

## Deglacial and postglacial climate history in east-central Isla Grande de Chiloé, southern Chile (43°S)

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### Abstract

Palynologic and stratigraphic data from Laguna Tahui (42°50'S, 73°30'W) indicate cool–temperate and humid conditions there between 14,000 and 10,000 <sup>14</sup>C yr B.P., followed by warmer and drier-than-present conditions between 10,000 and 7000 <sup>14</sup>C yr B.P., and subsequent cooling and rise in precipitation over the last 5800 <sup>14</sup>C yr. The thermophilous Valdivian trees *Eucryphia cordifolia* and *Caldcluvia paniculata* reached their maximum abundance during the early Holocene warm–dry phase (10,000–7000 <sup>14</sup>C yr B.P.), followed by a rise in lake levels and reexpansion of North Patagonian conifers starting at 7000 and 5800 <sup>14</sup>C yr B.P., respectively. Variations in the stratigraphic and geographic distribution of temperate rainforests in southern Chile suggest multimillennial trends in temperature and westerly activity, which are spatially and temporally coherent with paleoclimate records from neighboring regions. Climate variability at millennial and submillennial time scales may account for the establishment and persistence of fine-scale mosaics of Valdivian and North Patagonian rainforest species in low- to mid-elevation communities since ~5800 <sup>14</sup>C yr B.P.

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### Introduction

The modern distribution of temperate rainforests in southern Chile (Valdivian, North Patagonian, and Subantarctic) reflects latitudinal and altitudinal gradients of temperature and precipitation of westerly origin (Oberdorfer, 1960; Schmithüsen, 1956). This gradient is established by a combination of (i) the blocking effect of the Pacific Anticyclone, which causes an equatorward drop in annual precipitation, (ii) orographic rains, and the (iii) eastward rain shadow effect of the Coastal and Andean Ranges. Altitudinal and latitudinal overlap is superimposed upon this regional zonation pattern, in particular fine-scale mosaics of Valdivian and North Patagonian rainforest communities (Lusk, 1996), which occur in the lowlands between 40° and 42°S. The origin and persistence of this mosaic is not well understood; possible mechanisms may involve edaphic heterogeneity, varying disturbance regimes, ecological interactions, and

recent climatic change. Deciphering the biogeographic history of the temperate rainforests in this region through the last glacial–interglacial cycle might aid in determining the postglacial history of the southern westerlies.

Based on geomorphologic, stratigraphic, and biogeographic evidence from central Chile, Caviedes (1972) proposed changes in the intensity and position of the southern westerly winds during the last ice age. Subsequent palynological studies by Heusser (1974, 1983) and Villagrán (1988a) in the temperate and Mediterranean regions of southern Chile formalized this idea, and provided an initial radiocarbon chronology for this shift/intensification during the Last Glacial Maximum (LGM). Since then, numerous stratigraphic and modeling studies have elaborated on this problem (Heusser, 1989, 1990a, 1990b; Heusser et al., 1999; Hoganson and Ashworth, 1992; Lamy et al., 1999; Moreno, 1997; Moreno and León, 2003; Moreno et al., 1999; Veit, 1996; Villagrán, 1990; Wyrwoll et al., 2000), providing a better spatial and temporal understanding of the LGM climate. The timing, magnitude, and frequency of latitudinal changes in the westerly winds during and since the LGM are still poorly understood, and constitute an active area of research and discussion.

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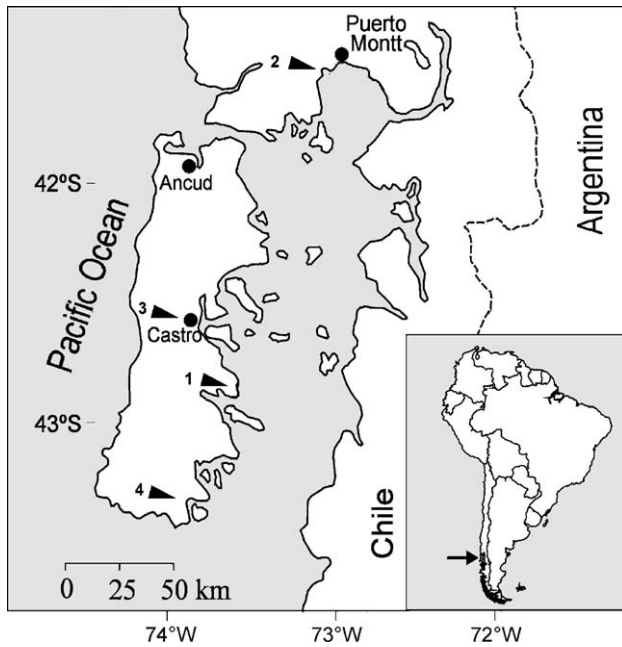


Fig. 1. Map of the study area showing the location of Laguna Tahui and other palynological pertinent to the discussion (1 = Laguna Tahui and L. Melli; 2 = Lago Condorito and Huelmo; 3 = L. Pastahué; 4 = Puerto Carmen).

The temperate region of southern Chile is one of the most intensively studied in southern South America, and the midlatitude region of the Southern Hemisphere (Fig. 1). Palynological and stratigraphic studies in this region have recognized important changes in the vegetation, glacial extent, and climate fluctuations throughout the Quaternary (Denton et al., 1999a, 199b; Heusser and Flint, 1977; Lowell et al., 1995). Available data shows that closed-canopy rainforests were already established in the Lake District and Isla Grande de Chiloé by 13,000  $^{14}\text{C}$  yr B.P., and have persisted until today with profound variations. According to Villagrán (2001), four major phases in vegetation development are evident in the temperate region of southern Chile: glacial, deglacial, early–mid, and late Holocene. During the glacial phase, cold-resistant North Patagonian taxa, along with Magellanic Moorland, expanded northward and downslope into the lowlands of latitudes 40–43°S. Climate conditions during the LGM have been interpreted as colder ( $\Delta T = -6.5^\circ\text{C}$ ) and wetter than today ( $\Delta P_p = \sim 2000$  mm/yr) (Heusser et al., 1996, 1999; Moreno, 1997; Moreno and León, 2003; Moreno et al., 1999; Villagrán, 1988a, 1990). During the deglacial phase, the “glacial vegetation” expanded into the newly deglaciated regions between 43° and 50°S, and the mountaintops of the Coastal and Andean ranges between 40° and 43°S. This migration is paralleled by a southward movement of thermophilous Valdivian and deciduous forests, occupying the region between 40° and 43°S. Important warming pulses and decline in precipitation are evident during this time (Heusser et al., 1996, 1999; Hoganson and Ashworth, 1992; Moreno, 1997; Moreno

and León, 2003; Moreno et al., 1999; Villagrán, 1988a, 1990). Thermophilous taxa characteristic of Valdivian rainforests became dominant during the subsequent warm–dry interval of the early–mid Holocene. Finally, during the late Holocene, an opposite trend leads to cooler/wetter conditions characteristic of the modern climate regime (Heusser, 1984, 1990a; Villagrán, 1988b). Precise stratigraphic, chronologic, and geographic control for these long-term trends, however, is still preliminary, in particular for the Holocene events.

The modern distribution and floristic composition of Isla Grande de Chiloé are largely a result of colonization and succession processes following the demise of Pleistocene glaciers, and subsequent reshuffling driven by climatic fluctuations. In this sense, Holocene climate variations would seem crucial for understanding plant distributions and the vegetation mosaic on this biodiverse island. Few studies, however, have focused on deciphering the complexity of Holocene vegetation and climate variability. In this paper, we report the stratigraphic and palynologic data obtained from sediment cores from Laguna Tahui (Fig. 1). These results allow assessment of the following questions: (i) What was the timing and direction of vegetation/climate changes since the LGM? (ii) How and when did the modern structure and distribution of evergreen rainforests establish? (iii) How did the westerly winds change during the last glacial–interglacial transition?

## Materials and methods

Laguna Tahui (42°50'S, 73°30'W, ~70 m above sea level = m.a.s.l.) is a small (~9 ha) closed-basin lake near the town of Queilen, on the east-central portion of Isla Grande de Chiloé (Fig. 1). The lake rests on an intermoraine depression dating to the LGM, on the Golfo Corcovado coast of eastern Chiloé.

We conducted vegetation surveys near Laguna Tahui with the aim of characterizing the modern forest and bog vegetation. We recorded all trees with a diameter at breast height  $\geq 9$  cm along 360-m transects, using the Point-Centered Quarter Method (Mueller-Dombois and Ellemberg, 1974). The wetland vegetation was characterized using the Point Intercept Method on 250-m-long transects near the lake perimeter.

Sediment cores from Laguna Tahui were obtained using a Wright piston corer from an anchored raft. The stratigraphy of these cores was characterized by textural descriptions, X-radiographs, and loss-on-ignition analysis following overnight drying in the oven (water content), followed by sequential burns at 550°C (total organic matter) for 2 h, and 925°C for 4 h in a muffle furnace (carbonate content) (Bengtsson and Enell, 1986). Sediment samples for palynological studies (1 cm<sup>3</sup> each) were processed following standard procedures (Faegri and Iversen,

1989), which include KOH deflocculation, HF digestion, and acetolysis.

A basic sum that included 250–300 pollen grains of trees, upland shrubs, and herbs were counted per each level. All ferns and aquatic/paludal taxa were combined in separate sums, and their percentages are expressed in reference to a supersum that includes the basic pollen sum and all ferns and aquatic/paludal taxa. A stratigraphically constrained ordination (CONISS) was performed on all terrestrial taxa (excluding ferns) with percentages  $\geq 2\%$  (after recalculating sums and percentages) to aid in the distinction and definition of pollen zones. We combined the pollen counts of *Eucryphia cordifolia* and *Caldcluvia paniculata*, into the taxon *Eucryphia/Caldcluvia*; *Escallonia* spp. and *Aextoxicon punctatum* into the taxon *Escallonia/Aextoxicon*; and *Lomatia* spp. and *Gevuina avellana* into the taxon *Lomatia/Gevuina* to facilitate comparisons with pollen records from previous studies, and in some cases because of difficulties in the distinction of these taxa at the species/genus level. Myrtaceae comprises numerous species and several genera, among which we were able to discriminate *Myrteola nummularia*, *Ugni*, and *Tepualia stipularis*. The remaining taxa were lumped in Myrtaceae undiff. We also combined the abundance of *Astelia pumila*, *Gentiana*-type, *Donatia fascicularis*, *Tribeles australis*, and *Euphrasia*-type under the category “Magellanic Moorland.”

## Results

Laguna Tahui (Fig. 1) is located in a region dominated by the North Patagonian rainforest type, which ranges in distribution from the central and southern portions of Isla Grande de Chiloé, the Channels region of southern Chile ( $43^{\circ}20'S$ – $45^{\circ}73'S$ ). The local vegetation on the slopes surrounding Laguna Tahui corresponds to a rainforest community dominated by *Drimys winteri*, *Amomyrtus luma*, *Luma apiculata*, along with *Weinmannia trichosperma*, *Embothrium coccineum*, and other trees. A *Sphagnum* bog dominates the areas adjacent to the northern edge of the lake, interspersed with (among others) *M. nummularia*, ericaceous shrubs (*G. mucronata*, *Gaultheria insana*, *G. antarctica*), the fern *Blechnum magellanicum*, and the woody *Tepualia stipularis* and *Griselinia racemosa* in the upper storey.

### Stratigraphy and chronology

Laguna Tahui has a single concave depression with gentle slopes that grade to peripheral fen, bog, and forest environments. We obtained three sets of overlapping sediment cores from the deepest (240-cm water depth), intermediate (165-cm water depth), and shallow (100-cm water depth) portions of the lake. We selected a 745-cm-long core (0004D) obtained from the intermediate portion of the lake

to conduct this study, based on its stratigraphic completeness, optimal recovery, and high sediment-accumulation rates (Figs. 2 and 3). Additional cores obtained from the deepest and peripheral areas of the lake afford valuable information for reconstructing past variations in lake levels (see Discussion) (Fig. 4).

The stratigraphy of core 0004D consists of brown organic mud (gyttja) between 995–932 cm ( $\sim 14,000$ – $9600$   $^{14}\text{C}$  yr B.P.), which shifts to dark-brown coarse-detritus gyttja with numerous, discrete, plant macrofossil layers between 916 and 847 cm (9600–7000  $^{14}\text{C}$  yr B.P.). The sediments then turn to a light-brown gyttja with abundant layers of periostracum remains of the freshwater bivalve *Diplodon* sp. between 847 and 723 cm (7000–4100  $^{14}\text{C}$  yr B.P.). Between 723 and 165 cm, the sediments consist of gyttja without molluscan remains (the last 4100  $^{14}\text{C}$  yr) (Fig. 2). We detected two distinctive tephra at 872–874- and 916–932-cm depth. The latter tephra has been reported and extensively dated at  $\sim 9600$   $^{14}\text{C}$  yr B.P. in the study area by previous studies (Hajdas et al., 2003; Heusser, 1966, 1974, 1981, 1990a; Heusser et al., 1999; Moreno, 1997, 2004; Moreno and León, 2003; Moreno et al., 1999, 2001). On the basis of the age model (see below), we obtained an interpolated age of  $\sim 8000$   $^{14}\text{C}$  yr B.P. for the tephra at 872–874-cm depth.

The loss-on-ignition results provide a proxy of the organic, inorganic, and carbonate content of the sediments. The organic and inorganic matter content varies in concert with the stratigraphic changes outlined above (Fig. 2). The carbonate content of the sediments is negligible or null (mean = 3.6% between 14,000 and 9000  $^{14}\text{C}$  yr B.P., and mean = 2% over the last 9000  $^{14}\text{C}$  yr). These low values most likely represent background noise by varying amounts of residual water molecules retained in clay lattices, and/or varying amounts of clay in the sediments (Fig. 2).

The chronology of core 0004D is controlled by five AMS radiocarbon dates, seven conventional radiocarbon dates (Table 1), chronostratigraphic correlation of a prominent tephra layer (9600  $^{14}\text{C}$  yr B.P. at 932-cm depth) (Fig. 2), and assignment of a modern age to the water/sediment interphase ( $-50$  yr at 165-cm depth). Our results suggest undisturbed, continuous, in situ deposition in Laguna Tahui over the last  $\sim 14,000$   $^{14}\text{C}$  yr (Figs. 2 and 3).

Two sets of age models were developed based on the radiocarbon and calendar dates, acknowledging a prominent increase in sediment accumulation rates at  $\sim 4750$   $^{14}\text{C}$  yr B.P. (Fig. 3). One set consists of 5th-order polynomials applied to the radiocarbon and calendar dates younger than 4750  $^{14}\text{C}$  yr B.P. The second set consists of 4th- and 5th-order polynomials applied to the radiocarbon and calendar dates, respectively, older than 4750  $^{14}\text{C}$  yr B.P. Considering the instantaneous deposition of the tephra horizon at 932–916 cm, we subtracted its thickness from the underlying deposits for the purpose of calculating interpolated ages for the pollen levels (Fig. 3).

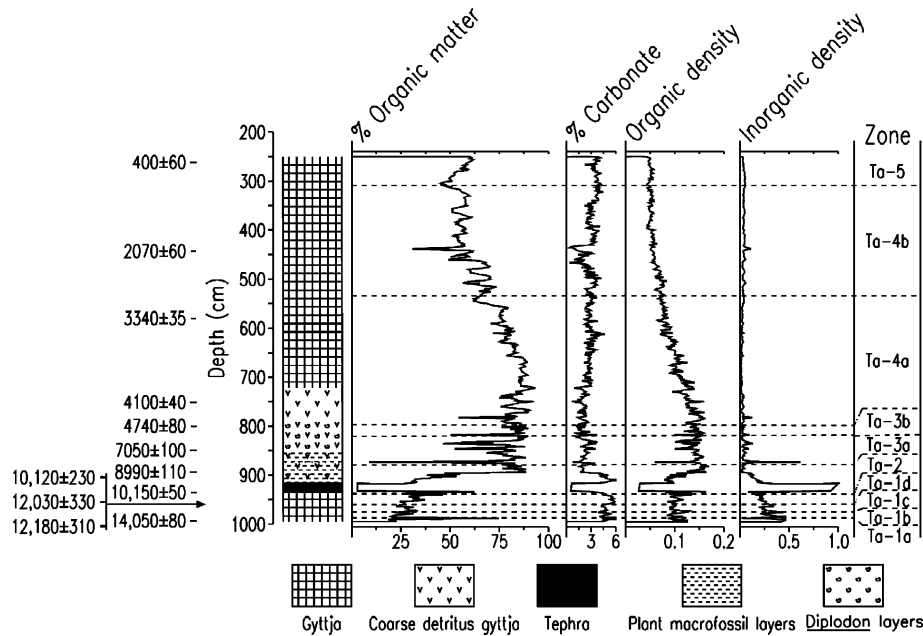


Fig. 2. Stratigraphy of core 0004D, showing all radiocarbon dates (expressed as  $^{14}\text{C}$  yr B.P.) and the results of the loss-on-ignition analysis. Dashed lines portray the boundaries of pollen assemblage zones. The labels on the right side of the diagram define the pollen assemblage zones. Notice the difference in scale among curves.

### Pollen stratigraphy

We analyzed the pollen and spores content of seventy-four 1-cm-thick sediment samples, each spanning an average of 19  $^{14}\text{C}$  yr (23 cal yr), with a median time resolution of 148  $^{14}\text{C}$  yr (192 cal yr) between samples. The results of the palynological analysis are shown as percent abundance (Figs. 5 and 6). From these results, we identified 10 pollen assemblage zones, based on a CONISS ordination (Fig. 5) and conspicuous changes in the stratigraphy of key indicator

taxa. In the following section, we describe in detail the pollen stratigraphy of core 0004D (Table 2).

**Zone Ta-1a** (995–987-cm depth, 14,000–13,400  $^{14}\text{C}$  yr B.P.) is dominated by the assemblage *Nothofagus dombeyi*-type-*Lomatia/Gevuina*-Poaceae ( $\Sigma = 81\%$  of the basic sum), along with *Empetrum*/Ericaceae (mean = 6%), Compositae/Tubuliflorae (mean = 3%), *Escallonia/Aextoxicon* (mean = 2%), and abundant spores of the fern *Blechnum*-type (mean = 47%) and *Lycopodium*. This is accompanied by trace percentages (mean < 2%) of *Fitzroya/Pilgerodendron*,

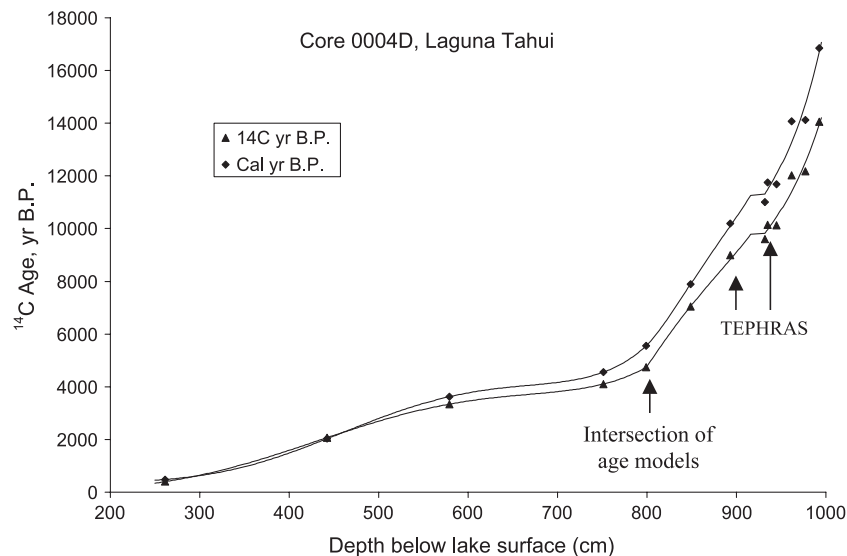


Fig. 3. Age models of core 0004D. Triangles represent uncalibrated radiocarbon dates; diamonds represent calibrated radiocarbon dates obtained from the program Calib 4.1.2. The age models explicitly reflect the instantaneous deposition of the  $\sim 9600$   $^{14}\text{C}$  yr B.P. tephra.

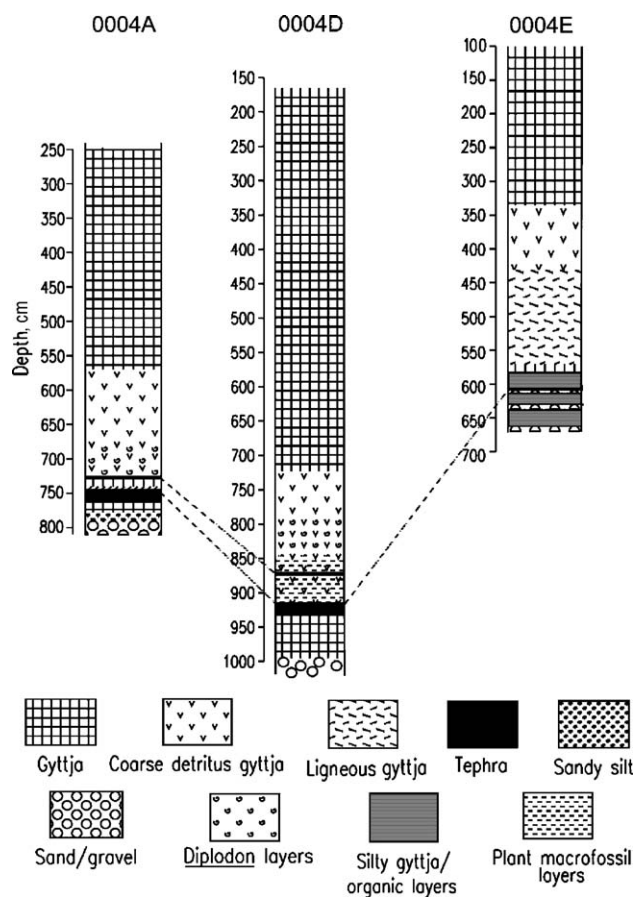


Fig. 4. Stratigraphic columns of cores 0004A, 0004D, and 0004E. All depths are expressed as centimeters below the modern lake surface. The dashed lines indicate correlation of the  $\sim 9600$  and  $\sim 8000$   $^{14}\text{C}$ -yr-old tephra.

*Embothrium coccineum*, *D. winteri*, and the epiphytic *Philesia magellanica*, *Lepidoceras kingii*, and *Nertera granadensis*. **Zone Ta-1b** (987–975-cm depth, 13,400–12,200  $^{14}\text{C}$  yr B.P.) features the assemblage Myrtaceae undiff.–*N. dombeyi*-type–*Escallonia/Aextoxicon* ( $\Sigma = 77\%$  of the basic pollen sum), along with *Lomatia/Gevuina* (mean = 5%), Poaceae (mean = 3%), *Empetrum*/Ericaceae, and *Donatia* (both with mean = 2%). Several forest taxa appear for the first time in trace amounts (*Laurelia*, *E. coccineum*, *Drimys*, *P. magellanica*, *T. stipularis*, *Hymenophyllum*), accompanied by traces of Compositae/Tubuliflorae, *M. nummularia*, peak abundance of the aquatic fern *Isoetes* (mean = 44%), and major declines in *N. dombeyi*-type (from mean = 61% to 9%) and *Blechnum*-type (from mean = 47% to 11%). Within the Myrtaceae, *Amomyrtus*-type attained its maximum percentage (33%) at  $\sim 12,500$   $^{14}\text{C}$  yr B.P. and declined steadily until 11,000  $^{14}\text{C}$  yr B.P. **Zone Ta-1c** (975–960-cm depth, 12,200–11,200  $^{14}\text{C}$  yr B.P.) is characterized by the assemblage Myrtaceae–*Escallonia/Aextoxicon*–*Saxegothaea conspicua* ( $\Sigma = 73\%$  of the basic pollen sum) along with *Lomatia/Gevuina*, *Pseudopanax laetevirens*, *Hydrangea serratifolia*, and *Podocarpus nubigena*. Peak abundance of *Hymenophyllum* and *Lycopodium* occurs during this zone,

along with declining abundance of *Empetrum*/Ericaceae, Compositae/Tubuliflorae, and *Blechnum*-type. The hygrophilous *Isoetes* and *M. nummularia* reach peak abundance during this zone (42% and 14%, respectively). **Zone Ta-1d** (960–938-cm depth, 11,200–10,000  $^{14}\text{C}$  yr B.P.) features the *H. serratifolia*–Myrtaceae–*Pseudopanax laetevirens* assemblage ( $\Sigma = 63\%$  of the basic pollen sum). Conspicuous changes during this zone include increases in *H. serratifolia* (from mean = 2% to 30%), *Laurelia* (from mean = 2% to 6%), *Podocarpus nubigena*, the fern *Polypodium feullei*, along with prominent declines in Myrtaceae (*Amomyrtus*-type, *Myrceogenia*-type, *M. nummularia*), *P. magellanica*, and aquatic taxa. Also present are trace percentages of *Eucryphia/Caldcluvia*, *N. dombeyi*-type, *E. coccineum*, *D. winteri*, *Lomatia/Gevuina*, *Fuchsia*, *T. stipularis*, *Ugni*, and epiphytes such as *L. kingii*, *Luzuriaga*, and *Nertera granadensis*. One sample dated at 11,100  $^{14}\text{C}$  yr B.P. (957 cm) features high abundance of *Eucryphia/Caldcluvia* (21%) and *W. trichosperma* (19%), in the context of trace percentages of both taxa both above and underneath this particular level.

**Zone Ta-2** (938–879-cm depth, 10,000–8300  $^{14}\text{C}$  yr B.P.): This zone starts with the abrupt expansion of *W. trichosperma*, and led to the assemblage *W. trichosperma*–Myrtaceae undiff.–*H. serratifolia* ( $\Sigma = 72\%$  of the basic sum), along with *P. laetevirens* (mean = 7%), Poaceae (mean = 6%), *Eucryphia/Caldcluvia* (mean = 5%), and *E. coccineum* (mean = 2%). Several taxa exhibit their minimum abundance or disappear during this zone: *N. dombeyi*-type, *H. serratifolia*, *Laurelia*, and the conifers *P. nubigena* and *S. conspicua*.

**Zone Ta-3a** (879–821-cm depth, 8300–5800  $^{14}\text{C}$  yr B.P.) is characterized by the dominance of *Eucryphia/Caldcluvia*, along with *W. trichosperma* and *P. laetevirens* ( $\Sigma = 63\%$  of the basic sum). Other important taxa are Myrtaceae undiff. (mean = 11%), *H. serratifolia* (mean = 10%), Poaceae (mean

Table 1  
Radiocarbon dates from core 0004D

Laboratory no.	Depth range (cm)	$^{14}\text{C}$ yr B.P. $\pm$ 1 $\sigma$ error	Cal yr B.P.	$\delta^{13}\text{C}$ (‰)
GX-28212	258–264	400 $\pm$ 60	482	–26.1
NSRL-12470	442–443	2070 $\pm$ 60	2030	–26.1
NSRL-12471	579–580	3340 $\pm$ 35	3622	–27.5
NSRL-12472	749–753	4100 $\pm$ 40	4551	–28.6
GX-28213	798–800	4740 $\pm$ 80	5549	–30.4
GX-28214	847–851	7050 $\pm$ 100	7899	–30.4
GX-28215	891–895	8990 $\pm$ 110	10,187	–30.2
NSRL-12473	934–936	10,150 $\pm$ 50	11,746	–28.1
GX-28142	944–946	10,120 $\pm$ 230	11,692	–30.2
GX-28143	961–962	12,030 $\pm$ 330	14,076	–30.0
GX-28144	976–978	12,180 $\pm$ 310	14,127	–27.9
NSRL-12474	990–995	14,050 $\pm$ 80	16,847	–26.8

Radiocarbon-age errors correspond to  $\pm 1\sigma$ . Radiocarbon dates were converted to “calendar” years (cal yr B.P.) using the Calib 4.1.2 program (Stuiver et al., 1998). The NSRL-radiocarbon analyses were made using the AMS technique.

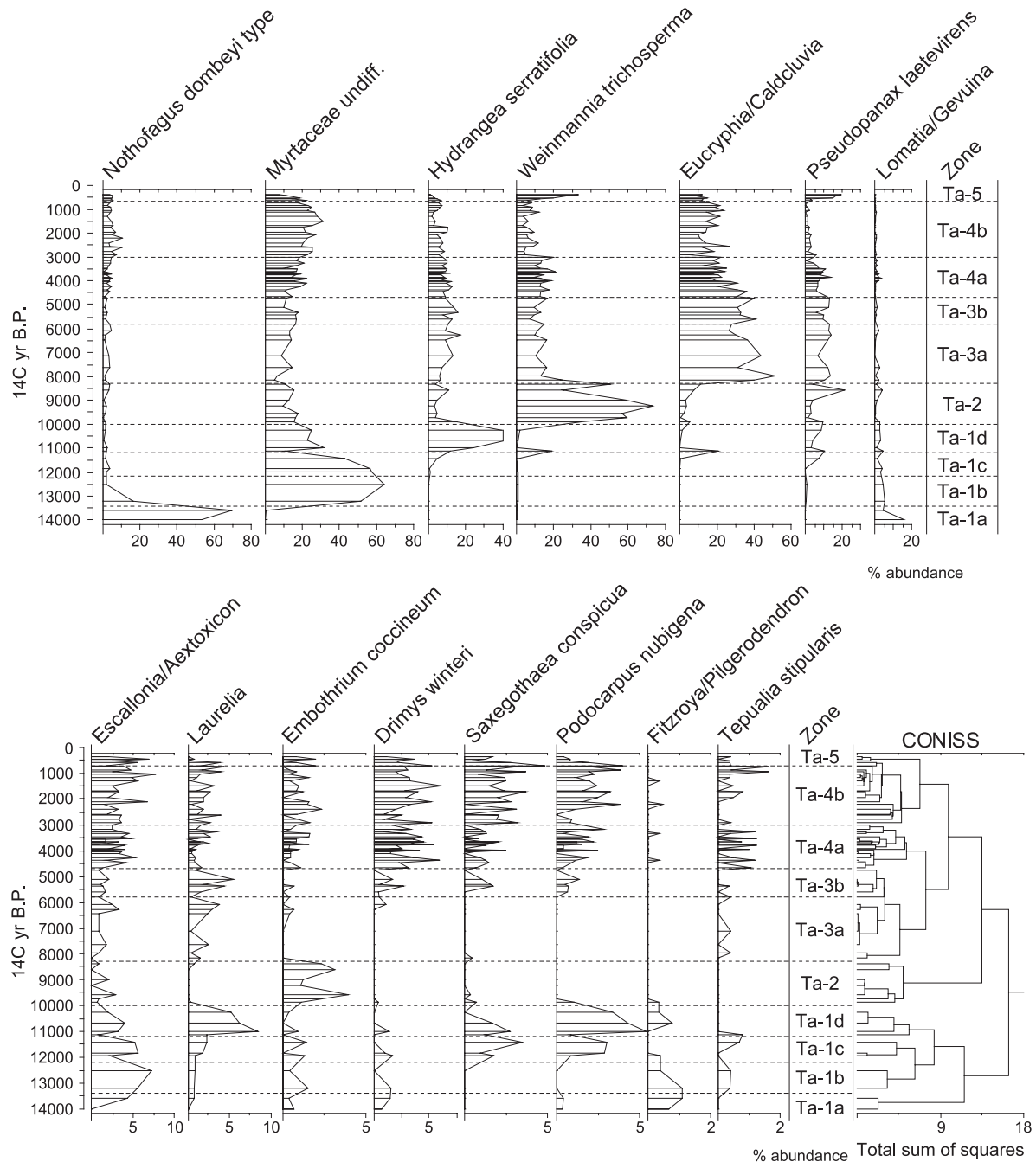


Fig. 5. Percentage pollen diagram of arboreal taxa of core 0004D and results of the CONISS ordination. Dashed lines portray the pollen assemblage zone boundaries. The labels on the right side of the diagram define the pollen assemblage zones (see text). Notice the difference in scale among taxa.

= 4%), and *Laurelia* (mean = 2%). The species *E. cordifolia* and *C. paniculata* display nearly identical stratigraphies during the early Holocene: both expanded simultaneously at 8600  $^{14}\text{C}$  yr B.P. and reached high abundance plateaus (20% and 17%, respectively). **Zone Ta-3b** (821–797-cm depth, 5800–4700  $^{14}\text{C}$  yr B.P.) features the assemblage *Eucryphia/Caldcluvia*–*W. trichosperma*–*Myrtaceae* ( $\Sigma$  = 62% of the basic sum), accompanied by *H. serratifolia* (mean = 12%), *P. laetevirens* (mean = 11%), along with *N. dombeyi*-type, *Misodendrum*, *D. winteri*, *Escallonia/Aextoxicon*, *Poa*-

*ceae*, and *Laurelia* (each with a mean = 2%). A distinctive feature of this zone is the reappearance of *Drimys*, and trace amounts of *Pod. nubigena* and *S. conspicua*.

**Zone Ta-4a** (797–534-cm depth, 4700–3000  $^{14}\text{C}$  yr B.P.) is dominated by the pollen assemblage *Eucryphia/Caldcluvia*–*Myrtaceae*–*W. trichosperma* ( $\Sigma$  = 54% of the basic sum), accompanied by *H. serratifolia* (mean = 9%), *P. laetevirens* (mean = 8%), *Poaceae* (mean = 6%), *N. dombeyi*-type (mean = 4%), and *Drimys*, *Escallonia/Aextoxicon* (each with a mean = 3%). Traces of *Ugni*, *Fuchsia*,

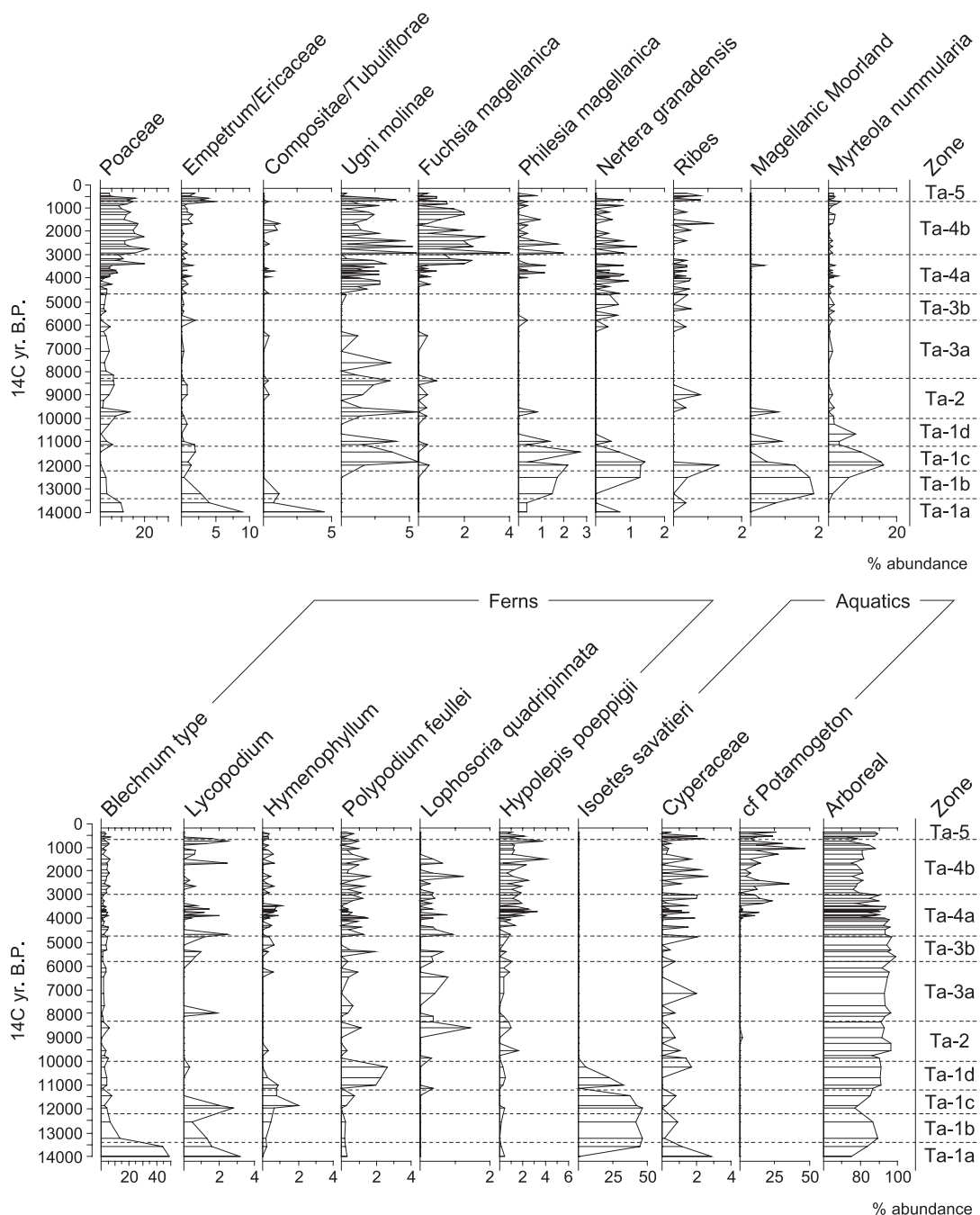


Fig. 6. Percentage pollen and spore diagram of nonarboreal taxa of core 0004D. Notice the difference in scale among taxa.

*E. coccineum*, *Lomatia*, *G. avellana*, *Ribes*, and the epiphytes *P. magellanica*, *L. kingii*, and *N. granadensis*. Prominent features of this zone are a drop in *Eucryphia/Caldcluvia* (from a mean = 34% to 23%), and increases in Poaceae (from a mean = 2% to 6%), *Drimys*, *P. nubigena*, and *S. conspicua* (from a combined mean of 2% to 5%), the fern *Hypolepis poeppigii*, and aquatic taxa (cf. *Potamogeton*). **Zone Ta-4b** (534–309-cm depth, 3000–700 <sup>14</sup>C yr B.P.), distinguished by the Myrtaceae–*Eucryphia/Caldcluvia*–Poaceae pollen assemblage ( $\Sigma = 55\%$  of the basic

sum). This zone has the minimal values of arboreal pollen (mean = 80%) for the last 10,000 <sup>14</sup>C yr B.P., reaching maximum abundance of Poaceae (mean = 13.4%). Other important taxa are *H. serratifolia* (mean = 6%), *N. dombeyi*-type (mean = 5%), and *Escallonia/Aextoxicon* (mean = 4%).

**Zone Ta 5** (309–259-cm depth, 700–400 <sup>14</sup>C yr B.P.): This zone, characterized by the assemblage *W. trichosperma*–*P. laetevirens*–Myrtaceae undiff. ( $\Sigma = 52\%$  of the basic sum), features abrupt expansions of *W. trichosperma* (from a mean = 7% to 24%) and *P. laetevirens* (from a mean =

Table 2

Summary of the pollen zones of core 0004D, showing their time span in radiocarbon and calendar time scale, the three dominant pollen taxa, and their cumulative percentages

Zones	<sup>14</sup> C yr B.P.	Cal yr B.P.	Assemblage	%Accum
Ta-5	400–700	470–650	<i>Weinmannia trichosperma</i> – <i>Pseudopanax laetevirens</i> –Myrtaceae	52
Ta-4b	700–3000	650–3200	Myrtaceae– <i>Eucryphia/Caldcluvia</i> –Poaceae	55
Ta-4a	3000–4700	3200–5500	<i>Eucryphia/Caldcluvia</i> –Myrtaceae– <i>Weinmannia trichosperma</i>	54
Ta-3b	4700–5800	5500–6500	<i>Eucryphia/Caldcluvia</i> – <i>Weinmannia trichosperma</i> –Myrtaceae	62
Ta-3a	5800–8300	6500–8000	<i>Eucryphia/Caldcluvia</i> – <i>Weinmannia trichosperma</i> – <i>Pseudopanax laetevirens</i>	63
Ta-2	8300–10,000	8000–11,500	<i>Weinmannia trichosperma</i> –Myrtaceae– <i>Hydrangea serratifolia</i>	72
Ta-1d	10,000–11,200	11,500–13,000	<i>Hydrangea serratifolia</i> –Myrtaceae– <i>Pseudopanax laetevirens</i>	63
Ta-1c	11,200–12,200	13,000–14,500	Myrtaceae– <i>Aextoxicon/Escaellonia</i> – <i>Saxegothea conspicua</i>	73
Ta-1b	12,200–13,400	14,500–16,000	Myrtaceae– <i>Nothofagus dombeyi</i> -type– <i>Aextoxicon/Escaellonia</i>	77
Ta-1a	13,400–14,000	16,000–16,800	<i>Nothofagus dombeyi</i> -type– <i>Lomatia</i> –Poaceae	81

2% to 13.4%), accompanying a generalized decline in all other trees and herbs.

## Discussion

Forest colonization in the Laguna Tahui record was underway by ~14,000 <sup>14</sup>C yr B.P. as indicated by the codominance of *Nothofagus* and abundant nonarboreal taxa, mainly grasses and heath. An abrupt increase of Myrtaceae, other trees, and forest ferns led to the establishment and diversification of a closed-canopy rainforest by ~13,400 <sup>14</sup>C yr B.P. This was followed by the expansion of podocarpaceous conifers (*S. conspicua*, *P. nubigena*) and the vine *H. serratifolia* between ~12,200 and 10,000 <sup>14</sup>C yr B.P. The presence of taxa characteristic of Magellanic Moorland communities, along with the aquatic fern *Isoetes savatieri* and the presence of lacustrine deposits, suggest low temperatures and high-precipitation regimes between ~14,000 and 10,000 <sup>14</sup>C yr B.P.

A prominent expansion of *W. trichosperma* occurred at 10,000 <sup>14</sup>C yr B.P., along with a decline in all North Patagonian rainforest taxa, which attained their maxima between ~14,000 and 10,000 <sup>14</sup>C yr B.P. This abrupt vegetation turnover coincides with a transition from lacustrine to boggy/swampy environments, as shown by lithological changes along a bathymetric transect. Cores 0004A, 0004D, and 0004E (Fig. 4) show a 9600 <sup>14</sup>C-yr-old tephra that overlies late glacial silts, gyttja, and basal sands/gravels. A regressive lacustrine phase is evident in all cores shortly after the deposition of this ash. This is expressed as (i) a shift to coarse detritus gyttja and plant macrofossil layers in core 0004D; (ii) hiatuses in cores 0004A and 0004E, as inferred based on an angular unconformity (>30°) for the ~8000 <sup>14</sup>C-yr-old tephra in 0004A, and its absence in the shallower core 0004E (nondeposition or erosion in a shallow environment); and (iii) the presence of ligneous (with wood pieces 3–5 cm in diameter) and coarse detritus gyttja in core 0004E, suggesting a marginal swamp forest environment.

The *W. trichosperma* expansion can be accounted by a transition to drier and warmer conditions, but it might also be

related with local disturbance regimes (Lara, 1991; Lusk, 1996). For example, this species expanded rapidly and became dominant at or before ~10,000 <sup>14</sup>C yr B.P. in the Huelmo (41°31'S, 73°00'W) (Moreno and León, 2003), Lago Condorito (41°45'S, 73°07'W) (Moreno, 2000, 2004; Moreno et al., 2001), and Laguna Melli sites (42°46'S, 73°33'W) (A. Abarzúa, unpublished data), when the local charcoal records show prominent and sustained increases. The Laguna Tahui record shows that this expansion was nearly simultaneous with the deposition of a 16-cm-thick tephra layer (Fig. 2). A possibility exists that the abrupt expansion of *W. trichosperma* was triggered either by edaphic changes and/or opening of the forest canopy, both linked directly or indirectly to the ecological effects of the volcanic event. The onset of the regressive lake phase in Laguna Tahui at ~10,000 <sup>14</sup>C yr B.P., however, suggests that an underlying climatic signal might have initiated important vegetation changes that would have altered local disturbance regimes, forest structure, and species composition.

The Valdivian rainforest elements *E. cordifolia* and *C. paniculata* expanded at ~8600 <sup>14</sup>C yr B.P., following a decline of *W. trichosperma*. The time span dominated by *W. trichosperma* and the early portion of the *E. cordifolia* and *C. paniculata*-dominated zone, between ~10,000 and 7000 <sup>14</sup>C yr B.P., represent the warmest and driest interval of the Last Glacial–Holocene transition. The end of this warm–dry phase in Laguna Tahui is established by a reversal in the terrestrialization process that had started at ~10,000 <sup>14</sup>C yr B.P., and the onset and culmination of a transgressive lake phase between ~7000 and 5800 <sup>14</sup>C yr B.P. This is observed along the bathymetric transect in the form of (i) disappearance of plant macrofossil-rich layers at 7000 <sup>14</sup>C yr B.P. (core 0004D), and the subsequent appearance of layers with abundant *Diplodon* remains in cores 0004A and 0004D; and (ii) a gradual change from coarse detritus gyttja with thick wood pieces to gyttja sediment with (smaller) organic detritus in core 0004E.

The pollen record from the Laguna Pastahué site (42°22'S, 73°49'W) (Villagrán, 1985), located ~70 km north of Laguna Tahui, shows the nearly simultaneous expansion of *W. trichosperma*, *E. cordifolia*, and *C. pan-*



*iculata* at ~9600 <sup>14</sup>C yr B.P. This pattern contrasts with the results from the Laguna Tahui, Laguna Melli (Abarzúa, in prep.), Lago Condorito (Moreno, 2000, 2004; Moreno et al., 2001), and Huelmo sites (Moreno and León, 2003; Moreno et al., 2001), which show a lag of 1400–2000 <sup>14</sup>C yr for the expansion of *E. cordifolia* and *C. paniculata*, relative to *W. trichosperma*. One explanation for this asynchrony might rely on the prevalence of higher frequency or severity of local disturbance regimes near these sites, which would have favored the persistence of fast-growth, shade-intolerant pioneer tree species on volcanically derived substrates (*W. trichosperma*) (Lusk, 1999) in detriment of other tree species characteristic shade-tolerant of secondary stages in the succession process (*E. cordifolia*) (Veblen and Ashton, 1978). Nevertheless, the palynologic and stratigraphic data from Laguna Tahui, and neighboring sites in the region, indicate a prominent rise in temperature, substantial reduction in annual precipitation, and quite possibly, increased rainfall seasonality between 10,000 and 7000 <sup>14</sup>C yr B.P.

The beginning of the transgressive lake phase at ~7000 <sup>14</sup>C yr B.P. was followed by a reexpansion of *D. winteri* and podocarpaceous conifers (*S. conspicua*, *P. nubigena*) starting at ~5800 <sup>14</sup>C yr B.P. Considering that the modern distribution of conifers is centered mainly at higher elevations (200–300 m.a.s.l.) near the study area, and above 400 m.a.s.l. in the Costal Range of Isla Grande de Chiloé (Fig. 1), we interpret these results as indicating the onset of a cooling trend and increase in precipitation at ~7000 <sup>14</sup>C yr B.P. This cooling trend intensified at 4750 <sup>14</sup>C yr B.P. with a drop in the Valdivian rainforest indicators, forest diversification, and a rise in North Patagonian rainforest trees (Myrtaceae, *D. winteri*, *S. conspicua*, *P. nubigena*). A subsequent increase in herbs (Poaceae, possibly *Chusquea* spp.) and shrubs (*Fuchsia magellanica*, *Escallonia* sp., *E. coccineum*, *Ugni* sp., among others) at ~3000 <sup>14</sup>C yr B.P. suggests an opening of the forest canopy and/or forest fragmentation within this cool–temperate, wet climate condition. The exact cause of this important vegetation change is unknown. It is likely that this vegetation signal was driven by increased variability in climate or disturbance regimes; however, additional studies will be needed to assess this hypothesis.

The pollen record shows that *W. trichosperma* and *P. laetevirens* expanded rapidly between 700 and 400 <sup>14</sup>C yr B.P. Our vegetation survey indicates that *P. laetevirens* thrives near the southern edge of Laguna Tahui, an area that has been severely disturbed by human activities. Thus, the vegetation signal that started at 700 <sup>14</sup>C yr B.P. may represent local human disturbance since pre-Hispanic times.

#### Regional and continental implications

The Laguna Tahui palynological record agrees with previous studies from the Chilean Lake District (Heusser, 1966, 1984; Heusser et al., 1999; Moreno, 1997, 2004; Moreno and León, 2003; Moreno et al., 1999), Isla Grande de Chiloé

(Heusser, 1990a; Heusser et al., 1999; Villagrán, 1985, 1988a, 1988b; 1990, 1991), and the Channels region of southern Chile (Ashworth and Markgraf, 1989; Ashworth et al., 1991; Bennett et al., 2000; Lumley and Switsur, 1993) in showing a rapid expansion of closed-canopy North Patagonian rainforests following the retreat of Andean glaciers shortly after ~14,700 <sup>14</sup>C yr B.P. (Denton et al., 1999a). This shift resulted from a 5° to 7°C warming pulse at the end of the last ice age (Denton et al., 1999b; Heusser et al., 1999; Lowell et al., 1995; Moreno et al., 1999; Villagrán, 1988a, 1990).

A multimillennial pattern in precipitation trends, attributable to changes in westerly activity, is evident in the Laguna Tahui record: (i) higher than present precipitation regimes prevailed between ~14,000 and 10,000 <sup>14</sup>C yr B.P.; (ii) lower than present rainfall between ~10,000 and 7000 <sup>14</sup>C yr B.P.; (iii) a transitional phase with rising precipitation regimes between ~7000 and 5800 <sup>14</sup>C yr B.P.; and (iv) modern precipitation since 4750 <sup>14</sup>C yr B.P. These findings suggest changes in the latitudinal position/strength of the zone of maximum westerly precipitation since the end of last ice age. A northward displacement of this zone occurred between ~14,000 and 10,000 <sup>14</sup>C yr B.P., followed by a southward shift between ~10,000 and 7000 <sup>14</sup>C yr B.P., and a recovery to modern values through discrete steps at ~7000, 5800, and 4700 <sup>14</sup>C yr B.P. These latitudinal shifts of the westerly winds between 10,000 and 7000 <sup>14</sup>C yr B.P. may have resulted from the interaction of tropical (strengthening/weakening or southward/northward shift of the Pacific Anticyclone) and extratropical/subpolar forcing (disintegration/expansion or poleward/equatorward shift in the northern limit of Antarctic sea ice).

Our results contrast with the climatic constancy advocated by Bennett et al. (2000) during the last glacial–Holocene transition in Southern Chile. The basis for this interpretation is the apparent vegetation homogeneity they found in pollen records between ~14,000 and 7000 <sup>14</sup>C yr B.P. from the Channels region (44–47°S). Although both areas of southern Chile are characterized by the dominance of broadleaf temperate rainforest, the native vegetation in the Chilean Lake District and Isla Grande de Chiloé is more diverse and heterogeneous along topographic, climatic, and edaphic gradients. This is reflected in the absence of Valdivian rainforest communities south of 43°30'S. Possible explanations for this southern limit may involve a combination of climatic and marine barriers that might have limited the migration of Valdivian elements to areas south of Isla Grande de Chiloé. Pollen records between 41°30' and 43°30'S show that two ecologically and floristically distinct rainforest communities (e.g., North Patagonian and Valdivian rainforests) have alternated their dominance in the lowlands since the end of the last ice age. Pollen records between 44° and 47°S, however, show the persistence of North Patagonian rainforests with little variation over the last 14,000 <sup>14</sup>C yr. A recent study on fossil midges from Peninsula de Taitao (Massaferro and Brooks, 2002), however, identified Holocene climate fluctuations in agreement

with our results from Laguna Tahui, in particular a reduction in moisture between 10,000 and 7000  $^{14}\text{C}$  yr B.P., and subsequent recovery to reach modern climate conditions.

Indeed, the timing and direction of temperature and precipitation changes over the last 14,000  $^{14}\text{C}$  yr B.P. at Laguna Tahui may have implications at a continental scale. Abraham et al. (2000) postulated Holocene variations in the aerial extent/magnitude of the Andean rain shadow, the so-called “South American Arid Diagonal Zone”, in broad agreement with our results. The warm–dry phase between 10,000 and 7000  $^{14}\text{C}$  yr B.P. is also recorded at Laguna Aculeo, central Chile (33°50'S), an area affected by winter rains of westerly origin. Paleoenvironmental studies show desiccation of the Laguna Aculeo between 8400 and 5000  $^{14}\text{C}$  yr B.P., followed by several pulses in lake level rise that led to modern conditions by 3000  $^{14}\text{C}$  yr B.P. Thus, the end of the warm–dry phase at Aculeo seems to lag by 2000  $^{14}\text{C}$  yr the Laguna Tahui record, generating an apparent discrepancy between these records/regions. One explanation for this lagged response could be that increased westerly activity observed in southern Chile at 7000  $^{14}\text{C}$  yr B.P. was of insufficient magnitude to trigger a rise in lake levels in central Chile. Thus, only by 5000  $^{14}\text{C}$  yr B.P. were subsequent intensifications of this trend able to finally influence the northern limit of the westerlies in central Chile.

The early Holocene warm–dry phase drove southward shifts in species ranges, as depicted by the Valdivian tree *E. cordifolia*, whose early Holocene expansion has also been reported in the Puerto Carmen palynological site in southern Isla Grande de Chiloé (Villagrán, 1988b), an area dominated today by North Patagonian rainforests. This may also apply to the presence of isolated populations of Sclerophyllous forest species such as *Peumus boldus* and *Cryptocaria alba* in the Valdivian rainforest-dominated Lake District. These biogeographic outliers can be interpreted as relicts of a former broader distribution, possibly related to the same climatic interval. We postulate that the fine-grained vegetation mosaic of North Patagonian rainforest conifers with thermophilous Valdivian rainforest tree species, characteristic of the lowlands of the NE Isla Grande de Chiloé and the Lake District originated ~5800  $^{14}\text{C}$  yr ago. This mixture owes its existence, in part, to multimillennial changes in westerly wind activity, and habitat/climatic heterogeneity at small spatial/temporal scales.

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