Expansion of Magellanic Moorland during the Late Pleistocene: Palynological Evidence from Northern Isla de Chiloé, Chile

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The late Quaternary vegetation of northern Isla de Chiloé is inferred from palynological analysis of a section in the Río Negro drainage (42°03'S, 73°50'W). At ca. 30,500 yr B.P., maxima of Astelia and Donatia occurred, suggesting wetland development. From that time until ca. 27,000 yr B.P., steppe indicators such as Compositae/Gramineae dominated, suggesting drier conditions. After 27,000 yr B.P., the moorland shrub Dacrydium gradually increased, reaching a maximum by 18,000 yr B.P. At this time Astelia increased again, suggesting development of cushion bog during cold and wet conditions. The glacial-postglacial transition is characterized by a marked change from peaty sediments to clays, a decrease in the cushion bog flora, and the prevalence of Gramineae/Compositae and swamp taxa. This vegetation prevailed until ca. 7000 yr B.P. when forest taxa became dominant. The floristic pattern inferred from the pollen spectra of the Río Negro section suggests that the late Pleistocene vegetation of Chiloé resembled modern Magellanic Moorland vegetation (52°–56°lat S). Based on climatic conditions presently associated with Magellanic Moorland, its occurrence in Chiloé at low elevations during the late Pleistocene implies a decrease in average temperature of at least 4°C and an increase in annual precipitation of at least 1500 mm.

INTRODUCTION

According to previous studies (Heusser and Flint, 1977; Porter, 1981; Mercer, 1984), the last glaciation affected the northeastern part of Isla de Chiloé, Chile (Fig. 1), while south of 42°40'S glaciers crossed the island and reached the Pacific Ocean.

Palynological evidence available from Chiloé (Heusser and Flint, 1977; Villagrán, 1985, 1988) reveals a pattern of late Quaternary forest succession of the three evergreen rain forest types that currently prevail in the region: Valdivian, Northpatagonian, and Subantarctic forests (Schmithüsen, 1956). For Patagonia and Tierra del Fuego in Chile and Argentina (40°–55°S) Auer (1948, 1958) described the gradual late- and postglacial colonization of Northpatagonian and Subantarctic elements from west to east and north to south from refugia in the Cordillera de la Costa between Valdivia and Chiloé. During the last glaciation, when temperatures are estimated to have been 8°C lower than present (Heusser 1981, 1982, 1984), shifts of vegetation should have occurred in the inverse direction.

The evidence on the late Pleistocene vegetation of Chiloé partially supports such a trend. The Subantarctic forest descended to occupy the lower elevations of the north-central part of the island between 43,000 and 31,000 yr B.P., while the Valdivian elements, which dominate the region at present, were absent (Heusser and Flint, 1977; Villagrán, 1985). During the height of the glaciation, between 27,000 and 14,000 yr B.P., a decline of the forest elements occurred (Heusser and Flint, 1977), except Nothofagus, and there appeared some Subantarctic taxa such as Huperzia selago (Heusser, 1972a) and Drapetes muscosus, presently restricted to areas south of latitude 48°S (Moore, 1983). However, no evidence has been found of the presence of elements of the Magellanic Moorland, which is the type of formation that one would expect to replace the Subantarctic forest under increasingly colder and wetter climatic conditions (Fig. 1).
Thus, the question posed by Heusser (1982) regarding the elements of the Magellanic Moorland has remained unanswered: 'Where were the plants during the height of the glaciation?' At present in Chiloé, Magellanic Moorland taxa are distributed on the summits of the Cordillera de Piuchué (Fig. 1) at more than 600 m elevation (Es-
pinosa, 1917; Godley, 1968). They are discontinuously distributed northward to the latitude of Valdivia (40°S) and, more scarcely, to the Nahuelbuta Range (38°S). The distributional center of Magellanic Moorland vegetation is along the Pacific coast of Tierra del Fuego, between 52° and 56°S (Fig. 1). The formation results from a combination of high rainfall (2000–5000 mm), relatively low temperatures (5–6°C), and poor drainage (Moore, 1983; Holdgate 1961). Taking into account the high moisture requirement of the moorland plant species, the pronounced rain shadow east of the Andes, the poor dispersability of cushion bog species (Wace, 1965; Villagran et al., 1986), and the widespread glaciation south of 42°30′S (Heusser, 1982), the only refugia available would have been low elevation areas near the Pacific coast at the northern border of the existing range of cushion plant species (40° to 42°). The apparent bipolarity of the present distributional range of the moorland taxa (Donat, 1933) could then be the consequence of (1) gradual postglacial recolonization by forest elements south of 42°S, thus disrupting the distributional continuity of moorland during the Holocene, and (2) gradual upward shift of the treeline during the postglacial period and consequent restriction of the cushion bogs to favorable habitats at the summits of the Cordillera de la Costa. If both movements occurred, the postglacial pollen data from south of 42°S should reveal a gradual north–south increase of the moorland species during the Holocene. North of 42°S, pollen data from west of the glacier limit should reveal the presence of cushion bog species at the glacial maximum.

Evidence for postglacial southward movement of cushion bog taxa has been found for Dacrydium fonckii, Drosera unijflora (Auer, 1958; Heusser, 1972b), Donatia fascicularis, Astelia pumila, and Gaimardia australis (V. Markgraf, unpublished data). Unfortunately, the profile studied by Auer came from the eastern slope of the Andes of Fuego-Patagonia. As Auer pointed out, however, proof for the latitudinal shifts of moorland vegetation would be far stronger in records from the wetter areas of the Chilean coast.

**STUDY AREA**

Isla de Chiloé, the major island of the Archipelago of Chiloé, is formed by Paleozoic metamorphic rocks of the Cordillera de la Costa (Cordillera de Piu-chué) to the west and by Quaternary sediments to the northeast (Fig. 1). Most of southern and eastern Chiloé has low and undulating terrain, with elevations up to 400 m. Only the northwestern and central area, the Cordillera de Piu-chué, rises to 700–800 m.

In general, the region has an oceanic climate. On the basis of its high annual precipitation it is included in the “Zone of perennial precipitation with a winter maximum” (Van Husen, 1967). The climate, however, changes along a W–E gradient (Table 1); stations located along the Pacific coast record an oceanic climate with smaller seasonal differences between the wettest and driest months, and between the maximum and minimum monthly temperatures. The summits of the Cordillera de Piu-chué are wetter and colder, while the east coast has a more Mediterranean climate, expressed mainly by greater summer dryness (di Castri and Hajek, 1976). Stations in Andean Chiloé record a more continental climate characterized by low winter temperatures and a wide temperature range (di Castri and Hajek, 1976).

Evergreen rain forests and herbaceous moors are presently the prevailing vegetation of the Isla de Chiloé. Forests at lower elevations have been markedly reduced by agricultural and livestock activities. Valdivian forest, dominated by Eucryphia cordifolia, Gevuina avellana, Calodculia paniculata, Laurelia philippiana, and various taxa in the family of Myrtaceae, is found up to 250 m, mainly in the northeast where there is some Mediterranean climatic influence. In the lower elevation areas of the Pacific coast, the dominating Valdivian el-
TABLE 1. METEOROLOGICAL DATA FROM STATIONS REPRESENTATIVE OF CHILOÉ ARCHIPELAGO (AFTER HAJEK AND DI CASTRI, 1975; HOLDGATE, 1961)

<table>
<thead>
<tr>
<th>Station</th>
<th>Position Lat. °S</th>
<th>Long. °W</th>
<th>Precipitation (mm)</th>
<th>Temperature (°C)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>Annual total</td>
<td>Oceanic</td>
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<tr>
<td></td>
<td></td>
<td></td>
<td>Wettest month</td>
<td>Mediterranean</td>
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<td>Driest month</td>
<td>Continental</td>
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<tr>
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<td></td>
<td></td>
<td>Annual mean</td>
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<td></td>
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<td>Max.</td>
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<td></td>
<td></td>
<td></td>
<td>Min.</td>
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</tr>
<tr>
<td>Punta Corona</td>
<td>41°47'</td>
<td>73°52'</td>
<td>2410.8</td>
<td>10.7</td>
</tr>
<tr>
<td>Isla Guayo</td>
<td>43°34'</td>
<td>74°45'</td>
<td>1409.0</td>
<td>9.7</td>
</tr>
<tr>
<td>Melinka</td>
<td>43°54'</td>
<td>73°46'</td>
<td>3137.7</td>
<td>10.0</td>
</tr>
<tr>
<td>San Pedro</td>
<td>42°15'</td>
<td>73°55'</td>
<td>3050.0</td>
<td>6.5</td>
</tr>
<tr>
<td>Pudeto</td>
<td>41°54'</td>
<td>73°48'</td>
<td>1808.7</td>
<td>11.0</td>
</tr>
<tr>
<td>Castro</td>
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<td>73°48'</td>
<td>1598.5</td>
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<tr>
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<td>73°43'</td>
<td>2047.7</td>
<td>10.6</td>
</tr>
<tr>
<td>Futaleufú</td>
<td>43°12'</td>
<td>71°52'</td>
<td>2150.3</td>
<td>10.1</td>
</tr>
<tr>
<td>Rio Cisnes</td>
<td>44°45'</td>
<td>72°00'</td>
<td>701.8</td>
<td>7.6</td>
</tr>
</tbody>
</table>

The core was obtained using a Dachnowsky borer. The sediments were
analyzed by Juan Varela, Department of Geology, Universidad de Chile, Santiago. The base of the core (depth 240–220 cm), is composed predominantly of white medium sand with a low clay (ca. 5%) and organic content. These sands are probably of fluviolacustrine origin. They are overlain by light yellowish medium sand with approximately 10% clay (220–205 cm). The sand grades upward into dark reddish-brown clayey peat with plant debris; between 120 and 60 cm reddish-brown peaty clays are found with abundant vegetal debris. Between 60 and 20 cm, light-greenish-gray clay appears with very little sand and some inclusions of reddish-brown peaty clay. In the upper part of the profile (20–0 cm), reddish-brown peaty clay reappears.

Samples for pollen analysis were taken at 5-cm intervals along the profile, except between 160 and 210 cm, where pollen concentration was low and samples were taken every 10 cm. For pollen analysis, samples were pretreated with 5% KOH solution, HF, and acetolysis. Pollen counts were made under a Nikon Biophot microscope. Three hundred pollen grains of arboreal and nonarboreal pollen were counted at each interval. Proportions of the taxa were calculated for the total arboreal and nonarboreal pollen sum, excluding Cyperaceae and spore-producing species. Figure 2 plots, from left to right, the frequencies of arboreal pollen (including tree species and their associated shrubs, vines, and the mistletoe Misodendrum), the frequencies of nonarboreal taxa, local aquatics (Cyperaceae), ferns, the total pollen sum, and radiocarbon dates. Taxonomic nomenclature follows Marticorena and Quezada (1985). Four radiocarbon dates are available: 7170 ± 120 yr B.P. (Beta-20984) at 25–40 cm, 18,090 ± 150 yr B.P. (Beta-21812) at 60–90 cm, 30,480 ± 630 yr B.P. (Beta-20895) at 140–160 cm, and 30,590 ± 600 yr B.P. (Beta-4728) at 200–220 cm. The last date, for the basal sandy level with a low carbon content, is believed to be too young because of possible infiltration of younger carbon from above. This explanation seems reasonable, since this sandy level is below one (140–160 cm) that gave a very similar date.

RESULTS

Six pollen zones have been distinguished (I–VI) in the diagram provided by the Rio Negro profile (Fig. 2). Zones I through V, corresponding predominantly to dark reddish-brown clayey peat, represent the late Pleistocene. At a depth of 60 cm, a sharp lithological and color change occurs from reddish-brown to a light greenish clay, corresponding to the appearance of pollen representative of postglacial vegetation (Zone VI).

ZONE I. Pollen content at the bottom of the profile, associated with the sandy clay, is low, and is characterized by the prevalence of nonarboreal taxa (42–88%). Successive maxima of Gunnera (up to 53% at the base), Gramineae (65–72% in the middle part), and Cyperaceae (at the top of the zone) occur. Close to the top of the zone, an increase of arboreal pollen, almost exclusively represented by Nothofagus (up to 58%), documents the beginning of arboreal colonization of sandy substrates.

ZONE II. This zone is characterized by a sharp increase of Astelia pumila (up to 44%), Ranunculaceae (up to 12%), Donatia fascicularis (up to 8%), Tetronecium magellanicum (up to 6%), and by traces of Nanodea muscosa, Gaimardia australis, and Drosera uniflora. All these taxa are characteristic of Subantarctic cushion bogs. While nonarboreal pollen is still dominant (57–69%), there is further increase in the representation of forest taxa, and another arboreal element, Drimys winteri, appears. This spectrum suggests an open landscape with moorlands and forests on the margins. The top of this zone is dated at 30,480 ± 630 yr B.P.

ZONE III. This zone is characterized by disappearance of the cushion bog taxa and the dominance of nonarboreal pollen (43–72%), Compositae/Tubuliflorae (up to 34%), and Gramineae (up to 32%). High
FIG. 2. Pollen diagram for the Río Negro profile, Isla de Chiloé, Chile.
proportions of Gramineae and Compositae characterize the pollen spectra of the Patagonian Steppe.

ZONE IV. In this zone Gramineae and Compositae decrease significantly, coupled with an increase of Nothofagus pollen (up to 54%) and of the dwarf conifer Dacrydium fonckii (up to 47%), a shrub characteristic of the borders of Subantarctic Magellanic Moorland. Various cushion bog taxa also increase relative to the previous zone. This change in the pollen spectrum suggests a return of Magellanic communities, with patches of subantarctic forest, probably of Nothofagus betuloides.

ZONE V. This zone is characterized by an increase in cushion bog taxa, Astelia pumila (up to 19%), Ranunculaceae (up to 10%), and by traces of Donatia fascicularis and Gaimardia australis. Simultaneously, pollen of Dacrydium and of the forest taxa decrease. Nonarboreal pollen dominates (54–57%). These changes suggest expansion of moorland vegetation and the retreat of forest. The zone is dated to 18,090 ± 150 yr B.P.

ZONE VIa. Zone VIa is characterized by nonarboreal pollen (50–60%). The prevalence of Gramineae (up to 22%) and Compositae-Tubuliflorae (up to 26%) suggests the expansion of steppe. The sudden and brief maxima of aquatic and swamp taxa, namely Isoetes savatieri (up to 23%) and Littorella (up to 7%), may result from flooding during deglaciation.

ZONE VId. A number of previously scarce arboreal taxa markedly increase from the lower levels of this zone: Podocarpus nubigena (up to 25%), Myrtaceae (up to 7%), and Drimys (up to 4%). Nothofagus remains represented by the same proportions as in the late Pleistocene zones. The first appearance of forest elements is distinctive: Pseudopanax, Hydrangea serratifolia, Lomatia/Gevuina, Maytenus, Desfontainia spinosa, Eucryphia/Caldcluvia, Weinmannia trichosperma, and Embothrium coccinum. Several ferns associated with forests also increase in their relative proportions: Polypodium feullei, Hypolepis rugosula, and Hymenophyllum. Arboreal pollen reaches a maximum of 88%. The onset of this zone is dated at 7170 ± 120 yr B.P.

ZONE Vlc. Characteristic are the brief decrease of forest taxa (45%), and the expansion of Gaimardia australis (38%) and of Cyperaceae, both wetland indicators.

ZONE Vld. Mixed forest taxa are prevalent (84–86%), of which the most abundant are hygrophilous Nothofagus, Podocarpus nubigena, Drimys winteri, and ferns.

DISCUSSION

The floristic composition of the Rio Negro sequence suggests that the late Pleistocene vegetation of Isla de Chiloe was equivalent to that of the modern Magellanic Moorland (Roig et al., 1985; Moore, 1983). According to Moore (1983), moorland communities include patches of evergreen forest, cushion bog, graminoid bog, and maritime tussock grassland.

From the beginning of the sequence (before 30,500 yr B.P.), a trend toward increasingly colder and wetter conditions is implied by the successive maxima of Gunnera, Gramineae, Cyperaceae (Zone I), Astelia, and Donatia (Zone II), documenting the development of cushion bogs from about 30,500 yr B.P. on. From this time until ca. 27,000 yr B.P. (Zone III), the dominance of grassland indicators, Compositae/Grumineae suggests a trend toward drier conditions. At ca. 27,000 yr B.P. a trend toward colder and wetter conditions began, as indicated by the dominance of the moorland shrub Dacrydium fonckii, followed at 18,090 yr B.P. by a second phase of Astelia pumila cushion bog. Throughout this sequence, high proportions of Nothofagus pollen (average 39%) and traces of Podocarpus nubigena, Myrtaceae, Drimys winteri, and Fitzroya/Pilgerodendron occur. All of these taxa are hygrophilous and floodplain species which occur in the patchy coastal evergreen forest of the Magellanic Moorland Complex (Roig et al., 1985). A pollen spectrum equivalent to this vegetational mosaic has been described by
Godley and Moar (1973) at an elevation of 650 m in the Cordillera de Puchué on Isla de Chiloé. The presence of this type of vegetation at 18,000 yr B.P. in the lower elevations of the island indicates a northward expansion of the Magellanic Moorland by at least 6° latitude, and a descent of at least 600 m in elevation. Assuming a wet adiabatic lapse rate of 0.65°C/100 m, the minimum implied lowering of mean annual temperature is 4°C. Based on the present amount of precipitation, the descent of the moorlands to sea level in Chiloé would have required an increase in annual precipitation of at least 1500 mm compared to the present level.

The little evidence available on the late Pleistocene vegetation prior to 27,000 yr B.P. of Isla de Chiloé supports such a climatic interpretation. Between 43,000 and 33,000 yr B.P. the Subantarctic forest descended by at least 500 m to occupy the lower elevations of the north-central part of the island, while the Valdivian forest elements which dominate the region at present were then absent (Heusser and Flint, 1977; Villagran 1985). The colder and wetter conditions inferred from our data to have followed this forest phase also agree with the interpretation of Heusser and Flint (1977) based on analysis of the section at Taiquemó (Fig. 1). The slight warming and greater dryness suggested by the decrease in herb percentages between 31,000 and 27,000 yr B.P. at Taiquemó also compares well the dominance of steppe indicators during this period in the Rio Negro profile. In northern Patagonia, Argentina, the Rahue deposit also shows a pollen spectrum similar to the Rio Negro profile, with dominance of Gramineae, Compositae, and Nothofagus, between 33,000 and 27,000 yr B.P. (Markgraf et al., 1986).

At 27,000 yr B.P., increases in the percentages of Gramineae and Compositae (Heusser 1966, 1974, 1981; Heusser and Flint, 1977) are believed to mark the beginning of a cooling trend that intensified after about 25,000 yr B.P. and continued until 14,000 yr B.P. The dominance of steppe indicators led Heusser and Flint (1977) and Heusser et al. (1981) to infer that drier conditions prevailed during the glacial maximum. In contrast with this interpretation, the pollen record between 27,000 and 18,000 yr B.P. in the Rio Negro profile shows a clear trend toward increasingly wetter conditions. This dissimilarity may be accounted for by the location of Heusser’s profiles, all of them in vicinity of glacier margins. There, the drier character of the vegetation could have resulted from the better-drained, sandy soils which predominate near glacier margins. For example, the Taiquemó section is located within the belt of end moraines and proximal outwash plains of the last glaciation (Heusser and Flint, 1977). In this connection, Sweda (1987) analyzed the vegetation cover in the vicinity of the retreating Soler Glacier, Patagonia, and recognized marked differences in the vegetation at different distances from the glacier margin. The coarse deposits of the proximal part of the outwash plain were so permeable that the available moisture could support only grass species and dwarf shrubs. The moraines had a higher content of silt and consequently a higher moisture-retention capacity, so that open woodland could form in this zone. The Nothofagus-parkland vegetation, with a dominance of Gramineae and Compositae during the 27,000 to 14,000 yr B.P. interval in Taiquemó, might result from the types of substrate available in a moraine-outwash complex. In contrast, the Rio Negro section is located over 15 km west of the ice margin during the last glaciation (Fig. 1), in the glaciofluvial area corresponding to the distal parts of the outwash plain. According to Sweda (1987), the silty deposits of this zone support lush and dense forests of Nothofagus species intermingled with marshy vegetation.

The wetter climate postulated for the last glacial maximum in the Rio Negro sector probably characterized the Isla de Chiloé in general. This conclusion derives from the
analysis of a pollen profile from the locality of Loncomilla in the north-central part of the island (C. Villagran, unpublished data). Here the vegetation at ca. 18,000 yr B.P. appears to have been dominated by *Nothofagus, Dacrydium, Astelia,* and *Donatia,* the same species which are dominant in Rio Negro.

The cause of this period of higher rainfall might lie in the changed atmospheric circulation at mid-latitudes in the Southern Hemisphere, which was in turn a consequence of the expansion of the ice cap on the Antarctic Ocean during the glacial maximum. Based on major changes in the relative abundance of radiolarians, which indicate changes in the position of the boundary zone between Antarctic and subantarctic waters, Hays *et al.* (1976) suggested that at 18,000 yr B.P. the Antarctic Convergence (Antarctic Polar Front) was displaced north of its present position by as much as 7° of latitude, whereas the Subtropical Convergence was little changed from its present position. The expansion of the Antarctic waters resulted in a compression of the subantarctic water mass, and a steepening of the thermal gradient throughout its extension. Along the Pacific coast of South America, the subantarctic water mass runs through the transition zone between the subantarctic and subtropical maritime air masses, between 30° and 60°S. This zone is under the influence of the westerly wind belt, which is responsible for the major rainfall patterns along the coast of Chile. Assuming that during the last glacial maximum the boundary of the subantarctic and subtropical air masses (Polar Front) was displaced 5°–7° north of its present position at 50°–55°S (Van Husen, 1967), as postulated by Heusser (1974), the steeper thermal gradient could have increased the baroclinicity and, consequently, the frontal activity within the zone under the influence of the westerly wind belt.

Therefore, hygrophyllous plant formations (Magellanic Moorland and *Nothofagus* rain forests), which are now dominant south of 38°S, would have extended northward. Concomitantly, the area covered by xeric plant formations (sclerophyllous forest and drought deciduous scrub) would have been narrower than today, when these formations are distributed between 30° and 38°S. The disjunct presence of forest stands dominated by *Nothofagus obliqua* (Casassa, 1986) or *Aextoxicon punctatum* (Villagran and Armesto, 1980; Perez and Villagran, 1985) on the mountaintops of the Coastal Range in central Chile (30°–34°S), could be interpreted as the result of northward extension of the hygrophyllous plant formations during the last glacial age. This northward movement of vegetation can also explain the present day existence of Magellanic Moorland relics on the Coastal Ranges in Nahuelbuta, Valdivia, and Chiloé (38°–42°S).

This climatic interpretation is consistent with palynological and stratigraphic evidence presented by Heusser (1983) and Varela (1976) for Laguna Tagua-Tagua in central Chile (34°30’S). These authors indicated a marked increase in precipitation in central Chile and a northward expansion of the limit of *Nothofagus* forest through ca. 5° of latitude between 28,000 and 14,000 yr B.P. In *Isla de Chiloé*, the very hygrophyllous Magellanic Moorland was dominant during the same time period, suggesting that the point of maximum rainfall was displaced from its present position at 50°S (Heusser, 1984) to a latitude close to the study area.

In the Rio Negro profile, the late glacial–postglacial transition is marked by a change in sediments from reddish-brown clayey peat to light grayish clay. In contrast to other postglacial records studied at higher elevations in the *Isla de Chiloé* (Villagran 1985, 1988), in which forest vegetation is continuously present after ca. 12,500 yr B.P., the vegetation in the Rio Negro profile is dominated by nonarboreal taxa until ca. 7000 yr B.P. The difference may result from contrasting permeability of the soils between different locations. Thus, the
poorly drained soils of the Rio Negro location could support aquatic and swamp taxa much longer than the better-drained upland locations. Wet conditions may have resulted from rapid deglaciation with increasing temperatures. Since ca. 7000 yr B.P., forest taxa of the North-Patagonian and Valdivian forests have prevailed. Forest development was interrupted by a brief period of forest decrease and expansion of Gaimardia australis cushion bogs, possibly a consequence of climatic changes associated with Neoglacialization after 5000 yr B.P. (Mercer, 1984).

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