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ORIGINAL ARTICLE

Equatorial mountain lakes show extended periods of thermal stratification with recent climate change

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ABSTRACT

Climate change in the Andes has already affected phenology, glaciology, and other ecosystem attributes, and now threatens to alter long-standing fundamental limnological properties. In the equatorial Andes, most lakes have traditionally been described as having waters that circulate continuously (polymictic), with only rare episodes of stratification. This characterization, albeit based on relatively few studies, is widely accepted, despite accelerated regional warming over the past 30 years. Here, we show that protracted periods of thermal stratification are presently the norm, not the exception, in equatorial mountain lakes. Annual circulation and stratification patterns recorded in four lakes from Ecuador's southern Sierra show extended periods of stratification, which are stable and do not break down with nocturnal cooling. These data contrast with earlier research from this region, which reported full water column mixing and only infrequent stratification, but are not surprising in light of recent trends toward rising temperatures and declining wind velocities. Paleolimnological studies show that changes to the thermal regimes of these lakes likely began several decades ago and have resulted in ecosystem-scale changes including regime shifts in phytoplankton and declines in aquatic production

Key words: Tropical Andes; Ecuador; lakes; climatic change; thermal stratification.

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INTRODUCTION

Lakes of the equatorial Andes sustain human life by supplying water for consumption, agriculture, fisheries and power generation (Herzog *et al.,* 2011). Climate changes of the last several decades stand to negatively impact these critical water resources (Vuille, 2013). Air temperatures in the Andes have risen by ~0.7°C between 1939 and 2006, with the most striking increases occurring since the 1970s (Vuille *et al.,* 2008). Moreover, future warming is projected to be amongst the greatest here than for any region on the planet (Magrin *et al.,* 2007; Diaz *et al.,* 2014).

Arguably, the most important feature that influences lake ecosystem properties on a global scale is thermal stratification (Gerten *et al.,* 2002). Lakes with water columns that circulate continuously function differently from those that are perennially stratified, with respect to fundamental properties including nutrient cycling, hypolimnetic oxygen concentrations, and plankton distribution (Hampton *et al.,* 2014). Changes to these basic properties can have repercussions that reverberate through the food web (Gerten *et al.,* 2002; Hampton *et al.,* 2014). Climate-related changes to circulation and stratification patterns can set into motion trophic cascades, the effects of which can have serious societal implications for those who rely directly on lakes for their livelihoods (O'Reilly *et al.,* 2003). This includes millions of Andean people for whom lakes serve as essential natural resources (Herzog *et al.,* 2011).

Categorizing tropical Andean lakes according to their thermal stratification regimes is difficult because of the paucity of physical limnological studies from the region. Amongst the first to study physical properties in equatorial mountain lakes were Hutchinson and Löffler (1956), who noted that the lack of seasonality that permits nearly perennial stratification in low elevation tropical lakes likewise permits nearly perennial circulation in mountain lakes of similar latitude. Although this statement does not capture the full complexity of stratification patterns that can occur in tropical lakes (Lewis *et al.,* 1973), in general, the few studies on equatorial high mountain lakes suggest that circulation is more or less continuous, and thermal stratification either does not occur or is short-lived and weak (Löffler, 1964; Steinitz-Kannan *et al.,* 1983; Gunkel *et al.,* 2002).

In the absence of direct measurements, paleolimnological studies can offer insight into historical patterns of mixing and circulation. For example, certain algal species require frequent mixing of the water column to survive, whereas others flourish under periods of sustained thermal stratification (Rühland et al 2015). In recent paleolimnological studies from the Andes of Ecuador and Peru, the examination of fossil algal assemblages showed sudden shifts in species composition during recent decades, which suggests a change in mixing regime from one of frequent circulation to extended periods of thermal stratification (Michelutti *et al*., 2015a, 2015b, 2016).

In this study, we documented patterns of mixing and circulation regimes from a suite of lakes in the equatorial Andes by recording temperature profiles over the time period of one year. Our study region in Cajas National Park, located in the southern Sierra of Ecuador (Fig. 1), is of high conservation value as it houses hundreds of lakes that are the source for ~60% of the drinking water to Cuenca, the country's third largest city. The available physical limnological data from Cajas National Park indicates the lakes have historically experienced frequent periods of water column circulation (Steinitz-Kannan *et al.,* 1983). However, recent paleolimnological studies from this lake-rich region have documented abrupt changes in planktonic algal assemblages beginning within the last 50 years, which suggests the lakes have entered new physical states of extended periods of thermal stratification (Michelutti *et al.,* 2015a). The timing of these changes coincides with regional records of rising air temperatures and declining wind speeds, which are two key variables that affect thermal stratification. Despite the paleolimnological evidence suggesting new limnological regimes for these lakes, the following questions still remained: Do the lakes in Cajas National Park stratify thermally? And if so, what is the duration and degree of stratification?

The intent of this study was to provide new data on stratification regimes for lakes in the equatorial Andes. The project was driven by the apparent disconnect between the few available studies of physical limnology that indicate circulation is more or less continuous (Steinitz-Kannan *et al.,* 1983) and the paleolimnological studies that suggest the lakes have entered new regimes of extended stratification (Michelutti *et al.,* 2015a). These newly acquired water temperature data will determine the validity of our paleolimnological assertion that thermal stratification is now prevalent in Cajas Park lakes. On a broader scale, these data will provide insight into whether the climate changes of recent decades (Vuille *et al.,* 2008) have initiated a potential regime shift in stratification patterns of lakes throughout the tropical Andes as inferred from paleolimnological studies (Michelutti *et al*. 2015a, 2015b, 2016).

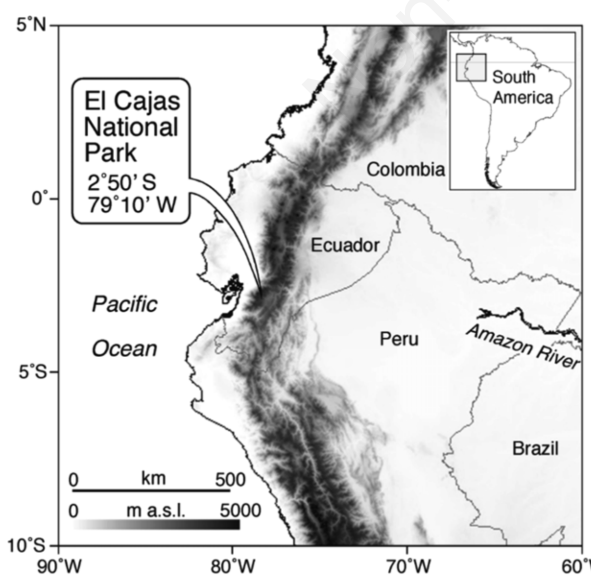

Fig. 1. Location of Cajas National Park in the southern Andes of Ecuador.

METHODS

In August 2014, water temperature data loggers (HOBO Water Temperature Pro v2 Data Logger) were deployed in four lakes in Cajas National Park (S 2° 83', W 79° 17'; Fig. 1). The four study sites (Supplementary Figs. 1-4) are located within ~10 km of one another and were selected to reflect differences in elevation and lake morphometry in order to obtain a regional signal of circulation and stratification patterns. The study lakes span an elevation gradient from 3,140 to 4,160 m asl and have comparable limnological properties, each being circumneutral in pH, dilute, and ultra-oligotrophic (Michelutti *et al.,* 2015a; Supplementary Tab. 1). Ten data loggers for each lake were positioned nearest the deepest portion of each basin, and placed along depth profiles at equidistant spacing from the surface to the bottom, at intervals ranging from ~1 to 2 m. Temperature was recorded every hour at each depth interval over a period of one year.

Mean annual temperature (1960 to 2008) recorded at the nearby Cañar meteorological station (~30 km away) was 11.3°C. Annual precipitation in the park ranges from 829 mm to 1343 mm. The seasonality of precipitation in the Ecuadorian Andes is bimodal, with two main wet seasons from March to May and September until November (Vuille *et al.,* 2013). Annual variations in daily solar radiation are minimal, and there is little evapotranspiration. Air temperature data for 2014 are from hourly readings from a temperature data logger (HOBO Water Temperature Pro v2 Data Logger) that was placed in a shaded region of the catchment of one of the study sites (Laguna Toreadora). Wind speeds are monthly means from NCEP/NCAR re-analyses (Kalnay *et al.,* 1996), at 500 hPa levels, based on a 3°×3° grid average covering Ecuador (0-5° S, 77.5-82.5° W).

RESULTS AND DISCUSSION

All study lakes showed extended periods of thermal stratification, with maximum temperature differences between surface and bottom waters in the range of ~6-7°C

(Fig. 2). Importantly, this stratification is stable and does not break down with nighttime cooling (Supplementary Fig 5). The lakes are thermally stratified by at least 2°C between 46% (Fondococha) to 76% (Patoquinas) of the year. Predictably, elevation and lake depth were important factors influencing the thermal regimes. The lowest elevation lake (Llaviucu at 3140 m asl) recorded the warmest surface water temperatures with fewest isothermal condi-

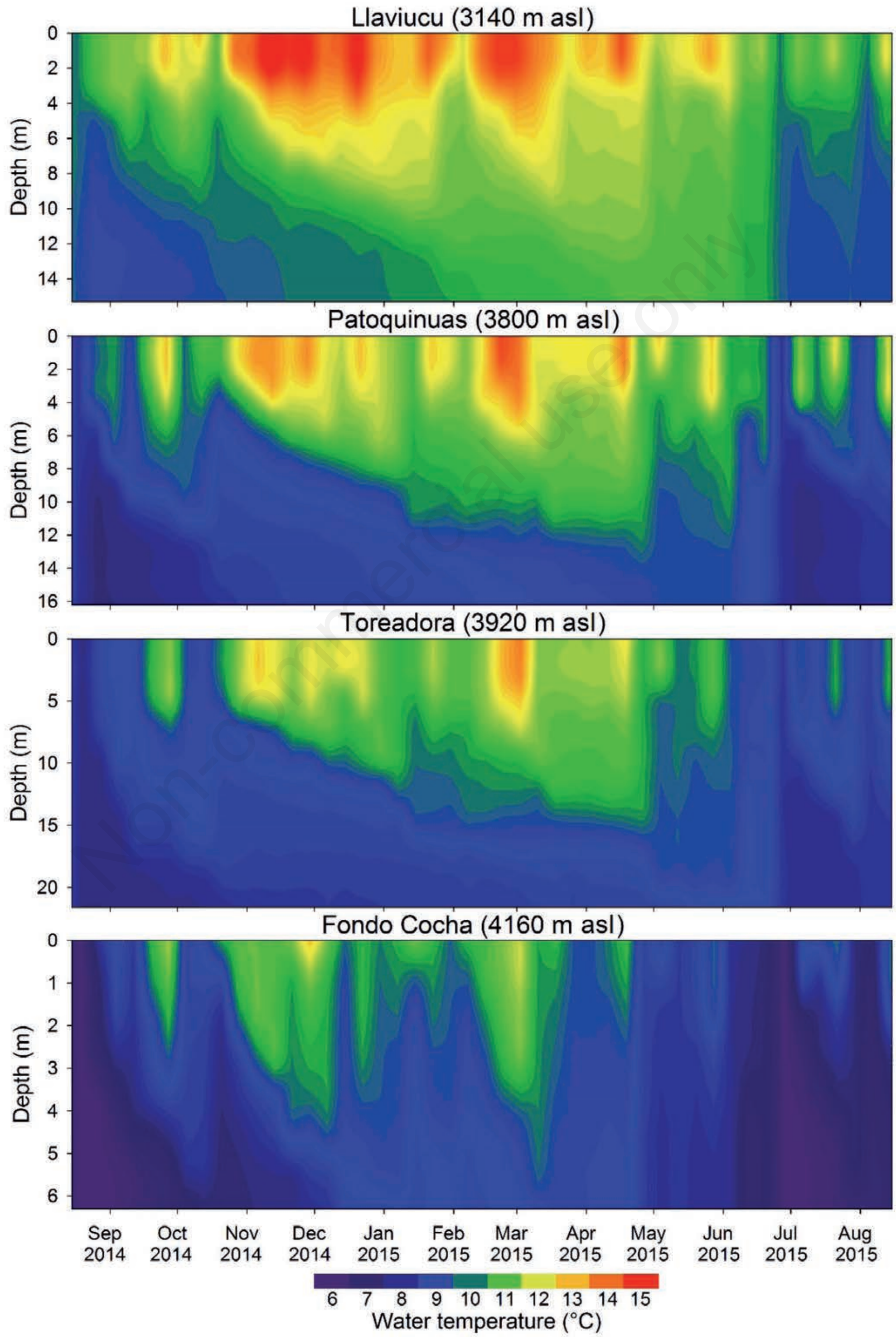

Fig. 2. Isothermal variations (°C) *versus* time for all study lakes.

tions, whereas the highest elevation, and shallowest lake (Fondo Cocha at 4160 m asl) recorded the coolest temperatures and the most frequent periods of isothermy (Fig. 2).

Despite differences in elevation gradients and basin morphometry, the study lakes show commonalities in their annual stratification and circulation patterns (Fig. 2), reflecting the influence of regional climatic variables, especially wind and temperature. Precipitation can also affect stratification, but a lack of high-quality stations with long-term data in these remote regions precludes assessment of its influence. The strongest and most continuous period of stratification occurred from early November to May, during which time mean monthly wind velocities were lowest and air temperatures were highest (Fig. 3). In contrast, the smallest temperature gradients and more isothermal periods occurred between May and October, when wind velocities were amongst their highest, and temperatures (particularly August - October, 2014) were low. Despite the variable climate that can occur in mountainous regions, the data from the nearby Cañar meteorological station (~30 km away) appears to correlate well with many of the variations in thermal profiles, at least on a broad scale.

Extended periods of thermal stratification in lakes from the equatorial Andes have, thus far, been considered atypical. In rare instances, landscape features such as steep-sided basin morphometry and a sheltered landscape can result in perennial stratification (Bird *et al.,* 2011); however, it is generally accepted that the thermal regime of equatorial mountain lakes, based on earlier limnological surveys, is cold polymictic with only infrequent periods of stratification (Hutchinson and Löffler, 1956; Steinitz-Kannan, 1997; Gunkel, 2000). In contrast, we show that extended periods of thermal stratification are now the norm in the study lakes, and the diatom-based paleolimnological studies (Michelutti *et al.,* 2015a) suggest these lakes likely experienced a recent shift with respect to their stratification regimes. This shift is entirely consistent with changing climate conditions in this region over the last few decades. Local records of air temperature from the Cañar meteorological station show a warming trend since the 1970s, with a temperature increase of 1.15°C since that time. Concurrent with increasing temperatures, wind velocities have declined, with modern values often 40% lower compared to those of the 1960s and 1970s (Michelutti *et al.,* 2015a).

A logical question is whether the thermal stratification of the study lakes represents an isolated event or a fundamental shift in physical properties driven by climatic changes of recent decades. Paleolimnological data from two of the study lakes (Toreadora and Llaviucu) provide temporal context for the temperature probe data. In fact, the sediment core studies predicted the density stratification patterns recorded here. High-resolution stratigraphic algal analyses from dated sediment cores revealed abrupt increases in the planktonic diatom *Discostella stelligera*

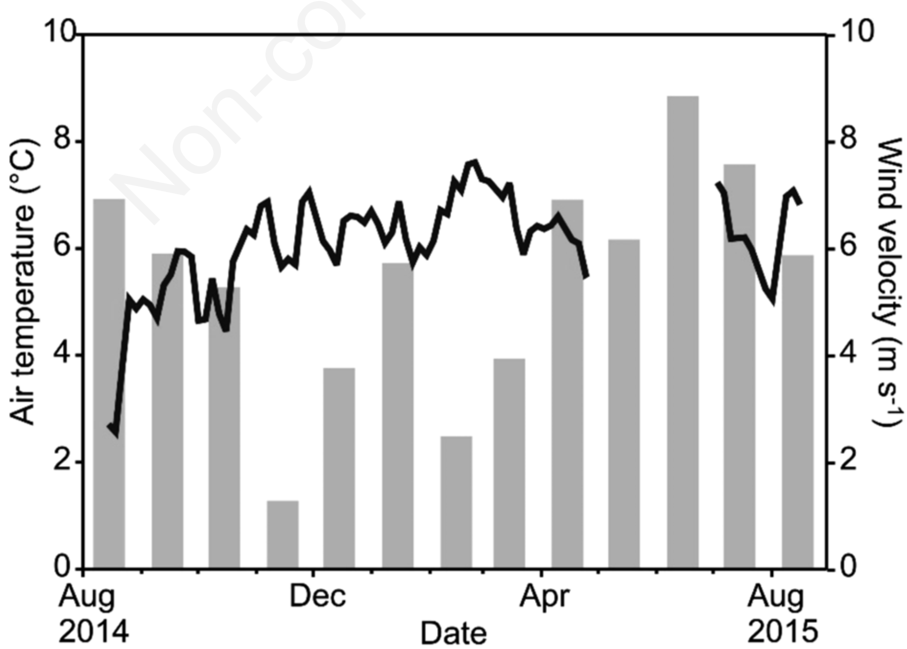

Fig. 3. Meteorological records of climatic drivers of thermal stratification including air temperatures plotted as a one week running mean (black line), and 500 hPa mean monthly wind velocities (bars). No temperature data were recorded during June and July because of equipment failures.

(basionym: *Cyclotella stelligera*) from trace abundances to dominance, concomitant with the increase in regional temperatures and declining wind speeds (Michelutti *et al.,* 2015a). The rapid rise of *D. stelligera* was attributed to climate changes that enhanced the duration and strength of thermal stratification and allowed this taxon to proliferate at the expense of other taxa that required a more turbulent, well-mixed water column (Rühland *et al.,* 2015). Greater periods of thermal stratification were also invoked to explain trends in whole lake production, as inferred from sedimentary chlorins, which decreased in the deepest study lake, Laguna Toreadora (Michelutti *et al.,* 2015a). Declines in aquatic production can occur as a result of greater periods of stratification that curtail the upwelling of hypolimnetic nutrients into the surface waters (O'Reilly *et al.,* 2003). Our temperature probe data (Fig. 2), together with the paleolimnological inferences, provide strong evidence that the study lakes have entered new physical states of enhanced water column stratification.

CONCLUSIONS

With the onset of intensified warming in this region, we suggest that the study lakes have crossed critical thermal thresholds, which ultimately can affect a wide spectrum of lake ecosystem properties. The earliest surveys from the 1980s reported that mountain lakes of Ecuador located above 3000 m asl rarely surpassed temperatures of 12°C (Steinitz-Kannan 1997), whereas our data show that it is not uncommon for surface temperatures to exceed 12°C (Fig. 2). However, these are still cold water lakes, and in comparison to warmer low elevation tropical lakes it is important to note that a similar degree difference between the epilimnion and hypolimnion does not result in equally stable stratification given the larger density difference per degree change at higher temperatures. Nonetheless, our data show that the study lakes experience extended periods of stable thermal stratification (Supplementary Fig. 5) and can no longer be considered cold polymictic, as originally described (Steinitz-Kannan *et al.,* 1983).

At present, the classification of the study lakes based on circulation patterns would likely fall somewhere between oligomictic and warm monomictic, which is not unlike many tropical lakes at lower altitudes. Climate-induced changes to lake physical mixing processes have already caused ecosystem-scale changes to the study sites including the reorganization of phytoplankton communities and changes in nutrient cycling with attendant declines in whole lake production (Michelutti *et al.,* 2015a). Similar changes appear underway for lakes elsewhere in the equatorial Andes (Michelutti *et al.,* 2015b). Given projections of rising temperatures in the Andes (Diaz *et al.,* 2014), equatorial mountain lakes will continue to experience dramatic changes that are likely to be exacerbated by increasing human pressure on water resources.

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