

Assessing the effects of climate and volcanism on diatom and chironomid assemblages in an Andean lake near Quito, Ecuador

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ABSTRACT

The tropical Andes are undergoing climate changes that rival those occurring anywhere else on the planet, and are likely to have profound consequences for ecosystems. Paleolimnological investigations of remote mountain lakes can provide details of past environmental change, especially where monitoring data are absent. Here, we reconstruct fossil diatom and chironomid communities spanning the last several hundred years from an Andean lake located in an ecological reserve near Quito, Ecuador. Both diatoms and chironomids recorded assemblage shifts reflective of changing climate conditions. The diatoms are likely responding primarily to temperature-related limnological changes, recording an increase in the number of planktonic taxa in the most recent sediments. This change is consistent with warmer conditions that result in enhanced periods of thermal stratification, allowing planktonic species to proliferate. The chironomids appear to respond mainly to a change in precipitation regime, recording a greater number of terrestrial and semi-terrestrial taxa that have been transported to the lake. A thick tephra deposit at the base of the sediment core affected both diatom and chironomid assemblages. The diatoms registered a change in species composition highlighting the ability of certain taxa to rapidly colonize new environments. In contrast, the chironomids showed a marked drop in abundance immediately following the tephra, but no change in species composition. In both cases the ecological response was short-lived, illustrating the resiliency of the lake to return to baseline conditions following volcanic inputs.

Key words: Tropical Andes; Ecuador; paleolimnology; diatoms; chironomids; climate change; tephra; mercury.

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INTRODUCTION

The climate of the Andes is changing rapidly. Meteorological data from mountain stations along the tropical Andes record temperature increases occurring at a rate nearly double the global average, with accelerated warming in the past 30 years (Vuille and Bradley 2000). The effects of this warming have been widespread and range from species-level responses such as the upslope advance of frogs towards unprecedented elevations (Seimon *et al.*, 2007), to landscape-level changes such as the rapid and pervasive thawing of the cryosphere (Rabatel *et al.*, 2013). General circulation models forecast continued warming based on a doubling of atmospheric CO₂, with the highest mountain peaks expected to increase in temperature by 4°C by the end of this century (reviewed in Herzog *et al.*, 2011).

There seems little doubt that the Andes will be sensitive to the projected warming of the 21st century, with profound consequences on natural ecosystems and societies (Herzog *et al.*, 2011). As a result, it has been argued that an expansion of climate monitoring networks is needed to better understand the climate change processes that af-

fect ecosystems and species (Rangwala and Miller, 2012; Herzog *et al.*, 2011). The logistical difficulties of instrument maintenance in remote regions, as well as financial constraints, strongly limit the initiation of new climate monitoring sites in the Andes. Lakes provide an alternate means of documenting climate change. They have been repeatedly shown to respond sensitively to climate variables (Williamson *et al.*, 2009), making them excellent sentinels of global change. Lake sediments act as natural archives of past environmental change (Smol, 2008), and paleolimnological investigations provide the advantage, over newly-implemented monitoring programs, of being able to place recent changes within the context of long-term variability (Hillyer *et al.*, 2009; Ekdahl *et al.*, 2008). The high Andes contain numerous lakes (Maldonado *et al.*, 2011) many of which are remote from human activities. This allows for a dense network of monitoring sites that are unaffected by local human impacts (*e.g.*, eutrophication, catchment alterations, industrial inputs), ensuring climate is the main driver of limnological change. Investigating climate change on the scale of an individual lake

ecosystem provides a perspective on the prevailing climatic processes operating at a local level that may be missed by larger scale climate models due to the dominant effects of orography (Herzog *et al.*, 2011). Lakes rarely respond to temperature shifts in a linear fashion, rather they often show threshold-type responses to warming (Smol and Douglas, 2007; Hobbs *et al.*, 2010; Rühland *et al.*, 2008, 2103, 2015). In paleolimnological studies, this has been recorded by rapid changes in the assemblages of sensitive bio-indicator groups such as algae, zooplankton and insects (Smol *et al.*, 2005). Often the response to temperature is indirect and caused by fundamental changes to limnological variables such as thermal stability and stratification, habitat alteration, and the availability of light and nutrient resources (Rühland *et al.*, 2015). Nonetheless, when long-term meteorological data are available to compare with paleolimnological data, the timing of biotic assemblage shifts often corresponds with the onset of temperature increases (Michelutti *et al.*, 2015b; Rühland *et al.*, 2013; Antoniadou *et al.*, 2005).

In this study, we document biotic changes in a sediment core recovered from Laguna Baños, which is located in an ecological reserve near Ecuador's capital city of Quito (Fig. 1). In previous paleolimnological investigations in the Andes, we recorded marked changes in diatom and chrysophyte algae in response to recent warming in the southern sierra of Ecuador near Cuenca (Michelutti *et al.*, 2015b) and in the cordillera central of Peru, southeast of Lima (Michelutti *et al.*, 2015a). Laguna Baños was selected for investigation as it is located near the equator from a region with little information on the response of

aquatic ecosystems to recent climate change. Below, we outline three specific objectives in this study.

First, we reconstruct fossil diatom and chironomid assemblages spanning the last several centuries of environmental change. In the Andes, diatom assemblages have been shown to respond sensitively to recent climatic change (Michelutti *et al.*, 2015a, 2015b), but far less research has been done on the response of chironomids, especially in paleolimnological studies (*e.g.*, Williams *et al.*, 2012; Urrutia *et al.*, 2010). The reconstruction of fossil records from both diatom and chironomid assemblages allows us to compare the timing and magnitude of responses between bio-indicators at two trophic levels.

Second, we compare changes recorded in the Laguna Baños core to previous studies elsewhere in the Andes, and assess the role of climate on these changes. Comparisons among studies from different regions is critical for the careful assessment of spatial and temporal variability of climate change in the Andes, especially when considering the complex topography of the region. The proximity of Laguna Baños to Quito allows us to take advantage of one of the longer-term temperature records from the Andes, dating back to the late 1800s, to compare with our paleolimnological data.

Third, we assess the response of aquatic biota to volcanic inputs. During the coring of Laguna Baños, we penetrated into a thick tephra deposit at least 10-cm thick. Although this deposit ultimately truncated our sediment record because we could not penetrate through it with our coring equipment, it provides an opportunity to assess the aquatic response to volcanic fallout. Investigating the aquatic response to volcanic eruptions is relevant as tephra can leach Hg and other elements into the surrounding environment, thereby affecting water and food supplies and ultimately human health (Weinstein and Cook 2005). In addition to metals and other elements, volcanic events can impact aquatic ecosystems by altering limnological properties including turbidity and light regimes, pH, silica, nutrients, and salinity (Barker *et al.*, 2000, Blong 1984). Changes to the diversity and abundance of diatom and chironomid assemblages following tephra deposits have been documented in mountain lakes in British Columbia, Canada (Hickman and Reasoner 1994), Mexico (Telford *et al.*, 2004), as well as in the Andes (Urrutia *et al.*, 2007; Massafiero and Corley 1998). In volcanically active regions, such as the northern portion of the Ecuadorian Andes, tephra may be important agents of change to aquatic ecosystems.

METHODS

Site description

Laguna Baños (S 00°19'10.16", W 078°09'34.79") is located in the Reserva Ecológica Cayambe-Coca, a nature



Fig. 1. Map showing the location of Laguna Baños in Ecuador.

reserve in Ecuador that straddles the equator, approximately 40 km east from the capital of Quito (Fig. 1). The lake is situated at an elevation of 3835 m asl, and is mostly surrounded by steep-sided slopes (Fig. 2a). Aside from a few hiking trails, there is little development in the catchment, which is dominated by the grasslands of the Páramo and low-lying shrubs. The nearest meteorological station to Laguna Baños is at Quito, and records a mean annual temperature of 13.6°C over the period from 1951–2000, with seasonal variations of less than half a degree Celsius (Osborn and Jones, 2014; Jones *et al.*, 2012). A general

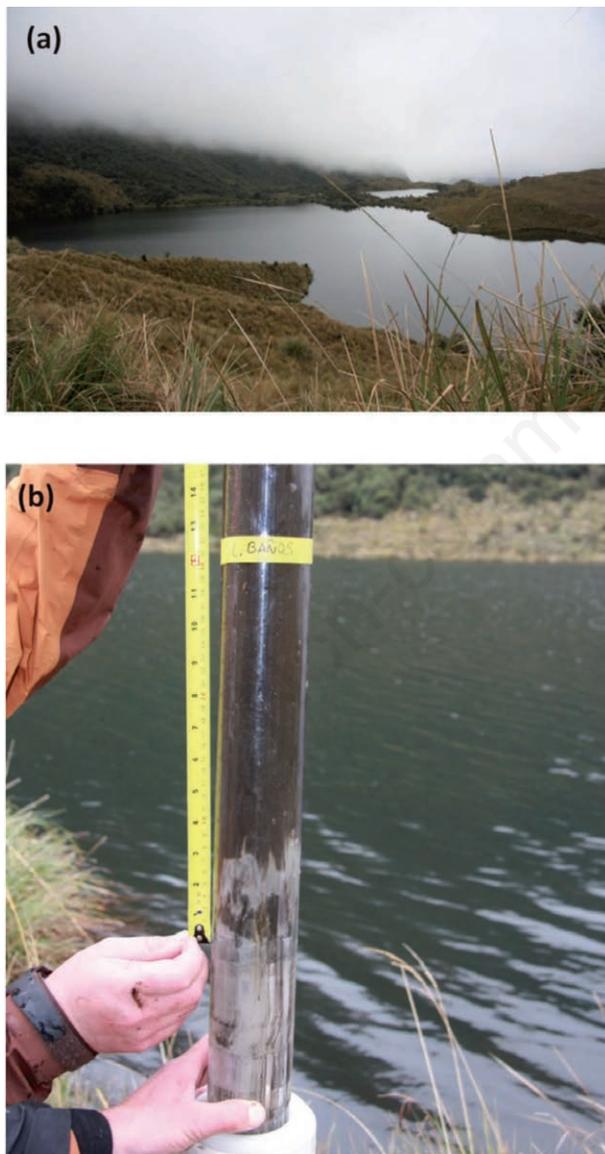


Fig. 2. Photographs of (a) Laguna Baños and (b) the sediment core recovered from Laguna Baños showing the tephra horizon near the bottom.

trend of increasing temperatures has been recorded since measurements began in the late 1800s (Fig. 3).

Sample recovery

On July 11, 2011, a sediment core was recovered from near the center of Laguna Baños ($Z_{\max} \approx 10$ m) using a universal gravity corer (i.d.=6.78 cm) with an attached hammer apparatus. During coring, we encountered a thick, white-grey tephra deposit that we could not penetrate (Fig. 2b). The surface of the core to ~24 cm depth was largely black-brown gyttia, after which depth the tephra became abundant and remained that way for at least 10 cm. The core was sectioned on-site into 0.25 cm intervals to 5 cm depth, then 0.5 cm intervals thereafter using a vertical core extruder (Glew *et al.*, 2001). Water samples for limnological analyses were collected near the center of the lake from a depth of ~30 cm. Lakewater pH, conductivity and temperature were measured in the field. All sediment and water samples were kept cool and dark until they were shipped back to the laboratory and stored in a cold room at 4°C.

Sample preparation

Water samples were analyzed for major/minor ions, metals, phosphorus, nitrogen, dissolved organic/inorganic carbon, particulate organic nitrogen, and chlorophyll *a* at the National Laboratory for Environmental Testing (NLET) in Burlington, ON, Canada. Protocols for bottling, filtering, and methods for chemical analyses followed Environment Canada (1994a, 1994b).

To establish sediment chronology, the core was measured for excess ^{210}Pb activities (Fig. 2), as well as ^{137}Cs , in an Ortec germanium crystal well detector following the procedures described in Schelske *et al.*, (1994) and Appleby (2001). Dates were developed from the constant rate of supply (CRS) model using the ScienTissIME package in MatLab® (ScheerSoftware Solutions, Barry's Bay,

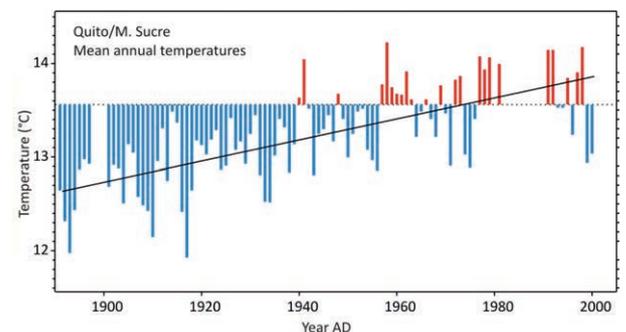


Fig. 3. Mean annual temperatures from the Quito airport (Mariscal Sucre) meteorological station plotted as departures from a 50-year mean (1951–2000).

ON, Canada). The tephra deposit at ~24 cm depth can be used as an independent dating marker, but without geochemical fingerprinting tracing its composition to the volcanic event, this can only be done tentatively based on chronologic means of known recent, nearby eruptions. Sediment mercury (Hg) concentrations were quantified on ~100 mg of dry, homogenized sediment using a DMA80 mercury analyzer at Yale University. Blanks, duplicates, and certified reference material (MESS-3) were run after every 10th unknown. Blanks were consistently <0.2 ng g⁻¹, duplicates were within 8% of each other, and measured MESS-3 concentrations were within 10% of the certified value (91 ng g⁻¹). Diatom slides were prepared following standard techniques for siliceous microfossils (Battarbee *et al.*, 2001). Sediment was oxidized using a 50:50 molar concentration of concentrated sulfuric and nitric acids, followed by repeated rinsing with distilled water until neutral pH was reached. Subsamples of the slurries were pipetted onto coverslips and allowed to dry before being permanently mounted to slides using Naphrax[®]. Diatoms were identified and enumerated at 0.5 cm intervals until 5 cm depth, then every 1 cm until 10 cm depth, followed by every 2 cm thereafter. For each interval, a minimum of 300 diatom valves was identified primarily to species level using a LEICA DMRB microscope equipped with Nomarski DIC optics under oil immersion at 1000X magnification. Taxonomy is based primarily upon Krammer and Lange-Bertalot (1986-1991) and Antoniadou *et al.*, (2008). Preparation of sediment for chironomid analyses followed procedure given in Walker (2001). Sediment was deflocculated in 5% KOH heated at 50°C for 20 minutes. This solution was then rinsed over a 100- μ m sieve, and the remaining sediment was washed into a small beaker with approximately 20 mL of deionized water. Chironomid head capsules from each sample were picked with forceps from a Bogorov tray under 20X magnification using a dissecting scope. The picked head capsules were placed on cover slips and subsequently permanently mounted onto microscope slides using Entellen[®]. Chironomid head capsules were identified using a Leica DMR HC light microscope at 40-400X magnification, at a resolution of approximately every 0.5 cm interval until 5 cm depth, and every 1 cm interval thereafter, for a total of 23 intervals analyzed. Each head capsule was identified to the lowest possible taxonomic level primarily following the taxonomy of Brooks *et al.* (2007), Wiederholm (1983) and Cranston (2010). Where possible, we attempted to collect a minimum of 50 head capsules per interval in order to adequately characterize the assemblage (Quinlan and Smol, 2001a). Low chironomid abundances were encountered in some intervals, especially near the surface and bottom-most sediment intervals. Still, a minimum of 20 head capsules were recovered for the majority of intervals, which, given the low chironomid diversity at

this lake, we believe sufficiently reflects the assemblage composition. In the top- and bottom-most samples less than 20 head capsules were recovered and they were combined with adjoining intervals to achieve appropriate count sizes. The dry sediment weight used in head capsule isolation ranged from 0.2-2.0 g, reflecting the variable head capsule concentration of the Laguna Baños sediment.

For both diatoms and chironomids, detrended canonical correspondence analysis (DCCA) constrained to depth were used to provide an estimate of the amount of compositional change between samples in the sediment core. Both data sets were analyzed identically by using square-root transformations of species-relative frequency data, no down-weighting of rare taxa, detrending by segments, and nonlinear rescaling (Smol *et al.*, 2005).

RESULTS

Limnology

Select limnological variables for Laguna Baños are provided in Tab. 1. Briefly, the lake is ultra-oligotrophic (TP=4.4 μ g L⁻¹) slightly alkaline (pH=7.6), with low specific conductivity (58 μ S cm⁻¹). At the time of sampling in July 2011, the lake was very weakly stratified recording water temperatures of 9.1°C from the surface to 2 m depth, after which temperatures decreased gradually to 8.1°C at 6 m depth and remained at that temperature to the lake bottom at ~10 m depth. There was little change in specific conductivity (<3 μ S cm⁻¹ difference) from the surface to the bottom waters.

Chronology

The plot of unsupported ²¹⁰Pb vs depth records a number of non-monotonic features and reversals, which are most likely caused by episodes of increased sediment input

Tab. 1. Select limnological variables for Laguna Baños.

Variables	
pH	7.6
Conductivity	58 μ S cm ⁻¹
Surface Temperature	9.1°C
Total phosphorus (unfilt.)	4.4 μ g L ⁻¹
Total phosphorus (filt.)	4 μ g L ⁻¹
Total nitrogen (filt.)	0.228 mg L ⁻¹
Chlorophyll <i>a</i>	1.0 mg L ⁻¹
Dissolved organic carbon	1.6 mg L ⁻¹
Dissolved inorganic carbon	9.4 mg L ⁻¹
Ca	11.9 mg L ⁻¹
Particulate organic carbon	0.177 mg L ⁻¹
Particulate organic nitrogen	0.015 mg L ⁻¹
SiO ₂	15.6 mg L ⁻¹

from the steep-sided catchment that dilute the ^{210}Pb . The percent organic matter (as inferred from loss on ignition at 550°C) profile is highly variable during this period suggesting episodic allochthonous inputs, although there is no clear relationship to the unsupported ^{210}Pb profile (Fig. 4 a,b). As is often the case in organic sediments, the ^{137}Cs data shows no clear peak associated with maximum fallout at ~ 1963 .

Mercury

The Hg profile shows a distinct peak centered ~ 21 cm depth reaching a maximum concentration of 727 ng g^{-1} ,

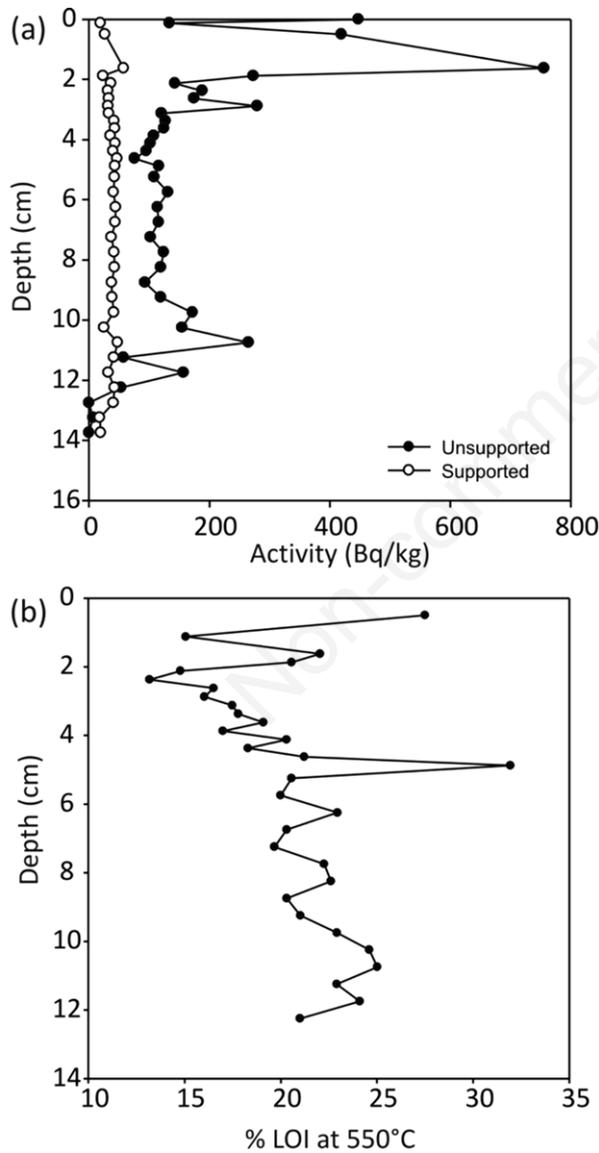


Fig. 4. Plots showing (a) activities of unsupported and supported ^{210}Pb (as ^{226}Ra), and (b) the percent organic matter as LOI 550°C .

which is approximately 7X greater than the baseline concentrations of $\sim 100 \text{ ng g}^{-1}$ (Fig. 5). The distinct Hg peak centered at ~ 21 cm depth (Fig. 5) provides confirmatory evidence of a tephra, as elevated Hg concentrations in lake sediments have been linked to volcanic activity (Guevara *et al.*, 2010). Natural volcanic sources of Hg appear to be far greater than atmospheric deposition of pollution Hg in this locality.

Diatoms

The core interval at 24 cm depth represents the transition between organic lake sediment and the tephra deposit, and below 24 cm the fossil diatom assemblages become too low to enumerate. The diatom assemblage at 24 cm stands apart from all other analyzed intervals in that it has the highest percentage of *Cocconeis placentula*, comprising 25% of the total assemblage. Above 24 cm, the assemblages are dominated by benthic taxa including *Achnanthis minutissimum*, and taxa belonging to the genera of small benthic fragiliariids (comprised of *Pseudostaurosira brevistriata*, *Staurosira venter*, and *Staurosirella pinnata*), *Nitzschia* spp. and *Achnanthes sensu lato*. The only planktonic taxon of note in the bottom portion of the core is *Aulacoseira alpigena*, comprising less than 20% of the total assemblage. However, beginning at the 12 cm depth, other planktonic taxa including *Discostella stelligera* and the pennate-planktonic *Tabellaria flocculosa* (str. IV) appear and maintain steady, albeit low, relative abundances until the surface. We note that both

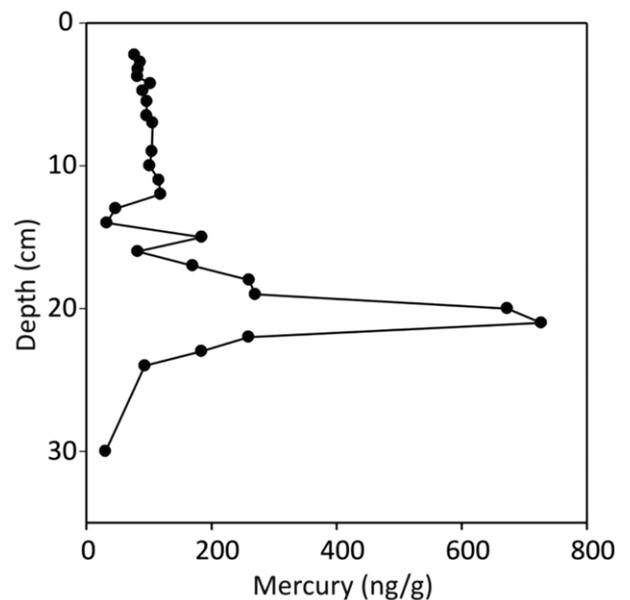


Fig. 5. Total Hg concentrations (ng/g) in the Laguna Baños sediment core.

D. stelligera and *T. flocculosa* were present in the bottom portion of the core, but in low (<2%) relative abundances. The *Fragilaria sensu lato* complex shows an increase in the uppermost 2 cm (Fig. 6), which appears to occur at the expense of other benthic *Nitzschia* taxa. The DCCA axis 1 sample scores reflect the compositional changes described above, with the largest changes occurring from the decline of *C. placentula*, the onset of the planktonic/tychoplanktonic taxa, and near the surface with the increase in small benthic fragilarioids.

Chironomids

The bottom-most interval (20.5-21 cm) contained very few head capsules (n=8), and therefore it was combined with the adjacent interval at 19.5-20 cm (n=36.5) to reach a reasonable count of 44.5 head capsules. Likewise the

upper-most 3 cm contained very few head capsules and the intervals from 0-1, 1-1.25, 1.75-2, and 2.75-3 cm were combined for a total of 27.5 head capsules. Head capsule numbers of > 50 were attained from the intervals of 18.5-19, 16.5-17, 14.5-15, 13.5-15, and 12.5-13 cm. All other intervals contained greater than 20, but less than 50 head capsules.

Polypedium, *Riethia* and *Orthocladus* were dominant throughout the entire record (Fig. 7). A minor assemblage change occurs at ~11 cm depth. Below this depth *Cricotopus*, *Pseudosmittia*, *Parachaetocladus*, and *Paracricotopus* are found exclusively, albeit in very low relative abundances. Above ~11 cm depth, *Paraphaenocladus*, *Limnophyes/Paralimnophyes*, *Rheotanytarsus* and *Corynoneura/Theinemaniella* increase in relative abundance, and to a lesser extent so does *Parochlus*. In general, *Polypedium* record lower relative abundances above 11-

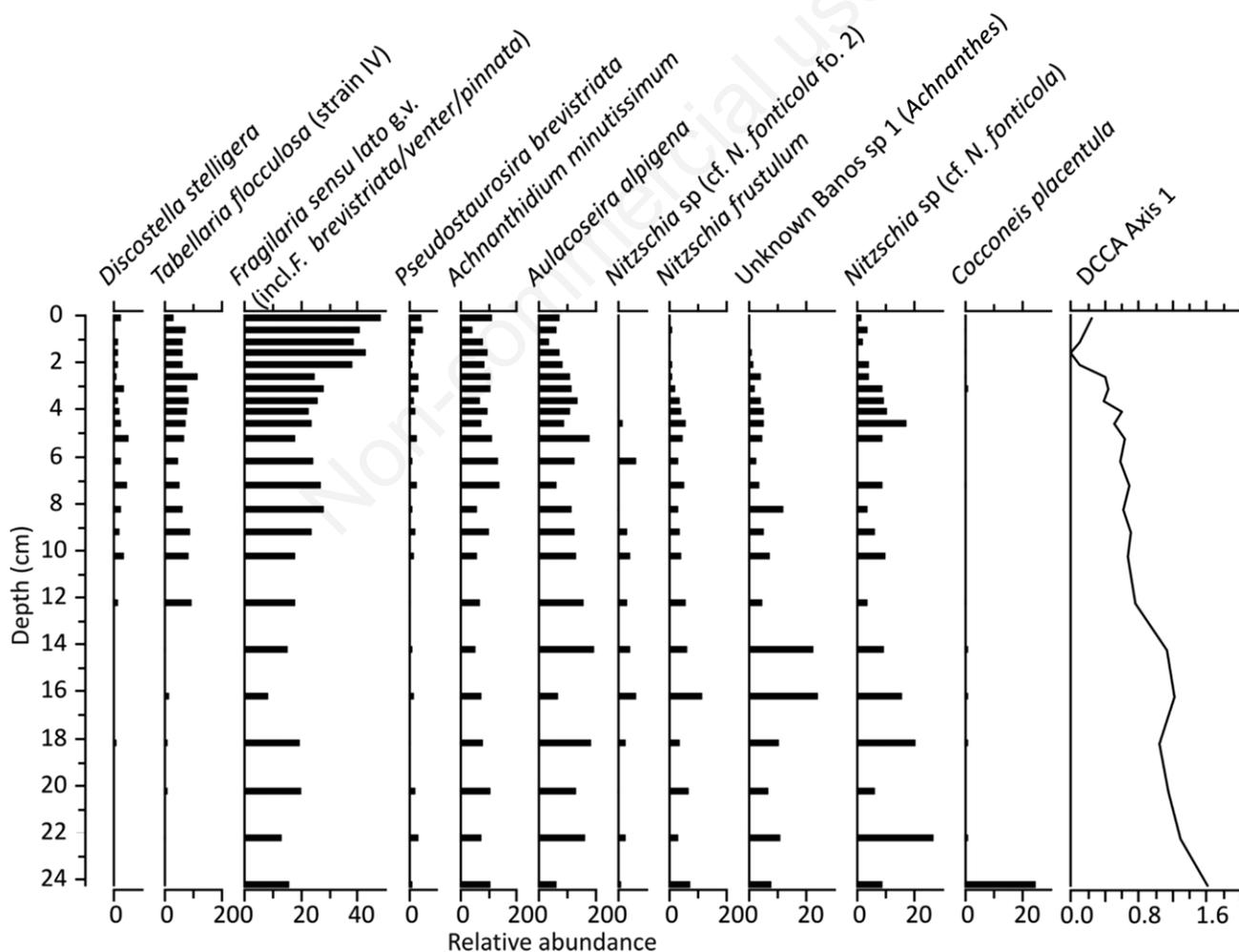


Fig. 6. Subfossil diatom assemblages from the Laguna Baños sediment core. Plotted on the far right are axis 1 sample scores from a DCCA constrained to depth.

cm depth, however it remains a dominant taxon (Fig. 7). The DCCA axis 1 sample scores reflect the compositional changes described above for the fossil chironomids, with the largest changes occurring at 11 cm and 3 cm depths.

DISCUSSION

Chronology

Establishing a reliable chronology on the Laguna Baños core proved challenging. The unsupported ^{210}Pb profile appears to be affected by stochastic sediment inputs from the catchment, which have diluted the signal. In particular there appears to be a massive dilution of unsupported ^{210}Pb from ~2-10 cm depth, although there is no clear relationship with the organic matter record (Fig. 4b). We do not suspect any significant degree of mixing as distinct biostratigraphic changes were recorded in both diatom and chironomid records (Figs. 6 and 7). The reliability of dates generated from the ^{210}Pb data is questionable, and with no way to independently verify the dates (e.g., ^{137}Cs), we apply a conservative approach to chronology, tentatively assigning the unsupported/supported ^{210}Pb

horizon at ~12.5 cm depth as corresponding to approximately 150 years before present. This depth is within the range of the unsupported/supported ^{210}Pb horizon recorded in other cores from the tropical Andes (Michelutti *et al.*, 2015a, 2015b), but should be viewed with caution.

The tephra located at ~24 cm depth provides a potential independent dating marker that could be used to evaluate the ^{210}Pb -derived dates. Even with geochemical fingerprinting data of this tephra, there is a general lack of geochemical data from source vents in northern Ecuador (Rodbell *et al.*, 2002), making the assignment of a particular volcanic eruption difficult. Thus, dating of this tephra can only be assigned tentatively based on chronological means of known recent, nearby eruptions. From what we gleaned of the literature with respect to volcanic eruptions near Laguna Baños within the last 500 years, the tephra deposit may correspond to the 1785-1786 Nevado Cayamabe (~40 km NNE of Laguna Baños) volcano eruption (Samaniengo *et al.*, 1998), or possibly the Pichincha (~50 km NW of Laguna Baños) eruptions of 1553 and 1660, which covered Quito in ~30 cm of ash (Hall and Mothes, 2008).

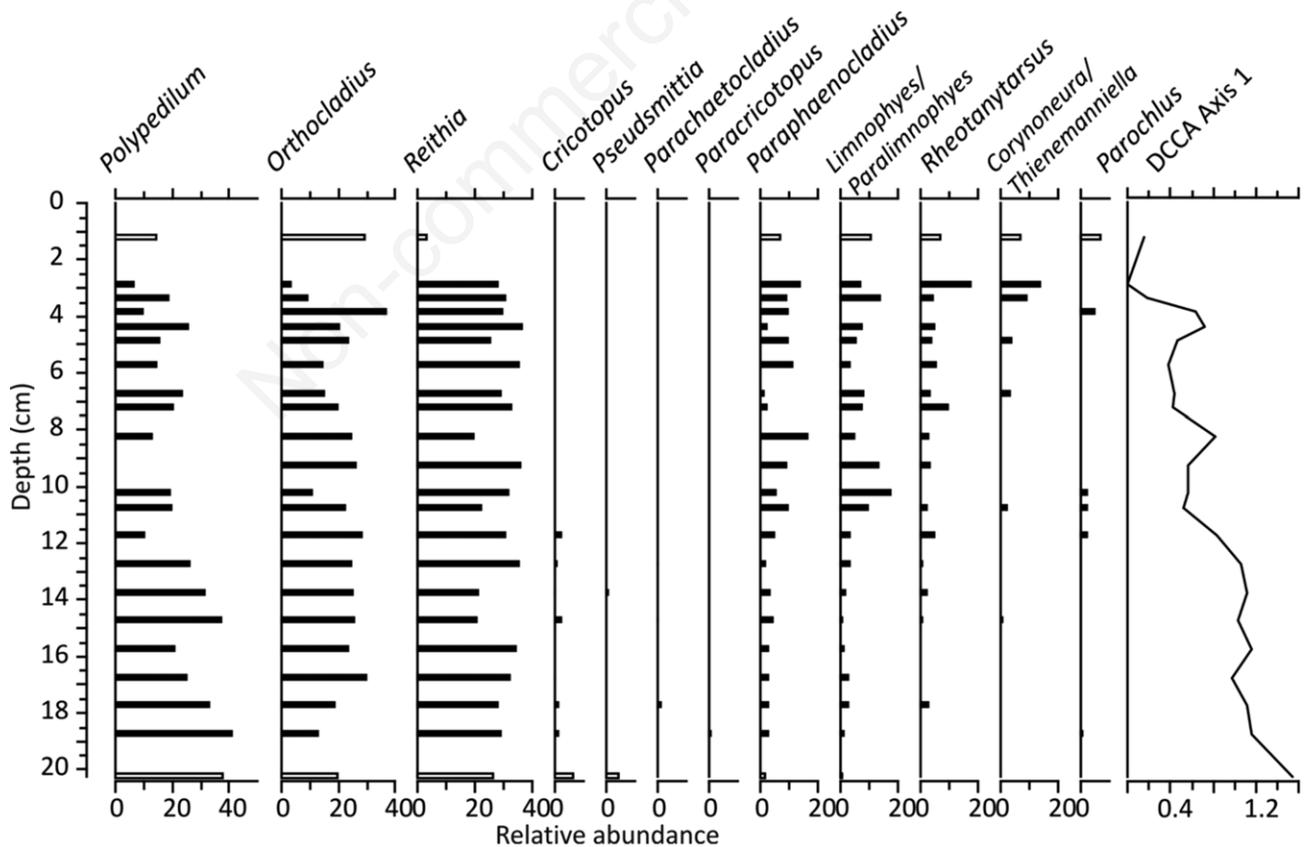


Fig. 7. Subfossil chironomid assemblages from the Laguna Baños sediment core. The hollow bars at the surface and bottom of the profile indicate two or more intervals have been combined to reach adequate head capsule numbers. Plotted on the far right are axis 1 sample scores from a DCCA constrained to depth.

Diatoms

The most ecologically significant change in the fossil diatom record occurs at 12 cm depth, with the increase of the planktonic taxa, *Discostella stelligera* and *Tabellaria flocculosa* (Fig. 6). Abrupt increases in both of these taxa, occurring within the last century, have also been recorded from Andean lakes in the southern sierra of Ecuador (Michelutti *et al.*, 2015b) and the cordillera central of Peru (Michelutti *et al.*, 2015a). Their increases are postulated to be a result of enhanced periods of thermal stratification, brought on by rising temperatures, which allow these planktonic species to flourish (Michelutti *et al.* 2016). In support of this hypothesis, other heavily silicified planktonics, such as *Aulacoseira* taxa, which require a more turbulent water column to remain in the photic zone, show concomitant declines. This also appears to be the case in Laguna Baños, with *Aulacoseira alpigena* registering generally lower abundances after the arrival of *D. stelligera* and *T. flocculosa*. The upper ~3 cm of the core also records the near disappearance of *Nitzschia* taxa, which appear to be outcompeted by small benthic fragilarioids. At present, it is unclear why the *Nitzschia* taxa decreased in surface sediments. These taxa are found in a wide range of environments ranging from high nutrient sites (Keatley *et al.*, 2011) to oligotrophic Arctic ponds (Michelutti *et al.*, 2003). Although this species shift is of interest, by far the more ecologically significant change is the aforementioned increase in planktonic taxa at 12 cm depth as this marks a change in both habitat and life strategy. This broad pattern of abrupt increases in *D. stelligera* and pennate planktonics within the last 100 years has been documented in hundreds of lakes from alpine, Arctic and temperate regions throughout Europe and North America (Rühland *et al.*, 2013, 2015).

Mountain lakes in Ecuador have been classified as being generally polymictic with only brief periods, if any, of thermal stratification (Steinitz-Kannan 1997). The steady increase in mean annual temperature recorded at the Quito meteorological station (Fig. 3), and across the tropical Andes (Vuille and Bradley 2000), adds plausibility to the hypothesis of enhanced periods of thermal stratification due to warming, although other factors can influence stratification, such as wind (Michelutti *et al.*, 2015b, 2016). The diatom shift in Laguna Baños is far more subtle compared to the dramatic changes recorded from lakes in southern Ecuador, where *D. stelligera* rapidly increased to dominance within the last several decades (Michelutti *et al.*, 2015b). The magnitude of changes in Laguna Baños more closely match those recorded in lakes from Peru's cordillera central, in which *T. flocculosa* records a modest increase and remains at relatively constant percent abundances until present-day (Michelutti *et al.*, 2015a). Although the increases in *D. stelligera* and *T. flocculosa* in Laguna Baños are modest, they still represent an important

shift in diatom composition as, prior to the 12 cm depth, these planktonic taxa were only present in trace amounts. Based on these data, we surmise that Laguna Baños presently may have longer periods of thermal stratification than in the past, likely due to rising temperatures, but still experiences frequent mixing that prevents planktonic taxa from dominating the assemblage. After crossing an initial threshold with respect to enhanced periods of thermal stratification, the lake appears to have remained this way with no escalation of change since the initial increase in planktonics. Given our assumption that ^{210}Pb activities reach supported levels at 12.5 cm depth, corresponding to ~150 yrs BP, the diatom shift in Laguna Baños occurs much earlier compared to similar shifts recorded elsewhere in the Andes thus far (Michelutti *et al.*, 2015a, 2015b).

Chironomids

The Laguna Baños chironomid record is dominated by taxa from three genera, namely *Polypedilum*, *Orthocladius* and *Riethia*. These genera are common throughout the Andes and have been described across a wide variety of habitats (Acosta and Prat, 2010; Ruiz *et al.*, 2000a, 2000b; Ospina *et al.*, 2000). In general, *Polypedilum* is considered typical of warm conditions (Larocque *et al.*, 2001; Eggermont *et al.*, 2010; Woodward and Schulmeister 2006), whereas *Orthocladius* and *Riethia* are commonly described as being cold tolerant (Eggermont and Heiri 2012; Massaferrero *et al.*, 2009). The approximately equal percent abundances of these taxa throughout the sediment record indicate they have overlapping tolerances with respect to temperature. There are no strong directional trends in the three dominant genera over time, with the exception of generally lower abundances of *Polypedilum* in the upper half of the core.

The most notable change in the fossil chironomid record is a subtle shift in species composition that occurs at ~11 cm depth. Notably, this shift happens at approximately the same time as the small relative increase in planktonic diatoms (Fig. 6). Although there are four genera that are only documented below 11 cm depth, including *Cricotopus*, *Pseudosmittia*, *Paracheaetocladius*, and *Paraphaenocladius*, their percent abundances are so low that any ecological inference based on their apparent disappearance from the most recent sediments is tenuous. The one exception may be *Cricotopus*, which, despite its low abundances, is present in most sediment intervals below 11 cm depth. Based on South American studies, the ecological preferences of *Cricotopus* remain enigmatic. In Patagonia, Massaferrero *et al.*, (2009) interpreted *Cricotopus* as warm-tolerant, but in the eastern Bolivian Andes, Williams *et al.* (2012) found no obvious correlation to temperature.

Likely, the most ecologically significant (and interpretable) change in the subfossil chironomid record is the

increase, at 11 cm depth, of *Paraphaenocladus*, *Limnophyes/Paralimnophyes*, and to a lesser extent of *Rheotanytarsus*, and *Corynoneura/Thienemanniella*. Both *Paraphaenocladus* and *Limnophyes* have been described as terrestrial or semi-terrestrial taxa needing only a film of water for survival (Hazra *et al.*, 2002; Boggero *et al.*, 2006). Changes to the precipitation regime may result in a greater proportion of these terrestrial and semi-terrestrial taxa being washed into the lake. In support of this hypothesis, *Corynoneura*, which also increases in recent sediment, was found to be more abundant during the rainy season in high altitude streams of the Peruvian Andes (Acosta and Prat, 2010). Likewise, an increase in *Rheotanytarsus*, which is commonly found in small rivers and streams, suggests an increase in running waters or streamflow to this site.

Unlike temperature trends which have increased unilaterally across most Andean regions (Vuille and Bradley 2000; Vuille *et al.*, 2003), precipitation has not displayed any significant trend over the last century (Rabatel *et al.*, 2013). However, changes in the type of precipitation may be relevant. For example, in the Andes, an increase in the ratio of vertical (*i.e.*, rain) to horizontal (*i.e.*, wind-blown mist) precipitation has been predicted for regions traditionally dominated by mist such as the Páramo found in the Reserva Ecológica Cayambe-Coca (Anderson *et al.*, 2011). Even with no change in total precipitation, a shift from mist to rain will affect how water is retained within the catchment, with precipitation falling as rain more likely to result in runoff. The effect of increased runoff is likely to be more pronounced in regions with steep-sided slopes, such as those surrounding Laguna Baños, which would increase seepage habitats and increase the transport of the terrestrial and semi-terrestrial taxa into the lake. It is also plausible that, under conditions of enhanced periods of thermal stratification, the abundances of benthic taxa may have declined. This, in turn, could account for the apparent increase in the terrestrial or semi-terrestrial taxa (Heiri and Lotter, 2003).

Response to volcanism

Tephra may affect the physical nature of lakes including changes to the light regime as well as habitat alteration by burying aquatic macrophytes and other benthic habitats. Changes to limnological variables have also been documented, including fluctuations to lakewater pH (Blong, 1984), increased inputs of silica and other nutrients (Barker *et al.*, 2000) and the release of contaminants including Hg and other metals (Weinstein and Cook 2005). Previous research on sediment cores from the Andes of northern Patagonia, Argentina, has shown elevated Hg concentrations immediately above tephra layers, suggesting a link to volcanic sources (Guevara *et al.*, 2010). In the Laguna Baños sediment core, Hg concen-

trations rise dramatically to ~7X above background in the region of the tephra (Fig. 5), showing that volcanic activity substantially increased the Hg load to the lake.

Changes to the diversity and abundance of diatom and chironomid assemblages following tephra deposits have been recorded elsewhere in the Andes (Urrutia *et al.*, 2007; Massaferrero and Corley 1998). In Laguna Baños, *Cocconeis placentula* records the single largest change in species relative abundance (>20%) between adjacent intervals (Fig. 6). This diatom assemblage at 24-cm depth sits atop the ~10-cm thick tephra deposit that ultimately truncated this Laguna Baños sediment record (Fig. 2b). *Cocconeis placentula* is a fast growing, pioneer species capable of rapidly colonizing bare substrates (Kelly *et al.*, 2005). We hypothesize that, after the tephra deposit (~10-cm thick) blanketed the lake bottom, *C. placentula* was able to outcompete the other diatom taxa. Following the disturbance event, *C. placentula* sharply decreased in percentage and the diatom species composition shows little change thereafter (until the planktonic taxa increase at ~12 cm depth) suggesting that the effect of the tephra on diatoms was short-lived.

The fossil chironomid assemblages did not record any major composition shift in response to the tephra. Rather, immediately above the tephra layer, chironomid head capsules were absent and abundances remained low until ~20-cm depth. A decrease in the concentration of head capsules following a tephra deposit was recorded in Andean lakes from Chile and Argentina (Urrutia *et al.*, 2007; Massaferrero and Corley 1998). This drop in abundance in the sediments following the tephra may be due to disruptions to chironomid habitat and food supply.

CONCLUSIONS

Both diatom and chironomid remains from Laguna Baños sediment recorded responses to changes in climate. Both occurred at approximately the same time and both assemblage shifts were subtle; however, changes in the two indicator groups may have been driven by different climate variables. The diatoms response is consistent with rising temperatures that, amongst other limnological changes, lead to enhanced periods of thermal stratification, which favors the growth of planktonic taxa. This is a commonly recorded response to warming globally (Rühland *et al.*, 2015). The sudden increase in the planktonic taxa suggest the crossing of a threshold with respect to greater periods of thermal stratification, and the stable percent abundances thereafter indicate similar conditions have persisted until present day, and no new ecological thresholds have, as of yet, been crossed. We surmise that the lake likely still undergoes frequent periods of mixing, but currently experiences longer periods of thermal stratification than in the past.

The chironomids appear to have responded primarily

to changes in precipitation, showing a recent increase in the number of terrestrial and semi-terrestrial taxa. This may be a response to overall increased precipitation or to changes in the precipitation regime, such as a shift from mist to rain, or even possibly a greater number of large episodic rainfall events. The possibility also exists that this apparent increase is due to a decline in benthic taxa that is occurring with increased periods of thermal stratification. Any temperature-driven changes to the thermal regime of Laguna Baños are not yet to the point where chironomids are affected by limnological change, such as increased anoxia that might accompany lengthy periods of stratification. This supports our conclusions from the diatom assemblages that the lake still likely undergoes frequent periods of mixing, even if periods of thermal stratification have likely increased in recent decades.

Both diatoms and chironomids recorded a response to volcanic inputs. The reason why the diatoms registered a change in species composition and the chironomids did not, may be related to the short life cycle of the diatoms, which allow species to take advantage of new environmental conditions very rapidly. Although we do not have data on the pre-tephra assemblages, both diatoms and chironomids appear to have stabilized following the tephra. These data suggest that the Laguna Baños diatom and chironomid assemblages may have been affected by the tephra; however, the ecological response was temporary.

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