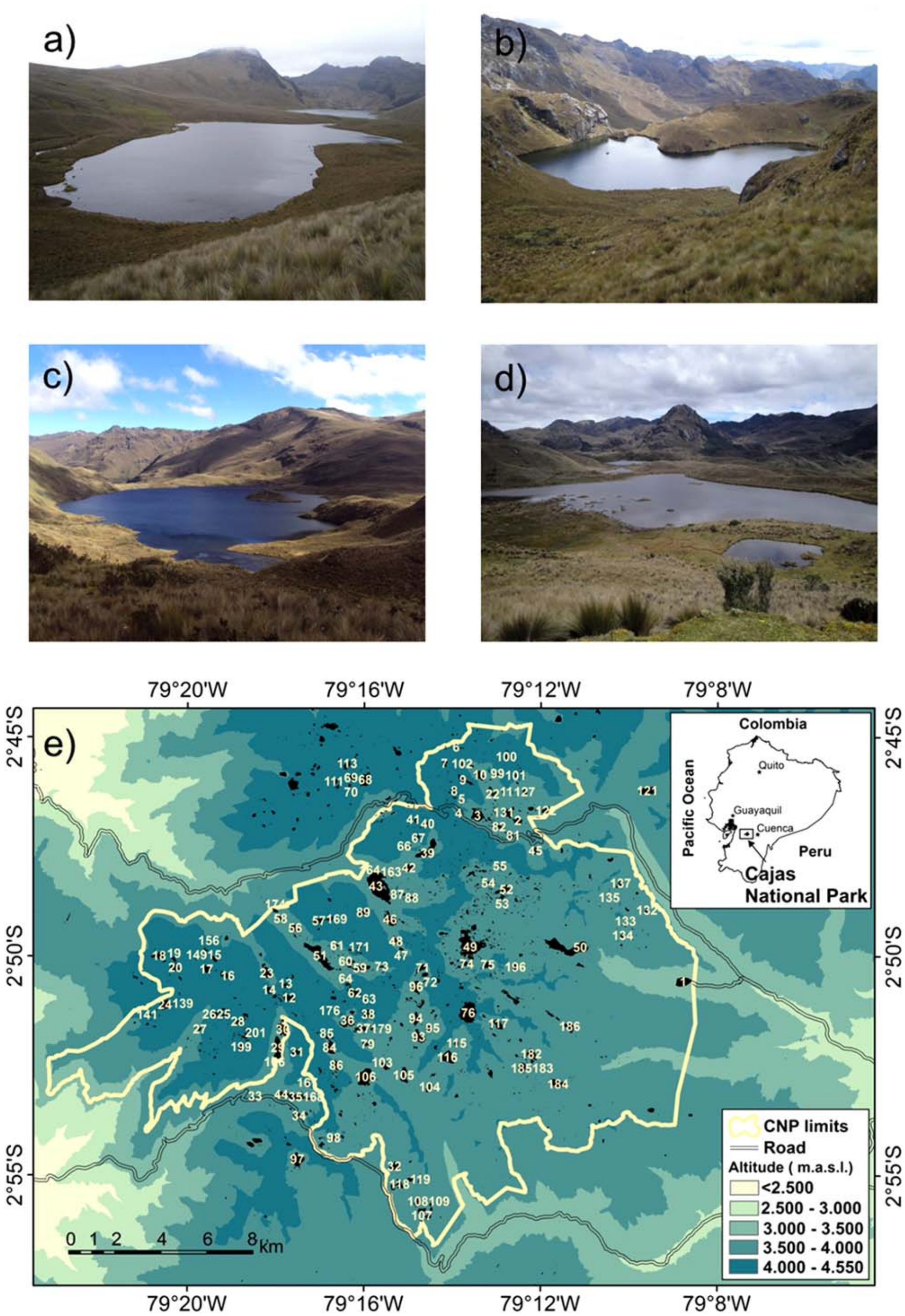

Figure 1. Some representative lake images from the Cajas National Park (CNP) ((a) Cascarilla 3–086, (b) Fondococha-007, (c) Luspa-043, and (d) Apicocha 1–081) and (e) a map with an indication of the lakes included in the bathymetry survey. The numbers refer to identification codes that have been used in the scope of the current study (see supporting information Table S1).

bodies of any size throughout most of the text. The 45% of the area drains to the Pacific Ocean, and the remaining 55% to the Atlantic. The primary bedrock is volcanic (Tarqui formation), including rhyolite, andesite, tuff, pyroclastic, and ignimbrites [*Hungerbühler et al*., 2002]. The regional geomorphology was shaped by glacier activities until the late Pleistocene when the ice retreated around 17,000–15,000 years ago [*Colinvaux et al*., 1997; *Hansen et al*., 2003; *Rodbell et al*., 2009]. Part of the glacier footprint is a large density of relatively small lakes above 3400 m above the sea level (asl), except Lake Llaviucu located at a lower altitude (3146 m asl) at the backside of a terminal frontal moraine of a large glacial tongue. The main soil types at the region are nonallophanic Andosols and Histosols from volcanic origin [*Borja and Cisneros*, 2009; *Crespo et al*., 2011]. Both types present dark colored epipedons characterized by high organic matter content, high porosity, low apparent density (400 kg m^{-3}) and a high water retention capacity (in average, 6 g g^{-1} at a pressure of 1500 kPa), with higher values in the H horizon [*Buytaert et al*., 2005]. Most of the rainfall is retained in soils and released gradually to the water courses, regulating the hydrology of these ecosystems [*Poulenard et al*., 2003; *Buytaert et al*., 2005]. The vegetation in 91% of the total extent of the Cajas NP and about 50% of the massif is herbaceous with a dominating presence of the genera *Stipa* and *Calamagrostis* [*Ramsay and Oxley*, 1997]. Concerning woody vegetation, only *Polylepis* species are present above the 3400 m asl. Lower altitudes—below the alpine lake inferior limit—are covered by the high-mountain forest ("bosque montano"). At present, the main impacts of land use and human activities on vegetation are tourism, fishery, grazing, and localized burning of the vegetation. Annual precipitation is between 900 and 1600 L m^{-2} yr^{-1} with contrasting seasons and high variation from year to year [*Vuille et al*., 2000; *Celleri et al*., 2007; *Padrón et al*., 2015]. High rainfall causes enhanced soil erosion with deposition of light-colored clastic laminae in the sediments of some lakes [*Rodbell et al*., 1999].

2.2. Lake Inventory and Area, and Perimeter Estimation

The boundaries of each lake were generated by heads-up digitalization of the aerial photographs of the project SIG-Tierras (2010–2014, www.sigtierras.gob.ec/) for the zone of the Cajas Massif. The images were orthorectified and georeferenced and had a spatial resolution of 30×30 cm^2. Only one digitizer performed the manual task, for consistency, and several people repeatedly checked for omissions and mistakes. ArcGIS 10.0 (ESRI Inc., Redlands, CA, USA) was used with a screen zoom of the photographs always below a scale of 1:200. The scale of cartographic digitalization was 1:5000. The area and perimeter of each lake were calculated from the digitized contour shapefile using the ArcGIS 10.0 calculator and the altitude from the raster of the SIG-Tierras digital elevation model that has a spatial resolution of 3×3 m^2.

2.3. Bathymetry Survey and Lake Basin Modeling

A selection of 202 lakes and ponds, covering the full-size gradient, was made to perform a bathymetry survey (supporting information Figure S1) within the Cajas NP (Figure 1). The survey was carried out with the aid of an inflatable rubber boat (Navigator II, RTS, China), approximately 3.5 m long, equipped with a propeller (2 HP, Yamaha, Japan) and an echo sounder Humminbird® model 1198c SI (Eufaula, AL, USA). The previously digitized lake boundary was used as zero-depth reference and for the planning of the number of gridded profiling transects and the spacing between them according to the lake size: for lakes with area > 0.2 km^2, the transect spacing was around 100 m; for lakes between 0.1 and 0.2 km^2, around 50 m; and for lakes < 0.1 km^2, around 25 m. The distance between the bathymetry points not exceeded 5 m. In the shallow lakes and ponds, where the use of the boat was not possible, measurements were taken at several points of the water body using a topographic measuring rod.

The digital bathymetry procedure is described in detail in the supporting information Text S1. The main steps included: (i) integration of the depth data collected in the field with the data derived from the digitalization of the orthophotos (i.e., boundaries of the lakes associated with zero depth); (ii) data preparation according to the demands of the following processing steps; (iii) selection and application of an appropriate interpolation algorithm for each lake, in total, ten interpolation methods were tested [*Franke and Nielson*, 1980; *Franke*, 1982; *Renka*, 1988; *Hanselman and Littlefield*, 1998; *Wise*, 2000; *Vivoni et al.*, 2005; *Vázquez and Feyen*, 2007; *Eldrandaly and Abu-Zaid*, 2011]; and (iv) production of the digital bathymetric models and geomorphological parameters. Given the number of lakes considered in the bathymetry survey, the interpolation and quality control analyses were carried out automatically, using the programming framework that Surfer® 13.0 enables in conjunction with PERL (Practical Extraction and Report Language) subroutines.

Table 1. Morphometric Descriptors of the 202 Lakes and Ponds Included in the Bathymetry Survey of the Cajas National Park (Ecuador)

Variable	Acronym	Unit	Mean	Median	Minimum	Maximum
Area	A	m^2	58,860	25,708	6	774,775
Perimeter	S	m	1,146	895	10	8,795
Fetch	Fetch	m	324	271	4	1,563
Maximum length	L_{max}	m	341	274	4	2,142
Maximum width	B_{max}	m	175	153	2	956
Mean width	B_{mean}	m	105	92	1	531
Volume	V	m^3	692,717	38,046	0.6	22,369,167
Maximum depth	Z_{max}	m	11.0	6.0	0.2	75.5
Mean depth	Z_{mean}	m	4.2	1.9	0.1	30.6
Shoreline development	D_L		1.6	1.5	1.0	3.1
Volume development	D_v		1.0	1.0	0.4	1.8
Z_{mean}/Z_{max} ratio	Z_{mean}/Z_{max}		0.3	0.3	0.1	0.6
L_{max}/B_{mean} ratio	L_{max}/B_{mean}		3.3	2.9	1.4	9.9
Relative depth	Z_r	%	4.6	4.2	0.1	15.5
Watershed area	A_w	km^2	2	1	0.000015	48
A_W/V ratio	A_W/V		173	12	0.1	10,113
Water renewal time	t_{WR}	Day	167	48	<1	4,261

From the digitalized lake basins several morphometric variables and indicative ratios were determined (Table 1). Fetch, defined as the maximum distance that the wind can travel on the surface of the water before it is intersected, was estimated according to *Hakanson* [1981].

3. Results

3.1. Lake Abundance and Size

In the Cajas Massif, all the lakes of glacial origin are < 1 km^2 in area. Lake abundance (N) increases with declining area (A). Although the fitting of a scaling factor (b) is significant, the distribution deviates from a true power law at both ends (Figure 2a).

$$N \sim A^b \tag{1}$$

The deviation in the low-size range is not related to a methodological bias as the distribution starts to diverge at values without orthophoto image resolution problems for digitalization [*Seekell and Pace*, 2011]. The distribution is also truncated at the large-size range. This kind of truncation has been attributed to the particular situation of mountain lake districts, where there is a decline of the available surface at higher elevations and, therefore, the probability to find large lakes drops above certain altitude [*Seekell et al*., 2013]. The maximum density of lakes in the Cajas Massif occurs about 3936 m asl and declines symmetrically towards both ends, although without following a normal distribution (supporting information Figure S2). The highest lake is located at 4424 m asl, and the lowest at 3146 m, although the latter is an exception corresponding to a terminal moraine and, in fact, the rest of the lakes are located at elevations $>$ 3400 m asl. If

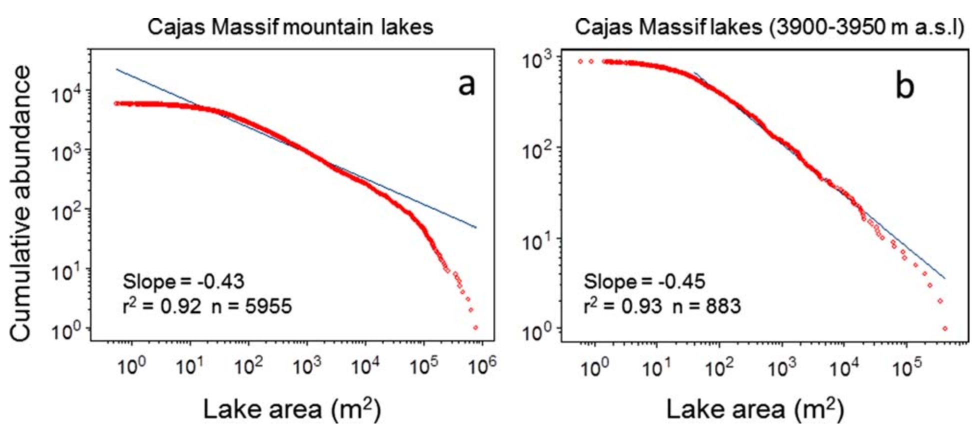

Figure 2. Lake-area distribution in the Cajas Massif (Southern Ecuador). (a) All high-mountain lakes and ponds from the Cajas Massif. (b) Subset of lakes around the average altitude of the lake distribution. The straight line indicates a power law fitting (equation (1)). In Figure 2b, only the right linear range was fitted.

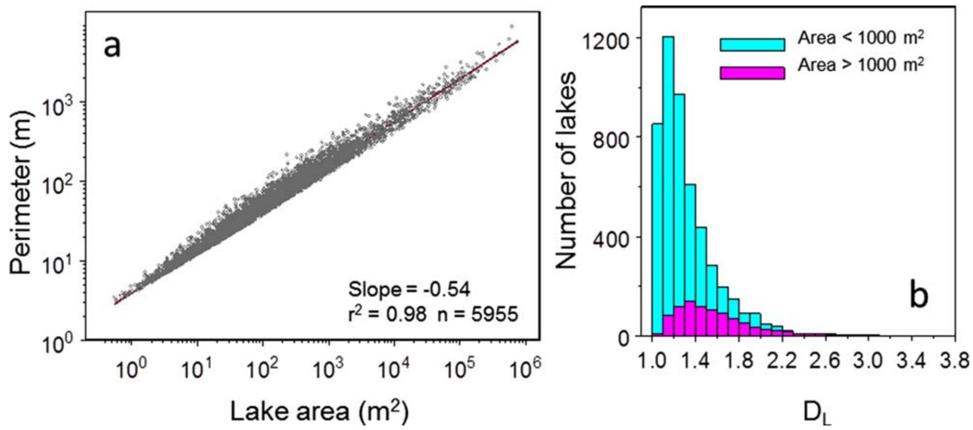

Figure 3. (a) Allometric relationship between the area and the perimeter of the Cajas Massif lakes. (b) Distribution of the shoreline development (D_L) for lakes with size above and below 1000 m^2, respectively.

one considers only the lakes around the mean altitude of the lakes (Figure 2b), the distribution becomes less bent at the large-size extreme, whereas, at the small-size end, the shape of the distribution scarcely changes respect to the whole lake set. This feature indicates that the deviation of a power law at each extreme does not respond to the same cause. The large lake-size tail of the distribution is much affected by altitude than the small lake-size end. Nevertheless, some restriction to the appearance of large lakes remains as the log-log representation of the tail is still not linear (Figure 2b). The truncation may also happen if the study extent is small, which could be the case with the altitudinal restriction.

3.2. Lake Shape

The complexity of the shoreline geometry is captured by the relationship between the lake area and the perimeter (Figure 3a). The fractal dimension (D), defined as

$$S \sim \sqrt{A}^{\,D} \tag{2}$$

is close to one (D = 1.079) for the whole lake set of the Cajas Massif, indicating as such that the lake shape, in general, corresponds to polygons scarcely ramified. Through the size range, there is no a significant deviation from this general pattern (Figure 3a).

The shoreline development (D_L) evaluates the departure of the shape from a circle ($D_L = 1$). Most of the lakes show D_L values close to one (Table 1 and Figure 3b). This feature, however, relaxes when the size of the lakes increases as larger lakes tend to be more convoluted than the smaller ones (Figure 3b and supporting information Figure S3). A few large lakes show elongated subrectangular or subcircular forms with sinuous shorelines such as Osohuayco ($D_L = 3.1$) and Toreadora ($D_L = 2.6$), both being within the Cajas NP.

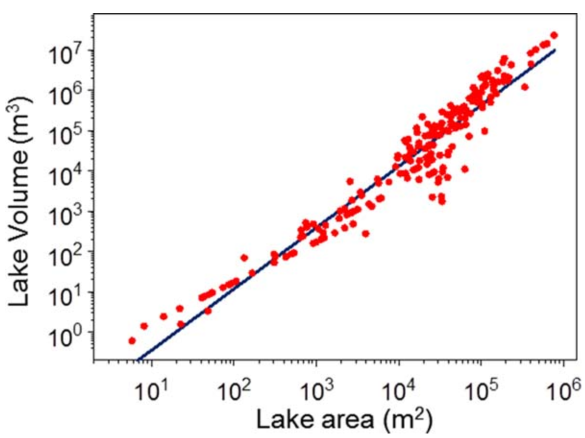

Figure 4. The relationship between area and volume for the lakes of the Cajas Massif based on a survey of 202 lakes and ponds in the Cajas National Park.

3.3. Lake 3-D Shape

The bathymetry survey in the Cajas NP provided the basis for extending the lake shape analysis to a third dimension. There is a general significant allometric relationship between lake area (A, m^2) and volume (V, m^3) that describes the invariance in shape as size changes:

$$V = 0.0107\ A^{1.52},\ \ r^2 = 0.93,\ \ n = 202 \tag{3}$$

The distribution of the deviations from the general relationship (Figure 4) does not appear to be homogeneous across the entire

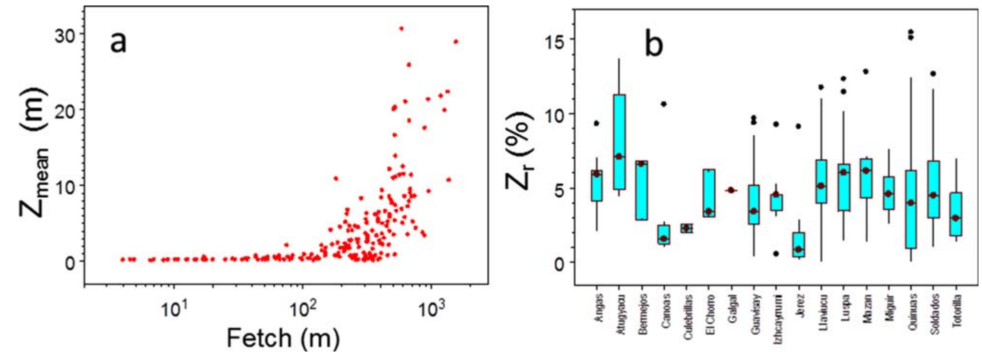

Figure 5. (a) Fetch versus Z_{mean} for the lakes of the Cajas National Park (Cajas NP). (b) Relative depth (Z_r) distribution (box-plots) for the main lakes in the Cajas NP.

lake-size gradient. Particularly, between 10^4 to 10^5 m^2 the range of lake volumes that correspond to the same lake area may cover two orders of magnitude. In this range, one could suspect the coexistence of two lake morphologies (supporting information Figure S4). However, the examination of available geological, geomorphological, and edaphological information did not provide any conclusive and robust evidence for such a distinction.

3.3.1. Mean and Relative Lake Depth

The majority of lakes are very shallow ($Z_{max} < 5$ m) (Table 1) as could be expected from the dominance of the small lake areas (supporting information Figure S5). Lakes from 10 to 20 m depth (Z_{max}) are relatively common, and there are only a few deep lakes ($40 < Z_{max} < 80$ m). The bias toward shallow forms accentuates when considering the mean depth of the lakes (supporting information Figure S5) as Z_{mean} is nearly isomorphically proportional to about one third of the maximum depth.

$$Z_{mean} = 0.33 \times Z_{max}^{1.0268}, \quad r^2 = 0.98, \quad n = 202 \tag{4}$$

A vast majority of the water bodies, therefore, show $Z_{mean} < 5$ m, only a few exhibits $Z_{mean} > 10$ m and none $Z_{mean} > 35$ m. The close relationship between Z_{max} and Z_{mean} facilitates a quick estimation of the lake volume of the Cajas Massif water bodies from a single bathymetric transect and the lake area.

Mean depth is a stabilizing factor against wind mixing action. The amount of momentum that the wind can transfer to the water column depends on the lake fetch. In general, it could be expected a large influence of the wind on the physical structure of most of the lakes. However, there can be contrasting situations among the Cajas NP lakes as there is more variation in fetch than in mean depth (Figure 5a).

The relative depth (Z_r) indicates the ratio between the lake's maximum depth and its mean diameter. It has been used as an indicator of the degree of the basin excavation by the glacier and posterior filling. The

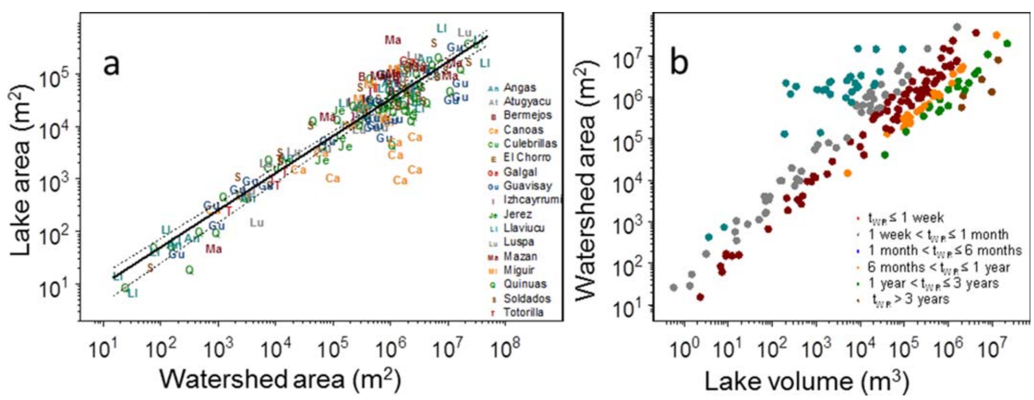

Figure 6. (a) Relationship between the watershed area and lake area. The legend lists the subbasins in the Cajas National Park. (b) The relationship between lake volume and watershed area as proxies for water retention capacity by the lake and watershed runoff, respectively. Colors indicate water renewal time (t_{WR}) estimated assuming 1000 L m^{-2} yr^{-1} and 35% average precipitation and evapotranspiration, respectively [*Crespo et al.*, 2011].

Cajas NP lakes show low Z_r values (Figure 5b). Only a few lakes show $Z_r > 10\%$; a value considered the threshold for high overexcavation. It can be thought that either the basins were not so much excavated as in other high-mountain ranges, the in-filling process has advanced more or a combination of both considerations. In fact, about 20% of the water bodies show $Z_r < 2\%$, which is considered an indication of being closer to an eventual complete filling. The Z_r patterns do not show any correspondence with the watershed orientation and main river basins distribution. Only at the level of relatively small subbasins, they display a geographical pattern (Figure 6b). Some of these subbasins show a high proportion of water bodies close to filling up (i.e., Canoas, Culebrillas, and Jerez), whereas the highly overexcavated lake basins are scattered over many subbasins, only Atugyacu is particularly rich in these latter lakes.

3.4. Lake Watershed

As could be expected from glacier erosive processes, the larger the watershed, the larger the lake (Figure 6a). However, the tendency is allometric so that the lake's area increases at a lower rate than the respective watershed.

$$A=1.95 \times A_w^{0.71}, \quad r^2=0.86, \quad n=202 \tag{5}$$

There is not a marked geographical pattern in the lake-size distribution across the main subbasins (Figure 6a). The watershed area and lake volume are the primary determinants of the average water renewal time (t_{WR}) in the lakes of the Cajas NP, provided the relatively homogeneous climate and geological landscape of the area. Under a similar amount of average precipitation, the runoff entering the lakes is proportional to the watershed area, whereas the retention capacity is proportional to the lake volume. Consequently, the morphological dissimilarities among lakes of a similar size result in marked differences in the t_{WR} (Figure 6b). Overall, t_{WR} of a few weeks to a few months largely predominate, and only a few lakes may show average t_{WR} above 1 or several years.

4. Discussion

4.1. Lake-Size Distribution

The shape of the distribution of the lake-area abundance from the Cajas Massif (Figure 2a) is similar to those found in other high-mountain lake districts of glacial origin [*Hanson et al*., 2007; *Seekell and Pace*, 2011]. The general features are deviations at both ends from a power law relationship and a slope around −0.5 of a log-log linear fitting (−0.66, −0.43, and −0.43 in the Adirondack Mountains, the Northern Highland Lake District, and our study, respectively) [*Seekell and Pace*, 2011]. It appears as a general feature that the mountain lake distribution differs from a power law, and the scaling slope is well below one; thus not following the two features that characterize the self-similar distribution of lakes >1 km^2 in the planet [*Lehner and Doll*, 2004; *Downing et al*., 2006; *Cael and Seekell*, 2016].

The deviation in the large-size lake extreme has been attributed to the restriction imposed by the departure from a flat surface so that the available area declines with altitude and thus the probability for large lakes diminishes [*Seekell et al*., 2013]. Considering a belt of lakes around the elevation of the highest lake density mitigates this restriction; however, even only fitting the large-size long tail, the slope remains around 0.5, and the distribution does not significantly fit a power law in the Cajas Massif. It seems, therefore, that there is an additional factor, beyond elevation, modifying the lake-size distribution in high-mountain lake districts. Periglacial processes, steep slopes, thin soils, and torrential stream flows may have enhanced the lake filling, perhaps at an early phase during deglaciation, when retreating glaciers move high amounts of detrital material and stream flows are rich in glacier flour. The large lakes in the central valleys may have been particularly affected by these processes so that their presence in the landscape has been substituted by flat lands of meandering streams or peatlands.

One of the consequences of the biased distribution is that within the Cajas Massif—and probably in similar mountain lake districts—most of the lentic water surface is in midsize lakes and not in ponds (Figure 7a). About 50% and more than 85% of the water surface area is on lakes $>10^5$ and $>10^4$ m^2, respectively. Biogeochemical processes in these systems are thus particularly relevant in the context of gas emissions and watershed and fluvial network dynamics. On the other hand, the still enormous numbers of ponds may be of interest for the metacommunity dynamics of some aquatic organisms restricted or with a preference for these systems (e.g., amphibians).

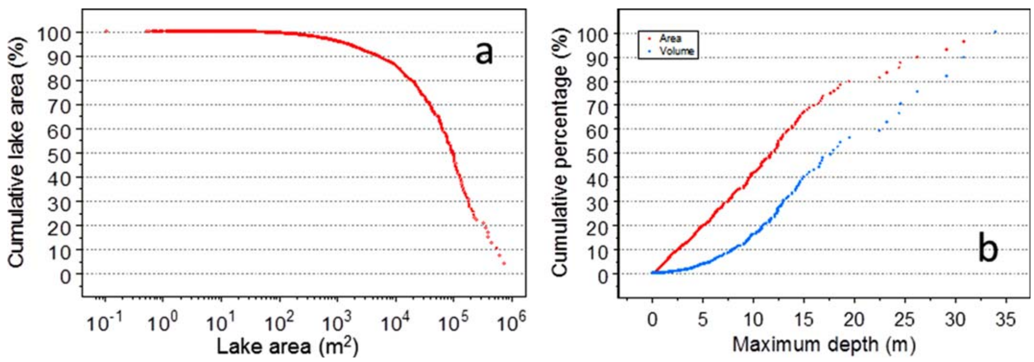

Figure 7. (a) Percentage of cumulative lake area from the largest lake to the smallest pond in the Cajas Massif. (b) Percentage of cumulative lake volume (blue) and lake area (red) with increasing maximum depth in the Cajas Massif as estimated with equations (3) and (5), respectively.

4.2. Lake Basin Morphology

Earth's lakes >4.7 km^2 show shorelines with a fractal dimension D = 1.34, close to expected predictions (D = 4/3) of the percolation theory [*Cael and Seekell*, 2016]; whereas lakes <4.7 km^2 depart from this pattern and show D = 1.00. The Cajas Massif lakes are close to the last model (D = 1.08), in this case in agreement with the general pattern in relatively flat landscapes. There is no clear departure from this scaling along the lake-size range (Figure 3a) as may occur if a subset of lakes or ponds become particularly convoluted [*Hohenegger et al.*, 2012]. Nevertheless, the shoreline development ratio (D_L) indicates that the larger the lake there is an increasing probability to become subrectangular and present sinuous shorelines in some cases (Figure 3b), yet the high scattering prevents from a significant departure from the general pattern. The lakes with higher D_L (e.g., >2) may correspond to cases of flooding of several subbasins (supporting information Figure S3). In any case, for most of the lakes, the differences are relatively small. One can conclude that in these lakes the interaction with terrestrial systems and littoral environments scale similarly throughout the lake-size range.

Large scattering in some parts of the lake-size gradient (e.g., 10^4 to 10^5 m^2) indicates some variation in the geomorphological process configuring the current lake basins. Several particularities point to a differential lake filling as the cause of the high depth (volume) variation at this mid lake-size range. (1) The markedly less noisy relationship between area and perimeter than between area and volume indicates that there has been a transformation of the lake bottoms processes posterior to the lake formation; otherwise, the shape heterogeneity in surface usually also correspond with the 3-D variation [*Hakanson*, 1981]. A comparison of the sediment records and detailed watershed bedrock and soil characteristics could provide the necessary evidence on this issue. Up to now, only the sediments of one of the "relatively shallow" lakes have been cored up to the bedrock (i.e., Pallcacoha) [*Rodbell et al.*, 1999]. The sedimentary record shows a relatively fast accumulation of light-colored inorganic sediment during Late Glacial and a transition to dark organic-rich gyttja at the onset of the Holocene, with lower accumulation rates. The average rates increase again and accelerate up to present by Mid-Holocene. Part of this acceleration may be due to the observed increasing frequency of ENSO events throughout the Holocene. This situation implies torrential rains that produce clastic laminae in the sediment profile. The volcanic bedrock of the watershed erodes easily, and debris flows and talus are abundant and located not far from the lake. However, the accumulation rate of the dark facies also increases. This feature may be due to natural processes, such as aquatic and subaquatic vegetation growth, with higher retention of fine sediment, or to human land perturbation (e.g., fire) as early cultures in the Andes have affected vegetation and soil stability since ancient times [*Coblentz and Keating*, 2008]. (2) The relative depth of many lakes ($Z_r \ll 10\%$) depart from values typical of overexcavation by glaciers. Assuming that there is no reason for a differential excavation of glaciers in tropical areas, the explanation should rely on an enhanced infilling compared to the temperate zone, which could be related to the soil erodibility and littoral vegetation development both enhanced in tropical volcanic humid regions. (3) The lakes deviating more from the general relationship between lake and watershed area (Figure 6a) also are lakes that are relatively shallow compared to their areas; for example, those in the Canoas subbasin. That is, the filling process may have also contributed to reducing the shoreline, although not as much as it

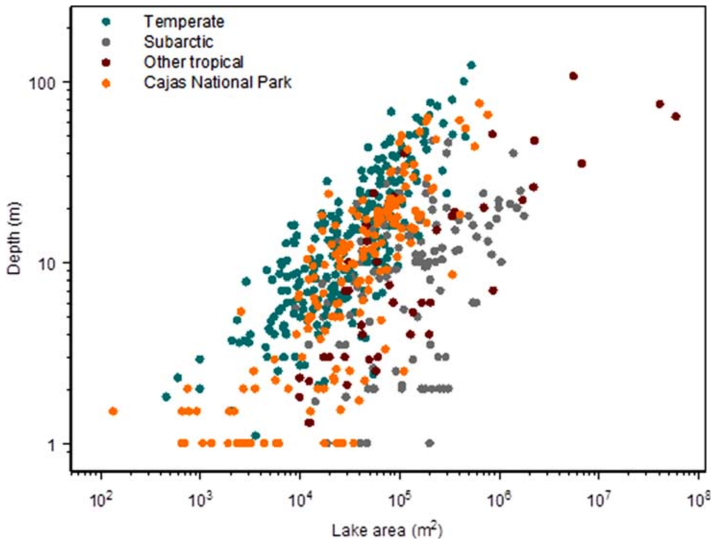

Figure 8. The relationship between lake area and maximum depths for remote lakes. Cajas National Park lakes are compared with a set of European temperate high-mountain lakes, subarctic lakes and tropical high-mountain from other parts of the world, mostly Colombian lakes.

has affected mean depth. (4) Lakes relatively deep and relative shallow for intermediate lake areas can be found in the same subbasins, which indicates that they do not respond to a geographical differentiation of the glacier erosion but rather to strictly nearby site geomorphological particularities.

Despite of the likely profound transformation of some of the Cajas Massif lakes after the excavation of the basin, the general pattern of lake basin formation, illustrated by the patterns between lake area and maximum depth (Figure 8), still agrees with that from alpine lakes in European ranges and differ from those in subarctic areas. In the latter region, lakes are much larger compared to depth than in high mountains [*Catalan et al*., 2009]. Glacier excavation in the ice accumulation zones depends on the steepness of the slope of the basin. In this aspect, the Cajas' lakes follow the pattern of some of the high-mountain lakes in the Colombian Andes and differ from others there that are closer to subarctic forms [*Catalan and Donato-Rondón*, 2016]. Accurate bathymetry surveys comprising a relatively large numbers of high-mountain lakes are not broadly available. It would be interesting to investigate whether the pattern of differential lake filling found in the Cajas NP lakes repeats elsewhere or, alternatively, they are more likely in particular climatic regions (e.g., tropical) and bedrock substrates (e.g., volcanic). Development of littoral and subaquatic vegetation may also play a role, and this could be particularly relevant in tropical high-mountain lakes.

5. Conclusions

Inventories of lake and pond areas are increasingly available at higher spatial resolution and become useful for multiple purposes. Lake-size distributions are the basis for upscaling biogeochemical processes to landscape scales, design research projects that depend on the selection of a few sites, and applying management criteria in protected or land used areas. The three activities require either some categorization of the water bodies or the characterization of the continuum variation. The use of lake surface area, which is broadly available, is not sufficient for an accurate functional classification of the water bodies in the Cajas Massif. At long term, the goal should be to increase the number of maximum depth measurements, at least for those lakes between 7000 and 40,000 m^2, the range of higher volume-area variation. Then, the use of the corresponding allometric equations can provide acceptable mean depth and lake volume estimations.

Concerning biogeochemical processes, the results presented herein show that lakes rather than ponds cover much more landscape surface and hold an even larger percentage of water volume (Figure 7). About 50% of the water is contained in a few lakes ($\sim$10) $>$18 m depth (Figure 7b). Water bodies $<$5 m depth, only account for about 5% of the total water stored. Research regarding the water column physical structure, biogeochemical process, and responses to global change merits concentrating in lakes $>$12 m depth as they hold about 80% of the volume and 50% of the pond and lake surface. However, lake morphology is not the only criteria to take into account. The size of the lake watershed cannot be ignored as they led to renewal times that differ markedly (Figure 6b). The issue becomes particularly critical for lakes with volume $>10^5$ m^3 as the water renewal times may vary from a few weeks to a few years depending on the watershed size and lake connectivity to the drainage network.

Beyond the identified allometric relationships that allow large-scale estimations and provide criteria for site selection, the detailed bathymetry survey within the Cajas NP constitutes a precise piece of information for research studies and management in the context of climate and other environmental changes. Studies on the thermal structure related to climate change may be preferentially accomplished in the relatively deep lakes, whereas those focusing on watershed transport may select relative-shallow lakes. In any case, all the lakes cannot be accommodated under a similar interpretative umbrella. For instance, in the Cajas NP, paleolimnological studies have been performed in several lakes, some of them referring to climatic and environmental changes during the Holocene and Late Glacial, others addressing current climatic change. The relatively shallow lake Pallcacocha provided a record of El Niño-Southern Oscillation (ENSO) throughout the last 15,000 years by the light-colored clastic laminae produced by storm-induced events [*Rodbell et al*., 1999]. The dynamics of these relatively shallow lakes, with high water renewal, are mainly dominated by what happens in the watershed and associated stream transport; therefore, they are excellent for reconstruction of extreme rainfall events, vegetation [*Hansen et al*., 2003] and land use changes. The relatively deep lakes, with water renewal longer than 1 year, are more appropriate for addressing issues related with proxies generated within the lake (e.g., diatom records) that respond to the physical and chemical characteristics of the water column and their changes throughout the year. These changes may also depend on extreme events, but also on more gentle climatic fluctuations and, particularly, interannual tendencies [*Michelutti et al*., 2015b]. The allometric patterns found in the tropical high-mountain lakes of Southern Ecuador are worth to be investigated in other ranges with the aim of building up a full understanding of the morphometric structure of high-mountain lakes and their implications for biogeochemical and ecological dynamics.

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