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Modern pollen rain and lake mud–water interface geochemistry along environmental gradients in southern Chile

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Abstract

This paper describes the vegetation–environment relationships deduced from descriptive and numerical analysis of pollen and spore percentages and mineral concentrations in mud–water interface samples from 47 small lakes in both forested and non-forested landscapes of the remote island region of southern Chile. The study shows (1) the spatial variation in pollen and geochemistry data derived from lake mud–water interface sediments in the Chonos Archipelago in southern Chile, and (2) the relative influence of a range of environmental variables (altitude, latitude, vegetation cover, fire, edaphic conditions) on lake sediment geochemistry concentration and pollen and spore percentage data. Multivariate analysis (Principle Components Analysis, Redundancy Analysis and Canonical Correspondence Analysis) of lake geochemistry and pollen and spore data show that there is a significant influence from both altitudinal and latitudinal gradients in the region. This is most likely reflecting plant and sedimentation response to temperature gradients.

Keywords: modern pollen rain; geochemistry; numerical analysis; treeline; Chile

1. Introduction

The analysis of plant community variation along environmental gradients is essential to our understanding of the dynamics of post-glacial succession and the reconstruction of past vegetation and landscapes. Today, on the west side of the southern Andes, the landscape between lat. 43°S–55°S encompasses an environmental gradient ranging from sub-Antarctic peatlands (‘Magellanic moorland’) through temperate woodland, to diverse Valdivian rainforests that include members of families with primarily subtropical distribution such as Cunoniaceae, Myrtaceae, and Araliaceae. Despite the importance of this region to global palaeoclimates, palaeoecology and historical biogeography (Ashworth et al., 1991; Lowell et al., 1995), little is known of the relationship between plant community variation and environmental variables.

Reconstruction of past environments from fossil biotic and geochemical evidence requires an understanding of the relationship between the fossil assemblage and the environment from which it is derived. To aid in the interpretation of fossil evidence palaeoecologists rely on the so called ‘modern analogue’. This approach can tell us much about the robustness of the proxy data used in environmental reconstruction’s including modern pollen rain as a proxy for vegetation patterns, charcoal particles as a

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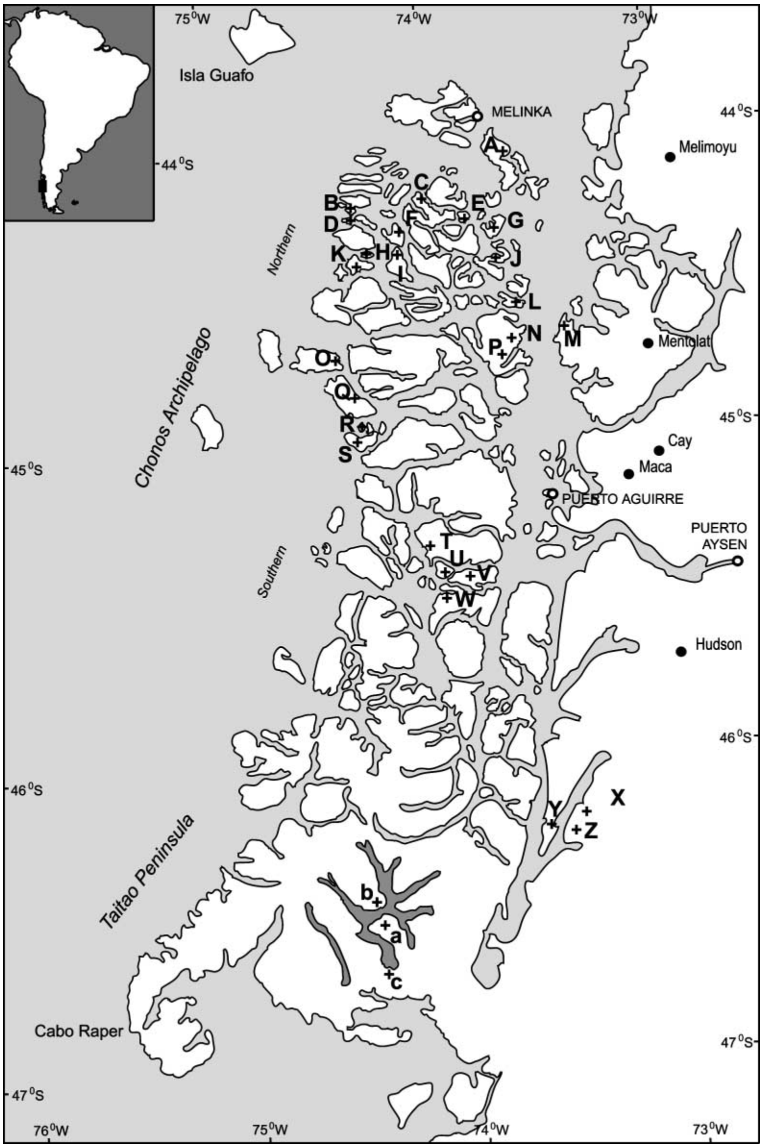


Fig. 1. Location of lake sites in the Chonos Archipelago and Taitao peninsula region of southern Chile (see Table 1 for alphabetic location codes).

proxy for regional fire occurrence, and geochemical data as a proxy for catchment sediment/water dynamics.

In this study we focus on modern pollen rain and geochemical data derived from mud–water interface samples from 47 small lakes in the Chonos Archipelago and Taitao Peninsula region of southern Chile (Fig. 1). As part of a program to reconstruct the post-glacial environmental changes of this region eight of these lakes were cored to basement rock. The results of this palaeoecological study are reported elsewhere (Bennett et al., 2000). The palynological and geochemical analysis of mud–water interface samples was designed to answer the following questions: (1) What are the general characteristics of modern pollen rain and geochemical data in the

Table 1
Lake site locations and associated environmental variables. Forest cover is a field based estimate of %canopy cover within the lake catchment area. Lake depth was measured at the center of each lake where the sediment sample was taken

Map	No.	Lake name	Latitude	Longitude	Altitude (masl)	Lake depth (m)	Charcoal (%)	Forest cover (%)
Northern Chonos Archipelago								
A	1	Laguna Caterina	44°01′20″S	73°38′40″W	25	3	44.4	100
B	2	Laguna Tomahawk	44°10′30″S	74°19′50″W	75	2	3.6	100
C	3	Laguna Luna Noche	44°10′30″S	73°59′40″W	30	7	2.2	100
D	4	Laguna Hugh	44°12′20″S	74°20′00″W	75	4	12.8	100
D	5	Laguna Bethen	44°12′30″S	74°19′40″W	75	4	30.9	100
D	6	Laguna Danica	44°12′40″S	74°19′50″W	75	2.5	23.4	100
E	7	Laguna Esorpion	44°14′20″S	73°50′00″W	50	3	17.6	100
F	8	Laguna Elisabeth	44°15′10″S	74°07′50″W	49	4	2.1	75
F	9	Laguna McNaughton	44°15′20″S	74°07′40″W	47	4	76.6	100
G	10	Laguna Scrogin	44°16′10″S	73°41′30″W	75	4	3.3	75
G	11	Laguna Keddie	44°17′30″S	73°43′10″W	75	8	56.4	100
G	12	Laguna Sara	44°17′40″S	73°43′00″W	75	4	2.2	75
H	13	Laguna Facil	44°19′30″S	74°17′00″W	10	3	1	75
H	14	Laguna Kyle	44°19′30″S	74°17′10″W	10	3	9.7	100
I	15	Laguna Linda	44°19′30″S	74°08′40″W	25	3	60.3	50
J	16	Laguna Veronica	44°21′20″S	73°39′30″W	50	3.5	13.9	100
J	17	Laguna Helena	44°21′20″S	73°39′20″W	50	3.5	11.6	100
J	18	Laguna Oprasa	44°21′20″S	73°39′20″W	50	3	94	100
K	19	Laguna Marion	44°22′30″S	74°19′40″W	125	1	67.1	100
L	20	Laguna Concierto	44°31′20″S	73°36′00″W	76	4	112.6	100
M	21	Laguna Barbera	44°35′20″S	73°24′00″W	20	2.5	3.4	100
N	22	Laguna Cuptana	44°35′40″S	73°38′50″W	30	5	72.2	50
N	23	Laguna Schistosome	44°36′10″S	73°37′30″W	30	2.5	8.8	50
N	24	Laguna Echo	44°37′30″S	73°36′10″W	20	4.5	25.8	25
N	25	Laguna Boal	44°39′20″S	73°39′30″W	400	4	26.9	25
O	26	Laguna Sybilline	44°40′20″S	74°27′10″W	25	1	81	50
P	27	Laguna Valentin	44°41′25″S	73°40′10″W	750	2.5	2.4	0
P	28	Laguna Alba	44°41′30″S	73°40′20″W	770	1.5	17.6	0
Q	29	Laguna Sputnik	44°45′40″S	74°24′10″W	25	3	93.8	100
Q	30	Laguna Beckett	44°46′50″S	74°23′20″W	25	1.5	7.8	100
R	31	Laguna Fro	44°51′40″S	74°14′10″W	75	1.5	8.5	100
R	32	Laguna Apache	44°52′40″S	74°19′50″W	25	3	24	100
R	33	Laguna Lofel	44°53′00″S	74°24′40″W	25	2	17.4	100
S	34	Laguna Dos Islas	44°55′20″S	74°19′30″W	75	0.5	14.3	100
Southern Chonos Archipelago								
T	35	Laguna Pescado	45°19′30″S	74°05′50″W	25	4	17.6	100
T	36	Laguna William	45°19′45″S	74°04′40″W	125	2	84.3	100
U	37	Laguna Lincoln	45°22′10″S	74°04′20″W	25	1.5	11.3	100
V	38	Laguna del Sol	45°23′00″S	73°51′00″W	25	1.8	81.8	100
V	39	Laguna Corazon	45°23′40″S	73°58′50″W	85	1.8	38.5	100
W	40	Laguna Charles	45°25′50″S	74°01′40″W	25	3	16.5	100
Mainland								
X	41	Laguna Miranda	46°08′40″S	73°26′40″W	120	4	1.5	100
Y	42	Laguna Coigue	46°10′50″S	73°34′10″W	825	5	11.2	0
Y	43	Laguna Pumilio	46°11′25″S	73°34′40″W	675	7.5	7.4	50
Z	44	Laguna Fantastico	46°13′40″S	73°30′50″W	75	13	1	100
Taitao Penninsula								
A	45	Laguna Percy	46°26′30″S	74°24′30″W	25	4	4.6	25
B	46	Laguna Melisa	46°31′20″S	74°29′10″W	25	0.5	2.5	25
C	47	Laguna Guernsey	46°38′30″S	74°24′20″W	25	0.5	3	25

Chonos-Taitao region? (2) What is the relative influence of a range of environmental variables (e.g. temperature, fire, edaphic conditions, volcanic activity) on the mud–water interface sediment geochemistry and regional modern pollen and spore spectra? (3) What are the implications of this modern pollen rain and geochemical data set for palaeoenvironmental reconstruction in the study area?

Assumptions in this work are as follows: (1) that the mud–water interface samples represent deposition within the last 200 years. Late Holocene sedimentation rates for lakes studied in this region suggest that this is a reasonable assumption (Bennett et al., 2000). (2) The mud–water interface pollen assemblage and geochemistry reflects variations in local vegetation–landscape units. In order to minimise the contribution of long-distance or regional pollen sources to the total pollen assemblage and maximise the contribution from local sources (within a few hundred metres of the lake basin (Jacobson and Bradshaw, 1981), the size of lakes sampled in this study was restricted to those less than 300 m diameter. Studies on the spatial representation of palaeoecological sites suggest that the larger the lake basin the more extensive the pollen source area (Jacobson and Bradshaw, 1981; Jackson, 1994).

Few studies of modern pollen rain have been carried out in southern South America, and those that have, focus on terrestrial deposits or moss polsters as receptacles for modern pollen (Heusser, 1974; Markgraf et al., 1981; Ashworth et al., 1991; Paez et al., 1994). In these studies *Nothofagus dombeyi*-type was found to be abundant in a range of samples including those from areas above the treeline due to the long-distance dispersal capacity of this pollen type. *Tepualia* and *Podocarpus* were also considered to be over-represented in the pollen spectra, whereas taxa such as *Maytenus*, *Desfontainia* and *Philesia* were shown to be under-represented. These studies have shown that, in general, the pollen spectra adequately represented the local vegetation type from which the sample was derived. In this study we provide the first examination of modern pollen rain from small lake basins in southern Chile across a range of environmental gradients, including latitude, longitude, altitude, forest cover, lake morphology, fire regime and lake sediment geochemistry.

1.1. Environmental setting

South of 44°S the westernmost high mountains overlook saltwater channels and fjords carved by extensive ice erosion from the Patagonian icefield that covered the region during the last glaciation (Clapperton and Sugden, 1988). The climate is strongly oceanic, with high precipitation produced by the coupled ocean-atmospheric influence of the Southern Polar Front that migrates seasonally between 50°S (austral summer) and 40–45°S (austral winter). Annual precipitation averages around 3000 mm, though the orographic impact of mountains rising to around 4300 m altitude may increase this threefold (Fujiyoshi et al., 1987). Annual average temperatures at sea level range from between 8–10°C, and decreases further to the east with increasing continentality. The geology of the region is highly complex Cretaceous granites overlain by Quaternary tills and volcanics (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).

The Taitao Peninsula and Chonos Archipelago region harbours North Patagonian rain forest, dominated by evergreen broadleaf and conifer taxa (Gajardo, 1995; Veblen et al., 1983). Lowland areas support a dense forest of evergreen *Nothofagus*, *Weinmannia trichosperma*, *Podocarpus nubigena*, *Drimys winteri*, *Caldcluvia paniculata*, *Pseudopanax laetevirens* and several species of the Myrtaceae. In general, *Nothofagus dombeyi* dominate the more continental forests to the east whereas *N. betuloides* and *N. nitida* dominate the coastal forests of the archipelago and peninsula. *Blechnum*, Hymenophyllaceae and other ferns and lichens are abundant. Poorly drained sites are dominated by open cover of *Pilgerodendron uviferum* and *Tepualia stipularis*. This same association, with an understorey dominated by *Philesia magellanica*, *Astelia pumila* and *Lepidothamnus fonkii*, is found in degraded or burnt areas, possibly as a result of selective logging practices over the last two centuries. *Chusquea*, a dense understorey bamboo that invades disturbed *Nothofagus* forest is generally restricted to the mainland areas and is only found in restricted pockets under the northern Chonos Archipelago *N. nitida* forests.

Forest diversity and stature tend to decrease with increasing elevation. Above 400 m, a number of heliophytic taxa, including *Weinmannia*, *Pseudopanax* and some Myrtaceae, drop out as the more open forests become dominated by *Nothofagus betuloides* and *Pilgerodendron uviferum*. Above about 600 m, dwarf trees with heights greater than 1.2 m are scarce, with cold-tolerant plants such as *Berberis buxifolia* and the deciduous *Nothofagus antarctica* becoming more important (*N. pumilio* is only rarely found in protected pockets near the treeline in the more oceanic climates). From 46–44°S the treeline lies at around 650–700 m altitude and is dominated by *N. betuloides* and *P. uviferum*. Above this, isolated stands of *N. betuloides*, *N. antarctica* and *Pilgerodendron* form 'Krummholtz', that gives way to cushion plants including *Astelia pumila*, *Donatia fascicularis*, and *Oreobolus obtusangulus*.

2. Methods

Fieldwork was conducted in the southern hemisphere summers of 1991, 1992, 1994, 1995 and 1996, with the logistic support of Raleigh International (UK) and CONAF (Corporación Nacional Forestal, Chile). Over the course of these five expeditions in the Chonos Archipelago-Taitao Peninsula region, lake sites were examined along transects running: (a) north–south from lat. 44°00′S to 46°39′S (latitudinal contrast); (b) west–east from long. 74°40′W to 73°26′W (decreasing oceanic influence); and (c) low-high altitude from 5 to 825 m above sea level. The focus of the site survey was on lakes that fell within specific morphological criteria, namely lakes that were small (<200 m diameter), deep (they have not filled with sediment to the point where rooted aquatics have colonised across the sediment surface), and with simple shapes so that complex patterns of sediment accumulation are reduced. Lakes fitting this criteria in the Chonos-Taitao study area were initially identified from aerial photographs and maps. Such lakes are ideal for the proposed work by reducing to a minimum stratigraphic complications of interpretation (for examples see Bennett et al., 1990 in the northern British Isles).

Table 1 lists the location and associated environmental variables for each site recorded in the study region. A total of 47 lakes were included in this analysis (Fig. 1). Surface samples were collected from each lake using a Höngve sampler (Wright, 1980) in order to ascertain the lake water depth, pollen content and geochemistry of mud–water interface sediments. All samples are stored at the cold-store facility in the Department of Quaternary Geology, University of Uppsala, Sweden.

2.1. Geochemical analysis

Mud–water interface samples were analysed for relative inorganic and organic content (loss on ignition (LOI) at 500°C for 5 h), biogenic silica, and allogenic and authigenic mineral components. The separation of the inorganic fraction into three components follows the fractional method introduced by Engstrom and Wright (1984) and modified by Lumley (1993). The wet-chemical extraction technique separates the acid-soluble 'authigenic fraction' and biogenic (diatom) silica from the clastic mineral 'allogenic fraction'. This provides information on the origin and relative contribution of mineral fractions in relation to erosional inputs (allogenic), redox conditions (authigenic) and lake productivity (biogenic Si). Elements considered in this study include Fe, Mn, Al, Mg, Na, K, Ca, Ti, Zn, Ba and Si. Element analysis was carried out on the ICPES at Royal Holloway and Bedford New College, UK, and calibrated with a series of matrix matched standard solutions.

2.2. Pollen and charcoal analysis

Pollen analysis follows the standard acetolysis method described by Faegri and Iversen (1989). Pollen identification was assisted by authored reference material (Heusser, 1971; Villagrán, 1980; Zhou and Heusser, 1996) and regional reference collections held at the Department of Plant Sciences, University of Cambridge. Pollen counts are expressed as percentages of the total pollen and spore sum, which generally falls between 300 and 500 grains, excluding pollen and spores of aquatic vascular plants. Charcoal analysis provides basic data on the abundance of charcoal in the sediment. 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

Table 2
Correlation coefficients between environmental variables (bold r values significant $P < 0.05$)

	Latitude (utm)	Longitude (utm)	Altitude (m.a.s.l.)	Forest cover (%)	Lake depth (m)	Charcoal particles (%)
Latitude (utm)	–	**0.75**	0.22	−0.35	0.09	−0.22
Longitude (utm)		–	**0.49**	−0.40	0.42	−0.23
Altitude (m.a.s.l.)			–	**−0.62**	0.12	−0.16
Forest cover (%)				–	0.06	0.20
Lake depth (m)					–	−0.09
Charcoal particles (%)						–

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).

2.3. Numerical analysis

To address the question about the relationship between environmental gradients and the response variables, namely mineral concentration and pollen and spore percentages, we used principal components analysis (PCA) and redundancy analysis (RDA) on the geochemical data set and canonical correspondence analysis (CCA) on the pollen and spore percentage data set (using the program CANOCO version 4.0, ter Braak and Šmilauer, 1998). Zonation of the pollen assemblage, constrained latitudinally and determined by binary splitting by sums-of-squares, and plotting of the pollen and geochemical diagrams have been implemented within psimpoll, a C program for plotting pollen data, developed by Bennett (1994).

3. Results and discussion

3.1. Correlation between site variables

Table 2 gives the correlation coefficients between the major site variables. Longitude and forest cover are all significantly correlated with altitude. Lake water depth at the sampling site and charcoal particle percentage (a proxy for fire occurrence in the pollen source area) are not significantly correlated with any variable.

3.2. Geochemistry

The mud–water interface geochemistry of the Chonos-Taitao lakes show a high degree of variability across the latitudinal gradient plotted in Fig. 2a and b. The element concentrations are divided into four regional zones based on the biogeographic grouping of Gajardo (1995) that show:

(1) LOI and biogenic silica (diatoms) are highly variable. LOI and biogenic silica often show low values at times of high allogenic mineral concentration;

(2) some allogenic elements have concentrations in general, higher across the southern Chonos archipelago than in the northern region. Al, Na and K are the dominant elements. High total allogenic mineral concentrations are reflected across all the contributing elements;

(3) some authigenic minerals, notably Na and K show a consistent increase in concentrations towards the southern part of the region. The authigenic minerals Mn, Ba, Ti and Si show very high concentrations in only a few samples from the southern Chonos.

3.3. Geochemical–environment relationship

PCA was used to depict the most important directions of variation in the whole sediment geochemistry dataset. The PCA biplot of LOI and geochemical element concentration is shown in Fig. 3. The first and second axes of the biplot are significant, with 42% of the variance in the data accounted for by the first PCA axis. There is a strong positive correlation along the first axis between the concentration of allogenic minerals. LOI is negatively correlated with the allogenic mineral concentrations. The second axis explains only 24% of the total variance, though there is a clear positive correlation between the concentration of authogenic minerals and to a lesser

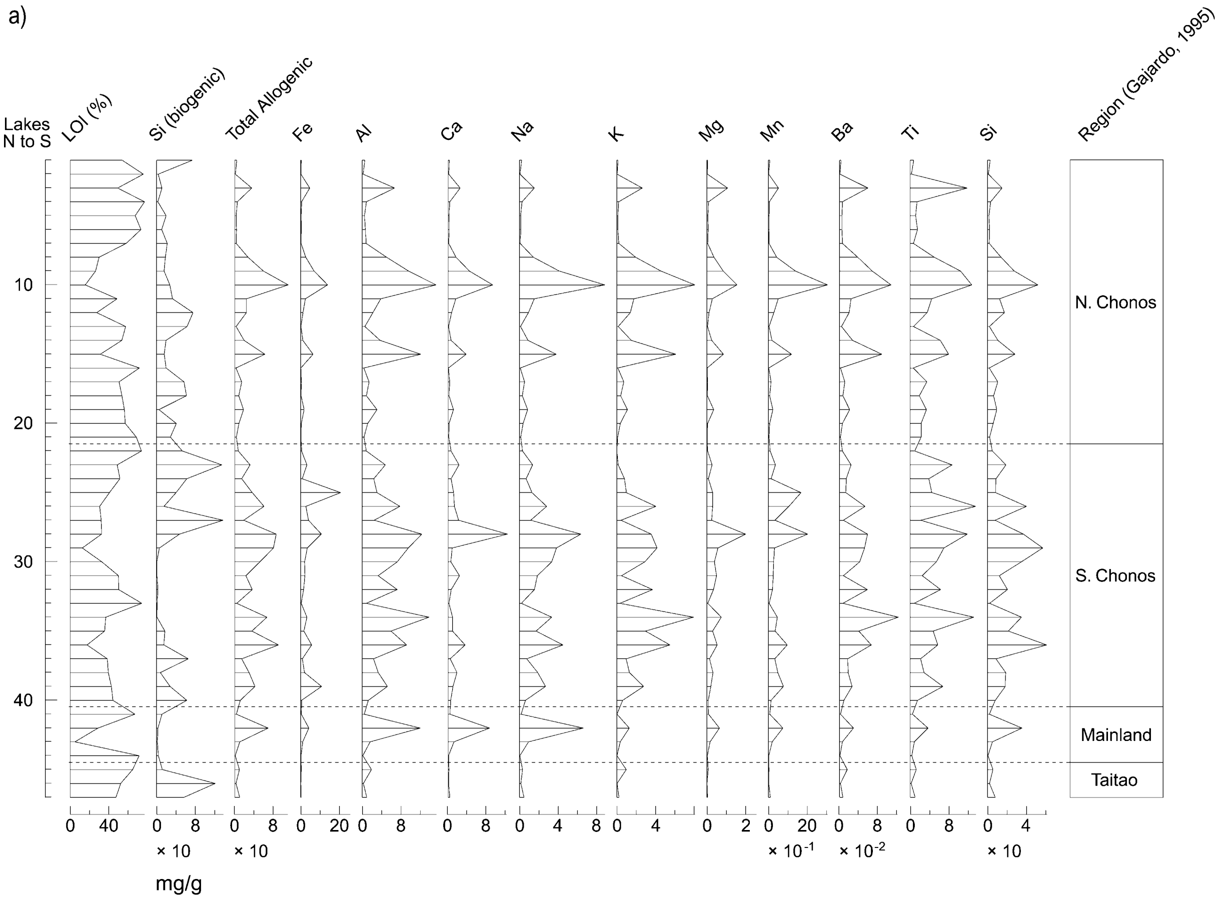


Fig. 2. Element concentration expressed as a weight fraction of dry sediment from the 47 lake mud–water interface samples (note independent scale for each mineral concentration curve). The sample series on the *y*-axis is running from northern to southern lake sites. (a) Loss on Ignition (LOI%), biogenic silica and allogenic mineral concentration (b) authogenic mineral concentration.

extent with biogenic Si. The associated biplot of lake sites is generally aligned along the first axis due to the strong inter-relationship between the relative organic matter measurement (LOI) and measures of inorganic concentration. The biogenic silica vector lies between LOI and authogenic mineral concentrations which may reflect high lake productivity as a function of available mineral content and organic matter.

RDA was used to relate the available environmental variables (see Table 2) to the geochemical dataset (Fig. 4). LOI (total organic content), biogenic silica and individual authigenic and allogenic mineral concentrations are considered as response variables. Unrestricted Monte Carlo permutation tests (ter Braak and Šmilauer, 1998) of the significance of the axes show that only the first axis is significant ($P = 0.05$, 99 permutations) and accounts for 16% of the variance of the data set. The RDA result indicates that altitude and then latitude are the main explanatory variables for the mud–water interface geochemistry data set. The RDA confirms the observations made from the geochemical diagram (Fig. 2a and b), in particular that the allogenic minerals Na, Ca, Al, and Mn and the authogenic minerals Si, Ti, Ba, and Al show strong positive correlation with altitude, whereas LOI, and authogenic minerals K, Na, Ca, and Mg show a weak negative correlation with altitude. These trends are most readily

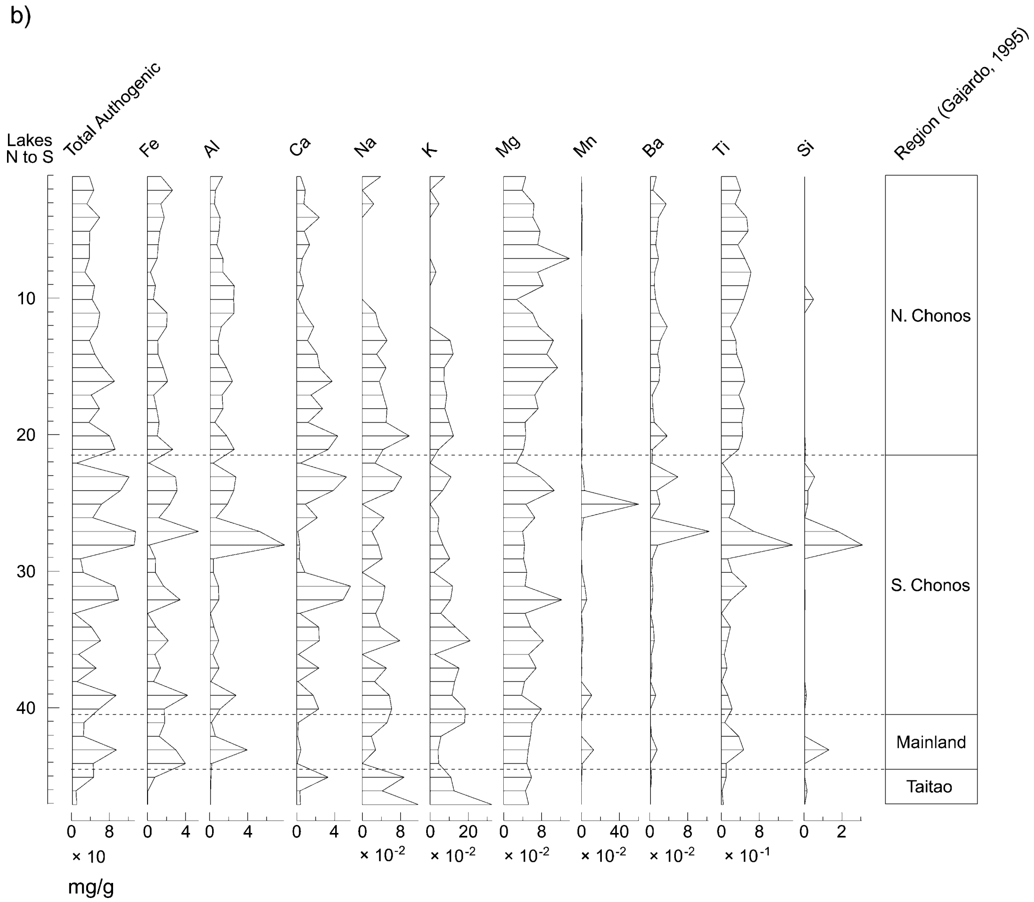


Fig. 2. (*continued*)

explained by lower organic productivity under lower temperatures as altitude increases and a more open vegetation cover exposing soils to high rainfall and wind conditions that are conducive to catchment erosion. Soil eluviation under the waterlogged peats around lakes above the treeline would increase the authogenic component (Engstrom and Hansen, 1985), though some authogenic elements (K, Na, Ca, and Mg) appear to decrease under these conditions. The authogenic minerals K and Na also appear to increase in concentration from north to south, which may be due to an increase in supply of these elements in the southern lake catchments possibly under conditions of either, greater availability in the environment, or increased soil eluviation of southern low altitude waterlogged soils.

3.4. Pollen and spores

The mud–water interface pollen and spore spectra from the Chonos-Taitao lake sites are plotted against a latitudinal gradient in Fig. 5a and b. The pollen and spore percentage data are divided into four zones based on sum of squares distance and is compared with the four regional zones based on the biogeographic grouping of Gajardo (1995). All mud–water interface samples are dominated by arboreal pollen types, notably *Nothofagus dombeyi*-type, *Podocarpus nubigena* and *Pilgerodendron uviferum*-type. This is the case even above treeline and suggests that these taxa are over-represented in the pollen assemblage. The general spore category, Filicales undif., is also important in most samples. Charcoal

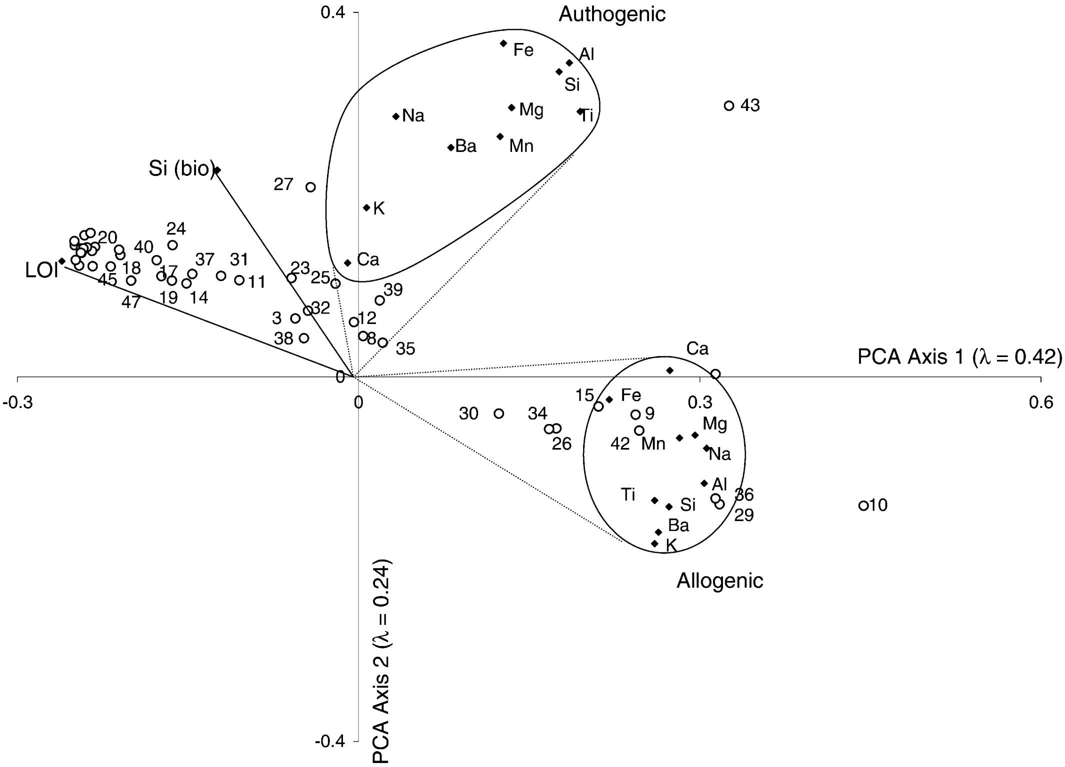


Fig. 3. Principal component analysis of geochemical variables using a linear correlation matrix to standardise data in different units. Sites are depicted by open circles and mineral elements are depicted by black diamonds with vectors from the origin shown as solid lines (or groupings) (first axis eigenvalue = 0.42, second axis eigenvalue = 0.24).

particles (%) are highly variable though are generally low to absent in the southern mainland and Taitao Peninsula sites.

3.4.1. Zone S-1

The pollen assemblage is dominated by the arboreal taxa *Nothofagus dombeyi*-type, *Lepidothamnus fonkii* and *Pilgerodendron uviferum*-type, with Filicales undif. dominating the fern spores. Herbaceous taxa, other fern spores and aquatics have very low percentage representation. Charcoal particle percentage is very low.

3.4.2. Zone S-2

The arboreal taxa dominate this zone with *Nothofagus dombeyi*-type peaking at around 70% of the total sum. *Lepidothamnus fonkii*, *Pilgerodendron uviferum*-type and Filicales undif. drop down to very low percentage values. Minor arboreal and herbaceous taxa, including *Berberis*, Gramineae, Rosaceae, and Saxifragaceae find their peak representation in the high altitude sites within this zone. Charcoal particle percentages remain very low.

3.4.3. Zone S-3

Nothofagus dombeyi-type percentage representation falls to around 30%, with *Podocarpus nubigena*, *Pilgerodendron uviferum*-type, *Tepualia stipularis* and Filicales undif increasing in relative dominance. Several minor arboreal taxa show the first appearance or peak percentage values in this zone including *Grevuina* and *Lomatia*. Herbaceous taxa remain very poorly represented and the aquatic forms are absent. Charcoal particles rise in this zone.

3.4.4. Zone S-4

The largest of the zones shows that *Nothofagus dombeyi*-type remained the dominant pollen

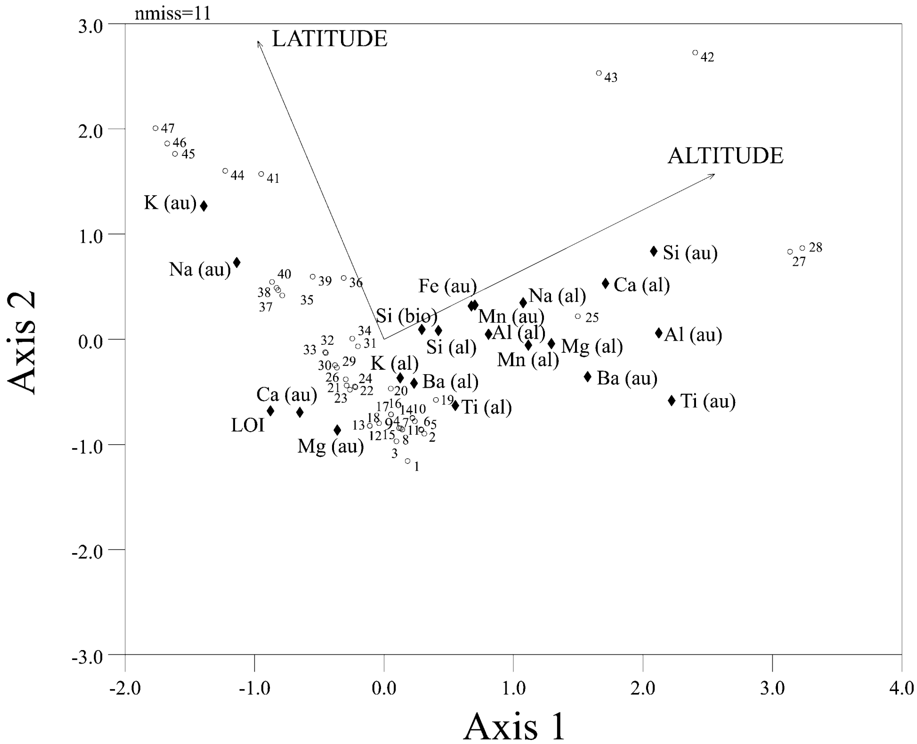


Fig. 4. Redundancy analysis of geochemical and environmental variables using a linear correlation matrix to standardize data in different units. Sites are depicted by open circles and mineral elements are depicted by black diamonds with significant environmental variables fitted as solid line vectors from the origin (temperature is depicted though it shows very strong collinearity with the other variables) (first axis eigenvalue = 0.16, second axis eigenvalue = 0.04).

contributor throughout the zone. *Podocarpus nubigena*, *Pilgerodendron uviferum*-type, *Tepualia stipularis* and *Lepidothamnus fonkii* are also important elements. The spores Filicales undif., *Blechnum*, and *Lophosoria quadripinnata* tend to decrease towards the north. Charcoal percentage generally increases though is highly variable.

The zonation has been constrained latitudinally with the divisions lying close to the biogeographic boundaries determined by Gajardo (1995) for the Chonos-Taitao region. There are clear trends in some species along this transect. Most notably, high soil moisture adapted *Lepidothamnus fonkii* and the fern spores Filicales undif. become dominant towards the south, possibly in response to higher annual rainfall and reduced seasonality at the southern latitudes. A number of the Myrtaceae pollen types, including *Tepualia stipularis*, are absent in the southern samples and only appear in the record towards the north, suggesting an increase in Myrtaceae diversity along the northward latitudinal gradient.

3.5. Pollen and spore-environment relationship

CCA is a technique for multivariate direct gradient analysis developed by ter Braak (1986) to examine the composition of biotic assemblages in relation to environmental gradients. Fig. 6 shows the CCA plot of the 47 mud–water interface samples and 53 selected pollen and spore types (occur with percentages >1% in the diagram) in relation to 29 environmental variables (those listed in Table 2 with the addition of the mud–water interface mineral concentrations). Of the 29 variables measured, statistical testing using forward selection of the environmental variables

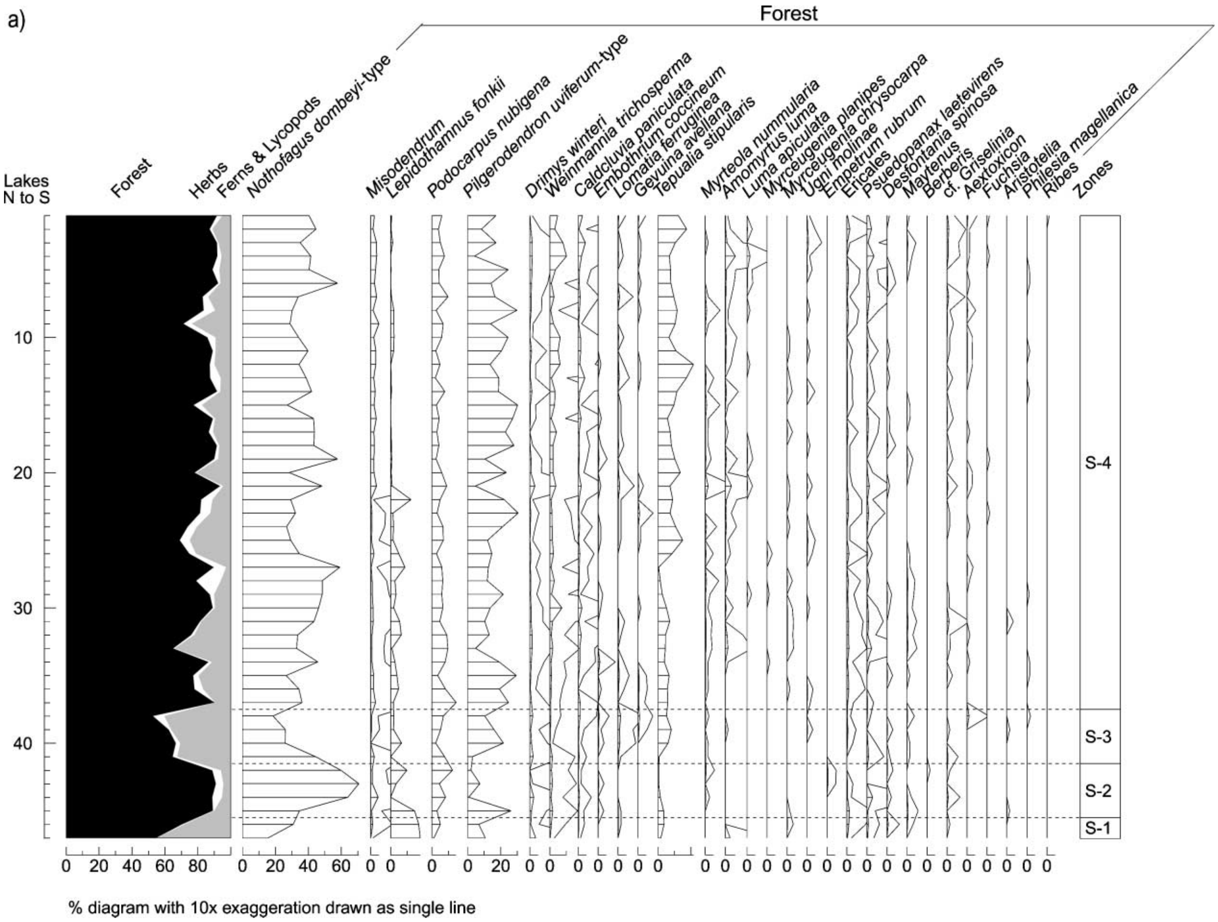


Fig. 5. Pollen, spore and charcoal particle percentage diagram, based on the total pollen and spore sum, from 47 lake mud–water interface samples. The sample series on the *y*-axis is running from northern to southern lake sites. (a) Summary diagram and taxa associated with forest. (b) Herbs, Ferns and Lycopods, aquatics and charcoal particles (expressed as a % of the total sum).

with Monte Carlo permutation tests showed that there were only four significant environmental variables: altitude, latitude, lake depth, and forest cover ($P < 0.05$ after 99 permutations). In Fig. 6(a) the lake sites are clearly separated along the first axis according to latitude and along the second axis according to altitude. Axis 1 ($\lambda = 0.16$) contrasts the latitude with forest cover, lake depth and LOI. Axis 2 ($\lambda = 0.10$) contrasts high and low altitude sites. Both axes are significant ($P = 0.005$ after 99 permutations) and capture 73% of the variation in the weighted averages of the 53 pollen and spore types in relation to environmental variables. In Fig. 6(b) the relationship between pollen and spore taxa and the environmental variables is depicted. There is a clear association between the southernmost sites and *Lepidothamnus fonkii*, *Lophosoria* and *Aristotelia* and in the north taxa such as *Ribes*, *Weinmannia*, *Cystopteris* and several Myrtaceae. There are also strong associations between the taxa found above treeline, mostly herbaceous taxa including *Astelia pumila*, Rosaceae, *Ranunculus*, Saxifragaceae, *Empetrum* and *Berberis*, with high altitude. The differentiation of the association between forest cover and lake depth with latitude is less clear in this analysis as these environmental variables are not strongly interelated in this region (Table 2). Other taxa situated near the origin, including the dominant arboreal taxa *Nothofagus dombeyi*-type, *Podocarpus nubigena* and *Pilgerodendron*

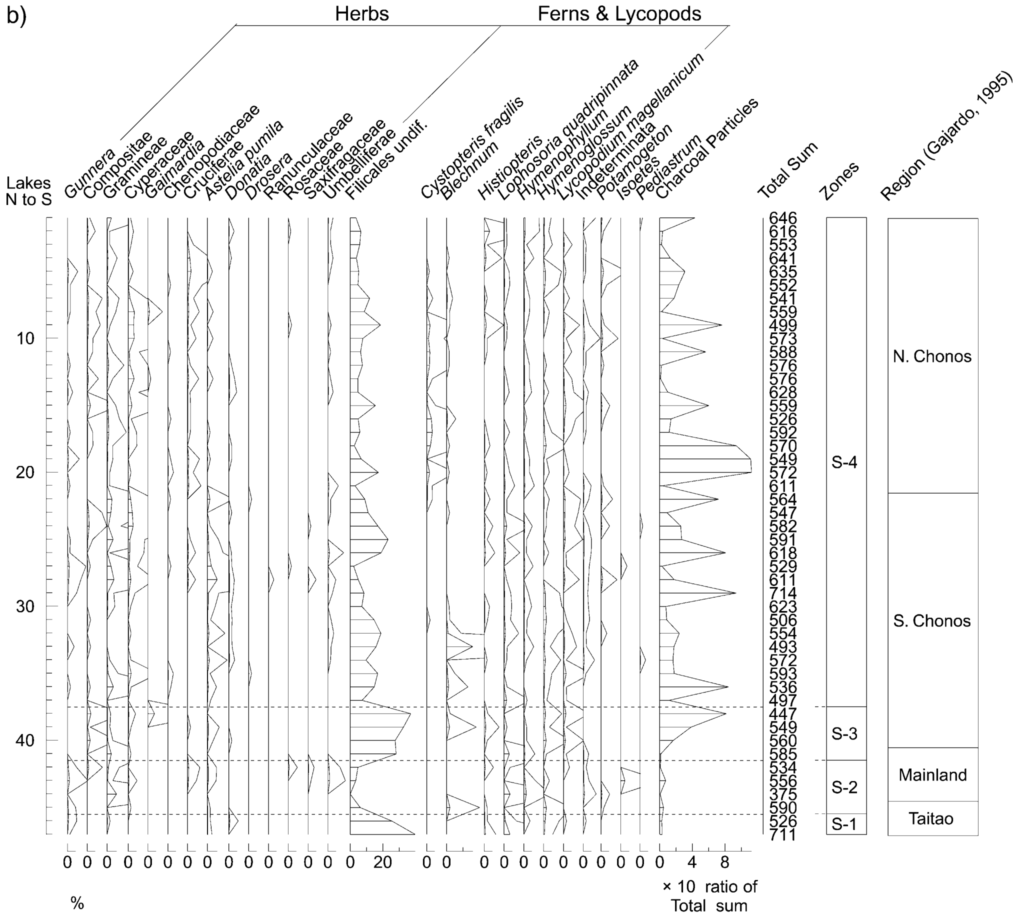
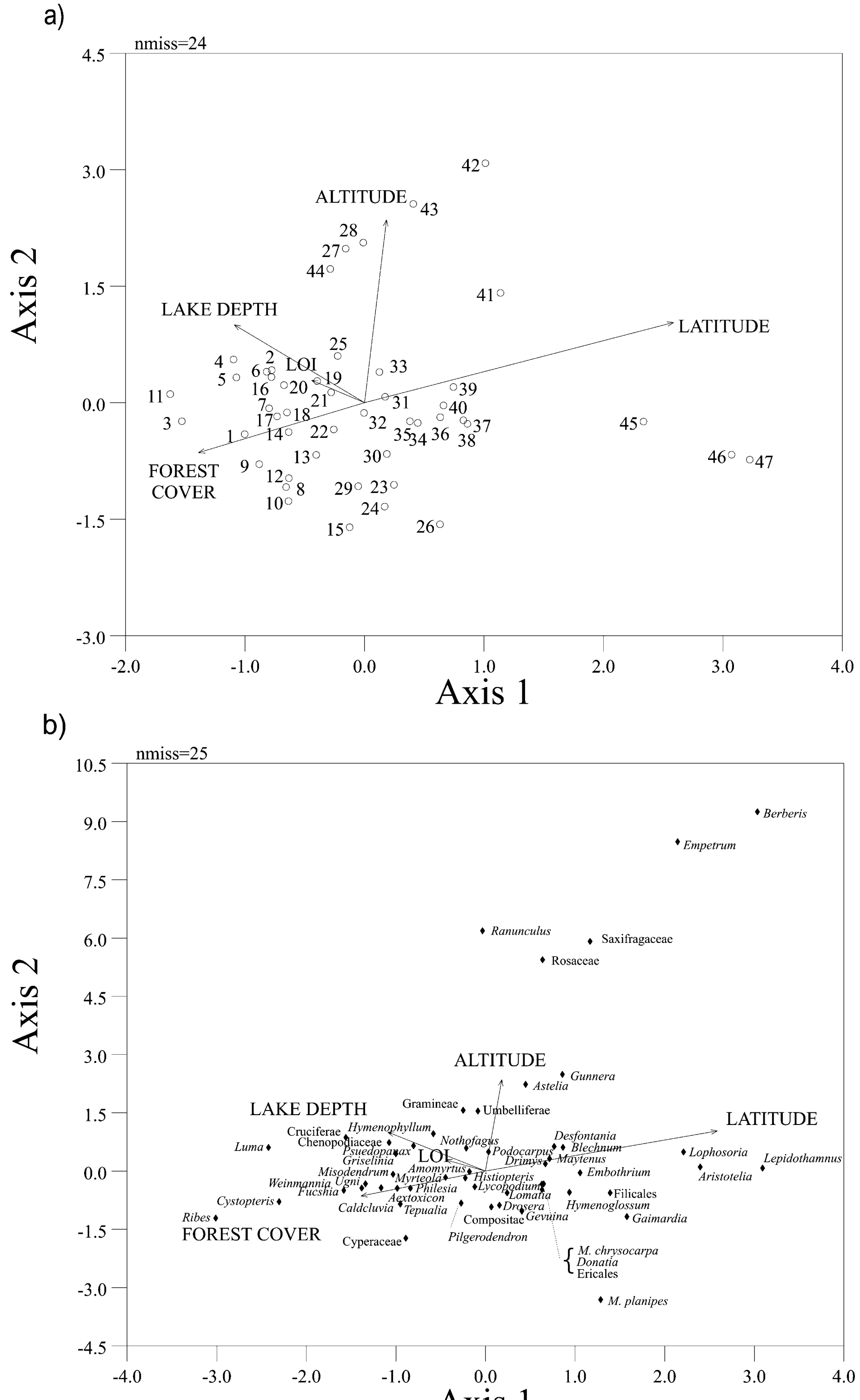


Fig. 5. (*continued*)

uviferum-type have little relation to the measured local environmental variables.

What are the implications of this modern pollen rain and geochemical dataset for palaeoenvironmental reconstruction in the study area? The lake mud–water interface samples were collected with the aim of examining present-day variability in proxy measures of landscape and vegetation cover as analogues for past environments. While this approach has been widely used in other studies, this is the first attempt to examine lake sediments in this region. Using descriptive and numerical analysis we have shown that lake sediment mineral and pollen and spore composition are strongly related to key environmental variables. The most significant environmental gradients for both data sets are altitude and latitude and there are clear species associations with these variables. These variables are most likely reflecting plant and sedimentation response to temperature gradients (precipitation data was not available in this analysis). Regional geology and edaphic conditions do not appear to influence the pollen and spore assemblage, supporting the suggestion that temperature is a significant environmental variable determining plant distributions in the region. The high altitude environments (above treeline) are the most distinct

Fig. 6. Canonical correspondence analysis of pollen and spore data and environmental variables. (a) Environmental variables vs. lake sites. (b) Environmental variables vs. taxa.


a)
nmiss=24
Axis 2
Axis 1
ALTITUDE
LAKE DEPTH
LOI
LATITUDE
FOREST COVER
b)
nmiss=25
Axis 2
Axis 1
ALTITUDE
LAKE DEPTH
LOI
LATITUDE
FOREST COVER
Berberis
Empetrum
Ranunculus
Saxifragaceae
Rosaceae
Gunnera
Astelia
Gramineae
Umbelliferae
Cruciferae
Chenopodiaceae
Hymenophyllum
Nothofagus
Luma
Psuedopanax
Griselinia
Podocarpus
Drimys
Desfontania
Blechnum
Maytenus
Lophosoria
Lepidothamnus
Aristotelia
Misodendrum
Amomyrtus
Histiopteris
Embothrium
Weinmannia
Ugni
Myrteola
Fucshia
Philesia
Lycopodium
Lomatia
Filicales
Cystopteris
Aextoxicon
Caldcluvia
Tepualia
Drosera
Hymenoglossum
Ribes
Compositae
Gevuina
Gaimardia
Cyperaceae
Pilgerodendron
M. chrysocarpa
Donatia
Ericales
M. planipes

assemblages in the modern data sets. Pollen taxa most useful for distinguishing treeline and above environments include *Berberis*, *Empetrum*, *Ranunculus*, *Astelia pumila*, *Gunnera*, Rosaceae, Saxifragaceae, and Gramineae. The dominant arboreal pollen taxa of *Nothofagus dombeyi*-type, *Podocarpus nubigena* and *Pilgerodendron uviferum*-type have little relation to the measured local environmental variables and are not likely to provide useful indicators of Holocene treeline/temperature conditions.

4. Conclusions

This paper is part of a larger, on-going integrated project (Bennett et al., 2000), that aims to develop a detailed reconstruction of post-glacial environmental change in southern Chile. The use of descriptive and numerical analysis of two different proxy data sets (geochemical and palynological) has provided a detailed picture of lake catchment geochemistry and vegetation patterns in the Chonos-Taitao region. Reconstruction of past environments, at least over Holocene time scales, from fossil plant and geochemical data can be enhanced by numerical analysis of modern data sets such as those presented here. The two most significant environmental variables are shown to be altitude and latitude, which is most likely reflecting plant and sedimentation response to temperature gradients.

(1) Altitude is the most significant environmental variable. In general, allogenic minerals increase as altitude increases, which is likely to be a consequence of more open vegetation cover at higher altitudes exposing soils to high rainfall and wind conditions that are conducive to catchment erosion. Soil eluviation under the waterlogged peats around lakes above the treeline increases the authogenic component. Above the tree-line the presence of the pollen taxa *Berberis*, *Empetrum*, *Ranunculus*, *Astelia pumila*, *Gunnera*, Rosaceae, Saxifragaceae, and Gramineae are strongly indicative of open alpine conditions.

(2) Latitude is also an important environmental variable, though is less significant for the geochemical data. The authogenic minerals K and Na tend to have higher concentrations in the southern lowland lake sites which may be due to an increase in supply of these elements in the southern lake catchments possibly under conditions of either, greater availability in the environment, or increased soil eluviation of southern low altitude waterlogged soils. The pollen and spore taxa show a significant latitudinal trend with southernmost sites being distinguished by increasing percentage representation of *Lepidothamnus fonkii*, *Lophosoria* and *Aristotelia*, and in the north, increasing representation of taxa such as *Ribes*, *Weinmannia*, *Cystopteris* and several Myrtaceae.

(3) Percentage representation of principal aboreal pollen taxa such as *Nothofagus dombeyi*-type, *Podocarpus nubigena*, and *Pilgerodendron uviferum*-type show no clear relationships with environmental variables in the region and are not likely to provide useful indicators of Holocene treeline/temperature conditions in this region.

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References

Ashworth, A.C., Markgraf, V., Villagrán, C., 1991. Late Quaternary climatic history of the Chilean Channels based on fossil pollen and beetle analyses, with an analysis of the modern vegetation and pollen rain. J. Quat. Sci. 6, 279–291.

Bennett, K.D., 1994. Confidence intervals for age estimates and deposition times in late-Quaternary sediment sequences. The Holocene 4, 337–348.

Bennett, K.D., Fossitt, J.A., Sharp, M.J., Switsur, V.R., 1990. Holocene vegetational and environmental history at Loch Lang, South Uist, Western Isles, Scotland. New Phyt. 114, 281–298.

Bennett, K.D., Haberle, S.G., Lumley, S.H., 2000. The Last Glacial-Holocene transition in southern Chile. Science 290, 325–328.

Clapperton, C.M., Sugden, D.E., 1988. Holocene glacier fluctuations in South America and Antarctica. Quat. Sci. Rev. 7, 185–198.

Clark, J.S., 1988. Particle motion and the theory of stratigraphic charcoal analysis: source area, transport, deposition, and sampling. Quat. Res. 30, 81–91.

Engstrom, D.R., Hansen, B.C.S., 1985. Postglacial vegetation change and soil development in southeastern Labrador as inferred from pollen and chemical stratigraphy. Can. J. Bot. 63, 543–561.

Engstrom, D.R., Wright Jr, H.E., 1984. Chemical stratigraphy of lake sediments as a record of environmental change. In: Haworth, E.Y., Lund, J.W.G. (Eds.), Lake Sediments and Environmental History. Leicester Univ. Press, Leicester, pp. 11–67.

Faegri, K., Iversen, J., 1989. Textbook of Pollen Analysis, 4th ed. (revised by Faegri, K., Kaland, P.E., Krywinski, K.). John Wiley and Sons, Chichester.

Fujiyoshi, Y., Kondo, H., Inoue, J., Yamada, T., 1987. Characteristics of precipitation and vertical structure of air temperature in northern Patagonia. Bull. Glac. Res. 4, 15–24.

Gajardo, R., 1995. La vegetatión natural de Chile: Clasificación y distribución geográfica. Editorial Universitaria, Santiago de Chile.

Heusser, C.J., 1974. Vegetation and climate of the southern Chilean lake district during and since the last interglaciation. Quat. Res. 4, 290–315.

Heusser, C.J., 1971. Pollen and Spores of Chile. Arizona Press, Tucson.

Jackson, S.T., 1994. Pollen and spores in Quaternary lake sediments as sensores of vegetation composition: theoretical models and empirical evidence. In: Traverse, A. (Ed.), Sedimentation of Organic Particles. Cambridge University Press, Cambridge, pp. 253–286.

Jacobson Jr, G.L., Bradshaw, R.H.W., 1981. The selection of sites for paleovegetational studies. Quat. Res. 16, 80–96.

Lowell, T.V., Huesser, C.J., Andersen, B.G., Moreno, P.I., Hauser, A., Huesser, L.E., Schlüchter, C., Marchant, D.R., Denton, G.H., 1995. Interhemispheric correlation of Late Pleistocene glacial events. Sci. 269, 1541–1549.

Lumley, S.H., 1993. Late Quaternary vegetational and environmental history of the Taitao Peninsula, Chile. Unpublished PhD Thesis, Cambridge University, Cambridge, 282 pp.

Markgraf, V., D'Antoni, H.L., Ager, T.A., 1981. Modern pollen dispersal in Argentina. Palyn. 5, 43–63.

Naranjo, J.A., Moreno, H., Bamks, N.G., 1993. La erupción del volcan Hudson en 1991 (46°S), Región XI, Aisén, Chile. Serv. Nac. Geol. Min. Bol. 44, 1–50.

Niemeyer, H.R., Skarmeta, J.M., Fuenzalida, R.P., Espinosa, W.N., 1984. Hojas Peninsula de Taitao y Puerto Aisen, Region Aisen del General Carlos Ibañez del Campo. Serv. Nac. Geol. Min. Bol., Carta Geologica de Chile, No. 60-61, 80 pp.

Paez, M.M., Villagran, C., Carrillo, R., 1994. Modelo de la dispersión polínica actual en la región templada chileno-argentina de Sudamérica y su relación con el clima y vegetación. Rev. Chil. Hist. Nat. 67, 417–433.

ter Braak, C.J.F., 1986. Canonical correspondence analysis: a new eigenvector method for multivariate direct gradient analysis. Ecol. 67, 1167–1179.

ter Braak, C.J.F., Šmilauer, P., 1998. CANOCO Reference Manual and User's Guide to Canoco for Windows. Software for Canonical Community Ordination (version 4). Centre for Biometry Wageningen (Wageningen, NL) and Microcomputer Power (Ithaca, NY, USA), 352 pp.

Veblen, T.T., Schlegel, F.M., Oltremari, J.V., 1983. Temperate broad-leaved evergreen forests of South America. In: Ovington, J.D. (Ed.), Temperate Broad-leaved Evergreen Forests. Elsevier, Amsterdam, pp. 5–31.

Villagrán, C., 1980. Vegetationsgeschichtliche und pflanzensoizio-logische Untersuchengen im Viecente Pérez Rosales National-park, Chile. Diss. Bot. 54, 1–165.

Wright Jr, H.E., 1980. Cores of soft lake sediments. Bor. 9, 107–114.

Zhou, M., Heusser, C.J., 1996. Late-glacial palynolog of the Myrtaceae of southern Chile. Rev. Palaeobot. Palynol. 91, 283–315.