

12 Late Quaternary environments and palaeoclimate

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Chile possesses one of the most pronounced climate gradients in the world, extending from the world's driest desert in the northern part of the country, where precipitation is measured in millimetres per decade, down to the channel and fiords region in southern Patagonia where rainfall can average up to 7 m per year or more. In contrast, thermal buffering by the Pacific Ocean contributes to ameliorating extreme temperatures, generating a latitudinal temperature gradient that is considerably less pronounced than across similar latitudinal ranges in other parts of the world (Miller 1976; Axelrod *et al.* 1991). Coupled with millions of years of geographic isolation induced by the massive barrier imposed by the Andean Cordillera, Chile today possesses a highly endemic fauna and flora whose distribution is tightly linked to these gradients (Arroyo *et al.* 1996; Hinojosa & Villagrán 1997).

Considering its geographic position and tectonic setting, it is hence not surprising that the geomorphology of Chile over the last two million years or so, i.e. the 'Quaternary' (see Gradstein *et al.* 2004), has been strongly influenced by climate along this broad latitudinal gradient. Whereas ancient landscapes preserved for millions of years exist in the hyperarid Atacama, repeatedly glaciated landscapes predominate in southern Chile. Elucidating the precise chronology of these Quaternary events affecting the western margin of southern South America is of great relevance to a number of scientific disciplines including ecology, palaeo-climatology, evolutionary biology, population genetics, phylogeography, biogeography and conservation.

Consequently, records of past climate and landscape change in Chile during the late Quaternary (an informal term generally spanning the last glacial-interglacial cycle) have been developed and described by an impressive number of researchers from many countries since the beginning of the twentieth century. The vast majority of such scientific endeavours have used either palaeo-ecological or geological/sedimentological evidence to describe palaeoclimate, geomorphology, neotectonics, biogeography and evolution in this region of South America. Over the past 20 years the pace of research has quickened, following a worldwide demand for ever increasing and more detailed palaeoclimate data. Recent developments in high-resolution ice core and marine records from the mid- and high latitudes of the southern hemisphere have led to new studies of climate linkages and controlling mechanisms at the interhemispheric level during and since the last ice age (Denton *et al.* 1999; Lowell *et al.* 1995; Kim *et al.* 2002; Mayewski *et al.* 2004).

To date, Quaternary research in Chile has produced a vast amount of data. Here, we provide an overview of the current knowledge based on work by active researchers (most reside in Chile) from a range of disciplines including Quaternary geology and stratigraphy, palaeoceanography, palaeo-ecology, biogeography and archaeology. Starting with a consideration of off-shore influences (see also Chapter 11), we move onland through Chile from north to south, including special sections on the rich flora of central ('mediterranean') Chile and the Chiloé Archipelago and the prominent terraces attributed to the last interglacial period around the coastal city of Valdivia (see Fig. 12.1 for site locations). We finally attempt to integrate what we know about past climate change with the earliest colonization of Chile by humans.

For the sake of consistency, all radiocarbon ages younger than 26 000 ¹⁴C yr BP in this chapter have been converted into calendar years before 1950 using CALIB 5.1 (<http://www.calib.org>). CALPAL using 2004 SFCP (www.calpal.de) was used for radiocarbon ages between 26 000 and 50 000 ¹⁴C yr BP. Ages older than 50 000 were left uncalibrated. Except were noted, all ages in this chapter are expressed either in calendar years before 1950 (yr BP), thousands of calendar years before 1950 (ka BP), or millions of years ago (Ma).

Past Quaternary research in Chile

Ever since the discovery of Mylodon Cave in southernmost Patagonia during the late 1800s, the Quaternary period in Chile, and in particular the late Pleistocene, has received worldwide attention. Excellent summaries of past Quaternary research in Chile have already been published (Paskoff 1977; Ortlieb 1995; Villagrán 1995b; Heusser 2003). Even though the Quaternary is a short 'blip' in the geological timescale, two million years is still quite a large chunk of time! We thus do not intend such a detailed synthesis in just one chapter of a book, but rather our aim here is to provide an overview of specific areas of ongoing research in Chile, especially focusing on late Quaternary palaeoclimates.

The first major review by Paskoff (1977) focused on several aspects of the Quaternary, with a strong emphasis on coastal geomorphology, together with his work on the geomorphology of semi-arid lands in north-central Chile (the 'Norte Chico') (see also Paskoff 1970). A synthesis of the palaeoclimate of northern Chile (the 'Norte Grande') was later provided by

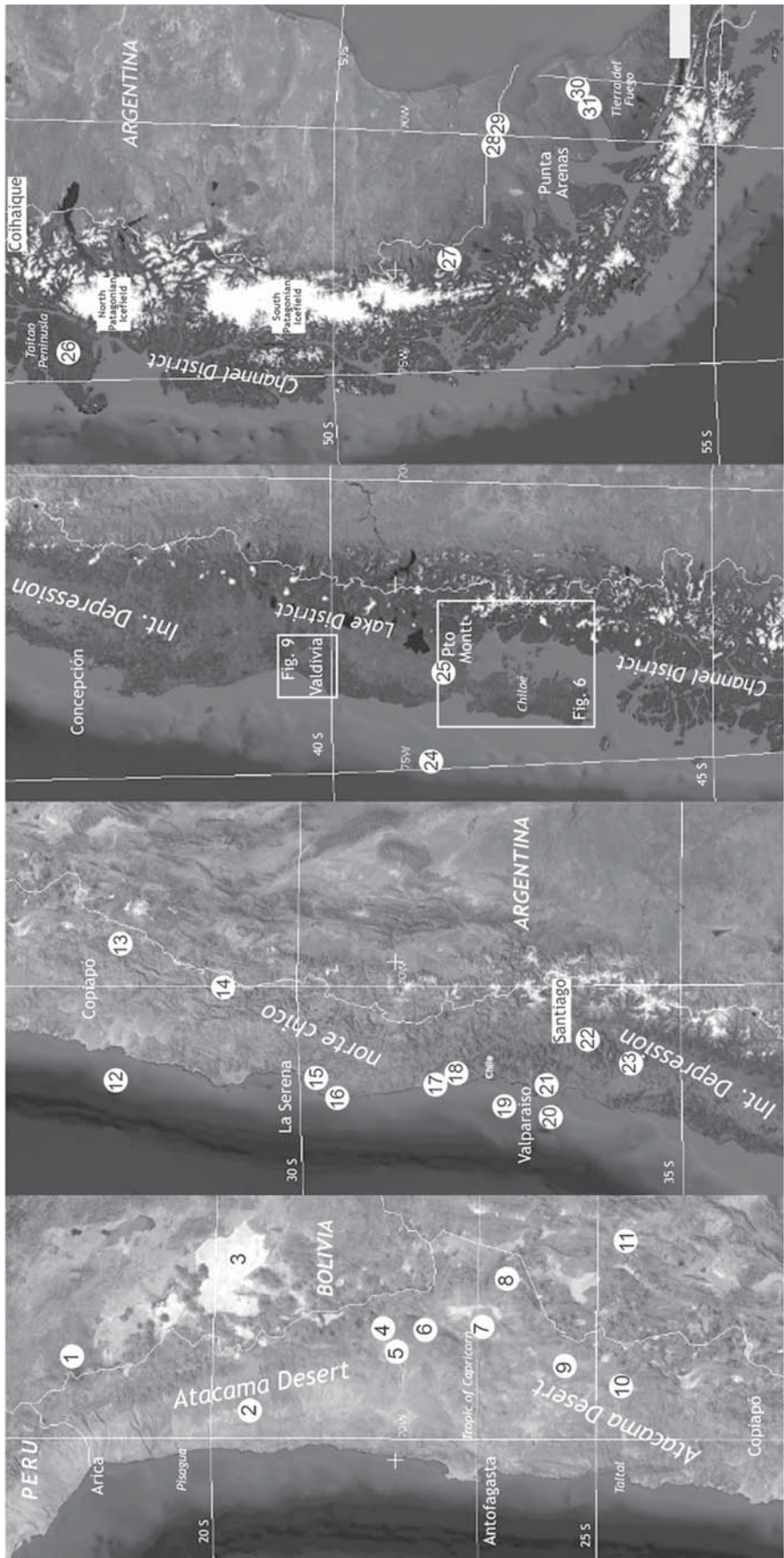


Fig. 12.1. A physical map of Chile. All localities discussed in this chapter including offshore core sites are indicated. Key: 1, Nevado Sajama; 2, Pampa del Tamarugal; 3, Salar de Uyuni; 4, Río Salado; 5, Calama; 6, Tuina; 7, Salar de Atacama; 8, Salar de Hombre Muerto; 9, Laguna Miscanti; 10, Quebrada del Chaco; 12, Marine core GeoB 3375-1; 13, Laguna Negro Francisco and Río La Gallina; 14, Valeriana and Encierro valleys; 15, Tongoy; 16, Fray Jorge and Talinay; 17, Ñague I, II and Quereo; 18, Palo Colorado; 19, Marine core GIK 17748-2; 20, Marine core GeoB 3302-1; 21, Algarrobo; 22, Laguna Aculeo; 23, Laguna Tagua Tagua; 24, Marine core GeoB 3313-1; 25, Monte Verde; 26, Laguna Stibnite; 27, Mylodon Cave and Cueva del Medio; 28, Fell's Cave; 29, Pali Alke; 30, Tres Arroyos; 31, Marazzi.

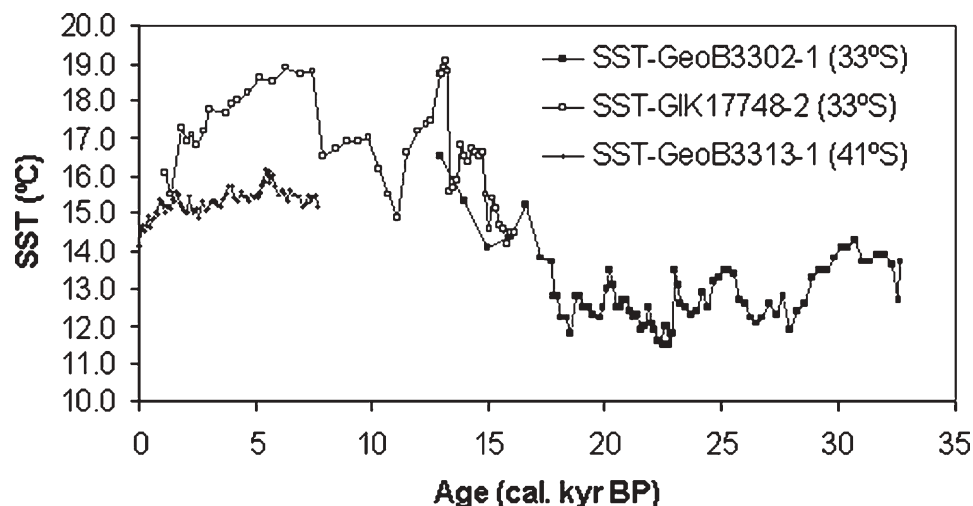


Fig. 12.2. Past sea surface temperature data spanning the last glacial–interglacial transition from marine cores off coastal Chile (Lamy *et al.* 1999, 2001; Marchant *et al.* 1999). Some dates have been recalibrated (see text).

Ortlieb (1995), although a considerable amount of research has taken place since this publication (see a recent update by Latorre *et al.* 2005) (also see below). Several important syntheses of the impacts of Quaternary climate and vegetation change in southern Chile have been written by palynologists Carolina Villagrán (Villagrán 1990, 1995*a, b*; Villagrán *et al.* 1998) and Calvin Heusser (2003). The latter publication includes not only a detailed historical narrative of past pioneers of the Quaternary in the southern Andes but also a summary of over 40 years of research including over 20 radiocarbon-dated palynological records. Quaternary impacts and distribution of past fauna were summarized in a review by Moreno *et al.* (1994) for northern and central Chile, by Latorre (1999) for Tierra del Fuego and more recently by Frassinetti & Alberdi (2000, 2001).

Late Pleistocene–Holocene palaeoceanography of the Peru–Chile Current (G.V.)

As detailed in the previous chapter, the Peru–Chile (or Humboldt) Current is a complex oceanographic system that modulates continental climate along the Chilean coastal margin. Off central and northern Chile, northward advection of cold Subantarctic Waters along its oceanic and coastal branches dominates the surface circulation, whereas a counter-current transports warm subtropical water masses poleward (Strub *et al.* 1998; Chaigneau & Pizarro 2005*a, b, c*). The subsurface Poleward Undercurrent transports nutrient-rich and oxygen-depleted Equatorial Subsurface Waters (Brandhorst 1971; Morales *et al.* 1996), and constitutes a main source of nutrients for the photic zone during upwelling processes, supporting not only primary production in the ocean surface layer, but also strong CO₂ outgassing particularly off central and northern Chile (Torres *et al.* 2002). South of approximately 42°S the West Wind Drift or Antarctic Circumpolar Current (ACC) intercepts the Chilean margin and flows southward into the Cape Horn Current (Strub *et al.* 1998; Chaigneau & Pizarro 2005*a, b, c*). The distribution of surface sediment properties off Chile confirms this oceanographic pattern, suggesting that upwelling processes are dominant as a key factor for primary production in central and northern Chile, whereas the ACC and nutrient fluvial input become dominant along the margin of southernmost Chile (e.g. south of 40°S) (Hebbeln *et al.* 2000*a*).

Detailed palaeoceanographic work on sediment cores collected between 27°S and 41°S all seem to indicate that oceanographic variations along coastal Chile during the late Pleistocene (Fig. 12.2), and particularly during the last glacial period, have been driven by high latitude climate change. These mostly include changes around Antarctica and implied latitudinal shifts of the Southern Westerlies and the ACC, following precession-driven changes in insolation, major changes in thermohaline circulation and global climate change.

Proxy analysis of terrigenous material present in sediment cores from central Chile (at 27°S and 33°S) (Lamy *et al.* 1998*a*, 1999, 2000) suggest strong precession-driven cyclic recurrences of more humid climates in both the High Andes, through increased snowfall, and in the Coastal Cordillera, with increased local rainfall during austral summer insolation maxima due to northward latitudinal shifts of the Southern Westerlies by *c.* 5°, coupled with increased influence of subpolar air masses. The intensified runoff in most of these records has been linked to an increase in fluvial input of continental iron together with heightened biological productivity (Dezileau *et al.* 2004).

During the Last Glacial Maximum (LGM: 23–19 ka BP), sedimentary records at 33°S and 41°S suggest sea surface temperatures (SSTs) of about 12°C and 9°C lower, respectively, than those during the Holocene (Kim *et al.* 2002; Lamy *et al.* 2002, 2004). This has been associated with a northward displacement of the position of the ACC and the Southern Westerlies, generating a considerably wetter climate in central Chile (Heusser 1990*b*; Lamy *et al.* 1999, 2000) as well as inducing high primary production rates off central Chile at 33°S (Hebbeln *et al.* 2002; Mohtadi & Hebbeln 2004) (also see below). According to these records, Termination 1 has been dated to 18.5 ka BP at 33°S and to 19.2 ka BP at 41°S, with a warm pulse, most evident at 33°S, occurring at *c.* 15 ka BP. These warming events culminated in maximum SSTs of 19°C at 13 ka BP and 15°C at 12.1 ka BP (41°S), respectively (Kim *et al.* 2002; Lamy *et al.* 2004).

The similar timing and direction present between the record of SSTs at this last site with the oxygen isotope (δ¹⁸O) record of the Byrd ice core in Antarctica (Blunier & Brook 2001), have led Lamy *et al.* (2004) to propose an Antarctic influence on the onset of the deglaciation and the maximum extension of glaciers in the Patagonian Ice Sheet (PIS), which occurred at 18–17.7 ka BP (Denton *et al.* 1999), some 1000 years after the increase of the SSTs at 41°S. A close dependence between ice sheet extent along the western slope of the Andes and offshore

SSTs during regional ice maxima has been suggested through model results by Hulton *et al.* (2002). The apparent inertia, however, of the PIS to ocean–climate forcing, which could have exerted a variable influence on continental environments, might explain the differences in timing between terrestrial records of the glacial and deglacial periods (Lowell *et al.* 1995; Denton *et al.* 1999; Moreno *et al.* 2001). According to Lamy *et al.* (1998a, 1999, 2000) increasing SSTs during deglaciation reflect a southward migration of the ACC and the Southern Westerlies, inducing overall more arid conditions at the Pleistocene–Holocene transition in central-southern Chile (Heusser 1990b; Villagrán & Varela 1990; Veit 1996; Lamy *et al.* 1998a, 1999, 2000). To date, marine records along coastal Chile have provided very little evidence for a Younger Dryas type event: only a weak signal is seen in the planktonic foraminifera record at 33°S (Marchant *et al.* 1999) which is absent in the alkenone-based SST reconstruction obtained from the same core (Kim *et al.* 2002).

The Holocene is characterized by lower primary production and increased climate variability from tropical sources such as El Niño events (Lamy *et al.* 1999, 2001, 2002; Marchant *et al.* 1999; Hebbeln *et al.* 2002; Mohtadi & Hebbeln 2004). A strong cooling event characterized by SSTs *c.* 1°C lower than present at 33°S, occurred at *c.* 11 ka BP, a time of reduced summer insolation and seasonality, followed by SST values similar to or slightly warmer than present (*c.* 17°C) until *c.* 8 ka BP (Kim *et al.* 2002). This may have supported more intense coastal fogs and wetter conditions in restricted water catchments along the semi-arid coast of Chile (e.g. Maldonado & Villagrán 2002). Afterwards, a strong warm pulse occurred between 8 and 7.5 ka BP, reaching a mid-Holocene maximum SST of about 19°C at *c.* 6 ka BP (Kim *et al.* 2002). This Holocene optimum closely matches the highest SST values of about 17°C at *c.* 5.5 ka BP recorded south at 41°S (Lamy *et al.* 2002). Although temperatures decreased gradually, high SSTs persisted during the mid-Holocene in both regions, probably associated with a southward shift of the ACC and the Southern Westerlies and strengthened SE Pacific Subtropical Anticyclone (SPA) (Kim *et al.* 2002; Lamy *et al.* 2002), roughly contemporaneously with warm phases and landward recession of ice sheets at coastal sites around Antarctica (Finocchiaro *et al.* 2005; Steig *et al.* 1998), and strong aridity in central Chile (Heusser 1990b; Villagrán & Varela 1990; Lamy *et al.* 1998a, 1999; Jenny *et al.* 2002b; Villa-Martínez *et al.* 2003). Increasing palaeo-productivity and oceanographic variability during the late Holocene reported in sediment cores from central and southern Chile (Marchant *et al.* 1999; Lamy *et al.* 2001, 2002), occurs concomitantly with trends towards decreasing SSTs, particularly during the last four millennia at 33°S and 41°S (Kim *et al.* 2002; Lamy *et al.* 2002). This decreasing temperature trend is also coeval with more humid climate conditions in central Chile and with decreasing air temperatures, increased sea-ice formation and ice-rafted debris around Antarctica (Steig *et al.* 1998; Domack *et al.* 2001). One probable cause is the influence exerted by increased El Niño–Southern Oscillation (ENSO) activity beginning at *c.* 5 ka BP (Rodbell *et al.* 1999). This caused poleward advection of warm subtropical water along the Chilean margin (Marchant *et al.* 1999), increased soil formation, runoff and clastic sedimentation in central-northern Chile (Veit 1996; Lamy *et al.* 1999; Jenny *et al.* 2002a; Villa-Martínez *et al.* 2003), more frequent debris flow events due to heavy rainfall episodes along the coastal Atacama Desert in northern Chile and southern Peru (Vargas *et al.* 2000), as well as possibly controlling the extent of Antarctic sea-ice (Clement *et al.* 1999). Recent work on drilling sites off coastal northern and southern Chile suggests significant ocean–climate variations during the last few centuries, as demonstrated by increased primary production and interdecadal variability in the coastal upwelling system off northern Chile (Vargas *et al.* 2004) and in the Chilean fiords (Rebolledo *et al.* 2005; Sepúlveda *et al.* 2005).

A major unsolved problem for these records remains in the changes associated with the Regional Radiocarbon Reservoir Effect (ΔR), especially during the last deglaciation and the Holocene, when intense global changes in the ventilation rates of seawater masses have been documented (Southon *et al.* 1990; Bard *et al.* 1994; Stuiver *et al.* 1998; Van Beek *et al.* 2002). This implies that significant, previously unconsidered, time lags may be present in chronologies of past ocean–climate change. This may also account for the apparent disagreement between ocean cores and continental records of climate change, in particular those from northern Patagonia (see below). For the Peru–Chile current system, recent work indicates that the equatorward advection of anomalously ^{14}C -depleted water masses from the Southern Ocean during the early Holocene, combined with intensified coastal upwelling during this time, were probably responsible for higher ΔR values of up to around 1000 years, with a mean $\Delta R = 496 \pm 304$ years in northern Chile and southern Peru (Fontugne *et al.* 2004). In comparison, mid-Holocene values characterized by a mean $\Delta R = 175 \pm 101$ are of considerably less impact. This implies that the chronostratigraphy of some sedimentary records from both central-northern and southern Chile should be revised, at least for these specific time periods at millennial and submillennial timescales.

Hyperarid northern Chile (Norte Grande) (18–27°S) (C.L.)

Northern Chile is well known throughout the world as home to the Atacama Desert, the driest and perhaps the oldest of the major subtropical deserts found in the southern hemisphere (Dunai *et al.* 2005; Hartley *et al.* 2005). Cosmogenic ^{21}Ne exposure dates on surfaces in Quebrada Tiliviche near Pisagua (19°35'S) indicate onset of extreme hyperaridity as early as 25–22 Ma (Dunai *et al.* 2005). The Atacama extends along the Pacific Andean slope from the southern border of Peru (18°S) to Copiapó, Chile (27°S) (Fig. 12.1). The region's hyperaridity owes its existence to a combination of: (1) the extreme rainshadow effect of the High Andes, blocking advection of tropical/subtropical moisture from the east; (2) limited influence of winter storm tracks from the south owing to the presence of the semi-permanent South Pacific Anticyclone (SPA); and (3) the generation of a temperature inversion at *c.* 1000 m by the cold, north-flowing Humboldt Current that constrains inland (upslope) penetration of Pacific moisture. The SPA has been anchored against the westward bend in the South American continent probably throughout the Neogene. Uplift of the central Andes to their current elevation may have occurred as early as 15 Ma (Vandervoort *et al.* 1995; Alpers & Brimhall 1988), although palaeobotanical evidence suggests that the central Andes were only at half their modern elevation at 10 Ma (Gregory-Wodzicki 2000). Recent palaeothermometry work using stable C and O isotopes from soil carbonates along the Bolivian orocline provides evidence for abrupt uplift (> 3 km) of the Altiplano between 10.3 and 6.7 Ma (Ghosh *et al.* 2006). The Humboldt Current is thought to have been active since early Tertiary times (Keller *et al.* 1997), but may have reached its present intensity as a result of the major expansion of the Antarctic ice sheet between 15 and 12.5 Ma (Flower & Kennett 1993), or after the Central American Seaway closed between 3.5 and 3.0 Ma (Ibaraki 1997).

In both summer and winter, precipitation variability is primarily modulated by Pacific SST gradients and associated upper air circulation anomalies with seasonal and annual precipitation totals determined by the number of precipitation days (Vuille *et al.* 2000; Garreaud & Aceituno 2001; Garreaud *et al.* 2003). These anomalies can promote greater spillover of summer moisture (either from the Amazon to the NE or the Gran Chaco to the SE), or conversely, greater penetration of winter storm tracks from the SW.

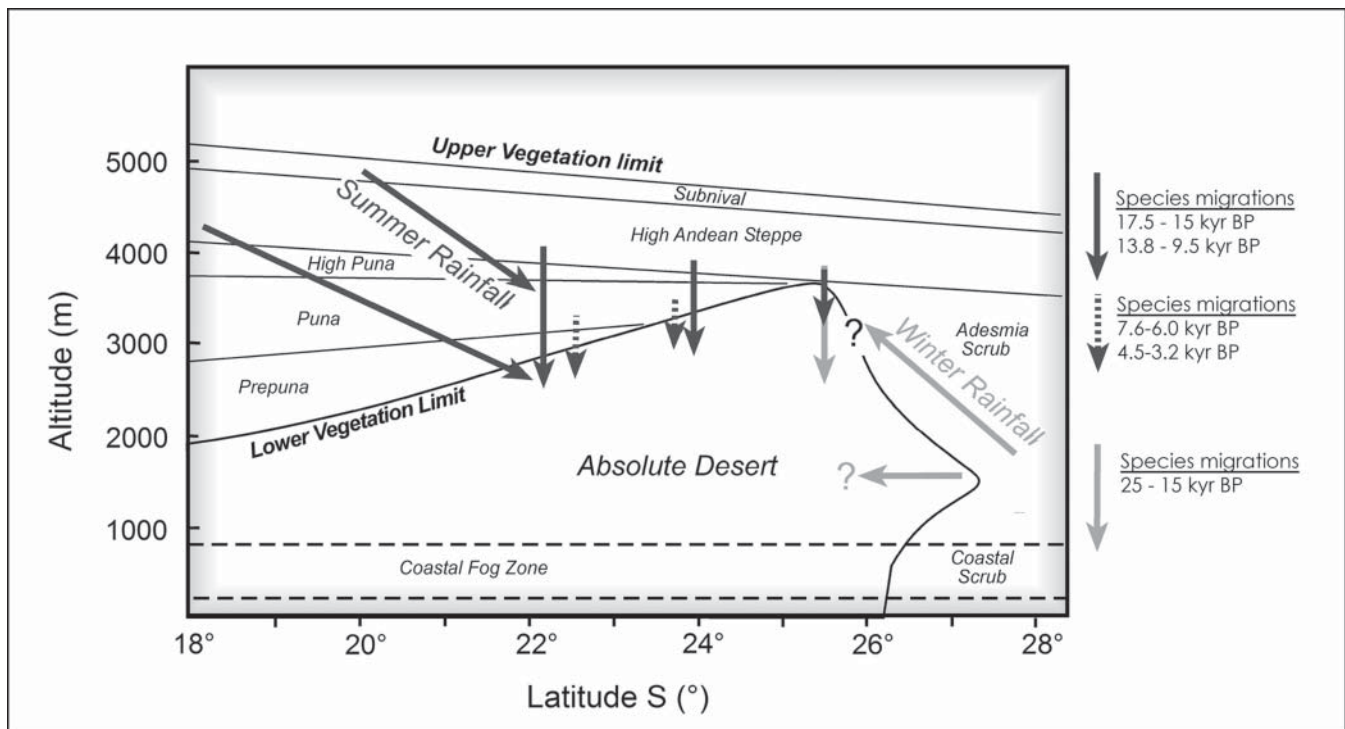


Fig. 12.3. Modern distribution of vegetation belts in northern Chile (after Villagrán *et al.* 1983). Grey arrows indicate plant species migrations during the late Quaternary (different shades are correlated with time of migration).

At millennial to glacial–interglacial scales the role of the tropics in global change is still poorly understood. Is regional insolation a major forcing factor of the Bolivian High, or is the intensity of South American summer rainfall forced instead by changes in equatorial Pacific SST gradients with both tropical and extratropical teleconnections?

Late Quaternary millennial-scale changes in the frequency and seasonality of the scant rainfall are associated with shifts in plant and animal distributions with elevation in the Atacama (Fig. 12.3). Today, plant diversity and distribution follow a gradient of mean annual precipitation, which in the central Atacama (22–24°S) increases from almost 0 mm/year at *c.* 2400 m to 200 mm/year at 4000 m. Along the Andean slope, a sparse vegetation zone known as Prepuna appears at 2900 m and gradually transitions into the Puna Belt (locally known as Tolar) between 3100 and 3900 m. This highly diverse vegetation belt is dominated by shrubs of the Asteraceae and Solanaceae families. The High Andean steppe is found above 3900 m, dominated by tussock grasses such as *Stipa*, *Nassella* and *Festuca*.

A large, ever-growing body of evidence has been obtained through vegetation changes analysed in rodent middens: bioaccumulations of plant and animal material made by rock-dwelling rodents (Betancourt *et al.* 1990; Betancourt & Saavedra 2002). Throughout the late Quaternary, midden (Betancourt *et al.* 2000; Latorre *et al.* 2002, 2003) and palaeo-wetland (Rech *et al.* 2002, 2003a) records from the central Atacama are in close agreement, in particular for a major wet phase between >15 and 9 ka BP. New evidence from midden research at Río Salado in the Calama Basin (Latorre *et al.* 2006) has revealed that this wet phase may have begun as early as 17.4 ka BP, coinciding closely with the onset of deglaciation at higher latitudes (Lowell *et al.* 1995; Moreno 1997), lake transgression at Salar de Uyuni (Sylvestre *et al.* 1998; Placzek *et al.* 2006) and post-LGM globally warmer temperatures. Palaeo-lake Tauca collapsed at 14.1 ka BP, slightly reviving afterwards between 13 and 11 ka BP during the minor Coipasa phase

(Placzek *et al.* 2006). This millennial-scale drought possibly occurred throughout the central Andes and is clearly evident in the Calama basin of northern Chile (Latorre *et al.* 2006).

A lesser wet phase during the mid-Holocene identified from preliminary evidence from rodent middens and palaeo-wetland stratigraphy in the central Atacama, was initially dated to between 7 and 3 ka BP (Betancourt *et al.* 2000). Recent work has replicated plant species migrations from upper into lower vegetation belts between 7.6–6.0 ka BP and 4.5–3.2 ka BP, with onset of drought at *c.* 5 ka BP (Latorre *et al.* 2003) (Fig. 12.3). Major regressive phases in high Andean lake records, however, as well as the timing of human occupation of the Salar de Atacama area ('silencio arqueológico' = archaeological silence: Núñez *et al.* 2002) have been interpreted in terms of extreme aridity (see below). Among the explanations proposed for this discrepancy are different sensitivities of the proxies used (e.g. Grosjean *et al.* 2003), hardwater contamination of ¹⁴C dates (Geyh *et al.* 1999) and regional impacts and interpretations (e.g. Grosjean 2001 versus Quade *et al.* 2001). As discussed in the last paragraph of this section, climate variability in the Atacama and the central Andes may be considerably more complex than previously thought.

The elaboration of preliminary new records from the southern Atacama at Quebrada del Chaco (25°30'S) constitute a step towards reconciling different palaeoclimate interpretations (Latorre *et al.* 2005; Maldonado *et al.* 2005). The majority of wetland deposits in Quebrada Chaco and tributaries, as well as midden records from upper elevations (>3450 m) dating between 15.4 and 10.2 ka BP are in good agreement with a late Glacial/early Holocene wet phase indicated in the central Atacama records. Early onset of aggradation beginning at *c.* 20.8 ka BP, however, agrees with low elevation midden evidence (<3000 m) for an earlier pluvial between 23.8 and 18.1 ka BP. One source for this earlier pluvial could be the enhancement or northward migration of westerly storm tracks during the LGM (23–19 ka BP).

In contrast to the central Atacama, absence of wetland deposits along with impoverished midden floras implies widespread aridity during the Holocene, with a slight increase in moisture over the last 1500 years (Maldonado *et al.* 2005). This pattern is clearly different from that visible in midden and wetland records further north, and implies that mid-Holocene increases in summer precipitation were of insufficient magnitude to have reached Quebrada Chaco at 25°30'S latitude. Further work in the southern Atacama is needed to place both a maximum northward limit to the westerly excursion during the LGM as well as to establish the southern limit of increased summer moisture during the late glacial and middle Holocene.

A diverse array of records of continental climate change for the central Andes is now available (see special issues of *Palaeogeography*, *Palaeoclimatology*, *Palaeoecology*, **194**, 2003 and *Journal of Quaternary Science*, **20**(7–8), 2005). Notable among these are lake and salt cores from Lake Titicaca and Salar de Uyuni (Baker *et al.* 2001a, b; Fornari *et al.* 2001), chronostratigraphic work on shoreline deposits throughout the Altiplano (Clapperton *et al.* 1997; Clayton & Clapperton 1997; Sylvestre *et al.* 1999; Placzek *et al.* 2006), ice cores from Nevado Sajama (Thompson *et al.* 1998) and Illimani (Ramirez *et al.* 2003), salt cores from Salar de Atacama (Bobst *et al.* 2001; Lowenstein *et al.* 2003), and Hombre Muerto (Godfrey *et al.* 2003) and a lake core from Laguna Miscanti (Grosjean *et al.* 2001). Discrepancies in palaeoclimate interpretation are still apparent, such as the slightly wetter mid-Holocene, an event that is completely absent from the High Andean lake records (all of which indicate intense drought). Although part of the discrepancy arises owing to the different sensitivities of the parameters involved as reconstructed from such diverse palaeoclimate methods, substantial geographic variation in the sources and mechanisms of precipitation over the central Andes can help understand part of the problem. Summertime precipitation variability in the central Andes was largely determined by the upper-air zonal wind component aloft, with an easterly (westerly) flow favouring wet (dry) conditions. The influence of these upper-air circulation anomalies on precipitation becomes more dominant when longer moisture transport distances are involved and hence is more prominent along the western slope of the Altiplano (Vuille *et al.* 2000). Different source areas also underlie summer rainfall patterns in the central Andes. Whereas the eastern Cordillera and northern Altiplano receive most of their moisture from the Amazon Basin, the Gran Chaco becomes more prevalent for the southern Altiplano and adjacent Cordillera (Vuille & Keimig 2004). Consequently, past rainfall changes in this region could very well display both a temporal and spatial component depending on latitude and altitude (e.g. Maldonado *et al.* 2005).

The semi-arid Norte Chico (27–32°S) (A.M.)

The Norte Chico lies along a transition between the hyperarid Atacama Desert to the north and the distinct mediterranean climate of central Chile to the south. The predominant blocking influence of the south Pacific Subtropical High is much stronger here than further south, causing occasional winter droughts that become more frequent with decreasing latitude (Van Husen 1967). Conversely, infrequent but heavy winter rainfalls associated with major El Niño events correlate with major animal population outbreaks and cycles of the flora and fauna (e.g. Lima *et al.* 1999; Gutierrez *et al.* 2000; Jaksic 2001; Gutierrez & Meserve 2003).

High resolution palaeoclimate archives from the Norte Chico are few, most not reaching even as far back as 6000 yr BP. Records of Pleistocene biotic and climate change are even less frequent. Despite this shortcoming, all published records (see Fig. 12.1 for locations) show an alternation of wet and dry periods, despite some disagreement regarding the exact timing

and duration of these phases. To date, four palaeoclimate records have been obtained from local swamp forests along the coast at c. 32°S (Villagrán & Varela 1990; Maldonado & Villagrán 2002, 2006), and three palaeopedological and limnogeological records from the Andean Cordillera (Grosjean *et al.* 1997, 1998; Earle *et al.* 2003). One study also establishes comparisons between palaeoclimates inferred from coastal and mountain palaeosols at the regional scale (27–33°S) (Veit 1996).

Pollen records from swamp forests at Quereo and Palo Colorado indicate a climate wetter than today during the early Holocene. These forests persisted at Palo Colorado (32°05'S) between c. 10 000 and 8700 yr BP (Maldonado & Villagrán 2006). The pollen record at Quereo, on the other hand, indicates that swamp forests dried out some time after 9370 yr BP (Villagrán & Varela 1990). Wetter conditions between 10 000 and 8300 yr BP have also been interpreted from palaeosols (Veit 1996).

Climate shifted towards extreme arid conditions after 9000 yr BP. The swamp forest at Palo Colorado disappeared and only matorral and herbaceous species persisted between 8700 and 7800 yr BP. Pollen-starved inorganic sediments suggest that these multimillennial-scale arid conditions persisted until 6000 yr BP. This also agrees with pollen evidence for a dry phase at Quereo (Villagrán & Varela 1990) and palaeosol evidence for temperatures that may have been up to 3°C higher between 8100 and 5700 yr BP (Veit 1996).

A gradual, stepwise rather than abrupt shift characterized the return of more mesic conditions starting at 4200 yr BP. Onset of sedimentation begins at 6200 yr BP at the sites Nague I and III (31°50'S), with absence of the swamp forests and predominance of herbs and matorral shrubs until 4200 yr BP. Swamp forests began to colonize the sector at this time, associated with increased moisture (Maldonado & Villagrán 2002). Wetter conditions began at 5300 yr BP at Palo Colorado, as indicated by the appearance of Myrtaceae pollen, which gradually increased until 4200 yr BP. Palaeolimnological evidence for increased moisture during this interval also comes from Laguna del Negro Francisco in the High Andes near Copiapó (27°S), where a saline lake that had existed since 6800 yr BP, shifted into a freshwater lake at c. 4200 yr BP (Grosjean *et al.* 1997).

High elevation records indicate an intensification of wetter conditions after 3200 yr BP when lake levels rose again at Laguna del Negro Francisco and glaciers advanced in the Valeriana and Encierro valleys at 29°S (Grosjean *et al.* 1998). A similar trend was seen on the coast where arboreal species began replacing herbaceous ones, although interrupted by several short drought episodes documented both at Nague (<2500 yr BP) and Palo Colorado (3000–2200 yr BP). An arid phase occurs slightly later in the High Andes, dated between 1700 and 1100 yr BP at Río La Gallina (Earle *et al.* 2003) and <1800 yr BP at Laguna del Negro Francisco. Wetter conditions during the late Holocene are also implied by palaeosol evidence across the region. Intense westerly activity may have reached as far north as Quebrada del Chaco at 25°30'S (see previous section) where pollen preserved in rodent middens indicates the altitudinal descent of hillslope species into the absolute desert at 1500 yr BP. Finally, the high variability seen in Myrtaceae pollen percentages at Palo Colorado together with relatively high percentages of annuals and geophytes between 2200 and 1300 yr BP (Maldonado & Villagrán 2006) may be related to increased frequency in ENSO events during the late Holocene, as reported by many other researchers for western South America (Rodbell *et al.* 1999; Moy *et al.* 2002; Riedinger *et al.* 2002; Jenny *et al.* 2003).

Central Chile (32–35°S) (R.V.M.)

As with the Norte Chico, Central Chile (32–35°S) occupies a transitional position between two major features that

characterize the western coast of southern South America, in this case the South Pacific Anticyclone (SPA) and the westerly wind belt. The variable climatic regime of this region is related to changes in the strength and position of the SPA. During the austral summer, this high pressure centre occupies a broad latitudinal range off South America that blocks the westerly flow of humid air masses moving across the Pacific Ocean, leaving central Chile completely dry. During the austral winter, however, the anticyclone weakens and moves equatorward, thereby allowing cyclonic storms and related frontal systems to progress towards central Chile.

A major component of the interannual variability in precipitation in central Chile is linked to ENSO (Aceituno 1988, 1990; Rutland & Fuenzalida 1991; Aceituno *et al.* 1993). During El Niño years, weakening of the anticyclone and decreased upwelling of cool ocean waters along the west coast of South America are factors that lead to large increases in total rainfall across the entire mediterranean-climate region of Chile. During pronounced La Niña episodes when the SPA is stronger, rainfall decreases well below the average, particularly in the northern part of the mediterranean region. These strong episodes can extend even to the wetter southern limit of the region, causing droughts during summer (Holmgren *et al.* 2001).

Despite such a key geographical position for understanding subtropical palaeoclimate changes, including the onset and subsequent evolution of ENSO, only a handful of palaeo-environmental records are known for central Chile. For example, the only locality that has produced a pollen record that encompasses glacial times is from Laguna Tagua Tagua (34°30'S), a lake drained artificially in historic times, which spans the last 54 000 years (Heusser 1983, 1990b; Valero-Garcés *et al.* 2005). The broad-leaved sclerophyllous woodland vegetation that surrounds the site today was dominated by the southern beech *Nothofagus* and *Prumnopitys* conifers, indicating a colder and considerably wetter climate during the late Pleistocene. These wet and cold phases occurred between 50 000 and 40 100 yr BP, and 32 600 and 13 260 yr BP. Arid phases, dominated by grasses (Poaceae) and halophytes (Chenopodiaceae), occurred between 54 000 and 50 000 ¹⁴C yr BP and between 40 150 and 32 950 yr BP. The climate became drier after 17 500 yr BP, as indicated by the decline of arboreal taxa and concomitant increase in grasses and halophytes (Heusser 1990b).

New sedimentological, geochemical and palynological data from the Laguna de Tagua Tagua, published recently by Valero-Garcés *et al.* (2005) are used to infer much higher precipitation between 40 100 and 21 000 yr BP, followed by a general increase in aridity that was interrupted by two humid spells (19 500–17 000 and 13 500–11 500 yr BP). This new record clearly demonstrates that the early to mid-Holocene was probably the driest period for the last 46 000 years in central Chile.

The few Holocene palaeoclimate records that exist document several major climate fluctuations, again in the form of alternating wet and dry phases, with a prevalence of warm, arid conditions during the early and middle Holocene. These studies include pollen records (Heusser 1983, 1990b; Villagrán & Varela 1990; Villa-Martínez & Villagrán 1997) and palaeosols (Veit 1996). The poorly constrained chronology and temporal resolution in most of these records, however, impedes further precision regarding our understanding of the timing and structure of these phases.

A more complete dataset of Holocene climate is now available from Laguna Aculeo (c. 34°S), a high-resolution multiproxy record from one of the few natural inland lakes present in the region (Jenny *et al.* 2002a, 2003; Villa-Martínez *et al.* 2003, 2004). The basal portion of this record is characterized by the absence of palynomorphs and presence of gravels, sands and saline silts in sediments older than 7500 yr BP, all of which suggest an ephemeral water body under very arid and warm

conditions. Palynomorphs appear at 7500 yr BP with elevated counts of halophytes between 7500 and 5700 yr BP, indicative of much warmer and arid conditions than at present.

An initially shallow freshwater lake appeared between 5700 and 3200 yr BP, associated with an increase in arboreal and herbaceous diversity. A marked rise of the lake level to near modern levels began at 3200 yr BP, along with the virtual disappearance of halophytes (which have reappeared in the last 100 years). Within this humid period, large-amplitude fluctuations in pollen influx occur coevally with numerous turbidite layers, suggesting a highly episodic and torrential rainfall. A similar pattern is also seen in the Matanzas pollen record over the last 3000 years on the coast of central Chile (c. 34°S) (Villa-Martínez 2002). This intense and episodic rainfall is probably associated with large-amplitude fluctuations of ENSO. Jenny *et al.* (2003), using a lake level curve from the Aculeo record coupled with a water balance model, have estimated precipitation changes for the Holocene in central Chile. From beginning of Holocene until 5700 yr BP, mean annual precipitation was on the order of 150–300 mm/year. Mean annual precipitation increased dramatically between 5700 and 3200 yr BP reaching 350–450 mm/year, and modern lake levels and the even higher mean annual precipitation of 450–550 mm/year became established only during the last 3000 years or so.

Vegetation diversity and change in central Chile (J.J.A.)

The climatic regime of central Chile differs in some important ways from other mediterranean ecosystems of the world because of the absence of summer rainfall and associated thunderstorm activity. This is a feature of great significance for understanding the disturbance regime that has historically affected Chilean mediterranean ecosystems. It also accounts for the negligible importance of spontaneous fire in the vegetation of central Chile. The rainshadow effect of the Andes, responsible for maintaining hyperarid conditions in the Atacama Desert, also isolates the mediterranean region from the easterly flow of warm moist air that brings summer rainfall and thunderstorms to the subtropical Andes. Lightning storms are generally confined to elevations above 3000 m in the Andes (Arroyo *et al.* 1981).

Mediterranean-type ecosystems occupy a narrow band along the western margin of South America, from 30°S to 36°S in central Chile. Because of their position in the transition zone between the southern Atacama Desert and the mixed deciduous-evergreen temperate forests which occur south of 36°S, they represent a highly heterogeneous vegetation mosaic. The major vegetation types are dry xerophytic thorn scrub dominated by deciduous shrubs and succulents, mesic communities dominated by evergreen sclerophyllous trees in the coastal and Andean foothills, and forests dominated by winter-deciduous trees in the south of the mediterranean area. Within the latitudinal range of the mediterranean climate, annual precipitation increases from less than 200 mm to more than 700 mm (Rundel 1981).

The mountainous topography of central Chile, contrasting radiation and moisture regimes, and strong rainshadow effects coupled with a mosaic of soil types and nutrient supplies, generate pronounced environmental gradients that have stimulated the evolutionary differentiation of the biota (Armesto & Martínez 1978; Rundel 1981; Rozzi *et al.* 1989). High floristic richness and a diversity of plant communities are a consequence of this environmental heterogeneity (Arroyo *et al.* 1993, 1995). In addition, strong climatic variability during the Quaternary (Villagrán 1995a; Holmgren *et al.* 2001) probably promoted increased genetic variability among local populations. The mediterranean region is also a depository of ancient tropical lineages that found refuge in coastal valleys from the sustained drying trend initiated by Andean tectonics during the late

Neogene (Troncoso *et al.* 1980; Villagrán & Armesto 1980; Arroyo *et al.* 1995; Hinojosa & Villagrán 2005). Plant migrations associated with climatic fluctuations during the Quaternary (Heusser 1983; Villagrán 1995a) contributed greatly to increase species richness and the heterogeneity of the vegetation mosaic in central Chile (Arroyo *et al.* 1995; Villagrán 1995a). Late Neogene Andean uplift has also provided new opportunities for colonization and differentiation of local alpine floras, increasing floristic richness and diversity even further.

In addition, the strong influence of insect and bird pollinators in the evolution of plant-reproductive strategies in mediterranean-type ecosystems (Arroyo & Uslar 1993; Arroyo *et al.* 1993, 1995), and the role of animals in the dispersal of seeds of sclerophyllous tree species (Hoffmann & Armesto 1995), are important conditions favouring genetic variability and speciation in biotic communities within the region. High levels of self-incompatibility are known for the woody species in montane sclerophyllous vegetation (Arroyo & Uslar 1993). The historical phytogeography of central Chile presented below follows the general floristic scheme proposed by Arroyo *et al.* (1995), although some names are different and additional vegetation types are included here (Armesto *et al.* 2007). We briefly discuss the more important vegetation types in terms of their relative floristic richness, endemism, distribution and natural history.

A widely distributed vegetation type in central Chile is the coastal forest dominated by the monotypic and endemic *Aextoxicon punctatum* ('olivillo'). These forests, described by Muñoz & Pisano (1947), Villagrán & Armesto (1980) and Pérez & Villagrán (1985), exhibit diverse species of climbers and epiphytes, including narrow endemics such as *Peperomia coquimbensis* (Piperaceae). Olivillo forests are generally immersed in a matrix of xerophytic vegetation, and reach as far north as La Serena (30°S) at Fray Jorge and Talinay (Troncoso *et al.* 1980), occurring as isolated relict forest fragments along the upper slopes of the Coastal Cordillera under the direct influence of maritime fogs which provide the main source of water and nutrients (Kummerow 1966; P. E. Vidiella & T. Dawson, pers. comm.). Patches of olivillo forest are found scattered across the coastal mountaintops from Fray Jorge south to central Chile, from where they are present more or less continuously southwards, especially on ocean-facing slopes and valleys.

The fragmented distribution of olivillo forests in Chile has intrigued biogeographers for many years (e.g. Muñoz & Pisano 1947; Skottsberg 1948; Schmithüsen 1956; Troncoso *et al.* 1980; Villagrán & Armesto 1980). Plant species found in the northernmost relicts (e.g. *Sarmienta repens* and *Mitraria coccinea*, Gesneriaceae, *Azara microphylla*, Celastraceae) also occur in Valdivian evergreen rainforests, 900 km to the south (Villagrán & Armesto 1980). Current interpretations of the phylogenetic relations, South American distribution, and fossil record of the main relict taxa, suggest that these floristic assemblages may be descendants of subtropical rainforests that occupied central Chile in the mid-Cenozoic, before the onset of events that shaped the mediterranean-type climate (Troncoso *et al.* 1980; Villagrán 1990; Villagrán & Hinojosa 1997).

The northernmost disjunct populations of *Nothofagus* in South America are found above 1000 m on the highest peaks of the Coastal Cordillera: El Roble, La Campana and Altos de Cantillana (Casassa 1985). The present-day continuous distribution of *Nothofagus obliqua* begins along the southern margin of the mediterranean region at 37°S, where several species of *Nothofagus* occur in mixed stands with both sclerophyllous species from central Chile and evergreen broadleaved trees from the Valdivian temperate rainforest. Locally known as Maulino forests (San Martín & Donoso 1996), they are populated by the narrow endemics *Nothofagus glauca* and *N. alessandrii*. High local endemism may reflect the conservative character of Coastal Cordillera habitats, compared to those of the Central Valley and Andean slopes (Villagrán & Hinojosa 1997).

Evergreen sclerophyllous vegetation extends more or less continuously in central Chile from the Coastal Cordillera to the Andean foothills. It is the most common plant formation here, dominated by evergreen trees and shrubs such as *Cryptocarya alba* (Lauraceae), *Lithrea caustica* (Anacardiaceae), *Quillaja saponaria* (Quillajaceae), *Maytenus boaria* (Celastraceae), *Kageneckia oblonga* (Rosaceae) and *Peumus boldus* (Monimiaceae). Communities commonly exhibit a patchy spatial structure with open spaces between shrub clumps (Fuentes *et al.* 1986). Along permanent water courses and on steep south-facing slopes, however, and especially in the Coastal Cordillera, these develop into a continuous 8–12-m-tall canopy and possess several tree species, such as *Beilschmiedia miersii* (Monimiaceae), *Drimys winteri* (Winteraceae), *Luma chequen* (Myrtaceae), *Citronella mucronata* (Icacinaeae) and *Persea lingue* (Lauraceae), restricted to such humid habitats (Armesto & Martínez 1978; Rundel 1981; Arroyo *et al.* 1995). On the ocean-facing slopes of the Coastal Cordillera sclerophyllous trees such as *Cryptocarya alba* often grow together with *Aextoxicon punctatum* (see above), often covered by profuse growth of climbers, such as *Proustia pyrifolia* (Asteraceae), *Bomarea salsilla* (Amaryllidaceae) and *Lardizabala biternata*, (Lardizabalaceae). On dry north-facing slopes, or on frequently disturbed sites (Armesto & Martínez 1978), the sclerophyllous matorral is often replaced by a xerophytic thorn scrub, with a combination of deciduous shrubs, such as *Trevoa trinervis* (Rhamnaceae), *Flourensia thurifera* (Asteraceae) and *Colliguaja odorifera* (Euphorbiaceae), and often includes succulent species such as bromeliads and columnar cacti, especially on steep rocky slopes.

The regional extent of dry xerophytic vegetation versus mesic sclerophyllous tree communities in central Chile seems to be held in a fragile balance. This balance is usually tipped by climatic cycles between cool, wet conditions and hot, dry episodes. These in turn may be linked to varying frequencies of ENSO during the Holocene (Villagrán 1995a; Maldonado & Villagrán 2006). Large-scale regeneration of sclerophyllous woodland is normally limited by drought stress and the lack of seed banks (Fuentes *et al.* 1986; Jiménez & Armesto 1992), except during unusually wet periods or along water courses. It is likely that the strong El Niño events (warm ENSO phases) in central Chile promote significant regeneration of sclerophyllous tree species, especially in dry or disturbed habitats. Owing to recurrent anthropogenic disturbance through fire and permanent grazing pressure, however, vegetation cover may be presently shifting regionally towards dominance by dry xerophytic species (Armesto & Martínez 1978), despite a regional trend towards increasing rainfall in the late Holocene (see previous section).

Xerophytic open woodlands, with the physiognomic aspect of a savanna (Fuentes *et al.* 1990), are currently widespread along the Central Valley in the mediterranean-climate region. These woodlands, dominated by leguminous trees, mainly *Acacia caven* and *Prosopis chilensis*, have a dense herb layer almost entirely made of introduced European annual herbs (e.g. *Erodium* spp.) and grasses, typically associated with grazing disturbance. Although some discussion has centred on the historical nature of this semi-arid formation (Arroyo *et al.* 1995), high percentages of introduced grasses found underneath *Acacia* trees, and the resprouting ability of persistent shrubs, suggests that this vegetation type has been shaped by human impact, especially through cattle grazing and fire.

Mixed sclerophyllous forest with abundant endemic palms *Jubaea chilensis* are a narrowly distributed and frequently overlooked component of the mosaic of vegetation types in coastal areas of central Chile. These evergreen forests are typical of very humid and mesic conditions found on slopes and deep canyons along the Coastal Cordillera (Arroyo *et al.* 1995). Only two small protected areas in central Chile contain significant palm populations at present, suggesting that mixed palm forests may have been more widespread, possibly in the recent past.

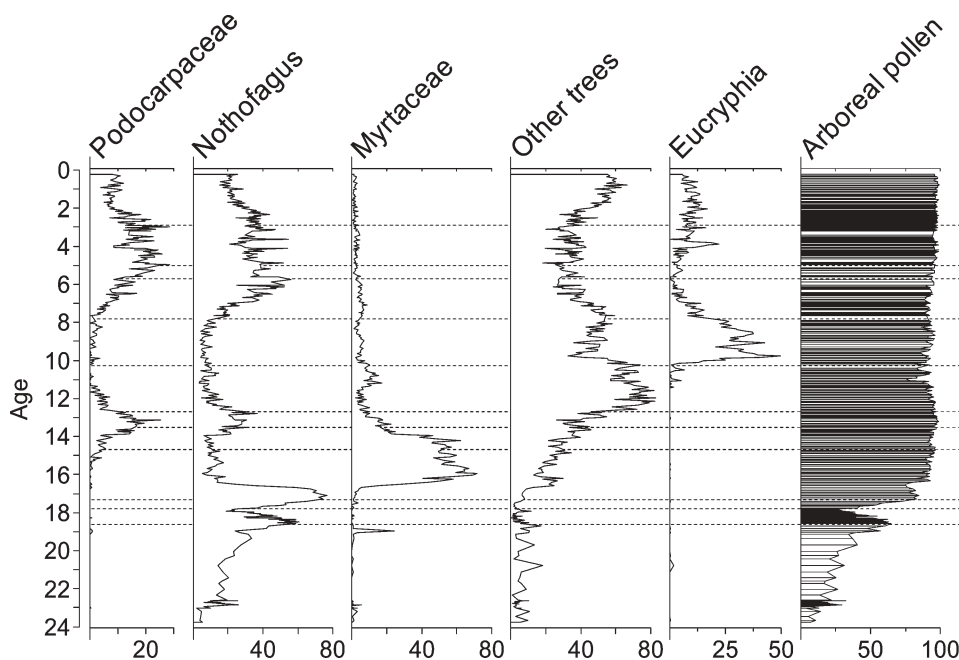


Fig. 12.4. Summary percentage diagram of key indicator taxa discussed in text, assembled from three overlapping pollen records obtained in the Chilean Lake District, northern Patagonia (ages in ka BP).

Finally, upland sclerophyllous woodland is found above 1500 m in the Andean mountains and differs both from the Andean foothill communities (Hoffmann & Hoffmann 1982; Arroyo *et al.* 1995) and from the upland *Nothofagus* communities of the Coastal Cordillera. This vegetation is dominated by *Kageneckia angustifolia* (Rosaceae), which constitutes a discontinuous treeline (Arroyo & Uslar 1993). Above the treeline, at 2300 m in central Chile, the montane woodland gives way to a low subalpine shrubland (Arroyo *et al.* 1981). Scattered patches of the long-lived mountain cypress *Austrocedrus chilensis* (Cupressaceae) may occur near the treeline at various locations between 32 and 36°S (Rundel 1981). The distribution of *Austrocedrus* is more continuous on the eastern side of the Andes south of 36°S. The presence in central Chile of these relict stands that possibly became established during wetter periods of the late Holocene, relying today on their sprouting ability to survive drought (C. Le-Quesne & J. C. Aravena, pers. comm.), further highlights the very sensitive nature of these vegetation formations to climatic variability over long timescales.

Northern Patagonia (39–41°S) (P.I.M.)

The study of interhemispheric climate linkages during and since the last ice age has benefited from the recent development of high-resolution ice core and marine records from the mid- and high latitudes of the southern hemisphere (Stenni *et al.* 2001; Lamy *et al.* 2004). Few palaeoclimate records from terrestrial environments in these regions, however, have the temporal continuity, time resolution and adequate chronologic control to allow a detailed examination of the timing, rates, direction and phasing of climate change at millennial timescales.

Northwest Patagonia is ideal for the study of interhemispheric linkages throughout the Quaternary because this region has insolation regimes out-of-phase with northern mid-latitudes, is highly sensitive to variations in the Southern Westerlies, and is far removed from the direct influence of northern hemisphere ice sheets and deep water circulation (Moreno 2002). Stratigraphic, palynologic and charcoal records from small, high-sediment accumulating lakes in the Chilean Lake

District (41°S) afford useful data for examining the interval from the LGM to the present.

A stacked palynological record (Fig. 12.4) from NW Patagonia that encompasses the last 24 000 years was developed to examine the timing, rates and direction of vegetation and climate change (Moreno *et al.* 1999; Moreno & León 2003; Moreno 2004a). The record shows extreme glacial climate ($\Delta T = -6.5^\circ\text{C}$, $\Delta Pp = c. 2000 \text{ mm/year}$) between 24 and 17.7 ka BP, followed by the abrupt expansion of north Patagonian rainforest taxa through successive warming events between 17.7 and 15.5 ka BP. Conditions approaching modern climate prevailed between 15.5 and 15 ka BP, followed by expansion of cold-resistant, hygrophilous north Patagonian rainforest trees at 15 and 13.5 ka BP, and subsequent warming pulses at 11.5 and 10.2 ka BP (Moreno *et al.* 2001; Hajdas *et al.* 2003). The earliest charcoal peaks, indicative of local fires between 15 and 14.5 ka BP, occurred despite the local dominance by temperate rainforests at the time under cool, temperate and wet conditions. Extreme warm, dry climate prevailed between 10.2 and 7.8 ka BP, as indicated by the predominance of the warmth-loving, drought-resistant Valdivian trees *Eucryphia cordifolia* and *Caldcluvia paniculata*, and lowered lake levels. Charcoal maxima and local vegetation disturbance are evident in several sites at different times between 13 and 8.5 ka BP. Cold-resistant north Patagonian rainforest trees underwent a step-like re-expansion between 7.5 and 5.5 ka BP, and reached peak abundance between 5 and 3 ka BP. *Eucryphia* and *Caldcluvia* re-expanded at 5 ka BP establishing a vegetation mosaic with podocarps and *Nothofagus* that persists until today. During the latter period, charcoal records indicate renewed fire activity with prominent increases at 5 and 3 ka BP. Modern vegetation and climatic conditions started at 2 ka BP, following a warm, dry phase between 3 and 2 ka BP.

Rainforest vegetation changed at ecological timescales (≤ 100 years) in response to climate forcing at millennial timescales since the last termination. Moreover, the timing and mean time spacing of events fall in the range of millennial-scale changes identified in the North Atlantic region (Bond *et al.* 1997, 1999; Bianchi & Mccave 1999). Submillennial-scale variability is also evident: El Niño years in NW Patagonia typically exhibit below-normal summer precipitation (Montecinos *et al.*

2000), hence the co-occurrence of thermophilous, drought-resistant Valdivian elements and cold-resistant, hygrophilous north Patagonian rainforest trees since *c.* 5 ka BP might represent a vegetation response to the onset of El Niño-like variability in the mid- to late Holocene.

The record from NW Patagonia indicates intense fire activity during the warm, dry early Holocene and in some cases during the final portion of the late glacial (Moreno 2004a). It is likely that the primary control on fire occurrence in this region lies in changes in the position and strength of the Southern Westerlies at multimillennial timescales, climate variability at subcentennial scales, as well as local (human?) ignition sources.

Biodiversity, glacial history and biogeography of the vegetation of Chiloé Archipelago (C.V.)

Biodiversity

The Chiloé Archipelago (41°47'–43°30'S; Fig. 12.5) possesses one of the most diverse and singular floras of Chile. Despite a lack of precise estimates for the total number of terrestrial plants in the Archipelago, it is probably over 1200 species, especially when the approximately 750 known species of vascular plants are considered (Ruthsatz & Villagrán 1991; Villagrán *et al.* 1986; Villagrán 2002) along with at least 360 known species of Bryophytes (Villagrán *et al.* 2003, 2005).

'Ulmo' (*Eucryphia cordifolia*) forests, one of the most important and diverse components of the Valdivian rainforest, reach their southern limits along the northern and central part of the Isla Grande (Schmithüsen 1956). North Patagonian rainforest communities are present along the Piuchué Cordillera, and along the southern portion of the Isla Grande and adjacent islets. These forests are dominated by 'canelo' (*Drimys winteri*), 'tepa' (*Laureliopsis philippiana*), myrtles such as 'luma' and 'petagüa' (*Amomyrtus luma* and *Myrceugenia ovata*) and by *Nothofagus nitida* and the conifers *Saxegothaea conspicua* and *Podocarpus nubigena* ('mañíos') at higher elevations. A more complex vegetational mosaic covers the broad summits of the Piuchué cordillera and low-elevation wetlands. This mosaic comprises small stands of Magellan 'coigue' (*Nothofagus betuloides*) and 'ñirre' (*Nothofagus antarctica*); magellanic moorlands (*Astelia pumila*, *Donatia fascicularis* and *Gaimardia australis*); 'alerce' (*Fitzroya cupressoides*); Guaitecas' cypress (*Pilgerodendron uviferum*); and 'tepú' (*Tepualia stipularis*). Many of these species, a true vanguard of the subantarctic floras, meet their northern limits here (Fig. 12.5).

Along the Pacific coast, diverse marsh, beach and intertidal rock communities are found adjacent to pristine forests of 'arrayan' (*Luma apiculata*) and 'olivillo' (*Aextoxicon punctatum*), one of the most unusual of Valdivian rainforest associations, with northern limits along the semi-arid coast of northern Chile (30°30'S) and southern limits at the Guapiquilán, Esmeralda and Guafo islets at the SW end of the main island. The olivillo forests of Chiloé house numerous species of vines, epiphytes and rare cryptogams that are endemic to Chilean forests, many of which have disappeared from most of their original ranges and today exhibit pronounced disjunct distributions in remote areas (Villagrán & Armesto 2003; Villagrán *et al.* 2003, 2004a, b, 2005).

Glacial history

Considering the dramatic extent of past glaciations during the Pleistocene, how did Chiloé come to have such levels of biodiversity? Glacial geological records from the last glaciation (Fig. 12.6) (Hollin & Schilling 1981; Denton *et al.* 1999), show that most of the southern and eastern portions of the main island, as well as continental Chiloé and the islets, were heavily covered by ice during the last ice age, the late Llanquihue Glaciation (LLG), dated between *c.* 37 000 and 17 500 yr BP,

with temperatures estimated to have been 6–8°C lower than today (C. J. Heusser *et al.* 1999). Periglacial processes such as solifluction, exerted considerable impact on the montane forests of the Piuchué Cordillera right down to the foothills (Veit & Garleff 1996). Figure 12.6 indicates the location of the pollen sites where these dramatic vegetation changes have been documented. Past changes in mean summer temperature during the LLG (Fig. 12.7) have been obtained from the pollen record at Taiquemó, the oldest such record in Chiloé (Heusser 1990a; Denton *et al.* 1999). Using this curve as reference, we can describe the following vegetation changes during the most extreme climate phases.

Interstadials during the early to middle LLG

Recent discoveries of *in situ* subfossil tree trunks of alerce (*Fitzroya cupressoides*) and Guaitecas' cypress (*Pilgerodendron uviferum*) in the Seno de Reloncaví and eastern margin of Chiloé Island (Fig. 12.6), dated between 45 470 and 51 050 yr BP, record the climate and glacial history of the north Patagonian rainforests as dominated by *Nothofagus* and conifers (Roig *et al.* 2001). Pollen analysed from three of these sites (Tenglo, Punta Pirquén and Molulco) evince dominance of arboreal taxa, mostly *Nothofagus dombeyi*-type and conifers such as *Fitzroya cupressoides*, *Pilgerodendron uviferum*, *Saxegothaea conspicua*, *Podocarpus nubigena* and *Lepidothamnium fonckii* (Villagrán *et al.* 1995, 2004b). This assemblage suggests relatively warm and wet interstadials during the early to middle LLG. Conifer forests expanded considerably across the central graben from their disjunct ranges in modern montane forests. Other pollen records with subfossil wood of similar age and similar assemblages, stratigraphy and chronology are Punta Tentén, Chiloé (Heusser *et al.* 1995), Punta Pelluco, Punta Penas and Canal Tenglo (Heusser 1981; L. E. Heusser *et al.* 1999).

Stadials of the late LLG

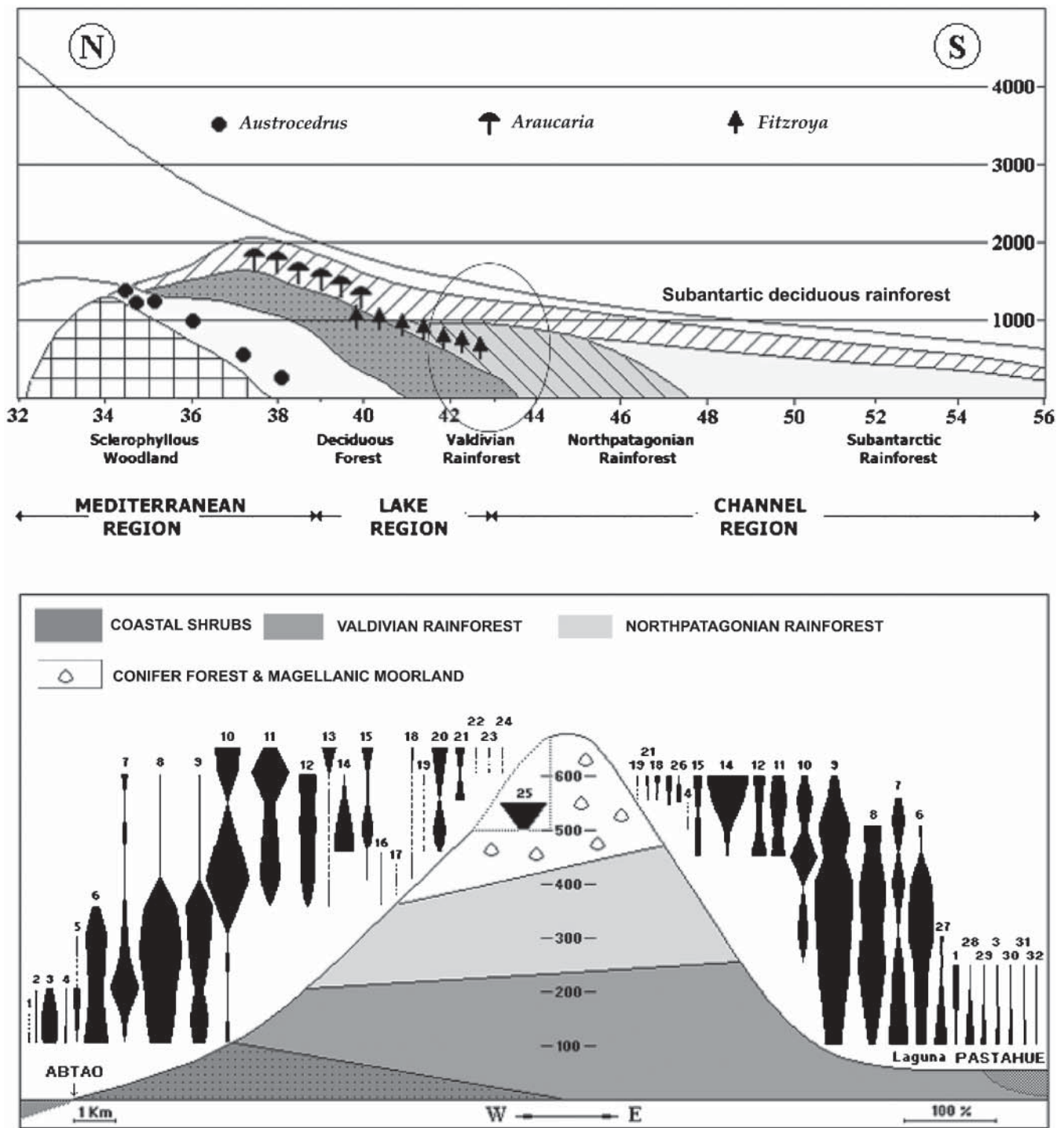
The dominant vegetation present during the stadials of the upper LLG, dated from *c.* 37 000 to 17 500 yr BP, has been described from three different pollen records taken from peatbogs in the NE part of Chiloé (Fig. 12.6): Taiquemó (Heusser 1990a), Loncomilla (Villagrán 1990) and Río Negro (Villagrán 1988a). Magellanic moorlands with grasses and composites alternated with small stands of *Nothofagus* and conifers. The middle to late LLG transition is documented by the discontinuous sections present at Pidpid, Tehuaco and Dalcahué, along the eastern-central coast of the island (Fig. 12.6), (Villagrán 1985; Heusser 1990a; C. J. Heusser *et al.* 1999).

Late glacial

After piedmont glacier collapse at *c.* 17 000 yr BP, quick colonization and rapid expansion of a closed-canopy north Patagonian rainforest with *Nothofagus*, conifers and Myrtaceae ensued at three pollen records along the central to southern sectors of the eastern coast of Chiloé: Lagunas Pastahué, Tahui and Melli (Villagrán 1985; Abarzúa *et al.* 2004). Vegetation also began colonizing previously glaciated areas in the southern part of the Isla Grande (Puerto Carmen, Laguna Soledad and Chaiguata (Villagrán 1988b). Forest colonization also commenced in the Channel District (Bennett *et al.* 2000), nearly synchronous with moorland ascent to the summits of the Piuchué cordillera and Andes (Villagrán 1991a), as evinced by pollen records from mainland Chiloé, Chaitén and Cuesta Moraga (Heusser *et al.* 1992).

The Holocene

A series of pollen records documents the transition from forests dominated by temperate-cold species to those dominated by more thermophilous species of the north Patagonian rainforest, such as 'tineo' (*Weinmannia trichosperma*) at the beginning of the Holocene (11 000 yr BP). This was followed by the



1. *Caldcluvia paniculata*, 2. *Rhaphithamnus spinosus*, 3. *Aextoxicon punctatum*, 4. *Weinmannia trichosperma*, 5. *Luma apiculata*, 6. *Myrceugenia ovata* var. *ovata*, 7. *M. planipes*, 8. *Laureliopsis philippiana*, 9. *Amomyrtus luma*, 10. *Drimys winteri*, 11. *Podocarpus nubigena*, 12. *Nothofagus dombeyi*, 13. *N. nitida*, 14. *Saxegothaea conspicua*, 15. *Tepualia stipularis*, 16. *Pseudopanax laetevirens*, 17. *Crinodendron hookerianum*, 18. *Myrceugenia chrysocarpa*, 19. *Embothrium coccineum*, 20. *Desfontainia spinosa*, 21. *Pilgerodendron uviferum*, 22. *Pernettya* sp., 23. *Escallonia alpina*, 24. *Nothofagus betuloides*, 25. *Fitzroya cupressoides*, 26. *Ovidia pillopillo*, 27. *Amomyrtus meli*, 28. *Gevuina avellana*, 29. *Eucryphia cordifolia*, 30. *Fuchsia magellanica*, 31. *Dasyphyllum diacanthoides*, 32. *Myrceugenia parviflora*.

Fig. 12.5. Upper panel: Altitudinal and latitudinal vegetation zones along the western slope of the Andes of south-central Chile (Schmithüsen 1956). Note merger between the Valdivian and north Patagonian rainforests at the latitude of Chiloé (41–44°S) as well as conifer distribution among both forests. Lower panel: Frequency distribution along a west-east altitudinal survey of native forest communities across the Piuchué Cordillera, NW Chiloé (Villagrán 1985).

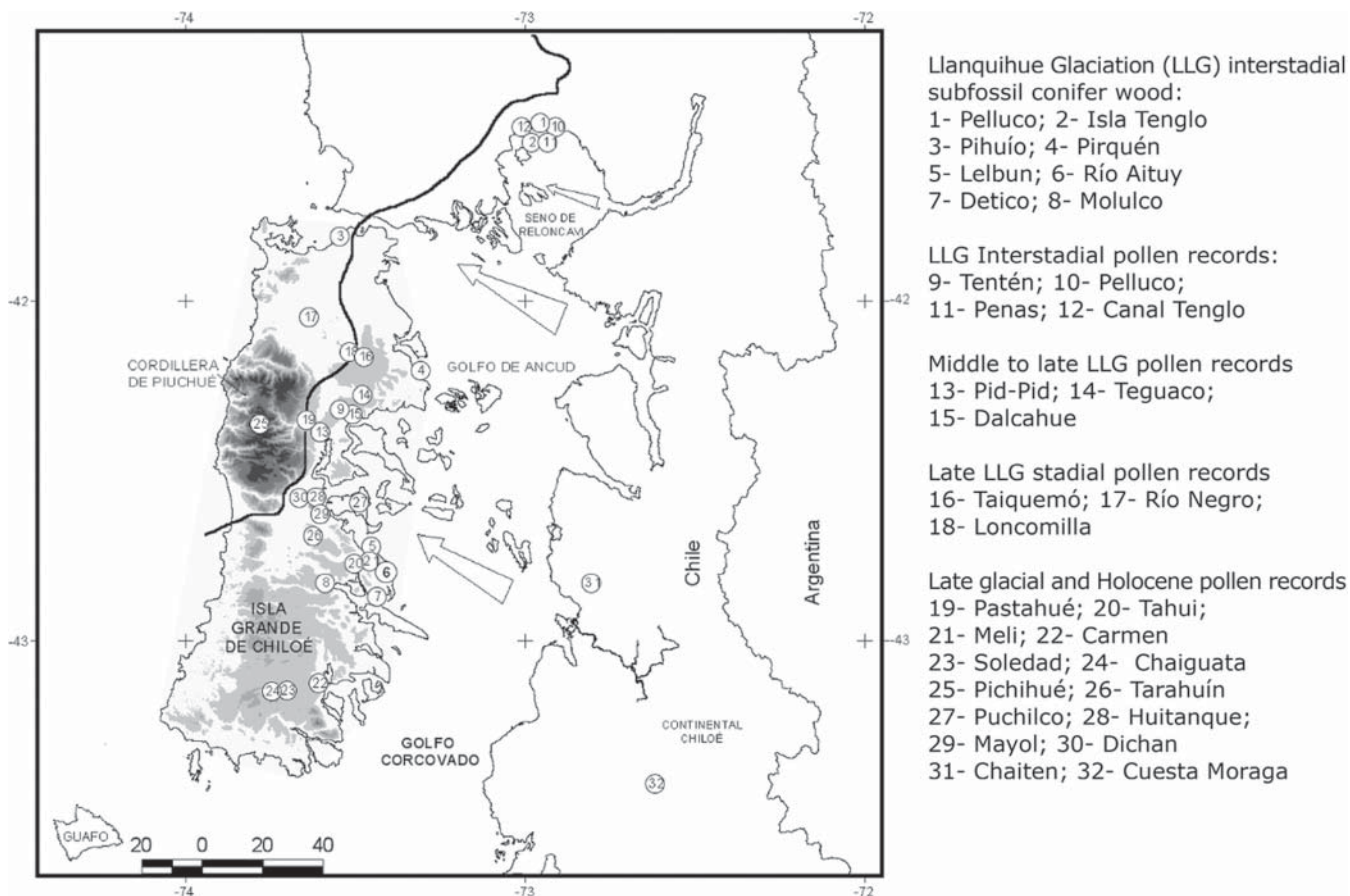


Fig. 12.6. Map of the Chiloé Archipelago indicating site locations discussed in text. Bold line indicates maximum ice extent during the LGM and main direction of flow (arrows) according to Heusser (1990a) and Denton *et al.* (1999).

widespread expansion of 'ulmo' (*Eucryphia cordifolia*) from *c.* 9200 to 6550 yr BP, dominating the vegetation along the SE sector of Isla Grande at Tahui, Melli and Puerto Carmen (Fig. 12.6). This event represents the largest southward expansion of the Valdivian rainforest over the last glacial cycle (Villagrán 1988b; Abarzúa *et al.* 2004).

Biogeographic consequences

An historical model based on the vegetation dynamics observed in the pollen records has been proposed by Villagrán (2001) (Fig. 12.8). This model hypothesizes that modern disjunct distributions of the conifer species in Chiloé, today found only in the coastal mountains and Andes (Villagrán *et al.* 1998; Villagrán & Armesto 2003), are the end result of forest recolonization of mountain habitats during deglaciations. The ranges occupied by these species would thus have been much more widespread and continuous during interstadials of the early to middle LLG along the low-lying intermediate valley of the Lake District and Chiloé. This hypothesis agrees well with recent phylogenetic molecular studies, which indicate high genetic diversity in all the isolated Chilean and Argentine conifer populations studied, as well as a high degree of divergence in the small stands of alerce *Fitzroya cupressoides* present in the Llanquihue central graben (Allnut *et al.* 1999, 2001, 2003; Premoli *et al.* 2000; Bekessy *et al.* 2002). These are most likely the last remnants of ancestral populations that occupied the entire valley during the aforementioned stages of the LLG.

The diversity of subantarctic flora present in Chiloé would thus be a consequence of the northward migration of Magellanic moorland mosaic during the stadials of LLG. Today, these moorland 'islands', present along the summits of the Piuchué

Cordillera, mark the northernmost limits of *Euphrasia antarctica*, *Gunnera lobata*, *Pratia repens*, *Abrotanella lineariifolia*, *Perezia lactuoides* spp. *palustris*, *Sisyrinchium patagonicum* and several species of Cyperaceae and Juncaceae (Ruthsatz & Villagrán 1991; Villagrán 2002). Some 229 species of liverworts have been recorded in Chiloé (Villagrán *et al.* 2005); most of these are endemic to southern Chile and Argentina with several endemic monotypic (*Roivainenia*, *Perdusenina*) or bitypic genera (*Nothostrepta*, *Arctoscyphus*) of Austral South America. Of these, 144 (63%) expand their ranges into the southern confines of the continent, south of 52°S (Hässel De Menéndez & Solari 1985). Fifty-seven of these (25%) reach their northern limits in the Chiloé Archipelago. The mosses of Chiloé also display a dominant subantarctic component (Villagrán *et al.* 2003).

In contrast, angiosperm species of the warm forest communities of southern Chile display maximum richness and restricted endemism between the Maule and Valdivia rivers (36–40°S), reaching their southern limits in Chiloé (Villagrán 1995a; Villagrán & Hinojosa 1997). This distribution, together with evidence from palaeopedological studies (Veit & Garleff 1996), the west–east direction of recolonization indicated by isopollen maps (Villagrán 1991b), and the southward recolonization of north Patagonian and Valdivian rainforests in the late glacial and early to mid-Holocene, has led researchers to hypothesize that the coast and western slopes of the Coastal Cordillera, between the Regions of Los Lagos and Bio Bio, have functioned as a major refuge for these temperate rainforests during past glaciations (Fig. 12.8).

Finally, the large disjunctions observed for Chilotan species of the Valdivian rainforest between central Chile (33°S) and semi-arid Chile (30°30'S) probably correspond to ancient

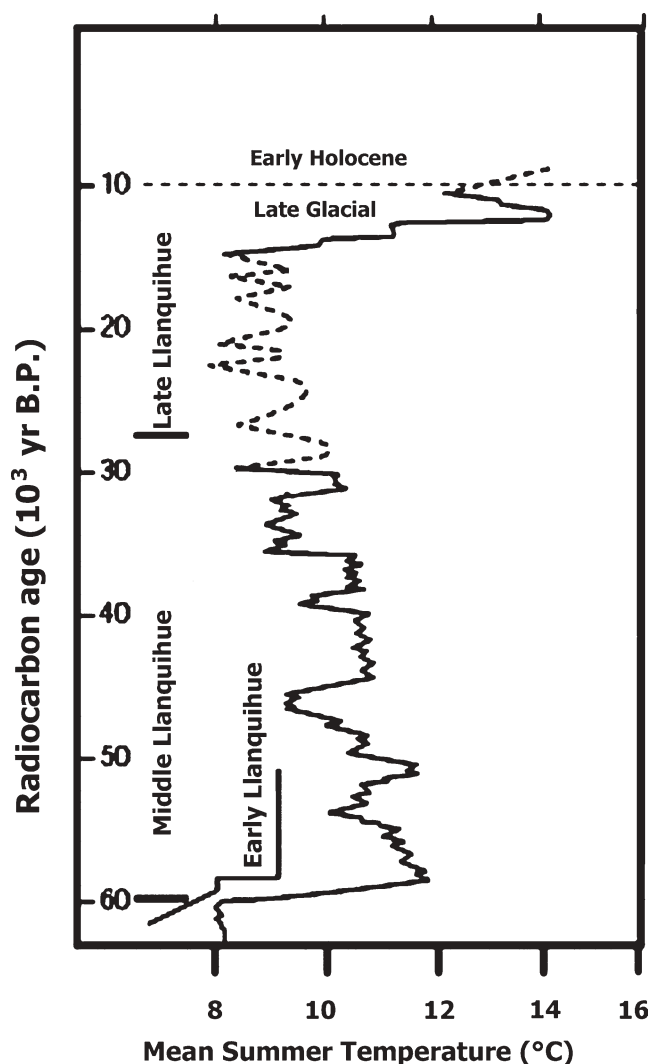


Fig. 12.7. A reconstruction of mean summer temperature of the Llanquihue Glaciation (LLG) indicating the presence of relatively warmer interstadials during the early to middle LLG (30 000–60 000 yr BP) based on past grass pollen fluctuations from the Taiquemó record (solid line). The dashed line corresponds to colder stadials during the late LLG (< 30 000 cal yr BP) inferred from the maximum extent of moraine deposition around Lago Llanquihue. The interval dated 14 600–10 000 ^{14}C yr BP (17.5–11.0 ka BP) (upper solid line) was developed using pollen records from Taiquemó, Fundo Llanquihue, Canal de la Puntilla and Huelmo (Denton *et al.* 1999)

endemisms of previous widespread distributions along coastal Chile before the Pleistocene and the formation of the 'arid diagonal' at the end of the Tertiary (Villagrán *et al.* 2004a). This agrees with fossil evidence from the Neogene of central Chile (Hinojosa & Villagrán 1997) and with recent molecular evidence that shows strong genetic divergence between the northernmost populations of two of these taxa (*Drimys* (Jara *et al.* 2002) and *Aextoxicon* (Nuñez 2004)). The persistence of these species in very restricted areas along the Pacific coast and islands is likely due to the highly oceanic character of these regions during Pleistocene glaciations (Villagrán 1991b). Among the Chilotan species of angiosperms with relict distributions in semi-arid Chile are *Nertera granadensis*, *Mitraria coccinea*, *Sarmienta repens*, *Peperomia fernandeziana*, *Dysopsis glechomoides* and *Uncinia phleoides*. Among the species of ferns with disjunct distributions between Chiloé, Valdivia and the Juan Fernandez islands are *Blechnum corralense*, *Trichomanes*

exsectum, *Hymenophyllum fuciforme*, *Histiopteris incisa* and *Gleichenia litoralis*. The species with disjunct distributions in semi-arid Chile are *Hymenophyllum peltatum*, *Asplenium dareoides*, *Rumohra adiantiformis*, *Hypolepis poeppigii*, *Polypodium feuiliei* var. *feuiliei* and *Megalastrum spectabile* var. *spectabile* (Villagrán *et al.* 2004a). Of the mosses, *Ptychomnion falcatum* is found on Chiloé, Valdivia and Juan Fernandez, whereas *Macromitrium longirostre*, *Fissidens berterii* and *Hemmediola kunzeana* are disjunct between Chiloé and central Chile (Villagrán *et al.* 2003). Perhaps the most surprising examples are the disjunct ranges exhibited by the Chilotan hepatics *Colura calyptrifolia*, *Frullania fertilis*, *Microlejeunea ulicina*, *Monoclea gottschei* ssp. *gottschei* and *Plagiochila rufescens*, all of which are also present in Fray Jorge–Talinay in semi-arid Chile, a major gap spanning more than 1600 km (Villagrán *et al.* 2005).

Interglacial terraces around Valdivia (M.P.)

Prominent terraces interpreted as either fluvial or marine in origin can be observed in the vicinity of the city of Valdivia (c. 38°30'–40°S) (Antinao & McDonough 1999; Brüggén 1944; Fuenzalida *et al.* 1965; Pino 1987, 1999; Rojas 1990). Their surface height varies from 10 m (in Porma, north of the Imperial River) to 67 m high (in Valdivia) (Fig. 12.9). According to the last interglacial sea-level reconstructions, these should not have been more than 8 m above the present level (Esat *et al.* 1999; Blum & Törnqvist 2000; Esat & Yokoyama 2000; Lambeck *et al.* 2002; Shackleton *et al.* 2003). Current thinking regarding these terrace surfaces is that they resulted from block neotectonics (Illies 1970). Faults that control the blocks (with north–south and NE–SW trending patterns) also control the orientation of the majority of local creeks (Grupo De Estudios Urbanos 1997). Relying on terrace altitude together with stratigraphical observations but lacking absolute dating, Lauer (1968) and Illies (1970) suggested a previous interglacial age, here termed the Valdivia Interglacial (VI). This age agrees with the degree of weathering present in these deposits.

Two different facies can clearly be recognized along the 160 km coastal zone. The first is composed of sediments derived from the local metamorphic basement (Metamorphic Complex of Mansa Bay: Duhart *et al.* 2001) associated with an accumulation of land-derived plant remains. This facies, defined as autochthonous, has surface development associated with present-day water courses. Coarse and fine alluvial gravels (including colluvial material) are interbedded within this facies, as well as several types of sand, silt and peat. Some of the gravel deposits consist mainly of quartz, while others are dominated by schist fragments. At least three levels of peat can be identified: the first is visible just above current sea-level (on the northern slope of Niebla's Playa Grande, on Huapi Island in the mouth of Tornagaleones estuary and on the northern slope of Curiñanco Beach); the second is at approximately 34 m above present sea level; and the third lies some 6 m above the previous level (these latter two peat deposits are in the terrace directly north of Los Molinos creek). The peats include numerous logs and branches all extraordinarily well preserved. These have been identified as southern beech (*Nothofagus* sp.), two species of myrtles (*Amomyrtus luma* and *Amomyrtus meli*) and Gaiatecas' cypress (*Pilgerodendron uviferum*). Unexpectedly, small-size leaves of 'ulmo' (*Eucryphia cordifolia*) have also been collected. Two infinite ^{14}C ages >45 000 yr BP obtained from wood samples at Los Molinos and from a carbonized log from the Chan Chan area provide the only chronology (Antinao & McDonough 1999).

The second facies, defined as allochthonous, is composed of medium to fine sandy sediments of volcanic origin, generally characterized by more than 15% ash matrix. Locally known as 'cancagua', it is interbedded with silt- and clay-sized sediments,

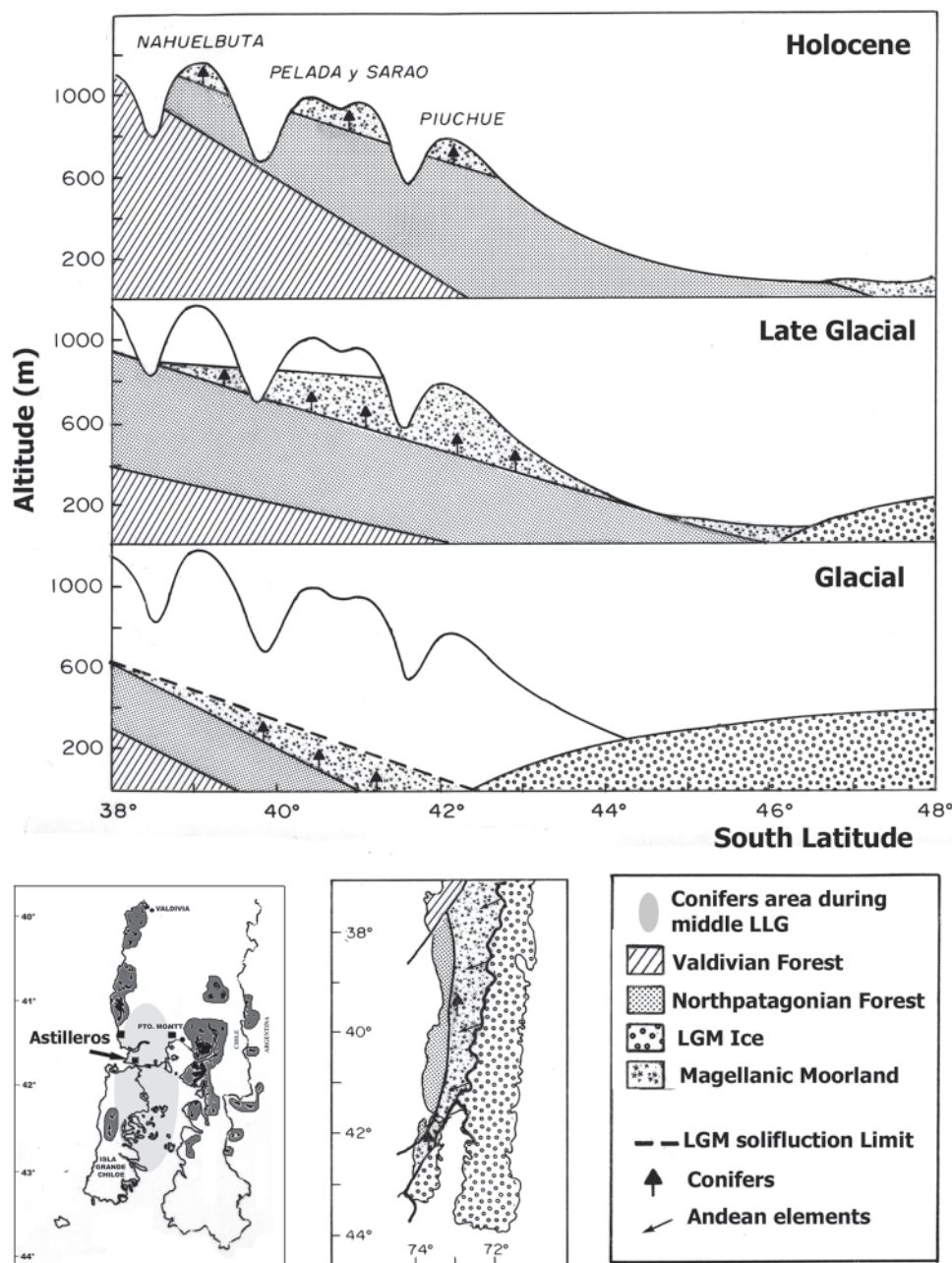


Fig. 12.8. A model of past vegetation changes in temperate Chile over the last glacial cycle (Villagrán 2001). The top three diagrams indicate the relative latitudinal and altitudinal distribution of temperate rainforests and magellanic moorland during the Holocene (present day), late glacial and glacial phases of the LLG (see text for details). The lower left diagram indicates a hypothetical palaeodistribution (light grey shading) of alerce (*Fitzroya cupressoides*) and Guaitecas cypress (*Pilgerodendron uviferum*) during LLG interstadials (Villagrán *et al.* 2004b). Present-day disjunct distribution along mountain ranges is indicated in dark grey shading. Arrow indicates the subpopulation with the highest genetic diversity at Astilleros. The lower middle panel indicates the main regions of refuge during glaciations for Valdivian and North Patagonian rainforests, based on glacial, palaeo-pedological and pollen evidence (Villagrán 1991b, 2001).

and is partially or totally reworked by weathering to kaolinite. The sandstone matrix has also undergone intense weathering, and has mostly converted into a sort of secondary cement. This second facies is abundant not only in the coastal area, but is also found along the most important estuaries and rivers, up to 15 km from their mouths. Outcrops in Playa Grande contain thin interbedded pumice ash layers. Two superimposed stratified flows, observable near the Niebla Spanish fort, dip towards the continent at an angle of c. 45°. The lower flow maintains this position throughout the whole outcrop, whereas the top flow is horizontal along the coastal cliff and starts to dip slowly

towards the continent, eliminating the possibility of tectonic tilting. A similar situation is observed at La Misión Beach in Valdivia and along the coast of Lake Budi. This primary structure was first interpreted as aeolian in origin (Antinao & McDonough 1999), but given the grain size, presence of matrix, thickness of strata and the transition from flat-lying to a 45° tilt, it is more easily explained as the result of a small frontal or lateral deltaic deposit into a channel or small body of water (Brown 2001). The volume of volcanic sand present reaches at least 5 km³ along the coastal area. Associated with the finest-grained sediments, generally a clay-silt mixture produced

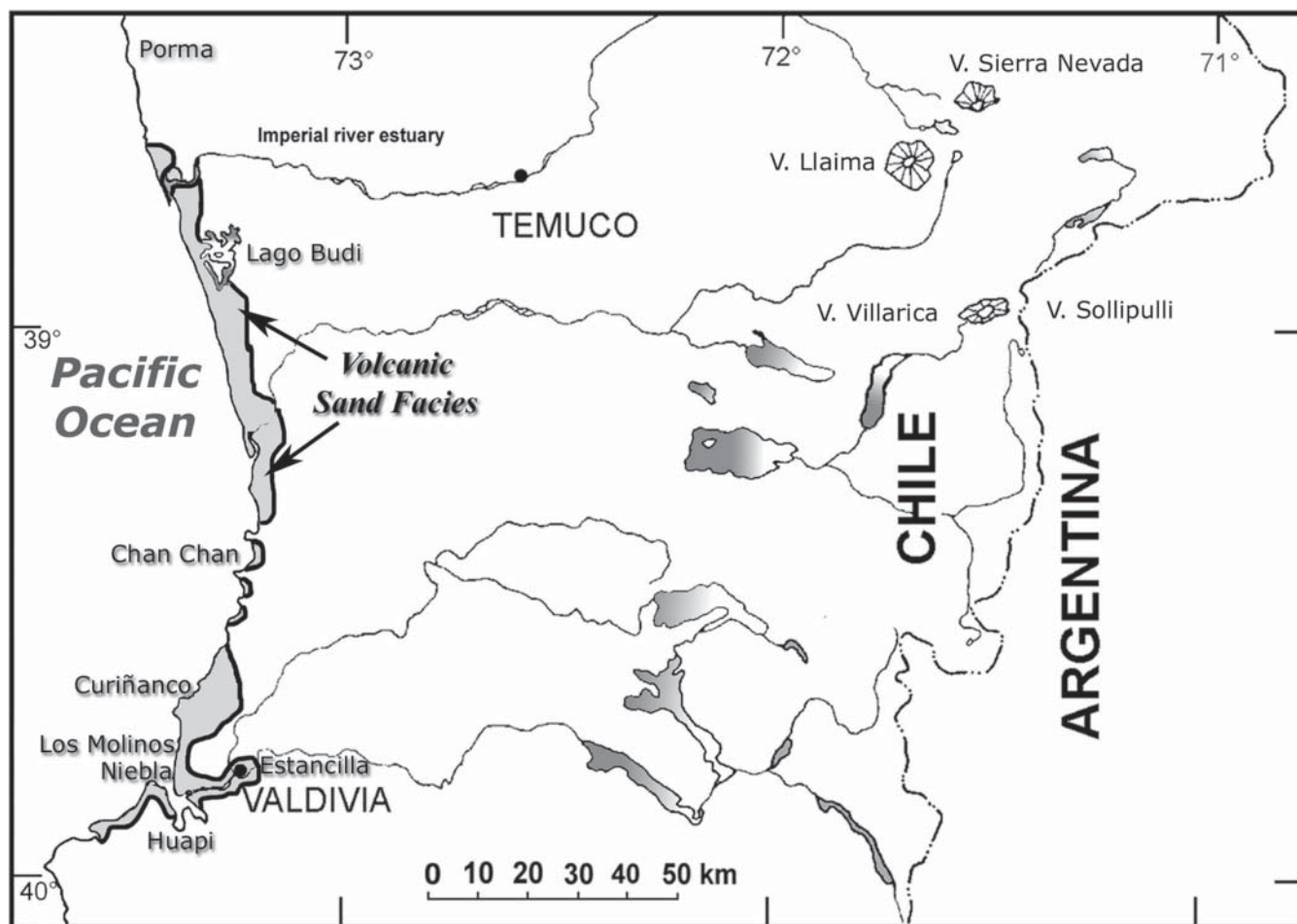


Fig. 12.9. Locality map of the area around Valdivia, southern Chile, indicating the spatial distribution of volcanic sand facies and key sites.

by weathering of volcanic ash, are estuarine and marine invertebrate fossil deposits (Estancilla, Niebla's Playa Grande, Huapi Island), with well preserved shells and/or casts, ostracods and tree leaves. The shellfish *Crepidula dilatata*, *Crepidula fecunda*, *Caecum chilense*, *Nassarius* sp. and *Aulacomya ater* have all been identified from the Huapi Island outcrop (Pino *et al.* 2002). With the exception of *Nassarius*, located in the upper strata, the other invertebrates are intermixed with broken shells and in disorder, which suggests that their soft body parts might have been eaten after deposition by *Nassarius*. The only leaf found at Estancilla was lying in a vertical position, indicative of deposition under a non-laminar flow. Based on the spatial arrangement of the fossils, these deposits seem to have been retransported by a hyperconcentrated flow, forming a thanatocenosis. The coquina fossils from Huapi Island have been interpreted as forming a subtropical association (Alvarez & Gallardo 1996), although the invertebrates identified up to now are indicative of an environmental setting similar to the one in nearby Corral Bay. Volcanic ash content decreases from north to south in this facies. Near the mouth of the Imperial River estuary (northern limit of the outcrops) the volcanic ash is present not only in the matrix, but also forms layers of pure ash, together with a thanatocenosis of estuarine invertebrates.

Although the Sollipulli, Sierra Nevada and Llaima volcanoes (all post-glacial in age) are located in the present Imperial River basin, the probable origin of this hyperconcentrated flow of sand and volcanic ash seems to be related to a pre-Llanquihue (last glacial) caldera of Villarica volcano. The volcanic sandstone is composed of fragments of andesite, basalt,

orthopyroxene, plagioclase, green hornblende, olivine and magnetite (Pino 1987). Most of the orthopyroxene crystals are not rounded, but rather have kept their euhedral shape, which supports the interpretation of a hyperconcentrated flow. Olivine and orthopyroxene are frequent products of post-glacial basaltic and dacitic volcanism (Naranjo & Moreno 1991), but the presence of green hornblende gives a measure of the importance of andesitic pyroclastic material, since it is not found in lavas (Smith & Lotosky 1995). Even today it has not been possible to associate the deposition of a hyperconcentrated sand flow to a particular volcanic event, as the pre-Llanquihue volcanic centres of the Andes have been buried or destroyed by successive glacier advances.

Both facies are vertically related in several ways. At Playa Grande and throughout the city of Valdivia, hyperconcentrated sand flows overlie peat with an undulating contact that corresponds to flame structures. In this particular case, evidence indicates transport and deposition of a viscous flow over a plastic material. At Los Molinos, allochthonous flows underlie autochthonous facies, whereas the opposite is true at Curiñanco.

If we accept that wavy-surface terrains in the Central Valley near Osorno are typically associated with lahar outcrops, such as at San Pablo (Corvalán 1974), then by analogy the same geomorphology in the Valdivia area indicates that the hyperconcentrated deposit of immature volcanic sand actually corresponds to a lahar. The Valdivia area and adjacent coastal zone exhibit this undulating pattern, alternating with the presence of terraces. The same wavy pattern can be seen along the

secondary road that links the main road (Ruta 5, Máfil) to the highway between San José de la Mariquina and Valdivia. This road cuts almost perpendicularly through the undulations of a coarse sand deposit which is somewhat less cemented than the traditional 'cancagua', but contains numerous pumice stones. Similar morphological structures can also be observed along the road towards Gorbea (Cuarta Faja), where very fine and immature volcanic sandstones appear in subsurface at the Santa María estate and correspond to what has been defined as 'cancagua'. Both outcrops lead towards the Villarica volcanic basin.

The reinterpretation of deposits containing marine or estuarine fossils as thanatocenosis associations transported by ash flows and the existence of typically continental facies and fossils along the present Valdivia coastline support the notion that the entire above-mentioned deposits, previously described as marine, are in fact fluvial, lacustrine and paludal in origin. If sea level was somewhat higher than today, then active sedimentation took place as the coastline was several kilometres further to the west. This agrees with the probable existence of a fluvial plain several kilometres wide, where ancient rivers meandered in more or less parallel directions to the coast and where hyperconcentrated flow deposits would have moved southward from the mouth of the Imperial River.

The colonization of Chile by *Homo sapiens* at the Pleistocene–Holocene boundary (L.N. & M.G.)

In this section, we review key sites of the first human occupations from the extreme arid north (18°S) to subantarctic south (56°S) and document their response to palaeo-environmental variability. We focus on the Pleistocene–Holocene boundary, a specific time with very favourable environmental conditions for human colonization in southernmost South America.

Arid and semi-arid regions

Scarce evidence exists for associations between human occupation and late Pleistocene faunas in the arid environments of Chile, despite widespread presence of the latter. For example, unpublished recent results from the Pleistocene lacustrine Calama basin document the presence of equids, camelids, megatheriids and macrauchenids (N. Hermosilla, pers. comm.). Other evidence for megafaunal presence includes a milodontid unearthed in the highlands surrounding Antofagasta de la Sierra (C. Aschero, pers. comm.), an equid from Salar de Surire in the High Andes of Arica (C. Santoro, pers. comm.) and a megatheriid from the *Prosopis tamarugo* forests in Pampa del Tamarugal (Casamiquela 1969–70). Cooler and moister climates around 14 000–11 000 yr BP are thought to have occurred at the Barro Negro site in the Argentine Puna, precisely the climate associated with extinct American species of equids, replaced by camelids c. 11 000 yr BP (Fernandez *et al.* 1991).

One of the few sites in northern Chile where associations between humans and megafauna have been established is along the pre-Andean range of the Tuina Hills in the vicinity of the Calama basin. Here, triangular projectile points (the 'Tuina tradition') are in the same stratigraphic position as American horse remains, with ¹⁴C dates between 11 700 and 11 200 yr BP. Of the 179 classifiable lithic artifacts discovered, two are bifacial triangular points made of allochthonous rocks together with 3879 camelid bone fragments. This find probably represents the last remnants of a Pleistocene fauna (Núñez *et al.* 2002).

The vast expanses of Puna and southern Altiplano (southern Bolivia, NW Argentina and northern Chile) were initially occupied by High Andean hunters of the Tuina tradition. Hunting sites were associated with modern camelids and were exclusively under rock shelters throughout the Andes between 12 050 and 11 000 yr BP, with strong evidence for a migrational regime

across large areas (Aschero 1988; De Souza 2004; Núñez *et al.* 2002). Recent studies, however, have identified open-air camps at Punta Negra-1, contemporaneous with Tuina-1, on the southern margin of Salar de Punta Negra (2976 m) (Grosjean *et al.* 2005). A number of differentiated artifacts with a 'Fell' (from Fell's Cave in southern Chile) tradition, including one 'fish tail' point and unifacial lithics, probably formed part of a migratory population that took advantage of the palaeo-springs and wetlands (with Andean recharge) that cropped out here at <3000 m (Grosjean *et al.* 2005). Fell points have also been found along the southern margin of the Argentine Puna (C. Aschero & A. Haber, pers. comm.) which implies that these peoples passed through the region at the end of the Pleistocene along the Andean highlands. At Punta Negra, lithic artifacts are intercalated with peat beads dated between 12 400 and 10 700 yr BP, including a ¹⁴C date on an adjacent hearth dated at 12 020 yr BP. Among a total of 964 unifacial lithic artifacts (scrapers, knives) only a single Fell point was found, along with four Punta Negra points similar to the Payjan tradition, and three triangular points of the Tuina tradition (Fig. 12.10).

As the 'Fell' groups passed through the Atacama Desert, they overcame all the biological and extreme climate barriers of the continent (Villagrán *et al.* 1983; Grosjean *et al.* 2005). After crossing over to the Pacific side of the Andes (Sandweiss *et al.* 1998), in a relatively short time these groups colonized palaeo-lacustrine basins rich in megafauna present in central-southern Chile (Núñez *et al.* 1994a, b). In all probability transients (Beaton 1991), they likely focused on assessing the availability of distant resources by passing through favourable sites along migratory paths. At Punta Negra, they made use of available wetlands rich in plant and animal (vicuñas) resources at a time when these were isolated from each other across the landscape. The record of large basaltic bifacial shards with expedite lateral retouches and nine bifacial points would imply, by and large, a group of low density, whose high rate of artifact output was enhanced by the close proximity of basalt outcrops (Grosjean *et al.* 2005).

The circum-Puna area experienced increased summer precipitation resulting in lake transgression throughout the region between 15 300 and 14 000 yr BP, with maximum levels present from 12 800 and 8900 yr BP, followed by lake collapse (Geyh *et al.* 1999; Grosjean *et al.* 2001). As previously stated, diverse interdisciplinary analyses have shown that the late Pleistocene of the Atacama Desert was a favourable environment for human settlement due to increased rainfall. It is thus almost beyond a doubt that the high abundance of Tuina tradition sites along the Andean front ranges resulted from the increased presence of wetlands adequate for the control of such a highly diverse territory.

Transitory Fell groups arrived in the semi-arid region further south by way of these same salar 'corridors' along the Andean front during the colder climates of the late glacial. This is indicated by the abundance of red soils, associated with wetter environments than today (Veit 1996), along the coast and lake shorelines, as well as the presence of relict forests and wetlands. These environments in particular would have concentrated resources such as megamammals, which further south occurred in association with *Nothofagus* parkland at the beginning of the Chilean Central Valley. An example is Quebrada Quereo, where shallow lake deposits contain an abundance of Pleistocene fauna (Núñez *et al.* 1994b; Jackson *et al.* 2004). This fauna disappeared with the abrupt onset of aridity at the beginning of the Holocene and coincided with the appearance of Fell point palaeo-indian predators (D. Jackson & C. Mendez, pers. comm.). The hunting of megamammals trapped among aquatic vegetation in these relict marshy areas was complemented by carrion feeding habits, eventually leading to extinction throughout the Central Valley in an amalgamation of climatic and cultural factors (Núñez *et al.* 1994b; López *et al.* 2004).

Human populations that reached Quereo did so in two waves associated with the abrupt collapse of surrounding forests,

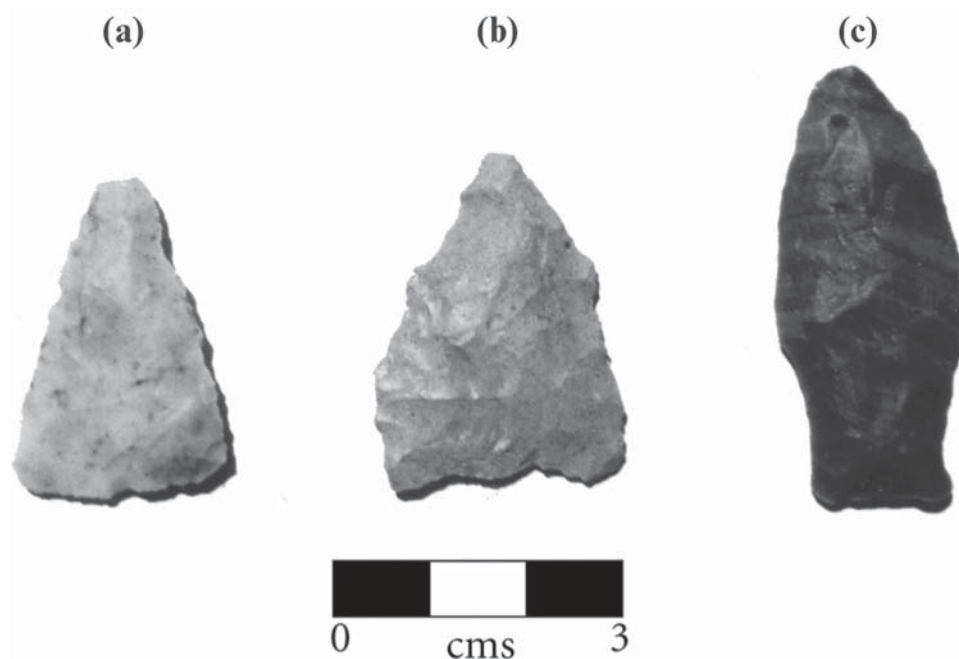


Fig. 12.10. Projectile points representative of the Punta Negra site: (a, b) triangular points of the Tuina tradition; (c) a 'fish-tail' point of the Fell tradition.

swamp and aquatic vegetation as well as encroaching semi-arid matorral in response to increasing aridity at the beginning of the Holocene (Heusser 1983; Villagrán & Varela 1990; Núñez *et al.* 1994b; also see section on Norte Chico). This 'adverse' scenario would have nevertheless allowed, and presumably even promoted, opportunistic strategies of megafauna hunting as resources became concentrated along remaining intermittent 'ecorefugia'. The earliest sequence of Quereo I occurred between 14 000 and 13 250 yr BP. Among the megafauna present were equids, mylodontids, 'paleo-llama', swamp deer and gomphotheres (e.g. *Stegomastodon* and *Cuvieronius*, commonly referred to as 'mastodonts' in the literature, although they are not true mastodonts, i.e. *Mammutidae*). Smaller species of felids, canids, birds, rodents and amphibians have also been described. Among the species actually hunted are the remains of a horse skull with caved-in frontal nasal bones surrounded by lithics, cut bones, tapered artifacts, impacted, fractured and splinted long bones with polished and eroded ends, perforated horse vertebrae, microdiorite shards with natural edges (to expedite cutting), and planar blocks or platforms *in situ* surrounded by long bones and scarce local refuse (Núñez *et al.* 1994b; López *et al.* 2004).

The Quereo II occupation occurred between 13 100 and 10 600 yr BP with remains of human activity and waste deposited along the margins of a meandering river, under a warmer and drier climate, again repeating the strategic importance of these ecorefugia under drought conditions for both megafauna and their human hunters. American horse, deer, gomphotheres and mylodontids have all been identified at this site. Although Quereo is close to the coast, marine resources are rare and were probably gathered elsewhere; they include two shells of *Concholepas concholepas* (Chilean abalone) and a whale vertebra of *Cetacea ballenidae*. Human activity seems to have been transient and possibly tied to dry camps such as those present at Quebrada El Membrillo (Jackson *et al.* 2004). Cut bones and bone artifacts modified for polishing and hammering, bones fractured before fossilization, placement of flat slabs *in situ* around areas with highly concentrated equid bone remains, together with laminar lithics and shards with percussion waves

and bulbs, including sharpened wood trunks, are all present at Quereo II and dated to 13 100 yr BP. The concentration of resources seen here, along with the species hunted, the lacustrine environment and the chronology, make this occupation contemporaneous with and similar in nature to the kill site located at Tagua Tagua (Montané 1968; Casamiquela 1969–70; Núñez *et al.* 1994a). Recent research along the upper reaches of the Quereo ravine has identified two additional occupations at Quebrada Membrillo, exposed by sediment deflation. The sites contain mylodontid bone with cut marks associated with surrounding flat slabs dated to 13 500 yr BP. A second layer, coeval with Quereo II, marks the presence of native horse and 'palaeolama' associated with knives, scrapers, choppers and marginal scrapers, together with splintered and impacted bones.

As previously stated (see Norte Chico section), the climate became increasingly more arid after the Quereo II occupation, with ^{14}C dates from immediately overlying peat layers dated to 10 600 yr BP. Overall, this would imply a collapse in the way of life of these 'Fell' groups, specialized as they were in the exploitation of these ecorefugia that began to disappear at a rapid pace throughout the interior basins of the central graben, as evidenced from Quereo and Tagua Tagua. This more than likely contributed to the general extinction of the megafauna at the end of this 'post-glacial' crisis (Varela 1976; Heusser 1983, 1990b; Villagrán & Varela 1990; Núñez *et al.* 1994a, b; Markgraf & Kenny 1997).

The fertile Central Valley

Exceptional lacustrine deposits from Lake Tagua Tagua (34°30'S) were discovered containing remains of megafauna in association with cultural remains, all initially dated to 13 250–12 800 yr BP (Montané 1968). More detailed studies eventually revealed a major (TT-1) location with five loci of skeletal remains, and discovered another location (TT-2) with nine loci including the remains of ten gomphotheres (juveniles and adults) all hunted and processed *in situ*, along with scarce horse and swamp deer remains. Many of these prey items were dismembered and piled onto ancient lacustrine beaches, along



Fig. 12.11. The Tagua Tagua-2 'mastodont' killing and butchering campsite. Inset: A 'fish-tail' Fell tradition point associated with megafaunal hunting and butchering at Tagua Tagua-2.

the shore of a palaeo-lake clearly sensitive to seasonal drought. An eventual return to wetter conditions (previously discussed) led to the burial and preservation of the evidence for human occupation at this site (Núñez *et al.* 1994a).

Judging by the lithics present at TT-1 (50 units) and TT-2 (79 units), both from open-air camps, and setting aside considerations regarding carrion feeding, the three Fell points (made of transparent quartz crystals) and numerous artifacts found provide unequivocal evidence for hunting and food processing (Fig. 12.11). Among these are unifacial implements (recloirs, side scrapers, knives, discoidal scrapers), hammering stones, an engraved gomphothere tusk dart and other bone artifacts, along with multiple cut and fractured bones, all indicative of processing *in situ* and accompanied by waste microdebitage (a by-product of on-site blade sharpening). All of these items were found in a single layer at TT-2 dated to 11 900–11 050 yr BP (Fig. 12.11). When compared to the earlier dates of TT-1 (13 250–12 800 yr BP) a pattern of lake regression becomes evident, with the earlier site located on a higher beach and the younger, lower site towards the middle, following overall increased aridity in the region. The dates are also in full agreement with the abrupt and widespread extinction of the megamammals at the end of the Pleistocene by *c.* 11 000 yr BP (Varela 1976; Núñez *et al.* 1994a, 2001).

Prolonged droughts during the Pleistocene–Holocene transition have been documented at numerous other ecorefugia associated with proboscideans in both North and South America (Bryan 1975; Correal 1981; Haynes 2002). The eventual concentration of these species in the few collapsing ecorefugia attracted palaeo-indian hunters to Tagua Tagua who specialized in large prey, in a similar fashion as at the classic mammoth sites in North America between 27°N and 33°N. Hence, the syngenetic events documented at Tagua Tagua, with the dramatic loss of resources altering proboscidean behaviour, were also synchronous with the North American Clovis groups during the late Pleistocene–early Holocene transition (10 600 yr BP) when abrupt onset of drought generated loss of wetlands and arboreal habitats (Haynes 1991, 2002). Thus, both Fell and Clovis cultures may have exploited similar ecocatastrophic scenarios, when opportunistic hunting strategies coupled

with stressful palaeoclimate conditions between 12 800 and 10 900 yr BP quickened the demise of an already collapsed biomass of megamammals.

The latest Pleistocene marked the onset of palaeolake desiccation along the southern part of the central graben. Further south, as piedmont glaciers retreated up-valley, many of these regions were subsequently reoccupied by temperate rainforests (Moreno 2000; Moreno *et al.* 2001) and a new drainage network of rivers and lakes became established along the Patagonian steppe (Tatur *et al.* 2002). This scenario is associated with Monte Verde near Puerto Montt, one of the earliest human occupations in South America, with cultural layers spanning from 15 100 to 14 200 yr BP (Dillehay & Collins 1988). Vegetation at the time consisted of wet and cold southern rainforests rich in conifers, 'avellano' (*Gevuina avellana*) and southern beech (*Nothofagus*), and the site has a collection of seeds, tubers, nuts and wild berries, indicating proximity to a wetland (Dillehay 1989; Heusser 1990a). Located along the margin of a small tributary of the Maullin River, the Monte Verde campsite was composed of 12 cabin foundations, with rectangular floor plans fixed with stakes and associated with communal hearths and fireplaces. Monte Verde represents a semi-stable and diversified adaptive culture without dependence on seasonal fluctuations. A wide range of resources were utilized, including fish, shellfish and marine algae obtained from the coast *c.* 80 km distant from the site. Megafauna present were limited to gomphotheres and 'palaeollama' as well as other smaller game, with pre-Clovis and Fell bifacial foliaceous lithic points similar to the Jobo tradition of northern South America (Dillehay 1989). An earlier event, with formed lithic artifacts dated to 33 000 ¹⁴C yr BP, located some 100 m from the classic site, is considered as a working hypothesis (Meltzer *et al.* 1997).

Finis Terrae: colonization of Fuego–Patagonia

Both small and large grazing herbivores found attractive habitats in the open and cold moist grasslands present at the threshold of human occupation of Fuego–Patagonia. Plant macrofossils analysed from ground sloth dung in Mylodon Cave dated to *c.* 14 400 yr BP indicate the presence of Cyperaceae, Juncaceae, grass and forbs (Moore 1978; Borrero *et al.* 1998). This moist grassland gave way, however, to a more xeric steppe between 13 000 and 11 000 yr BP with overall warmer temperatures (Markgraf 1988). Under environmental pressure, populations of large herbivores collapsed due to intense hunting by opportunistic hunters of the Fell tradition, which eventually became capable of colonizing the very southern tip of South America (Massone 1996; Borrero *et al.* 1998).

Optimum conditions existed for human existence at the end of the last glacial in Fuego–Patagonia: abundant game, both modern and extinct, extensive grasslands, water, prime material for lithics, and certainly the rich coastline. Fell's Cave (at Río Chico), surrounded by herbaceous steppe, is one the most representative sequences of these southernmost hunter-gatherers (12 800–11 100 yr BP) (Bird 1988; Markgraf 1988). Underneath this rock shelter, American horses, mylodontids and modern camelids have been preserved associated with excavated hearths and the remains of domestic artifact preparation typical of the Fell tradition, such as the 'fish-tail' points, long-frontal high-ridgeback scrapers, retouched unifacial shards, polishers, bone tools, knives, disc-shaped polished rocks and red pigments.

Other groups belonging to the Fell tradition came across a rock shelter at Tres Arroyos, in northern Tierra del Fuego. Both horse and mylodontids were consumed here between 12 720 and 11 750 yr BP in association with bifacial and unifacial artifacts, including several different scrapers with retouched edges (Jackson 1987; Massone 1987, 1996). Several hundred kilometres away at Cueva del Medio in the Ultima Esperanza area (Cerro Benítez), located only 1000 m to the

south of Mylodon Cave, another group of people piled up, amid campfires, bones of both extinct and modern fauna between 13 000 and 10 750 yr BP, in association with cutting tools and scrapers including 'fish-tail' points of the Fell tradition (Nami & Case 1988).

Similar occupations occurred 50 km from Fell's Cave, at Pali Aike cave, dated to 9680 yr BP (Bird 1988) and at Marazzi (Tierra del Fuego) dated to 10 920 yr BP (Laming-Emperaire & Humber 1972), and even thousands of kilometres away in the pampas of Buenos Aires (Flegenheimer 1987). Even though earlier hunters than the Fell tradition may have occupied Argentine Patagonia some 14 000 yr BP (Cardich 1987; Miotti 2003), the main wave of human expansion occurred synchronously with trends towards increased aridity and megafaunal extinctions, between 13 000 and 11 000 yr BP. At the front of this wave were the Fell hunters, specialized in exploiting big game already under palaeoenvironmental stress (Markgraf 1985).

To conclude, the data point to the arrival of *Homo sapiens* at the southernmost tip of the Americas between 15 200 and 11 000 yr BP in the context of abrupt climate change at the Pleistocene–Holocene boundary, although there are controversial claims of even earlier human presence. Two or more different waves of colonization from various origins were possible, presumably by relatively rapid passage through inhospitable landscapes across natural and desert barriers (Villagrán *et al.* 1983). Population movement would have been considerably slower, however, across the fertile landscapes of the Central Valley and Fuego–Patagonia.

To this effect, pre-Fell sites older than 13 000 yr BP are for now the earliest indicators of humanity present along the diverse environments of southernmost Chile and Argentina: from temperate rainforests (Monte Verde), Patagonian borderlands (Piedra Museo) and the Central Valley (Queiro I and Quebrada 'Membrillo') (Dillehay 1989; Núñez *et al.* 1994b; Miotti & Cattaneo 1997; Politis 2002; Jackson *et al.* 2004; López *et al.* 2004). The second well-represented wave of immigrants occurred between 13 000 and 11 000 yr BP, represented by typical Fell components and recognized throughout Chile and Argentina from 20°S to 56°S latitude. These occupations may have been made more effective through the greater availability of materials (Gamble & Soffer 1990; Borrero *et al.* 1998) with the 'popularization' of Fell points and large unifacial shards throughout southern South America occurring over no more than a millennium.

By 13 000–11 000 yr BP all of the analysed sites indicate occupation by an ever-growing and more diverse assemblage of peoples from 18°S to 56°S latitude, giving way to the coexistence of different cultural traditions. Cultural responses to ever-increasing aridity are known from the Tuina tradition (triangular points) associated with modern faunas (camelids) and very scarce megafauna (equids). This culture formed an effective, stable and lasting presence under wetter climate regimes in the central Andes.

Coeval with the Tuina tradition is the Fell tradition, which in contrast to Tuina, was formed by transient migratory groups exploiting point resources along the Andean piedmont (e.g. at Salar de Punta Negra) (Marshall 1993). The similarity of the points found at Punta Negra with the Payjan and classic Fell points of southernmost Chile (Fig. 12.10) would indicate that migration of the latter ensued from northern Peru, establishing contact with different occupations, such as Tuina, which were exclusively found only in the circum-Puna region (Dillehay *et al.* 2002; Chauchat & Pelegrin 2004; Grosjean *et al.* 2005).

In a similar fashion to the way that resources today increase from north to south, a colonizing wave would have orientated itself towards more productive and wetter areas with better, more continuous resources. From the scarce presence of Fell cultures in the northern desert, to ecotopia exploitation of semi-arid and central Chile, it was in the Central Valley where

these cultures seem to have flourished the most, most likely due to increased availability of big game, both extinct and modern. As climate became drier at the end of the last glacial, megafaunal resources became more concentrated but did not last very long. Exploitation eventually became untenable, making the palaeo-indian way of life considerably more difficult. The identification of an intense Fell occupation at Lake Tagua Tagua affords an exemplary account of how proboscidean populations under palaeo-environmental stress collapsed and became extinct across the threshold of the Pleistocene–Holocene boundary. Subantarctic steppe also became quickly colonized by Fell hunters, who then suffered abrupt collapse as climate became increasingly arid inducing an abrupt crisis in wild animal fodder.

Maritime cultures quickly became established between 13 000 and 11 000 yr BP along the entire length of the coast, evidenced by the Huentelauquen and Acha traditions (Muñoz & Chacama 1993; Llagostera *et al.* 1997). Along the Andean Precordillera, occupations of the Fell tradition applied Subandean cultural responses that were dependent on habitats found at lower altitudes (Saavedra & Cornejo 1995; Stehberg 1997). This included the Arica highlands, where a different response from the Tuina tradition was present (Santoro 1989). We thus propose that during the late glacial all the resources of the country were being used synchronously by hunter-gatherers (Núñez *et al.* 2001). The high variability inherent to abrupt climate changes at the Pleistocene–Holocene transition never constituted a barrier to colonization by the first *Homo sapiens*. By undergoing severe cultural adjustments, including applying opportunistic strategies, humans proved very capable of enduring colonization in the complex and dynamic post-glacial landscapes of southernmost South America.

Future challenges for Quaternary studies in Chile

Ongoing Quaternary research in Chile is highly diverse and cross-disciplinary. Among the major challenges posed for any overview of the subject is the need to provide a process-orientated integration of diverse settings, interpretations and scenarios that have been proposed previously, in the light of the ever-growing dataset of global palaeoclimate changes. A significant amount of interest is now invested in understanding the mechanisms involved in the generation and propagation of palaeoclimate signals at a global scale. Chile's natural geography is key for testing the contribution of low, mid- and high-latitude palaeoclimate processes to global climate change. This is a major and ambitious enterprise, as palaeo-ecologists and palaeo-climatologists leave behind the purely descriptive phase and lead the Quaternary sciences into a more predictive stage. To accomplish this, the development of high-resolution 'bullet-proof' chronologies is of utmost importance. With the advent of AMS radiocarbon dating as well standardized cosmogenic dating techniques, many records are now datable with considerable precision. In the long run, the more precisely we know our recent past, the greater our confidence will be in model predictions and outcomes.

This chapter has also made evident some of the more poorly known regions of Chile in terms of past climate and vegetation change and in particular over the last glacial–interglacial transition (the last 25 000 years). Of these, the Norte Chico and central Chile stand out, especially the former. Hence, many of the scenarios for plant colonization and the origin of modern-day plant associations proposed by biogeographic evidence (e.g. see section on vegetation diversity and change in central Chile) will remain mostly circumstantial until falsified or confirmed by geohistorical records. Greater integration between marine and land records will be essential for palaeo-climatologists working

in northern/central Chile. The ideal situation is for data from one type of record to be used in developing working hypotheses for other kinds of records. Outcomes may not always be predictable, however, and previously unsuspected scenarios of either climate or vegetation change may arise.

Even more conspicuous is the lack of data from older portions of the Quaternary. Here, we have presented evidence of interstadial conifer forests and previous interglacial (although undated) deposits near Valdivia. In northern Chile, we note that marine records (Lamy *et al.* 2000) and records of salt facies changes at Salar de Atacama (Bobst *et al.* 2001; Lowenstein *et al.* 2003) provide evidence for climate change over the last 80 to 100 ka. No records of that antiquity exist in southern Chile: the oldest known date back to 50 ka BP (L. E. Heusser *et al.* 1999; Villagrán *et al.* 2004b). To date, there are no other precisely dated records of either past climate or vegetation change in Chile that cover older time periods.

An exciting new area of research has been the extraction of fossil DNA from animal coprolites preserved in middens and cave deposits (Hofreiter *et al.* 2000, 2003; Kuch *et al.* 2002; Hadly *et al.* 2004). By merging powerful laboratory DNA extraction techniques with well constructed records of past climate change, a strong potential exists for understanding not

only present but also past population genetics and how modern biodiversity has arisen in the recent past.

Finally, Quaternary research is fast becoming a mature science discipline in Chile, with many new researchers devoted to developing precisely dated geohistorical records. This is perhaps the greatest difference from the situation almost 30 years ago, when Paskoff (1977) published his initial 'state of research'.

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