The dynamics of chironomid assemblages and vegetation during the Late Quaternary at Laguna Facil, Chonos Archipelago, southern Chile

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Abstract

We compare high-resolution pollen and chironomid records from the last 15,000 yr in Laguna Facil, southern Chile. Major vegetation and chironomid changes are recorded between ca 14,900 and 14,700 cal. yr BP. During the Lateglacial, changes in the chironomid stratigraphy lag behind changes in the pollen stratigraphy suggesting that the chironomids are responding to changes in the tree canopy or in soil chemistry brought about by vegetational development. At about 7200 cal. yr BP there is a change in the chironomid stratigraphy in advance of changes in the vegetation. This suggests that the response is to regional climatic change. The relatively close correlation of the chironomid and pollen stratigraphies with changes in charcoal concentrations also implicates the importance of fire and/or vulcanism in influencing the dynamics of forest and limnological systems. There is no clear evidence of cooling during the Younger Dryas chronozone in Laguna Facil.

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1. Introduction

Detailed, well-dated proxy data of Late Quaternary climate change in southern South America is the key to an understanding of inter-hemispheric climate linkages. However, compared with the north temperate region, there have been relatively few studies of climate dynamics in temperate South America. Most of these studies have focused on the response of abiotic climate proxies, such as glaciers and oxygen isotopes, and biotic proxies, specially pollen, to interpret climate change in the Late Quaternary (Markgraf and Kenny, 1997; Bennett et al., 2000; Moreno, 2000, 2004; Moreno et al, 2001; Heusser, 2002). The value of multi-proxy studies using independent indicators to provide a detailed and unambiguous impression of ecosystem responses to environmental change has been emphasised by Ammann et al. (2000) and Birks et al. (2000). In the present study, one of the first of its kind in this region, we have combined pollen and chironomids to investigate environmental change during the Late Quaternary at a site in southern Chile.

Chironomidae are powerful indicators of past environmental change. Most species are stenotopic and, because the adults are winged, they respond rapidly to environmental change. The larvae are aquatic and the remains of their head capsules are abundant and diverse in lake sediment samples, and they are readily identifiable to generic and species-group level. Chironomids are now well established in the repertoire of palaeoecological proxy indicators where they have been used most effectively to quantify past climate changes during the Lateglacial and Holocene in the northern hemisphere (Levesque et al., 1996; Korhola et al., 2000; Brooks and

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Birks, 2001). However, at present they have featured in comparatively few palaeoecological studies in the Southern Hemisphere (Paterson and Walker, 1974; Kokkin, 1986; Porch and Elias, 2000; Dimitriadis and Cranston, 2001). An examination of the response of chironomid assemblages to environmental change can compliment and augment a palynological approach. Vegetational responses to environmental change can be relatively slow, because of slow recruitment and migration rates, whereas the response of a chironomid fauna is rapid. While the vegetation responds to changes in the terrestrial environment, chironomids are sensitive to changes in the aquatic environment. Sometimes these two systems are linked, and may even be causative, but at other times the response is independent.

In a recent paper, Massaferro and Brooks (2002) presented the first high-resolution chironomid stratigraphy, covering the whole of the Late Quaternary, for any site in southern South America. The site, at Laguna Stibnite on the Taitao Peninsula in southern Chile, covering the whole of the Late Quaternary, for any presented the first high-resolution chironomid stratigraphy. The sequence is dominated by species of Nothofagus, Weinmannia and the conifers Podocarpus and Pilgerodendron (Gajardo, 1995). Laguna Facil lies at an altitude of 10 m a.s.l., has a surface area of 100 × 70 m and a maximum depth of 3 m (Fig. 1). The hydrological catchment is small (approx. 300 × 250 m) and with an outlet draining northwards to the coast. A second smaller lake is located 50 m to the west and drains into Laguna Facil. The catchment vegetation is a mosaic of open Astelia, Donatia and Oreobolus bog, open Pilgerodendron uviferum stands, and northern Patagonian rainforest. The lake edge is covered by a dense stand of Nothofagus betuloides and occasional P. uviferum in the wetter margins with the southeastern margin of the lake accessible over a Donatia–Astelia bog. The geomorphology of the catchment is highly complex Cretaceous granites scoured by glacial ice (Niemeyer et al., 1984). Several active volcanoes are located directly to the east of the region, with the most recent eruptions occurring during the 1990s from Mount Hudson (Naranjo et al., 1993).

2. Site description

Laguna Facil (44°19′S, 74°17′W) lies in the northern Chonos Archipelago, a complex island and channel landscape formed by extensive ice erosion from the Patagonian icefield that covered this region during the last glaciation (Hollin and Shilling, 1981; Haberle and Lumley, 1998). The area is dominated by a typical oceanic climate, strongly influenced by westerly winds and high precipitation (ca 3000 mm per yr). The mean annual temperature is around 8–10 °C. The surrounding vegetation is mixed northern Patagonian rainforest dominated by species of Nothofagus, Weinmannia and the conifers Podocarpus and Pilgerodendron (Gajardo, 1995). Laguna Facil lies at an altitude of 10 m a.s.l., has a surface area of 100 × 70 m and a maximum depth of 3 m (Fig. 1). The hydrological catchment is small (approx. 300 × 250 m) and with an outlet draining northwards to the coast. A second smaller lake is located 50 m to the west and drains into Laguna Facil. The catchment vegetation is a mosaic of open Astelia, Donatia and Oreobolus bog, open Pilgerodendron uviferum stands, and northern Patagonian rainforest. The lake edge is covered by a dense stand of Nothofagus betuloides and occasional P. uviferum in the wetter margins with the southeastern margin of the lake accessible over a Donatia–Astelia bog. The geomorphology of the catchment is highly complex Cretaceous granites scoured by glacial ice (Niemeyer et al., 1984). Several active volcanoes are located directly to the east of the region, with the most recent eruptions occurring during the 1990s from Mount Hudson (Naranjo et al., 1993).

3. Methods

3.1. Coring

Laguna Facil was cored using a 5-cm diameter Livingstone piston corer (Wright, 1967). The lithology of the full 10 m sequence was described carefully and before subsampling, magnetic susceptibility was performed (Haberle and Bennett, 2004). The core was subsampled for pollen, charcoal, chironomids and LOI.
analysis. Subsamples of the tephra layers were sampled for geochemical analysis to compare with other volcanic eruptions during the time span of the core (Haberle and Lumley, 1998).

### 3.2. Chironomid analysis

Subfossil Chironomidae larvae were analysed from 1–2 g wet sediment subsamples cut into 1 cm slices and sampled at intervals of about 8 cm. The samples were deflocculated with 10% KOH heated to 70 °C for 5 min. The sediment was sieved through 212 and 95 µm mesh sieves and the chironomid head capsules were hand sorted under a 25 × stereo-microscope using a Bogorov sorting tray. Finally, the head capsules were mounted in Euparal for identification under a compound microscope at 400 × magnification. Taxa were identified using the keys of Cranston (1997) and Wiederholm (1983). Due to the current rudimentary knowledge of the South American chironomid fauna, most of the specimens were identified to genus-level only, although some endemic species were recognised (e.g. *Parapsectrocladius accuminatus*). The genus *Tanytarsus* was split in four morpho-taxa identified as type - A, B, C and D (Massaferro and Brooks, 2002). The slides are deposited in the collections of The Natural History Museum, London, UK.

### 3.3. Pollen and charcoal analysis

Pollen analysis follows the standard acetolysis method described by Faegri and Iversen (1989). Pollen identification was assisted by published reference material (Heusser, 1971; Villagran, 1980; Zhou and Heusser, 1996) and regional reference collections held by SGH. Pollen counts are expressed as percentages of the total pollen and spore sum, which generally falls between 300–500 grains, excluding pollen and spores of aquatic vascular plants. Sample resolution was the same as for chironomids. Detailed counting of microscopic charcoal particles (opaque angular particles 5–100 µm in diameter) is done at the same time as pollen counting. The total number of charcoal particles counted is presented as a percentage of the total pollen and spore sum, which
is considered to be reflection of fire occurrence within the pollen source area (Clark, 1988).

3.4. Stratigraphical and numerical analysis

Stratigraphic diagrams were produced using TILIA v.21 and TILIA GRAPH 1.25 (Grimm, 1991). Zones were determined by eye and by optimal partitioning (Birks and Gordon, 1985) using the programme ZONE v. 1.2 and subsequent comparison of the partitions with the broken-stick model (Bennett, 1996; Birks, 1998) using the programme BSTICK v. 1.0. Principal components analysis (PCA), correspondence analysis (CA) and detrended correspondence analysis (DCA) were performed using CANOCO v. 4.5 (ter Braak and Smilauer, 2002) with square root-transformation of species data, non-linear rescaling of axes and down-weighting of rare taxa. These analyses were used to compare trends in the chironomid and pollen stratigraphical data.

3.5. Chronology

Tephra layers were used as markers to date the sediment sequence. Two of these tephras correspond to Hudson eruptions and have been dated as part of a regional tephrochronological analysis (Haberle and Lumley, 1998). Additionally, a series of 5 AMS radiocarbon analyses (on bulk samples) were carried out in order to establish an age-depth model for the lake sediments (Haberle and Lumley, 1998; Haberle and Bennett, 2004). An age-depth model (Haberle and Bennett, 2004) was used to convert calibrated radiocarbon years to calendar years (Fig. 2).

4. Results

4.1. Lithology, magnetic susceptibility and loss-on-ignition

Full details of lithology, magnetic susceptibility and loss-on-ignition are provided by Haberle and Bennett (2004). A summary diagram of the lithology, including the position of tephra bands, loss-on-ignition and magnetic susceptibility plots are given in Fig. 2.

A total of 763 cm of lake muds and clays was recovered from the centre of Lake Facil from 255 to 1018 cm below water surface (bws). The basal core encountered solid bedrock at a depth of 1018 cm bws. Overlying the bedrock are sediments composed of olive/grey, massive...
silty clays to 997 cm bws that are characterised by low LOI values (Fig. 2). Between 997 and 850 cm bws the sediments are dark brown lake muds with occasional bands (<1 cm thick) of olive grey sandy clay decreasing in frequency up-core. Magnetic susceptibility values show a decreasing trend to minimum values at 800 cm bws. The LOI values increase up core with a sharp peak from 850 to 800 cm bws. Above 850 cm bws to the mud water interface at 255 cm bws the sediments are uniformly dark brown lake muds. LOI continues to increase until 480 cm bws followed by a decline to the top of the core. Three tephra deposits are located at 830 cm bws (Fac-1, olive grey sandy silt, 3 mm thick), 751 cm bws (Fac-2, olive grey sandy silt, 10 mm thick), and 315 cm bws (Fac-3, olive grey sandy silt, 5 mm thick), with troughs in LOI values characterising the tephra deposits.

4.2. Chironomids

A total of 8384 chironomid larval head capsules belonging to 30 taxa was recovered from the Laguna Fácil sediment core (Fig. 3). However only those taxa occurring in more than five samples or at an abundance of more than 5% are shown in the stratigraphic diagram. Dominating the assemblage throughout the core were Parakiefferiella, Tanytarsus (specially Tanytarsus type-A) and Tanypodinae (specially Labrundinia, Apsectrotanypus and Ablabesmyia). Despite the great diversity of Chironomini in the core, this taxon was not abundant in the sequence. Using cluster analysis we recognised four chironomid zones which are characterised below. The two samples deposited at 750 and 744 cm contained large quantities of tephra ash that effectively diluted the head capsules, and fewer than 50 were recovered from these samples. For this reason they were omitted from the zonation analysis.

Zone Fa-c1 (1008–849 cm; >15,900–14,700 cal. yr BP)

This zone is characterised by low abundance and poor preservation of head capsules which made identification difficult. However the diversity is high, and most of the taxa present in the sequence are represented in this zone. The dominant taxon is Tanytarsus type-A followed by Pseudochironomus, Limnophyes, Parakiefferiella and Polypleldium. Podonominae and Tanypodinae, specially Ablabesmyia, are at their highest abundance in this zone. In the second half of the zone, Chironomus, Parapsectrocladius and later Labrundinia appear while Tanytarsus type-D disappears. The high abundance of Polypleldium, Pseudochironomus and Podonominae is characteristic of this zone.

Zone Fa-c2 (849–748 cm; 14,700–10,700 cal. yr BP)

Zone Fa-c2 is characterised by declines in the abundance of many taxa, specially Tanytarsus-type A, Apsectrotanypus, Ablabesmyia, Chironomus, Limnophyes, Polypleldium, Pseudochironomus and Podonominae, and an increase in abundance of Tanytarsus type-C and Parapsectrocladius. There is a delayed response in Labrundinia which declines after the start of the zone, and in Macropelopia and Corynoneura which both increase later in the zone. These three taxa return to their former levels before the zone ends. At the end of the zone, there is a decline in head capsule concentration and a sharp rise in abundance of Tanytarsus type-C and Parapsectrocladius.

Zone Fa-c3 (748–684 cm; 10,700–7200 cal. yr BP)

At, or shortly after, the start of this zone most of the taxa which changed abundance in zone Fa-c2 return to their former levels. The exceptions are Polypleldium, Pseudochironomus and Podonominae that continue at low abundance levels for most of the rest of the sequence.

Zone Fa-c4 (684–304 cm; 7200–0 cal. yr BP)

This zone boundary was not identified by optimal partitioning but sharp changes in the chironomid stratigraphy occur at this time which is also closely coincident with a pollen zone boundary. Parapsectrocladius declines at about 684 cm and this level also coincides with increases in the abundance of Phaenopsectra, Corynoneura, Harrisius and Gymnometriocnemus.

4.3. Pollen

A full description of the pollen stratigraphy is given by Haberle and Bennett (2004). The pollen zones are briefly described here summarising the changes in the dominant taxa that characterise each zone (Fig. 4).

Zone Fa-p1 (1018–868 cm; >15,900–14,900 cal. yr BP)

The zone is dominated by Gramineae, Compositae, Cyperaceae and Filicales. High levels of charcoal appear at the top of the zone.

Zone Fa-p2 (868–828 cm; 14,900–14,500 cal. yr BP)

The lower zone boundary is marked by sharp declines in Gramineae, Compositae, Cyperaceae, Filicales and charcoal and sharp increases in Pilgerodendron and a gradual rise in Drimys and Nothofagus. Charcoal levels are low throughout the zone.

Zone Fa-p3 (828–772 cm; 14,500–12,000 cal. yr BP)

The lower zone boundary is marked by a sharp decline in Pilgerodendron. Nothofagus begins a gradual decline
Fig. 3. Late Quaternary chironomid stratigraphy from Laguna Facil. Only the dominant taxa are shown. Solid horizontal lines indicate position of chironomid zone boundaries identified by optimal partitioning and a broken-stick model. For comparison, pollen zone boundaries are indicated by dash-lines and show how some elements of the chironomid fauna show synchronous change with vegetation change.
throughout the zone and there is a gradual increase in *Podocarpus* which peaks around 13,000–12,500 cal. yr BP. Charcoal levels are low throughout the zone.

**Zone Fa-p4 (772–668 cm; 12,000–6800 cal. yr BP)**

The lower zone boundary is marked by the appearance of *Tepualia* and *Weinmannia* which continue to rise through the zone coupled with a decline in *Pilgerodendron, Drimys* and *Nothofagus*. After ca 9500 cal. yr BP *Podocarpus* and *Weinmannia* begin to decline and there is a resurgence in *Nothofagus*. Charcoal levels increase throughout the zone.

**Zone Fa-p5 (668–255 cm; 6800–0 cal. yr BP)**

The lower zone boundary is marked by a rise in *Pilgerodendron, Nothofagus* and *Tepualia* continue to dominate for most of the zone. After ca 2000 cal. yr BP *Tepualia* declines and there is an increase in *Pilgerodendron* and *Cyperaceae*. Charcoal levels remain high and increase after about 2500 cal. yr BP.

### 4.4. Comparison between chironomid and pollen stratigraphy

Four chironomid zones and five pollen zones were identified as significant by optimal partitioning and comparison with the broken stick model. The four chironomid zones correspond closely but not exactly with four of the pollen zones (Figs. 3 and 4).

The termination of chironomid zone Fa-c1 follows the end of pollen zone Fa-p1 by between 100 and 300 cal. years as far as can be estimated within the sampling resolution of the two stratigraphies. However, there are some changes in the chironomid stratigraphy that
coincide with the upper boundary of Fa-p1, namely rises in *Parakiefferiella*, *Tanytarsus* C and declines in *Limnophyes*. Chironomid zone Fa-c2 corresponds broadly with the combined pollen zones Fa-p2 and Fa-p3. The boundary between pollen zones Fa-p2 and Fa-p3 reflects the decline of *Pilgerodendron* and the appearance of *Podocarpus*. However, although optimal partitioning did not identify a significant change in the chironomid fauna at this point, some changes in the chironomid fauna are evident. In particular, there is a strong increase in *Corynoneura* and declines in *Chironomus* and *Laborundina*. The upper boundary of pollen zone Fa-p3 lies at about 12,000 cal. yr BP and leads the end of chironomid zone Fa-c2 by about cal. 300–1600 years. However, there are some changes in the chironomid assemblage that coincide with the rise in *Tepualia* and *Weinmannia*, specially a rise in *Laborundina* and declines in *Corynoneura* and *Tanytarsus* B. Chironomid zone Fa-3 is encompassed by pollen zone Fa-p4. Chironomid zone Fa-3 ends between 300–500 years before the end of pollen zone Fa-p4. The upper boundary of Fa-p4, which marks an increase in *Pilgerodendron* coincides with a decrease in *Limnophyes* and an increase in *Chironomus*.

DCA was performed in order to determine whether the chironomid and pollen species response to environmental change was unimodal or linear. For the chironomid species data the length of the first DCA axis was 2.02 and explained 17.2% of the variance. This result indicates that the species response is linear and that PCA is most appropriate. For the pollen data the length of the first DCA axis was 2.80 and explained 40% of the variance. This result indicates that the pollen response is unimodal and that CA is appropriate. PCA and CA sample scores for chironomids and pollen are shown in Fig. 5. The plots show similar trends with the major change in both assemblages occurring at about 14,900 cal. yr BP. This change coincides with the disappearance of the herbs and shrubs and the establishment of the *Nothofagus* forest and an increase in the organic matter, expressed as LOI (Figs. 2 and 4). Another important change in the pollen CA scores appears at ca 11,500 cal. yr BP reflecting the increase of *Weinmannia* and *Tepualia*. However, the changes in the chironomid PCA axis 1 sample scores are rather small at this time.

5. Discussion

5.1. Response of chironomids and vegetational changes

There have been relatively few studies of the ecology of chironomids in Patagonia (Brundin, 1966; Fitkau and Reiss, 1973; Reiss, 1977). However, many of the genera that occur in Patagonia also occur in Australia and north temperate regions where their ecology is better known. Work on the ecology of Holartic chironomid taxa by Saether (1975) suggests that the general ecological tolerances of chironomid genera are the same throughout their range even though species within those genera may be different in North America and northern Europe. From this it follows that it is reasonable to suppose congeneric species will also occupy similar ecological niches in southern temperate regions as they do in Australian and north temperate regions, permitting tentative conclusions to be drawn about the responses of these taxa to environmental change at Laguna Facil.

Most of the taxa in the Laguna Facil Late Quaternary sequence are typical of relatively warm productive lakes. The exception is Podonominae, species of which are typical of cool, glacier-fed, oligotrophic waters. Tanytarsines, such as *Asectrotanytus* and *Ablabesmyia*, are carnivorous, but most of the other taxa can be generally described as either detrivores in the case of Chironomini or algivores in the case of Orthocladiinae and Podonominae. Most of the taxa in the sequence typically occur in the littoral of lakes, reflecting the shallow maximum depth of Laguna Facil (3 m), although *Chironomus* is also often associated with deeper waters (Saether, 1975). The larvae of *Harrisius* and *Gymnometrocnenus* are terrestrial and *Limnophyes* is also often associated with terrestrial semi-terrestrial or hygropetric environments (Cranston et al., 1983).

Species of Podonominae are at their most abundant in the sequence in zone Fa-c1 (ca 15,900–14,700 cal. yr BP) suggesting the lake waters were at their coolest at this time. LOI values were relatively low during this zone suggesting that lake productivity was relatively low and/or mineralogenic in-wash was high. Head capsule concentrations are also low for most of the zone, only increasing towards the top. However, rather than reflecting low lake productivity, this may be as a result of the high sedimentation rate in the basal part of the core. The domination of non-arbooreal pollen taxa, specially Gramineae, Compositae and Cyperaceae and the near absence of forest trees also point to a cool climate prior to about 14,900 cal. yr BP.

In the upper part of zone Fa-c1 (ca 15,000 cal. yr BP), prior to the arrival of forest, the abundance of several chironomid taxa begins to change as *Pseudochironomus*, *Polyplectrum*, *Chironomus* and *Tanytarsus* type-B decline. Since there is not a sudden change in the chironomid fauna at the Fa-c1/Fa-c2 zone boundary, this suggests that environmental change was gradual and of relatively small amplitude. The decline of Podonominae and Gramineae suggests that the climate may have been warming. The increase in charcoal concentrations is also consistent with climatic warming or vulcanism (Moreno, 2000, Szeicz et al., 2003). An ecological threshold finally may have been crossed at

849 cm (ca 14,700 cal. yr BP) when there is a sharp change in the abundance of several chironomid taxa.

Major vegetation changes are recorded at ca 14,900 cal. yr BP when the sharp decline in non-arboreal pollen taxa and the increase of *Nothofagus* and *Pilgerodendron* pollen indicate a significant change in the vegetation as forest began to get established in the area. At the same time, LOI increases suggesting an increase in lake productivity. Charcoal concentration during this period decreases, suggesting a change in regional climate towards more humid conditions. The steep rise in *Pilgerodendron*, a tree that is characteristic of wet soils, suggests increasing precipitation. This coincides with a decline in *Limnophyes* which may be responding to lake level rise since this taxon is characteristic of very shallow water.

The arrival of forest is followed by a shift in the chironomid assemblage when *Chironomus, Limnophyes, Polypedilum* and *Pseudochironomus* are finally replaced by *Tanytarsus* type-C, *Parapsectrocladius, Macropelopia* and *Corynoneura*. Interpreting this change can only be tentative until more is known about the ecology of Patagonian midges, but all the taxa that decline are typical of productive lakes. Moreover, species of *Tanytarsus* are often associated with less-productive lakes.

*Labrundina, Macropelopia* and *Corynoneura* all show strong changes in abundance during chironomid zone Fa-c2 (between 14,700 and 11,000 cal. yr BP) but the changes in abundance of these taxa do not coincide exactly with the boundaries of zone Fa-c2. Instead these taxa show a late response at the beginning of the chironomid zone and anticipate the end of the zone. Changes of these taxa are more closely tied in with vegetational changes and suggest they may be responding to catchment changes or perhaps physical changes brought about by the presence of increasing tree cover adjacent to the lake.

The only change in the chironomid fauna that coincides with lithological change occurs at 750 cm (ca 11,000 cal. yr BP) where there is a deposition of volcanic ash. Few head capsules were recovered from the sample
including the tephra probably because of the dilution effect of the rapid deposition of a large volume of sediment. The high percentage of *Tanytarsus* type-C in the sample is probably best interpreted as a consequence of the low numbers of head capsules rather than as a direct response by *Tanytarsus* type-C to a change in substrate. Head capsule concentrations remain low in the sample following the tephra band and this may also account for the abundance peak of *Parapsectrocladius*. Samples that include fewer than 50 head capsules are unlikely to be representative of the midge assemblage and therefore cannot be reliably interpreted (Heiri and Lotter, 2001; Larocque, 2001). Consequently these two samples were omitted from the zonation analysis.

At ca 11,200 cal. yr BP *Tepualia* and *Weinmannia* appear for the first time in the pollen record (Fa-p3/Fa-p4 boundary). *Weinmannia* is a shade-intolerant emergent tree that is found in poorly drained soils, whereas *Tepualia* is known to expand following disturbance in temperate forest communities. Thus, the presence of both species indicates a change from a closed-canopy rain forest community to a forest dominated by species favoured by local disturbance. Sometime after this (ca 10,000 cal. yr BP) *Pilgerodendron* declines to very low levels indicating a drying of the soils. The high percentage of charcoal in this period, suggesting an increase in fires, also indicates the climate became drier. At this time there is an increase in the abundance of *Limnophyes* and *Chironomus* which suggests that the lake had probably become lower as a result of decreasing precipitation and possibly more eutrophic. The subsequent decline in *Weinmannia* and increase in *Pilgerodendron* at ca 6700 cal. yr BP coincides with a decline in *Limnophyes* suggesting the lake levels had risen once more. At Laguna Stibnite (Massaferro and Brooks, 2002) *Limnophyes* and *Chironomus* also showed similar patterns in abundance in response to putative changes in lake level.

The reappearance of Podonominae after about 4200 cal. yr BP suggests that temperatures in the latter half of the Holocene may have begun to decline once more.

5.2. Comparison with other sites

Pollen stratigraphies are often fairly similar across a climatic region because of long distance pollen transport and also because regional vegetational assemblages are often dominated by the same species of trees. Event stratigraphies can therefore be developed in which contemporary vegetational responses can be identified in the same taxa across a biogeographic region (Walker et al., 1997).

Chironomids, on the other hand, are often not amenable to this approach because assemblages tend to differ from lake to lake since the detailed composition of the fauna is influenced by in-lake variables such as pH and trophic status. Nevertheless, although the assemblages may differ from lake to lake they can be expected to show a synchronous response to regional climate change which often over-rides the influence of local in-lake variables (Walker et al., 1992; Brooks, 2000).

Therefore, it is instructive to compare the changes in midge assemblages from various sites to see whether a regional response to climate change can be detected. Unfortunately, there is a limited number of studies of Late Quaternary chironomid assemblages in southern South America (Arlot et al., 1997; Corley and Massaferro, 1998; Massaferro and Brooks, 2002). The highest resolution study to-date, covering the period from 17,000 cal. yr BP to the present day, focused on midge and pollen assemblages at Laguna Facil, Taitao Peninsula, about 300 km south of Laguna Facil (Massaferro and Brooks, 2002) (Fig. 1). There are many similarities in the composition of the midge faunas at both sites. At both sites, a decline in Podonominae after 14,500 cal. yr BP suggests that the climate was cooler in the Late Glacial than during the Holocene. Furthermore, at Laguna Stibnite, an increase in Podonominae between 13,200 and 11,000 cal. yr BP suggests a response to cooling at a time that coincides with the Younger Dryas Chronozone (YDC). However, no response to a cooling event coinciding with the YDC is apparent at Laguna Facil. The change in the midge assemblage at about 14,700 cal. yr BP is too early to be a response to YDC cooling but the response at about 10,700 could be connected to warming at the end of the YDC. A recent study of pollen records form Laguna Facil and Laguna Oprasa (located 50 km east of Laguna Facil) showed no cooling at that time (Haberle and Bennett, 2004). The authors suggest that YDC and ACR were periods of very stable climate in southern Chile and that conditions were warmer and wetter than the period after deglaciation. The more northerly location of Laguna Facil means that it is less likely than Laguna Stibnite to have been influenced by any resurgence of Andean glaciers during the YDC (Fig. 1). At these latitudes, the behaviour and extent of the glaciers during the Last Glacial Maximum is almost completely unknown. Changing patterns of atmospheric moisture, from latitudinal movement of southern Westerlies, resulted in a high variable glacier system (Heusser, 2002; Glasser et al., 2004). Geographic variability in glacial activity would indicate that climatic conditions were possibly insufficiently intense and/or of insufficient duration to affect uniform regional palaeobiotic changes, therefore a response during the YD may be recognizable at some sites but not at others.

During the Holocene a series of cyclical changes in the Laguna Stibnite chironomid fauna, most notably *Limnophyes* and *Chironomus* alternating with Podonominae and *Polypedilum*, and coinciding with
fluctuations in Pilgerodendron pollen, suggested a response to trophic change or changes in precipitation. There are no such cyclical changes at Laguna Facil and, although the abundance of these four chironomid taxa does fluctuate, the changes are coincidental rather than being reciprocal and, in addition, these changes do not coincide with changes in Pilgerodendron. Nevertheless, a common feature of both the Laguna Facil and Laguna Stibnite sequences is that as trees are recruited into the vegetational assemblage this is reflected by changes in the chironomid assemblage. At both sites, the chironomid assemblage shows a significant change after the arrival of Nothofagus and Pilgerodendron and after the arrival of Tepualia and Weinmannia. At Laguna Facil, the chironomid and pollen zones do not exactly coincide, in fact the pollen zone boundaries tend to predate the chironomid zone boundaries. This suggests that the chironomids may be responding to changes in water chemistry variables brought about by catchment changes as a result of vegetational development or perhaps to physical changes in the vegetational structure.

There is no close relationship between the dates of the chironomid zones at Laguna Stibnite or Laguna Facil. This suggests that at Laguna Facil the chironomids are responding to local rather than regional environmental changes, perhaps in response to the gradual migration and colonisation of trees in the lake catchment.

6. Conclusions

This study has allowed us to compare the development of southern temperate forest and limnological systems, reflected in changes in chironomid assemblages, at one site during the Late Glacial and Holocene. This has contributed to our understanding of the extent to which vegetation and chironomid assemblage development are a function of a response to regional climate change or to local environmental changes.

The study shows that changes in pollen assemblages are synchronous with changes in charcoal concentrations. The presence of charcoal particles in a sediment core is related to fires and/or vulcanism. This suggests that, in Laguna Facil, a cycle of dry (high charcoal) and wet (low charcoal) periods occurred during the last 15,000 cal. yr BP. By ca 14,800 cal. yr BP, the replacement of open vegetation by tree-forest elements is coincident with a sharp drop in charcoal indicating an increase in moisture. From ca 14,500 to 11,200 cal. yr BP there is a decline in Nothofagus and Pilgerodendron followed by an increase in Tepualia and Weinmannia after 11,200 cal. yr BP. An increase in charcoal at the same time points towards drier (warmer) conditions.

Significant changes in the chironomid profile, as indicated by zone boundaries, coincide closely but not synchronously with changes in the pollen and charcoal stratigraphies. The fast generation time of chironomids and the abilities of the winged adults to disperse rapidly and widely across the landscape imply that midges are likely to respond more quickly to climatic change than trees. The lag in the response of midges compared with the forest trees would therefore suggest that the midge fauna is responding to changes brought about by the migration of these trees. This could be in response to changes in the structure of the forest canopy and amount of tree shade close to the shores of the lake, or to changes in water chemistry brought about by soil development. However, a change in the chironomid assemblage at ca 7200 cal. yr BP anticipates the resurgence of Pilgerodendron so this suggests a response to regional climatic change.

Although there have been an increasing number of palaeoecological studies in Patagonia there is still much work to be done to fully understand and interpret the regional Quaternary scenarios, involving changes in biodiversity, tree refugia, species dispersion, successional changes, and migration patterns since the last ice age.

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References


Moreno, P., 2000. Climate, fire, and vegetation between about 13,000 and 9,200 C-14 yr BP in the Chilean lake district. Quaternary Research 54, 81–89.


