Chironomids as indicators of natural and human impacts in a 700-yr record from the northern Patagonian Andes

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ABSTRACT

Chironomid communities were studied in a sediment core collected from Lake Moreno Oeste, located in Nahuel Huapi National Park. A major change in midge assemblages occurred at ~AD 1760, which was characterized by a decrease of "cold taxa" including *Polypedilum* sp.2 and *Dicrotendipes*, and an increase of "warm taxa" including *Apsectrotanypus* and *Polypedilum* sp.1. These taxa are likely related to climatic conditions concurrent with the end of a cold period at ~AD 1500−1700 and the beginning of a drying climate at ~AD 1740−1900 in northern Patagonia. Coarse tephra layers had low midge diversity; however they did not disrupt the climatic trend as the community recovered rapidly after the event. Since AD 1910, after the increase in suburban housing, fish introduction, and the construction of a road, there was an increase in the relative abundances of taxa typically associated with the littoral zone, such as *Parapsectrocladius*, *Riethia*, *Apsectrotanypus*, and some Tanytarsini morphotypes. The main change in the chironomid community appears to be associated with long-term climate change. At the beginning of the 20th century, other site-specific environmental factors (catchment change and fish introduction) altered the chironomid assemblages, making it more difficult to understand the relative importance of each driver of assemblage change.

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Introduction

Chironomidae (Insecta: Diptera) comprise one of the most abundant, diverse, and representative aquatic insect taxa with their larval stages serving as an important link in the ecology of aquatic environments (Walker, 2001). This family is one of the few groups of freshwater benthic macroinvertebrates that can be readily used in palaeoenvironmental reconstructions. Since larvae have head capsules composed of chitin, their remains are generally very well preserved in lake sediments (Millet et al., 2014). Many species are stenotopic and their chitinous head capsules can be recovered from sediment and identified (Francis, 2004), enabling the reconstruction of the chironomid community composition over-time. For these reasons, chironomids have proved to be excellent proxy indicators in lake studies throughout the world (Lotter et al., 1997). In the Southern Hemisphere, and particularly in Patagonia, few palaeolimnological studies involving chironomids have been conducted (Corley and Massaferro, 1998; Massaferro and Brooks, 2002; Massaferro et al., 2005; Massaferro and Larocque, 2013; among others), and there is still much work to be done to improve our understanding of their ecology.

Palaeolimnological studies are a useful tool for assessing the impact of various types of global events in the environment. Multiproxy analyses are useful for assessing the impact of different types of anthropogenic and natural environmental changes on macroinvertebrate communities (Millet et al., 2014). In particular, chironomid assemblages are potentially affected by a variety of environmental parameters and complex ecological processes, with climate (temperature) and in-lake processes (trophic condition)

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serving as potential forcing factors driving changes in chironomid communities (Brodersen and Anderson, 2002). During low-amplitude temperature changes, the influence of temperature on chironomid assemblages may be exceeded by the influence of other environmental factors, such as anthropogenic changes in the catchment (Millet et al., 2014). In recent years, paleolimnological studies in Patagonia have used chironomids as proxies for understanding past climatic variations (Massaferro and Brooks, 2002; Massaferro, 2009; Massaferro and Larocque, 2013). Additional studies have used chironomids to track the impact of volcanic ash (tephra) deposition on lacustrine ecosystems (Araneda et al., 2007) and to evaluate the influence of different environmental changes on chironomid communities occurring during the last ~100 yr in Lake Morenito (Massaferro et al., 2005). Knowledge of the ecology of Patagonian chironomids is still poor and too limited to provide consistent ecological interpretations (Verschuren and Eggermont, 2006; Araneda et al., 2007) or to make inferences about the main drivers that determine their life histories and species distribution compared to studies undertaken in the Northern Hemisphere.

Paleoclimate data from Patagonia are still not sufficient to allow the development of a detailed quantitative reconstruction. There are few records of the regional climate over the last millennium. Until now, dendrochronology studies in northern Patagonia in Argentina and a multi-proxy analysis in Lake Puyehue in southern Chile have identified two important climatic periods: a humid period associated with the onset of the European little ice age (LIA) between AD 1490 and 1700, and another period characterized by a drying climate between AD 1740 and 1900 (Villalba, 1990, 1994; Lara and Villalba, 1993; Bertrand et al., 2005).

Northern Patagonia, considered a region with low anthropogenic impact, is characterized by a large diversity of glacial oligotrophic lakes. The Nahuel Huapi National Park (NHNP), situated in this region, is the largest protected natural area in Argentina and is characterized by its remoteness and is a large reservoir of freshwater resources. However, human activities, e.g., deforestation, erosion, and domestic sewage disposal, have impacted this region over the past few decades mostly due to the increasing immigration from other parts of Argentina (Massaferro et al., 2005). Furthermore, since this region is part of the Southern Volcanic Zone (Stern, 2004), numerous volcanic eruptions have also impacted this area during the last millennium. Consequently, numerous aquatic environments in the NHNP have been adversely affected by volcanic events (Massaferro et al., 2005).

The overarching goal of this study is to document the responses of subfossil chironomid taxa to environmental changes associated with known natural and anthropogenic events or conditions that affected Lake Moreno Oeste in the NHNP and its surrounding environment during the past 700 yr. The chironomids were obtained from a sediment core extracted from Llao-Llao Bay. We chose the chironomid fauna as bioindicator group to assess the ecosystem response to the influence of human-induced (i.e., catchment change and fish introduction) and natural-induced (i.e., temperature and volcanic eruptions changes) with two specific objectives: 1) reconstruct subfossil chironomid assemblages spanning the last centuries of environmental change and 2) relate changes in subfossil chironomid assemblages to known local and regional events.

Site description

The NHNP (~7100 km^2) is located in northern Patagonia (40°15′–41°34′S, 71°4′–72°54′W), on the eastern slope of the southern Andes, comprising a catchment area that includes three major river systems, thirteen lakes with larger than 10 km^2 in area, and several hundred small lakes and ponds (Daga et al., 2008). The NHNP is part of the Southern Volcanic Zone, which includes at least

60 historically, and potentially active volcanoes in Chile and Argentina, three giant silicic caldera systems, and numerous minor eruptive centers (Stern, 2004).

Like most of the lakes in the NHNP, Lake Moreno (41°5′S; 71°33′W, 758 m above sea level) is a deep, clear and warm monomictic lake of glacial origin. Lake Moreno has an extended euphotic zone (Secchi disk ~20 m), low dissolved organic carbon (DOC; 0.82 mg L^{-1}), total phosphorous (TP; 3.89 μg L^{-1}), and nitrogen concentrations (TN; 144.1 μg L^{-1}). The vertical oxygen distribution follows an orthograde curve year-round, typical of unproductive lakes during thermal stratification (Modenutti et al., 2000; Díaz et al., 2007).

Lake Moreno consists of two relatively large and connected lakes: Moreno Este (ME) with an area of 5.42 km^2 and maximum depth of 106 m, and Oeste (MO) with an area of 5.22 km^2 and maximum depth of 90 m, plus a smaller lake, Morenito, with an area of 0.82 km^2 and maximum depth of 12 m that is connected to the larger lakes by a shallow channel open from mid-autumn to late-spring (Buria et al., 2007; Fig. 1). De la Virgen, Casa de Piedra, and Goye rivers, flow into ME, and the López River flows into MO, which in turn is connected by a short channel to Lake Nahuel Huapi, the largest lake in the NHNP that is at an altitude of 764 m asl, an area of 557 km^2 and a maximum depth of 464 m (Ribeiro Guevara et al., 2005). The MO basin has a highly irregular coastline, with peninsulas, bays, and flooded areas inhabited by macrophytes, both submerged (*Myriophyllum quitense* and *Nitella* sp.) and emergent (*Schoenoplectus californicus*, *Ranunculus* sp., *Hydrocotyle chamaemorus*, and *Galium* sp.; Arcagni et al., 2013), and surrounded by temperate rainforest dominated by *Nothofagus dombeyi* and *Austrocedrus chilensis* (Queimaliños et al., 1999).

During the 20th century, human activity has affected Lake Moreno and its surrounding environment. This has included the introduction of exotic salmonid in AD 1910 that comprising *Oncorhynchus mykiss* (rainbow trout), *Salmo trutta* (brown trout) and *Salvelinus fontinalis* (brook trout) (Macchi et al., 2007), and deforestation, construction of suburban housing in the catchment since 1930, and a dam construction that artificially isolated Lake Morenito from MO in 1960 (Modenutti and Pérez, 2001; Massaferro et al., 2005).

Methods

Sampling, sedimentology and chronology

A 43 cm-long sediment core, which we call LL, was extracted in AD 2000 with a messenger-activated gravity corer from the deepest point of Llao-Llao Bay (at a depth of 20 m) in MO (Fig. 1). The sediment core was longitudinally cut using a portable circular saw to section the tube walls, and afterwards a copper plate was slid through the sediment to divide it into two semi-circular sections. The open core was photographed and sediment characteristics, granulometric properties and color, were described. Several tephra layers were identified as the most significant sedimentological features in the core. Both semi-circular sections were sub-sampled every 1 cm and the sub-samples were freeze-dried until they were completely dry (constant mass). Afterwards, they were homogenized and organic matter (OM) content was estimated using loss on ignition (LOI) at 550°C for 4 h (Heiri et al., 2001). The geochemical and morphological characteristics of LL core, including a discussion of the composition and origin of tephra layers, was previously described by Daga et al. (2010).

The sediment accumulation rate was determined using ^{210}Pb and ^{137}Cs dating. ^{210}Pb dating technique relies on the nuclear decay of ^{210}Pb isotope deposited together with sediments, which exhibits an exponential specific activity profile in the sedimentary
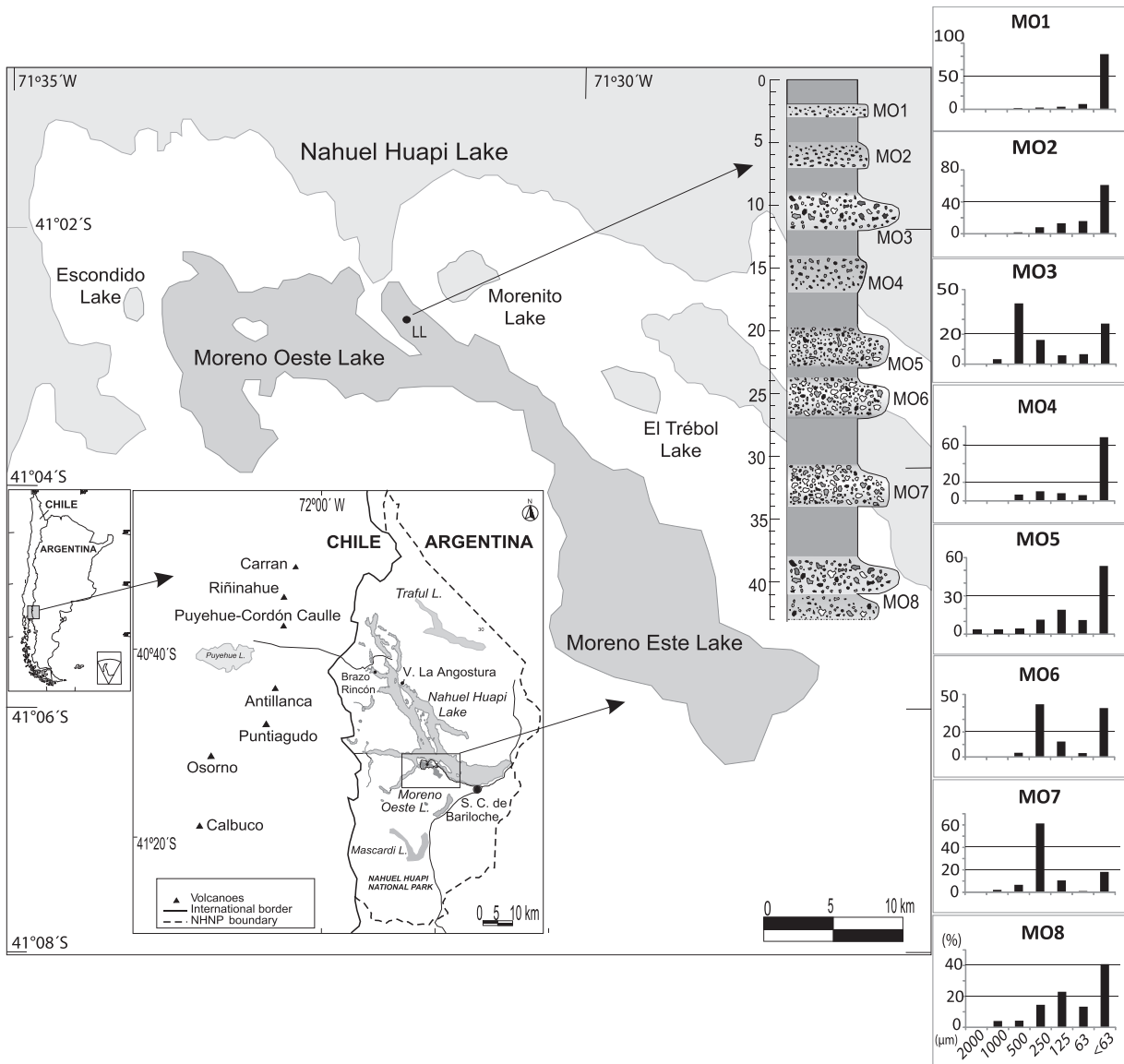
Figure 1. Map of the study area with detail of the sequence extracted from Lake Moreno Oeste. Granulometry composition of each tephra is showed. Modified from Daga et al. (2010). LL indicates the site from which the sediment core was extracted.

sequence. The evaluation of the specific activity profile with a proper model, the CRS (Constant Rate of Supply) in this case, allows a determination of the sequence chronology and the sedimentation rate. The ^{210}Pb specific activity profile in MO sequence showed significant determinations, with the expected exponential behavior, from core top until 1 g cm^{-2} depth, hence allowing ^{210}Pb dating in the upper 5 cm layers. The sedimentation rate determined was 13.3 ± 1.0 mg cm^{-2} yr^{-1} (0.0584 ± 0.0044 cm yr^{-1}; Daga et al., 2008). ^{137}Cs dating technique correlates ^{137}Cs specific activity peaks in the sedimentary sequence profile with the historical ^{137}Cs fallout sequence in the study region (Ribeiro Guevara and Arribére, 2002), allowing to associate sediment layers with ^{137}Cs fallout dates. The results of both dating techniques are in good agreement. Ages for deeper sediments were obtained by extrapolation with sediment mass by using the sedimentation rate determined by the ^{210}Pb dating in the upper 5 cm of the core. To avoid in the extrapolation the effect of sediment dilution by inputs not associated with the regular sedimentation dynamics, such as pyroclastic material, volcanic ashes were subtracted from sediments by estimating the fraction in each layer from the analysis under binocular microscope.

Dating estimation by extrapolation of ^{210}Pb determination, which assumes no change in sedimentation rate before AD 1900, was complemented with tephrochronological correlations. The geochemical characterization of the tephra layers deposited before AD 1900 allowed the identification of the volcanic source, showing good agreement between extrapolated ^{210}Pb ages and volcanic events records (Daga et al., 2008). Therefore, both independent methods allowed the establishment of a consistent sediment succession chronology, covering 700 yr of sedimentation.

Chironomids

The analysis of the chironomid head capsules was conducted on subsamples that had a dry mass of 1 g, which were extracted from the sediment matrix using the standard methods of Walker (2001). Chironomid head capsules were mounted on slides and identified with reference to available taxonomic literature (Wiederholm, 1983; Coffman and Ferrington, 1996; Cranston, 2000; Epler, 2001). To identify members of the Tanypodinae, we used the identification method of Rieradevall and Brooks (2001) based on cephalic

setation; and Massaferro et al. (2013) for morphotypes of the Tanytarsini tribe (Chironominae) based on the antennal pedestal, premandible teeth, mentum and ventromental plates. Photomicrographs were taken of each taxon to preserve a record of the subfossil content (Fig. 4).

Statistical analysis

The taxonomic diversity (H′) of chironomid assemblages in each sub-sample was calculated using the Shannon index and the balance of the community through the richness index (R) (Begon et al., 1999; Zar, 2010). To test the differences between two diversity indexes, we used the Hutcheson's test (1970) $(t = (H'_1 - H'_2)/(sH'_1 - H'_2)$; considering "s" the variance between diversity "H′" values) (Zar, 2010).

The relative abundance of each taxon was presented as a percentage of the total abundance in each sub-sample using TILIA and TILIA GRAPH v.1.7.16 (Grimm, 1987). To distinguish different associations in chironomid communities within the core, a stratigraphically constrained sum-of-squares cluster analysis (CONISS) was applied. Zones were determined using major differences in CONISS groupings; significant differences in changes among the zones were determined with an analysis of similarity (ANOSIM, Clarke and Warwick, 2001), with zones as factors. The similarity percentage procedure (SIMPER) on transformed variables (Primer 6.1.6, Clarke and Gorley, 2005) was used to determine which taxa contributed most to the differences among the groups.

Principal component analysis (PCA) was applied to the chironomid assemblages to assess compositional structure and faunal turnover throughout the core (Birks, 1998) and percentage data was square root transformed. PCA was performed using CANOCO version 4.5 (ter Braak, 1991).

Results

Core lithostratigraphy

The LL core consisted of homogeneous silty clay-size material composed of siliciclastic sediment and organic matter in variable proportions, with subtle changes in particle size and color in tephra layers. The sequence contained eight intercalated tephra layers named as MO1– MO8 (Fig. 1), composed by variable proportions of coarse grain size particles (2000–63 μm) and fine sediment (<63 μm). Visual inspection of the tephras revealed that most of the <63 μm particle size comprised lake sediment. Tephras MO1, MO2 and MO4 are composed of a large proportion (60–80%) of fine lake sediment, while tephras MO3, MO7 and MO8 recorded a high proportion (60–80%) of coarse particles of volcanic origin (63–1000 μm; Fig. 1). MO5 is composed of almost 50% of <63 μm particles that corresponds to volcanic ash according to its geochemical composition (Daga, personal communication), and the maximum size particles reach >2000 μm. MO6 is characterized by 40% of host fine sediment and 60% of coarse particles, however the most abundant coarse particles correspond to the 500–250 μm fraction (Fig. 1). According to their granulometric properties and geochemical composition, MO1, MO2, MO4, and MO6 are considered as fine tephras, while MO3, MO5, MO7, and MO8 are referred as coarse tephras in the following sections.

Organic matter (OM) content and its relationship with tephra layers

The percentage of organic matter was relatively constant along the core, with an average of 5.5%, although the OM content increased to an average of 10% in the upper-most 7 cm of the core (starting at an age of ~AD, 1920). The greatest content of OM (14.9%) was in the

top 1 cm of the core and was coincident with the highest values for chironomid abundance and richness (Fig. 2). As detailed previously, the tephra layers showed different grain size distribution (Fig. 1). Variable geochemical composition is also observed depending on the different volcanic sources (Daga et al., 2010). Beyond these differences, all tephra layers marked a noticeably decrease in OM content, related to the deposition of high quantities of allochthonous inorganic material in very short periods.

Chironomid community

A total of 1594 head capsules were recorded in the 43 sediment samples analyzed from the core. A minimum of 50 head capsules were identified in most samples except in of coarse tephra layers which contained very few head capsules. Despite some layers from the lowest part of the core also had a low amount of head capsules, they always had more than 30, which also allowed to make inferences (Larocque et al., 2009) (Fig. 2; Table 1). Twenty-nine of the taxa belong to the subfamilies Chironominae, Tanypodinae, Orthocladiinae, Prodiamesinae and Podonominae. Taxa belonging to Chironominae were the most abundant in the entire sequence comprising 55.8% of the total taxa found (Tribe Chironomini: 36.3% − Tribe Tanytarsini: 14.4% − Tribe Pseudochironomini: 5.1%), followed by Tanypodinae (34.7%), Orthocladiinae (7.8%), Prodiamesinae (1.6%), and Podonominae (0.1%) (Fig. 2).

The H′ and R values for all sub-samples were calculated (Fig. 2). The highest values of H′ and R are at 1 cm (H′ = 1.14; R = 22) and the lowest (H′ = 0.45; R = 3) at 33 cm (MO7). There is a sharp decrease in total abundance, R and H′ values associated to the coarse tephras MO3, MO5, MO7 and MO8 (Fig. 2). However, there were no statistical differences (test *t*: p > 0.05) between diversity values of the immediate upper and lower layers of coarse tephras. As detailed previously, tephra layers had the lowest abundance of chironomid head capsules and, as a consequence, fewer taxa, e.g., *Parapsectrocladius*, *Polypedilum* sp.2, *Parakiefferiella*, and some Tanytarsini morphotypes (Fig. 3).

The most abundant taxa included *Apsectrotanypus* (26.4%), followed by *Polypedilum* sp.2 (11.2%), and *Polypedilum* sp.1 (8.5%) (Fig. 3). Less abundant taxa included *Dicrotendipes* (6.6%), *Ablabesmyia* (6.6%), *Riethia* (5.1%), *Parapsectrocladius* (4.5%), *Cryptochironomus* (3.4%), *Paracladopelma* (2.7%), *Parakiefferiella* (2.3%), Chironominae ind.1 (2.1%), *Monodiamesa* (1.6%), *Djalmabatista* (1.2%), *Parachironomus* (0.9%), *Apedilum* (0.7%), and *Limnophyes* (0.7%). Taxa such as *Cricotopus*, *Labrundinia*, *Chironomus*, Chironominae ind.2, Podonominae ind.1, Podonominae ind.2 and Tanypodinae ind.1 represent less than 0.5% of the samples. We also identified different morphotypes of the Tribe Tanytarsini (Chironominae) such as Tanytarsini D2 (4.5%), 1C (3.8%), D (3.1%) and other types with abundances less than 1% such as Tanytarsini 1A, 1B, B, C and 1D (Massaferro et al., 2013). All taxa shown in Figure 3 were present in at least two samples. Representative images of the chironomids are shown in Figure 4.

The CONISS analysis divided the core in two main biozones, A and B, based on the relative abundance of chironomids, which were further sub-divided into A1, A2, B1, B2 and B3 (Fig. 3). There were significant differences in the composition of chironomid assemblages among different biozones according to the ANOSIM test (R = 0.18, p = 0.001). The main characteristics of the different biozones are shown in Table 1 and described below.

Biozone A

This biozone was characterized by Chironominae (Tribe Chironomini) and the dominant taxon was *Polypedilum* sp.2. Although the taxa composition was similar in A1 and in A2, *Polypedilum* sp.2
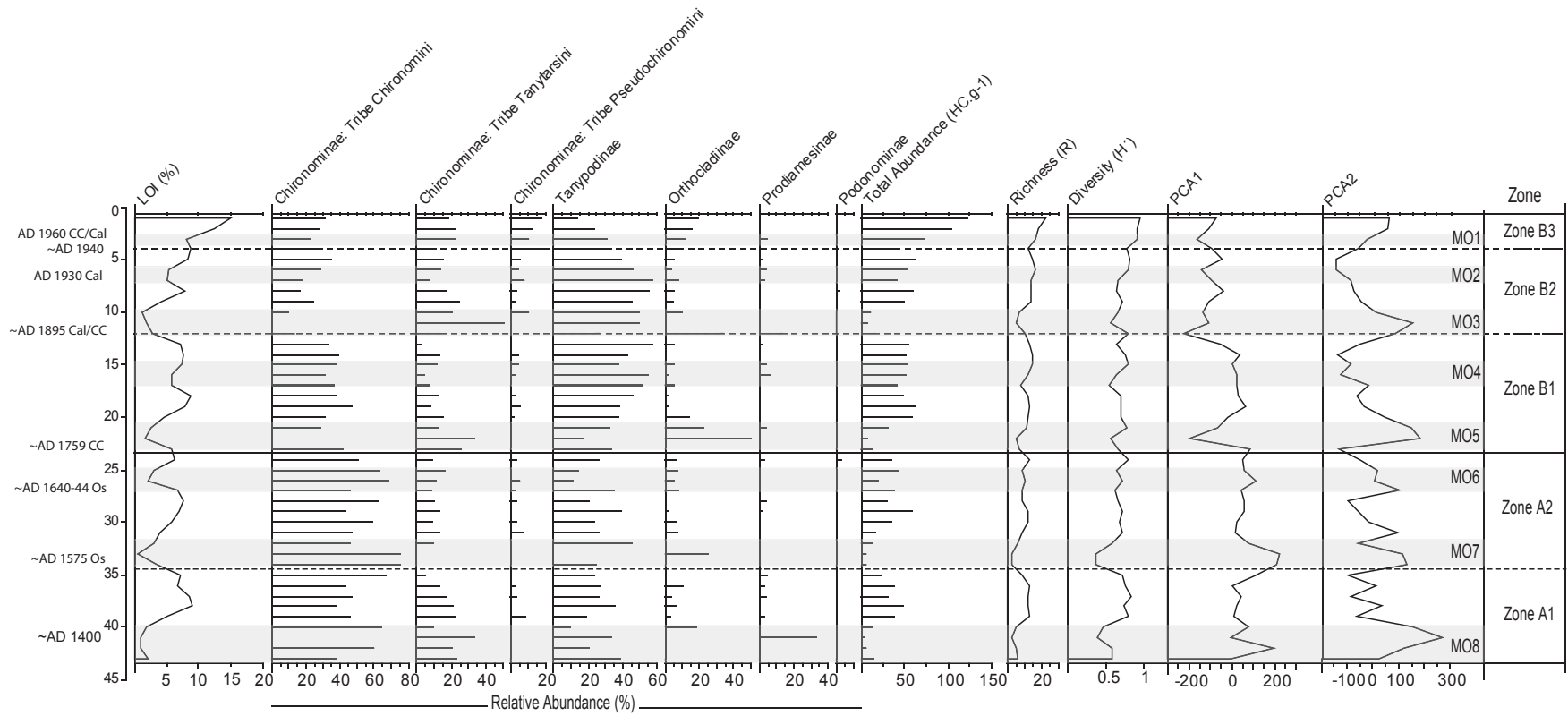
Figure 2. Loss on ignition: LOI (%) profile, relative abundance (%) of Chironomidae subfamilies, total abundance (HC/g), richness (R) and diversity (H′) indices, PCA scores, biozones, and volcanic ash layers (gray rows). Volcanoes that showed a principal influence: Cordon Caulle Complex (CC), Calbuco (Cal) and Osorno (Os).
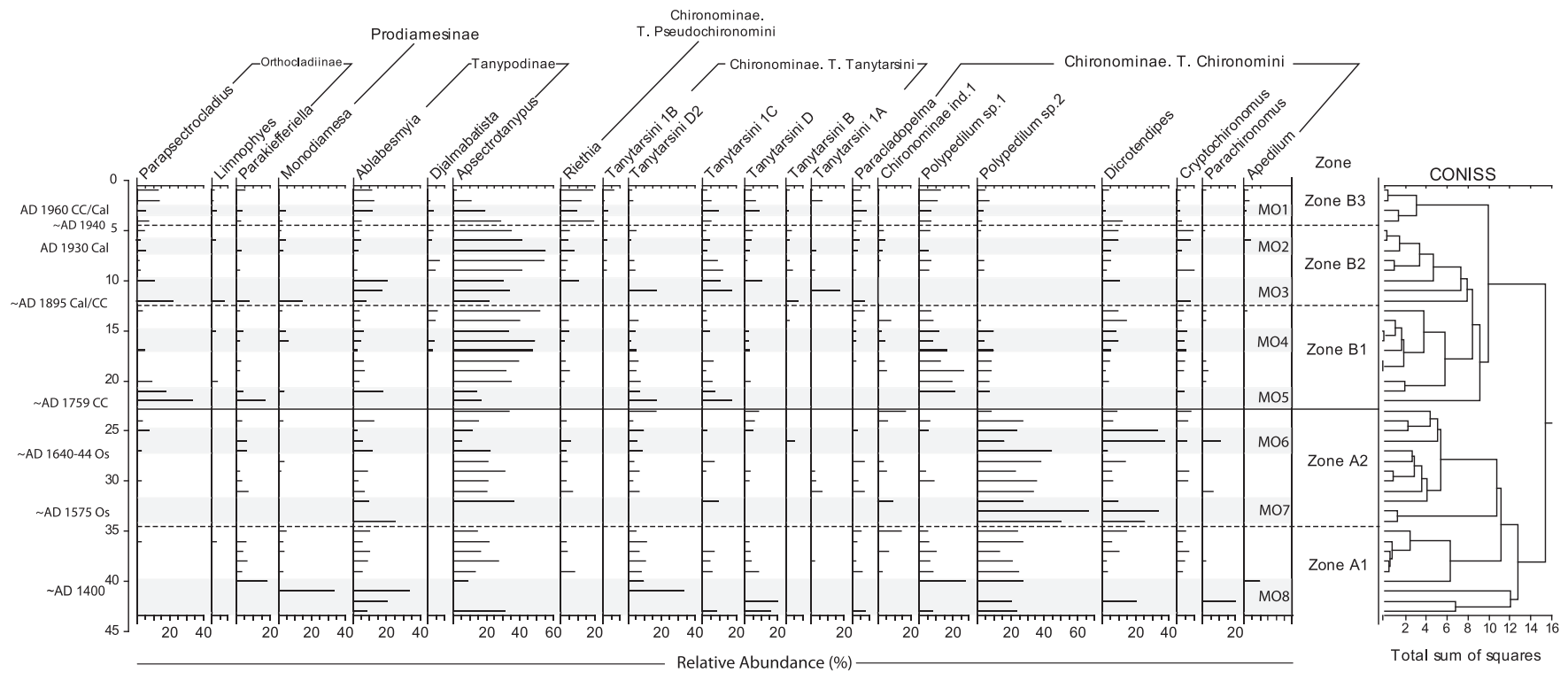
Figure 3. Relative abundance of Chironomidae taxa from Lake Moreno Oeste sediment. Chironomid zones were determined based on a CONISS cluster analysis on the different taxa relative abundances.
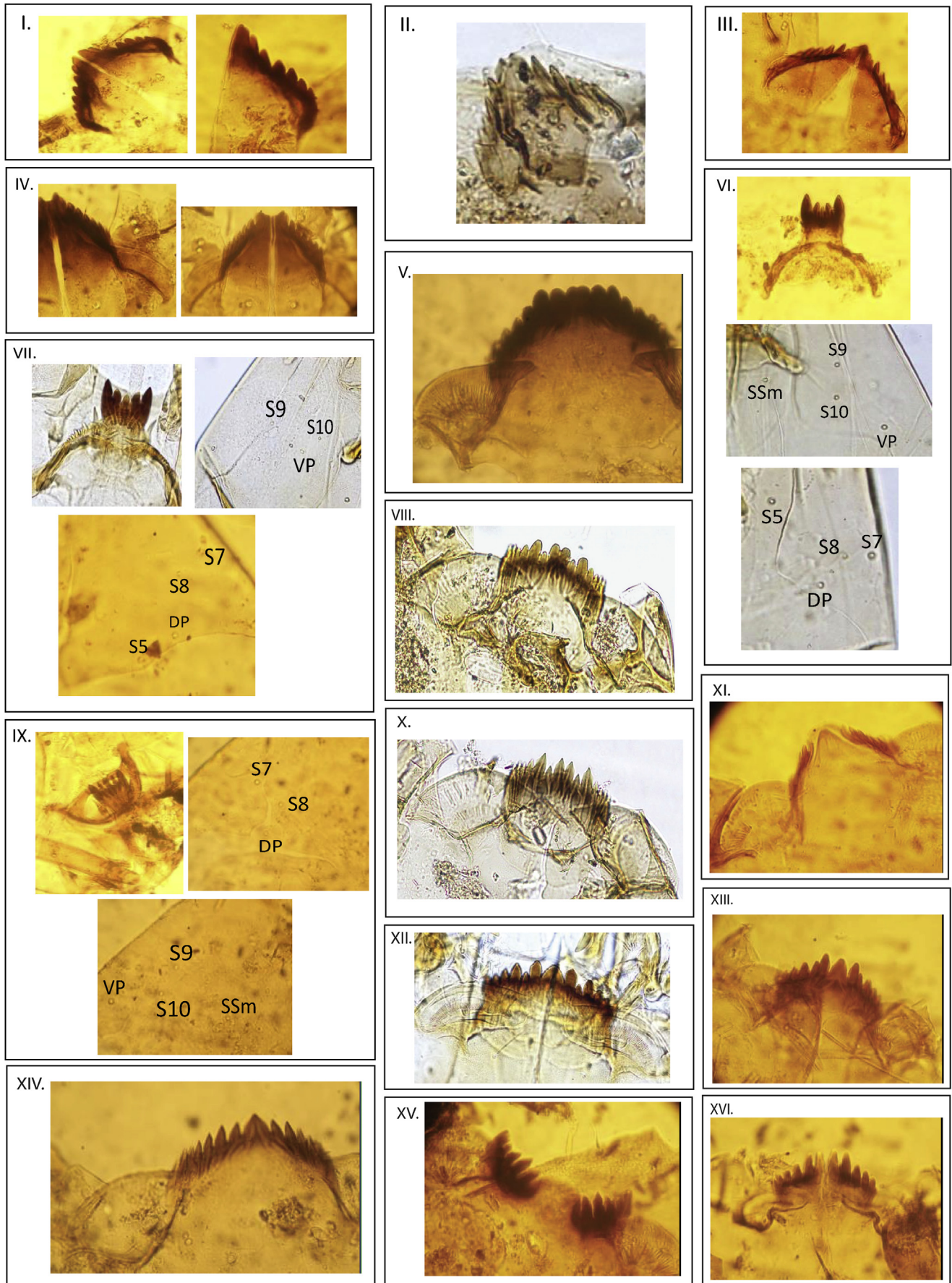
Figure 4. Photomicrographs of key fossil chironomid head capsules from Lake Moreno Oeste. I. *Parapsectrocladius*, II. *Limnophyes*, III. *Parakiefferiella*, IV. *Monodiamesa*, V. Chironominae ind.1, VI. *Djalmabatista*, VII. *Ablabesmyia*, VIII. *Polypedilum* sp.1, IX. *Apsectrotanypus*, X. *Polypedilum* sp.2, XI. *Paracladopelma*, XII. *Riethia*, XIII. *Dicrotendipes*, XIV. *Parachironomus*, XV. *Cryptochironomus*, XVI. *Apedilum*.

and *Dicrotendipes* increased and *Ablabesmyia* and *Polypedilum* sp.1 decreased in A2, while the opposite trend was observed in A1 (Table 1).

Biozone B

Tanypodinae was the most abundant subfamily and *Apsectrotanypus* the main taxa in this biozone. Higher abundances of *Apsectrotanypus*, *Parapsectrocladius*, *Polypedilum* sp.1, Tanytarsini 1C and *Riethia* were present in this biozone, with taxa such as *Djalmabatista* and Tanytarsini 1B, and others with abundances lower than 0.5% (e.g. *Chronomus*, Tanytarsini C, and Tanytarsini 1D; not represented in Fig. 3), were only registered in this biozone towards the top. The highest values of abundance, R (17) and H′ (1.05) were recorded in zone B3, with an average abundance of 85.5 capsules g^{-1} (Fig. 2).

On the basis of the SIMPER analysis, the most important taxa that determined the differences between the main zones A and B, were *Apsectrotanypus* (contribution to dissimilarity: 12%), *Polypedilum* sp.2 (8%), *Polypedilum* sp.1 (7.4%), *Parapsectrocladius* (6.2%), Tanytarsini 1C (5.4%), and *Dicrotendipes* (5.4%).

PCA analysis

Coarse tephra layers MO3, MO5, MO7, and MO8 were excluded from the PCA analysis because their abundance, richness, and diversity were considered anomalous. The deposition of a tephra layer, particularly coarse tephras, corresponds to an almost instantaneous event that results in greater than normal sedimentation rate. Samples MO1, MO2, MO4, and MO6 represent minor or more distal eruptions characterized by a slower deposition rate and composed principally of <63 μm diameter particles (Fig. 1). Chironomid assemblages from these tephras were not affected, hence they were included in the PCA analysis (Fig. 2).

Differences between the main biozones are apparent in the PCA analysis (Fig. 2). PCA1 and PCA 2 axes (Fig. 5) make it possible to distinguish the specific changes in chironomid assemblages and their relationship with the defined biozones. The first axis explains 24.5% of the total variance and both axes explain 39.9% of the total variance. The PCA biplot shows two main groups of samples concurrent with the biozones determined from the cluster analysis (Figs. 3 and 5). Samples in biozone A (black in Fig. 5) are pooled at the positive end of axis one of the PCA, and the samples in biozone B (red in Fig. 5) are pooled at the negative end of axis one. The main taxa that determined the distribution of the samples are also indicated in Figure 5.

Discussion

The importance of ash fall events in chironomid assemblages

Volcanic ash deposition in lacustrine environments may have had a major impact on the fauna, producing changes and sharp instantaneous drops in diversity and abundance in chironomid assemblages (Massaferro and Corley, 1998; Massaferro et al., 2005; Araneda et al., 2007). This response could be associated with an increased nutrient input, diminution of light penetration, the sealing of the sediment–water interface, burial of the macrophytes in littoral zones, and changes in the pH and salinity of the lake water (Eastwood et al., 2002). The ash deposition also produces changes in the lake sedimentological structure with lower organic content and coarser grain size (Araneda et al., 2007).

Daga et al. (2010) presented an accurate characterization of the volcanic products recognized in the LL sequence where they described eight tephra layers with different grain size distributions and geochemical composition. With regard to the chironomid assemblages, it was evident that in fine tephras (MO1, MO2, MO4, and MO6), composed by a higher proportion of particles <63 μm corresponding to the silty clay host sediment, chironomid abundance, R and, H′ values remained unchanged. In contrast, in coarse tephras (MO3, MO5, MO7, and MO8) there was a notable decrease in chironomid abundance, R and, diversity values (Fig. 2). Despite this, we did not recognise any significant difference between diversity values of the immediate upper and lower layers of coarse tephras. Therefore, we suggest that the chironomid community rapidly recovered its abundance and diversity after coarse tephra deposition, restoring the previous structure from the pulse disturbance and exhibiting a high resilience capacity (Massaferro and Corley, 1998; Massaferro et al., 2005; Araneda et al., 2007). Due to the low sedimentation rate of MO (1 cm in ~10−25 yr) determined by ^{210}Pb and tephrochronological analyses, we could not precisely estimate the recovery time, however previous works have observed that chironomids appeared to recover rapidly after tephra deposition, perhaps taking advantage of the organic material trapped in the new sediments (Massaferro et al., 2005). According to Miserendino et al. (2012, and references there in), the recovery process of benthic communities, after ashfall episodes takes between 5 and 10 yr.

Table 1
Summary of the chironomid assemblage biozones, layer depth (cm), age period, HC (head capsules) average, dominant and subdominant taxa, and corresponding tephras for each zone. Average of relative abundances of each taxa are showed in parenthesis.

| Chironomid assemblage zone	Depth (cm)	Age Period	HC average (HC g^{-1})		Dominant taxon	Subdominant taxa	Tephras
			All samples	without coarse tephra layers			
B3	4−0	~AD 1940−2000	86	86	*Apsectrotanypus* (14.9%)	*Riethia* (14.4%) *Ablabesmyia* (9.6%) *Parapsectrocladius* (9.5%)	MO1
B2	12−5	~AD 1895−1940	38	53	*Apsectrotanypus* (38.3%)	*Ablabesmyia* (6.8%) Tanytarsini 1C (6.8%) *Parapsectrocladius* (5.6%)	MO2 MO3
B1	22−13	~AD 1760−1895	46	53	*Apsectrotanypus* (35.2%)	*Polypedilum* sp.1 (12.7%) *Parapsectrocladius* (6.6%) Tanytarsini D2 (5.7%)	MO4 MO5
A2	34−23	~AD 1500−1760	25	34	*Polypedilum* sp.2 (31%)	*Apsectrotanypus* (17.9%) *Dicrotendipes* (14.2%) *Ablabesmyia* (6.9%)	MO6 MO7
A1	43−35	~AD 1400−1500	22	34	*Polypedilum* sp.2 (20%)	*Apsectrotanypus* (14.8%) *Ablabesmyia* (11.1%) Tanytarsini D2 (9.2%)	MO8
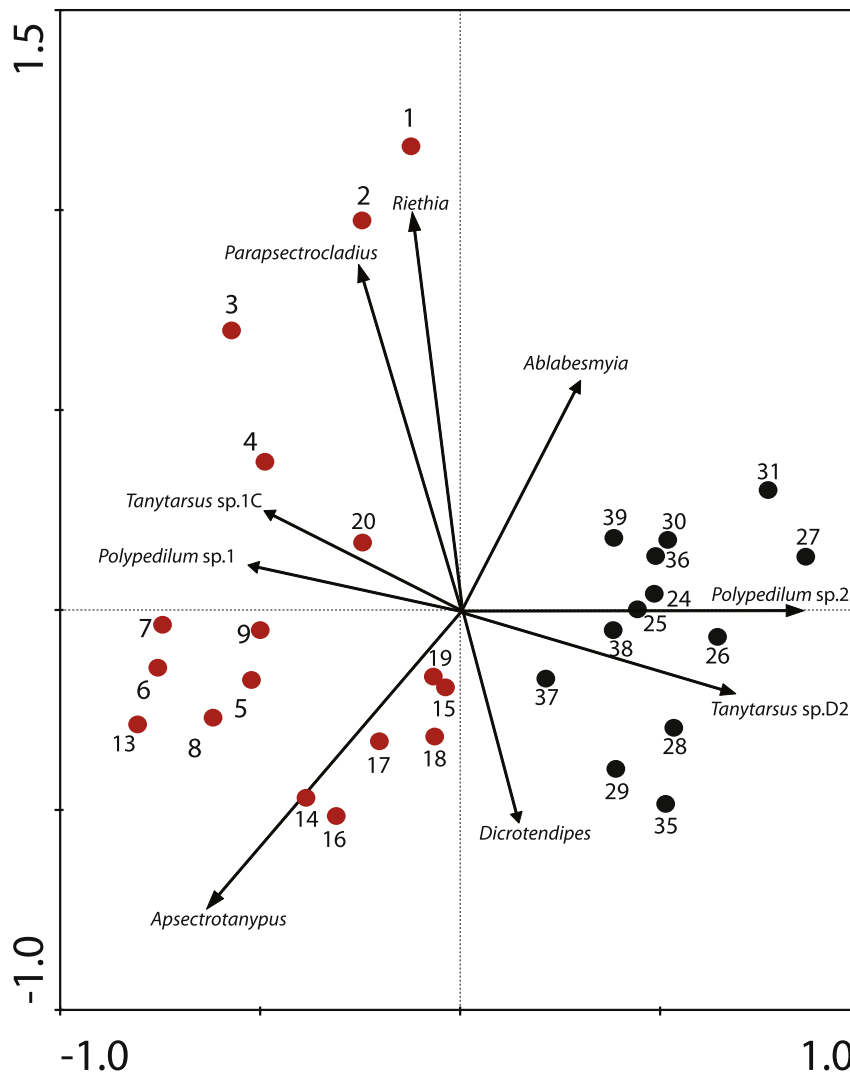
Figure 5. PCA biplot of the sediment core samples. Black dots samples belonging to Biozone A. Red dots samples belonging to Biozone B. The main taxa that determined the distribution of the samples are also shown. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

The coarse tephras with particles >63 μm could have generated notable decreases in midge assemblages due to the input of high amounts of material accumulating several centimeters at the bottom of the lake in a short period of time, thus altering the normal sedimentation pattern. This kind of process was evident during the 2011 Cordón Caulle eruption, where 2 cm of tephra was deposited in the bottom of Lake Moreno, mostly during the first weeks after the eruption (Daga et al., 2013). Alternatively, fine tephras could correspond to volcanic ashes from minor or more distal eruptions reaching the lake catchment. In such cases, the minor amounts of volcanic material together with the hydrodynamic properties of fine volcanic particles in water (suspension, drifting) and late inputs from the catchment (surface runoff, winds) could generate less clear, or diluted, deposits at the bottom lake (Lowe, 2011). The 2015 Calbuco eruption (Romero et al., 2016) could be considered as the type of eruption that generates this kind of fine tephras, with less notable effect on the biological communities.

Cordón Caulle, Calbuco, and Osorno volcanoes showed a dominant influence in the sedimentary succession, each characterized by different geochemical composition (Daga et al., 2010). The chironomid assemblages, however, did not present a response associated to the different tephra sources, so we could infer that the chemistry of tephra layers recorded in the LL core would not be a determining driver on past changes in this community, as it is the particle size.

Lake Moreno Oeste chironomid community as temperature indicator

The chironomid composition of MO is typical of lakes surrounded by *Nothofagus* spp. forest from NHNP in Patagonia as described by Donato et al. (2008) and Añón Suarez (1991). Within the LL core, the dominant taxa were *Apsectrotanypus*, *Polypedilum* sp.1, *Polypedilum* sp.2, *Dicrotendipes*, *Ablabesmyia*, and *Riethia*. Although there is a lack of studies from northern Patagonia that focus on the ecological preferences of the Chironomidae, Massaferro and Larocque (2013) developed chironomid transfer functions based on sixty-seven lakes in southern Patagonia. They observed that *Dicrotendipes* is more abundant in lakes with temperatures between 3 and 5°C, and *Riethia* is most abundant in lakes with temperatures between 5 and 5.5°C. Although in Patagonia, *Polypedilum* sp. and *P. quinquesetosus* are mainly associated with warm climates (Donato et al., 2008; Massaferro and Larocque, 2013), in Tasmania *P. vespertinus* Skuse and *P. watsoni* Freeman are restricted to cooler lakes (Rees et al., 2008), which suggest that particular requirements of temperature of *Polypedilum* are species dependent. Moreover, currently in MO there are two species of

Polypedilum: *Polypedilum* sp.1, associated with higher temperatures and littoral habitats; and *Polypedilum* sp.2, associated with lower temperatures and deeper distribution (Williams, personal observation).

The main changes in chironomid assemblages evident between biozones A and B identified in the PCA and in the cluster analysis, occurred at the end of the LIA (AD 1500–1700). A period of lower temperatures in the area have been estimated in the mid-15th century from dendrochronological studies (Villalba et al., 2001) and in a multi-proxy analysis of sediments from Lake Puyehue (Bertrand et al., 2005). A glacial geologic study (Villalba, 1990) and tree-ring studies (Lara and Villalba, 1993; Villalba, 1994) in northern Patagonia have characterized the periods from ~AD 1740–1900 as having a dry climate. Neukom et al. (2011), through a multi proxy analysis (lake sediments, tree rings, ice cores), performed a reconstruction of austral summer (winter) surface air temperature fields back to AD 900 from southern South America (SSA), where they also observed a period of lower summer temperatures (~AD 1400–1650) in northern Patagonia. The coincidence of all these different proxies with periods of lower temperatures confirms that the LIA was evident in the southern hemisphere (Fig. 6).

The main shift in the chironomid assemblages at the A/B transition in the LL core was characterized by a sharp drop in *Polypedilum* sp. 2 and *Dicrotendipes*, which were dominant in the deeper part of the core and are mainly associated with colder temperatures (Massaferro and Larocque, 2013; Williams, personal observation). A trend towards a more thermophilous community after ~AD 1760 in the lower section of the core (23 cm), indicated by an increase in the relative abundances of *Apsectrotanypus* and *Parapsectrocladius*, was generally associated with higher temperatures and littoral zones (Ashe et al., 1987; Fig. 6).

The drying climate period (~AD 1740–1900) was recognized in the biozone B by the increase in the relative abundance of *Parapsectrocladius*, *Apsectrotanypus*, and *Djalmabatista*. These genera, which are generally adapted to warmer waters, prefer standing and littoral water (Ashe et al., 1987), and live in areas inhabited by aquatic vegetation in Llao-Llao Bay (Williams, personal observation). Other less common midge taxa (<0.5%) from our core, like *Chironomus*, Tanytarsini C and Tanytarsini 1D are also associated with higher temperatures (Massaferro and Larocque, 2013) or warmer seasons in MO (Williams, personal observation). As such, the main changes in the chironomid assemblages in the lower and middle parts of the core may have been driven by temperature changes. Higher temperatures and drier climate may be associated with a decrease in the water level and a greater development of the littoral zone in the lake (Vermaire et al., 2013). This situation produces an increase in the development of the macrophyte stands (*Myriophyllum* sp. and *S. californicus)*, that in turn are responsible of the appearance of some new thermophilous and stenothermic chironomid genera and the lower abundance of the colder stenothermic taxa. The increase of temperatures in the area, indicated by dendrochronological studies and the glacier retreat (Villalba, 1990, 1994), were the driven factors for the warming up of the lake water and the change in subfossil chironomid assemblages.

Human impacts: increasing the complexity of paleolimnological results

Since AD 1900, the chironomid richness and abundance reached the highest values within the core, concurrent with the first human impacts (Fig. 2) and with a period of higher summer and winter average temperatures, as summer temperatures reached conditions similar to earlier warmer periods (Neukom et al., 2011) (Fig. 6). Salmonid introduction in Lake Moreno at ~AD 1910 (Macchi et al., 2007) could be one of the drivers for the changes observed in

zone B2, which enhances the changes in midge assemblages generated by higher temperatures. This situation represents a trend towards an increase of taxa such as *Apsectrotanypus*, *Parapsectrocladius*, and some Tanytarsus morphotypes, like Tanytarsini 1B, B and 1A, associated to the littoral zone of the lakes (Ashe et al., 1987; Añón Suarez, 1991).

Takamura et al. (2009) stated that fish introduction has an indirect influence in the community structure of benthic macroinvertebrates through their excretion and directly or indirectly by habitat disturbance or modification. Moreover, changes in zooplankton structure following fish introduction can cause a direct impact in the sediments by increasing the pelagic organic matter. This increase in nutrient concentrations can result in enhanced macrophyte development in the littoral zone that supports flourishing chironomid assemblages (Frossard et al., 2013), intensifying the effect of the higher temperature and the lower precipitation already observed in zone B1. However, in Lake Moreno, as the introduction of exotic fish is relatively contemporary with the higher temperatures resulting in milder winters and hotter summers (Neukom et al., 2011), it is difficult to establish which factor is the main environmental driver for the changes in the midge assemblage (Fig. 6).

The construction of the first buildings around MO (foundation of Llao-Llao village in 1937 and Llao-Llao hotel in 1938), and the construction of a road that isolated Lake Morenito in 1960 (Modenutti and Pérez, 2001; Massaferro et al., 2005) generated further changes in the lake limnology. This was concurrent with the deep changes recorded in the chironomid assemblages from zone B3. From AD 1960, just after the isolation of Lake Morenito, we registered the highest abundance and richness values of the past chironomids community, with capsules averaging 100 g^{-1} at 3–1 cm. In this period, some taxa, such as *Parapsectrocladius*, *Ablabesmyia*, *Riethia*, and *Polypedilum* sp.1, which inhabit mainly on *M. quitense*, and sediment under *M. quitense*, *Nitella* sp. and *S. californicus* in MO (Williams, personal observation) increased their relative abundance noticeably. In Lake Morenito, Massaferro et al. (2005) reconstructed similar changes and suggested that the lake has become more productive since its isolation, mostly related to in-lake processes such as an increase in nutrients or algal productivity. In the long term, the construction of a dam, which substantially expanded the littoral habitat causing greater vegetation development, could have resulted in an increase of the abundance and diversity of littoral taxa as was observed by Vermaire et al. (2013) in Lake Chenago. In this sense, Takamura et al. (2009) affirmed that the quantity and species richness of submerged plants are important determinants of the community structure of macroinvertebrates inhabiting sediments in Lake Takkobu in northern Japan. This could be associated with the vegetation, which is important for the benthic community because it provides physically stable habitats, better food conditions, refuge from predators, and higher concentration of dissolved oxygen (Takamura et al., 2009). Moreover, the habitat preferences of larval chironomids in a shallow clear-water lake are related to the biomass of periphytic algae on host plants and to environmental variables (oxygen, nutrients) specific to the macrophyte stand (Vermaire et al., 2013; Tarkowska-Kukuryk, 2014). This relationship is consistent with numerous contemporary studies that have documented a relationship between chironomid community assemblage and macrophyte abundance (Langdon et al., 2010; Vermaire et al., 2013; Tarkowska-Kukuryk, 2014).

Conclusions

The main changes in chironomid assemblages in MO are due to climatic changes in the area with relatively sudden changes during
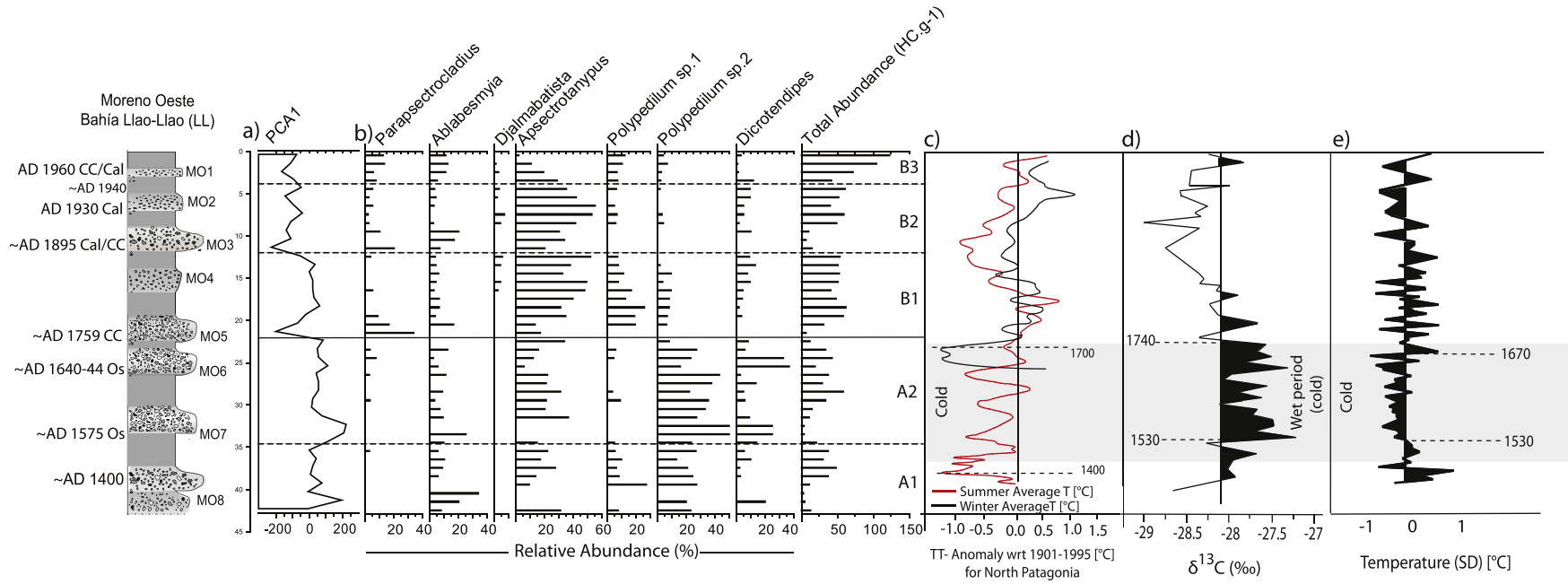
Figure 6. a) PCA axis 1 profile b) Relative abundance of main temperature-related taxa and total abundance of Chironomidae from Lake Moreno Oeste sequence. Comparison of Llao-Llao profile with Northern Patagonia climatic reconstructions with different proxy records: c) 30-yr filtered summer (year 1400–2000) and winter (year 1750–2000) temperature anomalies 900–1995 (wrt 1901–1995) for north Patagonia reconstructed by PCR (Modified from Neukom et al., 2011) d) Reconstruction of changes of paleoproductivity (δ^{13}C) from Puyehue Lake, indicating a wet period associated with lower temperatures during 1530–1740 (Modified from Bertrand et al., 2005) e) Reconstruction of summer temperature in northern Patagonia based on tree ring records (Modified from Villalba, 1994). The gray row indicates the comparable cold period in the different studies.

A/B biozone transition (~AD 1760), which according to the chronology in the LL core is concordant in Northern Patagonia with the end of a cold period (~AD 1500–1700), probably associated with LIA, and with the beginning of a period characterized by a drying climate (~AD 1740–1900). The role of climate changes in the determination of subfossil chironomid assemblages is later obscured by anthropogenic influences including the first human settlements, the introduction of salmonids, and the isolation of Lake Morenito from the main lake. The sharp instantaneous drop in the diversity and abundance of chironomid assemblages evident in the coarse volcanic layers did not disrupt the main changes through time because the community rapidly recovered to its previous condition. We can confirm that subfossil chironomids can be used as good proxies for natural and human-induced changes in Lake Moreno in the past 700 yr.

Acknowledgments

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