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A Record of Environmental and Climatic Change from the West Coast, South Island, New Zealand, using Beetle Fossils

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by

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Abstract

Fossil beetle based palaeoclimatic and palaeoenvironmental reconstructions are presented from the Westport region, West Coast, South Island, New Zealand for the last glacial cycle. They include the longest continuous fossil beetle record from New Zealand, covering 16,000 years over the OIS 3/OIS 2 transition. Early last glacial (OIS 4) and mid-Holocene (OIS 1) reconstructions are also presented.

The assumptions underlying fossil beetle research in New Zealand are tested indicating beetles are suitable proxies for reconstructing palaeotemperature and palaeoprecipitation. This thesis provides the first quantitative estimates of temperature and precipitation from the Westport region for the last glacial.

Reconstructed temperatures indicate stadial cooling was seasonal. Maximum cooling was ca. 5°C in winter and ca. 2-3°C in summer. Winter cooling is consistent with previous quantitative estimates from New Zealand. Mean annual precipitation decreased a maximum 35-40% during stadials. Temperatures and precipitation varied during OIS 3/2 indicating multiple possible drivers for glaciation. A glacial advance ca. 34-28ka BP correlates with ca. 5°C winter cooling and ca. 40% less precipitation, which supports temperature driven glaciation whereas a glacial advance ca. 24-22ka BP correlates with ca. 3°C winter cooling and precipitation similar to present, which supports precipitation forced glaciation.

Palaeoenvironmental reconstructions of stadial vegetation from the Westport region indicate lowland *Nothofagus fusca*-type forest during OIS 4 and a forest-grassland mosaic during OIS 3/2. These records contrast with pollen-based reconstructions of a treeless landscape in Westport during stadials but are consistent with quantitative estimates of stadial cooling. A shift of reproductive strategy in arboreal vegetation may explain the lack of tree pollen in stadial pollen records. This is significant for our understanding of glacial palaeoecology and palaeoclimatology as pollen records may not accurately represent stadial vegetation.

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The technical and academic staff of the Department of Geological Sciences (University of Canterbury) also deserve special mention for making welcome the rogue biologist in their midst. The production of this Ph.D would not have been possible without their assistance and support. The time and expertise of the staff at the New Zealand Arthropod Collection (Landcare Research Ltd., Auckland) and the Lincoln University Entomology Museum (Linclon University, Christchurch) was also appreciated and I thank all of those who assisted in the identification of beetle fossils.

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Chapter 1

Introduction

1.1. Background

Fossil beetles have long been used as proxies for palaeoenvironmental and palaeoclimatic change (e.g. Coope, 1959; Atkinson et al., 1987; Elias, 1991, 1994, 2006; Whitehouse, 2004, 2006) but they have seen only limited use outside the Northern Hemisphere (e.g. Hoganson & Ashworth, 1992; Porch & Elias, 2000). Recent work (e.g. Marra & Leschen, 2004; Marra et al., 2004, 2006) has developed fossil beetles as robust proxies of palaeoclimatic and palaeoenvironmental change in New Zealand. This thesis uses fossil beetles to produce palaeoenvironmental and palaeoclimatic reconstructions from the West Coast of the South Island of New Zealand, an area which has not yet been examined using beetle-based reconstructions but one which is of great significance in understanding Quaternary climate change in New Zealand and the wider Southern Hemisphere.

The West Coast of New Zealand's South Island is an imporant area for examining the patterns and forcing mechanisms of climatic change in the Southern Hemisphere mid-latitudes. This region is situated directly in the path of the Southern Hemisphere mid-latitude westerlies between 40ºS and 60ºS (Fig. 1.1a-b) and variations in the climate of the West Coast are controlled by sea surface temperatures in the Tasman Sea, immediately upwind of this region. Changes in climate should be therefore be able to be related back to variations in westerly atmospheric circulation and regional insolation budgets (e.g. Vandergoes et al., 2005) as the westerlies are driven by equator-pole

Figure 1.1a: Map of the Pacific Ocean indicating the position of New Zealand in relation to atmospheric circulation.

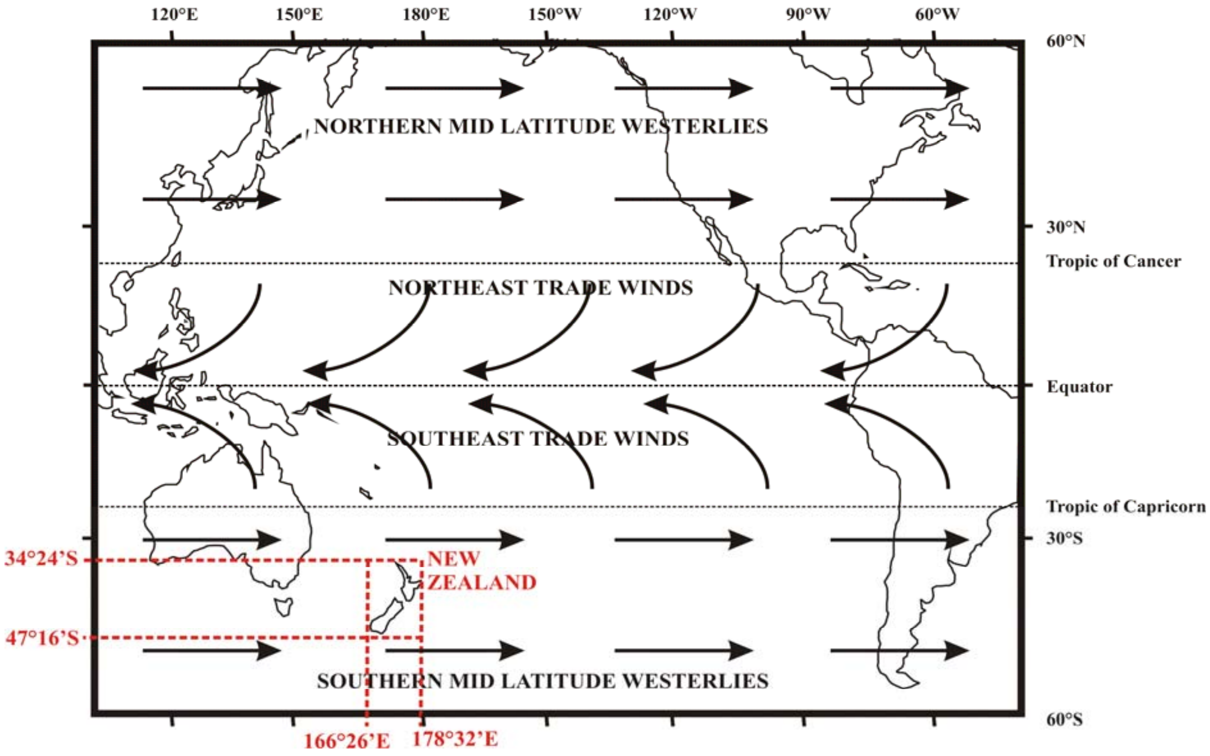
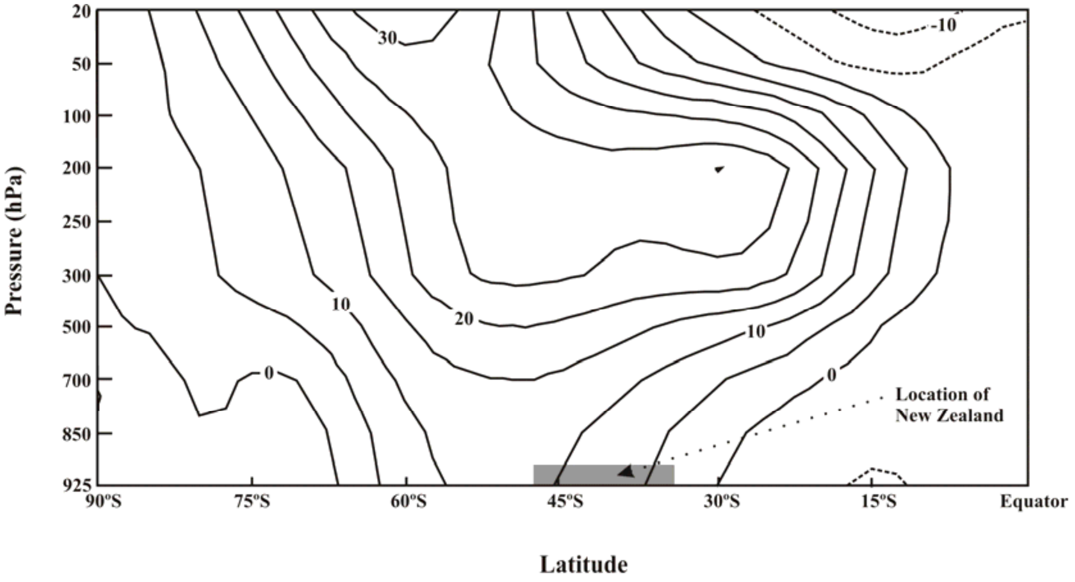


Figure 1.1b: The Southern Hemisphere zonal mean zonal wind averaged over all times of the year. The contour interval is 5 m.s^{-1} with negative contours represented by dashed lines. The latitude of New Zealand is indicated by the shaded grey box on the x-axis. Figure is adapted from Shulmeister et al., (2004).



pressure and temperature gradients which in turn appear to be driven by variation in Southern Hemisphere insolation (Shulmeister et al., 2004; Vandergoes et al., 2005). Given the importance of this region, studies of palaeoclimate are remarkably limited and, like most of New Zealand, dominantly comprise palynological investigations (e.g. Moar & Suggate, 1979; 1996). While these studies have provided reconstructions of the palaeoenvironment, quantification of the palaeoclimate from pollen records is difficult as the flora of New Zealand is temperature-tolerant (Norton et al., 1986). This has meant that only qualitative inferences (e.g. colder, wetter) of palaeoclimate have been made.

Furthermore, the palynological interpretation of the palaeoenvironment of New Zealand during the last glacial maximum (LGM) (ca. 20,000 years BP) is one of the long standing conundrums in New Zealand science. The vegetation reconstruction for this period is one of a generally deforested landscape (McGlone, 1988; McGlone et al., 1993), however, this type of environment fails to mesh with the few existing quantitative estimates of temperature at the LGM (e.g. Porter, 1975; Barrows & Juggins, 2005) which indicate that conditions remained warm enough to allow forest to survive over most of the North Island and in the north of the South Island (Willett, 1950; Barrows & Juggins, 2005).

In attempting to reconcile the pollen record with the rather moderate cooling inferred for the glacial maximum some workers (e.g. Wardle, 1988) have suggested that forest survived in refugia in the north of the South Island. This hypothesis was previously suggested by Willett (1950) based on inferred temperature depression from equilibrium line altitude estimates (ELAs) from glacial periods. However re-forestation of lowland

New Zealand was extremely rapid, occurring within a few hundred years of regional deglaciation (McGlone, 1988). While the seeds of many New Zealand forest taxa are bird-dispersed they are unlikely to have been able to spread rapidly enough from northern refugia to explain the rapid re-forestation (McGlone, 1988). Other workers (e.g. McGlone et al., 1993) have therefore inferred the survival of stands of sub-alpine forest in hilly regions of the North Island and in isolated pockets along the length of the South Island. Both models still require the restriction of forest beyond what would be expected from the reconstructed temperatures.

1.2 Thesis aims and objectives

Data, especially quantitative data, on climate during the last glacial from the western side of New Zealand are sorely lacking and are vital to understanding Quaternary climate change in this important region. Furthermore the discrepancy between the palaeoenvironment indicated by the pollen record and the palaeoclimate indicated by other palaeoclimatic proxies (ELAs, SSTs etc.) needs to be addressed.

In order to help resolve these problems this thesis examines a series of fossil beetle assemblages from the Westport region of the West Coast, South Island, New Zealand. The assemblages cover the period of the last glacial cycle (ca. 74 ka BP to present (Martinson et al., 1987)) and changes in their faunistic composition should identify the timing and magnitude of climatic and environmental change during this period.

This thesis therefore has the following aims and objectives:

- To produce a fossil beetle record of palaeoenvironmental change for the last glacial cycle (OIS 5a to OIS 1) in the Westport region of the West Coast, South Island, New Zealand.
- To produce a quantitative climatic reconstructions for the last glacial cycle in the Westport region of the West Coast, South Island, New Zealand.
- To interpret the palaeoenviromental and quantitative palaeoclimatic records to;
    1. clarify the relationship between the pollen record and physical proxies of climate change and;
    2. improve the understanding of the scale of cooling and precipitation change in the western South Island during the last glacial cycle.

Fulfilling these aims and objectives will contribute to the current understanding of the New Zealand during the last glacial cycle by providing much needed quantiative estimates of the climate of this important region over the last glacial cycle. Furthermore the palaeoenvironmental reconstructions may help to reconcile the discrepancies between the the pollen record and the physical climate proxies.

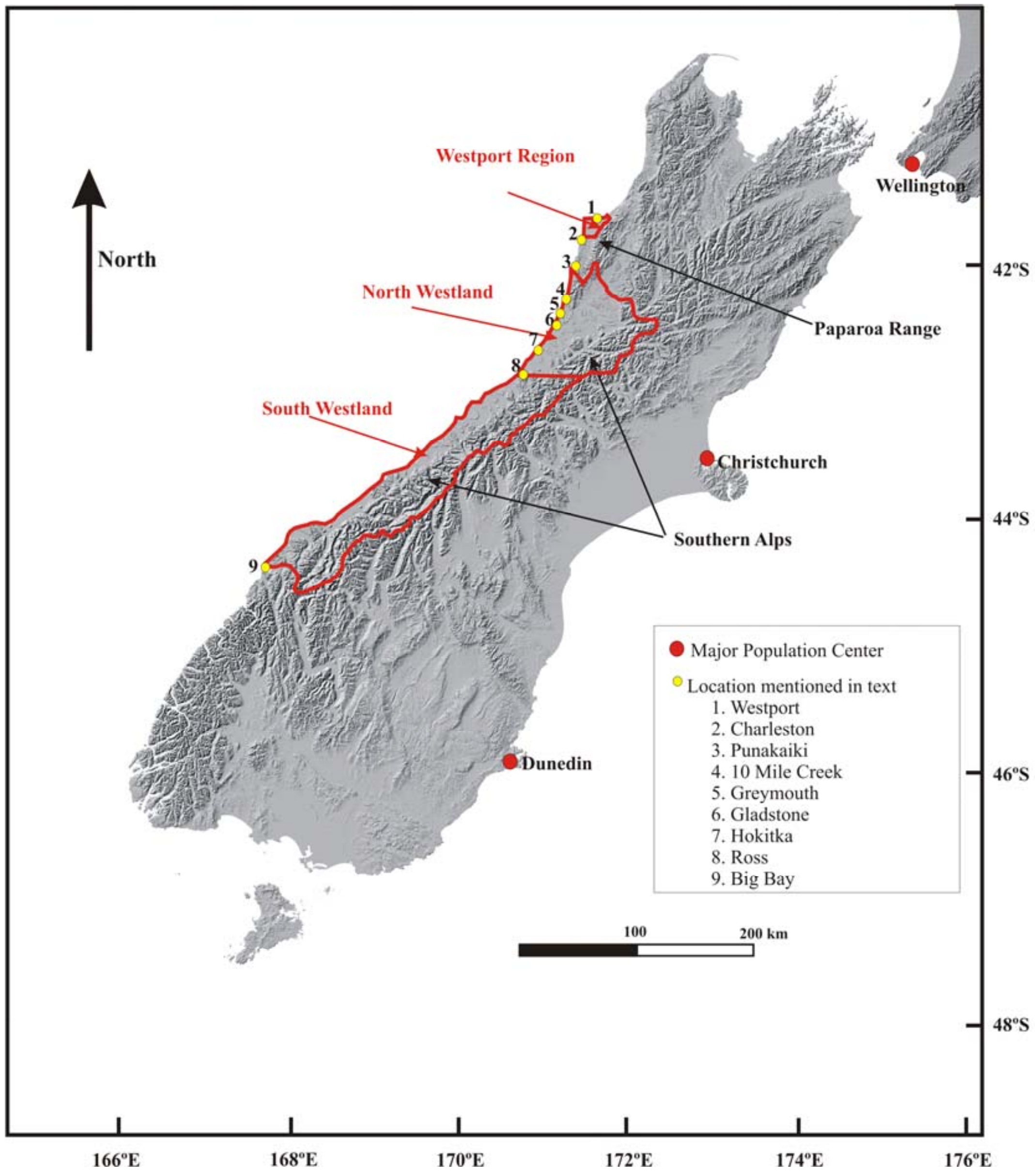
This thesis also builds upon the previous palaeoentomological work of Marra (2003), Marra & Leschen (2004), and Marra et al. (2004), by confirming which environmental variables are the dominant factors controlling the distribution of the New Zealand beetle fauna.

1.3 Modern Physiography

1.3.1 Regions of the West Coast

Throughout this thesis references are made to three regions on the West Coast of the South Island. These regions are Westport, North Westland and South Westland (Fig. 1.2).

Figure 1.2. Map of South Island, New Zealand showing the West Coast divisions used in this thesis (outlined in red), the major mountain ranges (black arrows), and the location of sites mentioned in section 1.3 (yellow dots).



The Westport region is the area within ca. 15 km of the town of Westport (ca. 41°45’S, 171°36’E). The boundaries of the region have previously been defined as “almost to Charleston” (ca. 41°54’S, 171°26’E) (but excluding the Charleston mining area) in the south, the Paparoa Range in the southeast, the Waimangaroa River (ca. 41°43’S, 171°46’E) in the northeast and the Tasman Sea to the west (Fig. 1.2) (McPherson, 1978). These also appear to be the boundaries used by Moar & Suggate (1979) for their pollen based palaeoenvironmental reconstruction of the Westport region. This thesis retains these boundaries for consistency with these previous studies.

The boundaries of North and South Westland are less well defined in the literature and this thesis draws on the boundaries of the Meteorological Service of New Zealand’s Westland Forecast District (Kelly & Marshall, 1996) and the political boundaries of the region of New Zealand administered by the Grey and Westland District Councils (Kelly & Marshall, 1996) region of New Zealand administered by the Grey and Westland District Councils (Kelly & Marshall, 1996) (Fig. 1.2) region of New Zealand administered by the Grey and Westland District Councils (Kelly & Marshall, 1996) (Fig. 1.2). These sources place the northern limit of the overall Westland region at the town of Punakaiki (ca. 42°06’S, 171º20’E) in the north (Grey District Council, 2005) and the southern limit at Big Bay (ca. 44°19’S, 168º07’E) (Westland District Council, 2005) (Fig. 1.2). The eastern limit appears to be the main divide of the Southern Alps. The division between North and South Westland is an arbitrary one that has become generally accepted in the literature and is typically made at the town of Ross (ca. 42°54’S, 170º49’E) (Fig. 1.2) based on the local rugby competition! (Peter Almond, pers. comm.

2005). Again to retain consistency with published studies from the West Coast this thesis continue to use this nomenclature.

1.3.2 Physiography & geology

The northwest coastal margin of South Island, New Zealand (Fig. 1.2) is characterised by a coastal plain backed by a series of uplifted marine benches (McPherson, 1978; Suggate, 1989; 1992). In the area around Westport the exposed gneiss and granites of the Paparoa Range rise sharply to the east (McPherson, 1978; Nathan et al., 2002). Further south in Westland the higher peaks of the Southern Alps back the coastal plain and marine benches.

The breadth of the marine benches varies depending upon the underlying lithology. In the area around Westport (ca. 41°45'S, 171°36'E) (Fig. 1.2) the coastal plain and marine benches are broad due to the easily eroded underlying Pliocene and Miocene mudstones. Elsewhere the coastal margin narrows (e.g. near Ten Mile Creek (ca. 42°20'S, 171°16'E)) (Fig. 1.2) due to a change in the underlying sediments to harder basement rocks of Paleozoic and Mesozic origin (Suggate, 1992). The coastal plain and marine benches widen again in North Westland between Greymouth and Hokitika (e.g. near Gladstone (ca. 42°32'S, 171°09'E)) (Fig. 1.2) where the underlying sediments are again softer Miocene sediments (Suggate, 1992).

The marine benches are preserved due to continuing regional uplift (Suggate, 1965; Nathan et al., 2002) and consist primarily of packages of organic sediments with interglacial climate affinities (e.g. Moar & Suggate 1979; Moar & Suggate 1996). These overlie marine sediments and are capped by dunes or alluvial gravels. The alluvial gravels are correlated to (in the north) or derived from (in the south) glacial advances. Each bench has been assigned to an Oxygen Isotope Stage (OIS) on the principle that each successively higher terrace is associated with an interglacial sea-level. While there is little age control on the assigned ages of the marine benches in the Westport region, careful mapping (Suggate & Waight, 1999; Nathan et al., 2002) has enabled them to be correlated to the sequence of terraces between Hokitika and Greymouth approximately 100 km to the south (Fig. 1.2). Luminescence dating by Preusser et al. (2005) has demonstrated that age inferences of the terraces near Hokitika are robust to the last interglaciation. By extension the ages of the Westport terraces associated with the last glacial cycle are also probably reliable.

1.3.3 Climate

The Westport region (Fig. 1.2) has a temperate oceanic climate. Winds are dominantly (55%) 5-30km/h in strength (Beaufort Scale 2-4) (Hessell, 1982) and are most commonly derived from the southwest (21.2%) although a significant component are north-easterly (13.7%) or westerly (13.0%) in origin (Hessell, 1982). Easterly winds are primarily katabatic and are created by cold air moving down river valleys from the inland ranges. These winds are enhanced during the winter months. Coastal regions are subject to few frosts; the severity and frequency of frost increasing with distance inland (Hessell, 1982). Measurements from the Westport airport (41°44’S, 171°35’E, 4m a.m.s.l.) indicate that winter (July) temperatures fall to a mean minimum of 4.3°C with an overall mean winter temperature of 8.1°C (Anonymous, 1982). Summer (February) temperature averages 16.0°C and reaches a mean maximum of 19.8ºC (Anonymous, 1982). Overall mean annual temperature is 12.1°C (Hessell, 1982). Precipitation averages 2,150mm annually and increases inland with rising elevation (Hessell, 1982). Precipitation is spread evenly throughout the year and is high enough to maintain soil water balance at saturation level during all seasons allowing plenty of moisture for evaporation (9am humidity levels are 80-90% saturation (Hessell, 1982)).

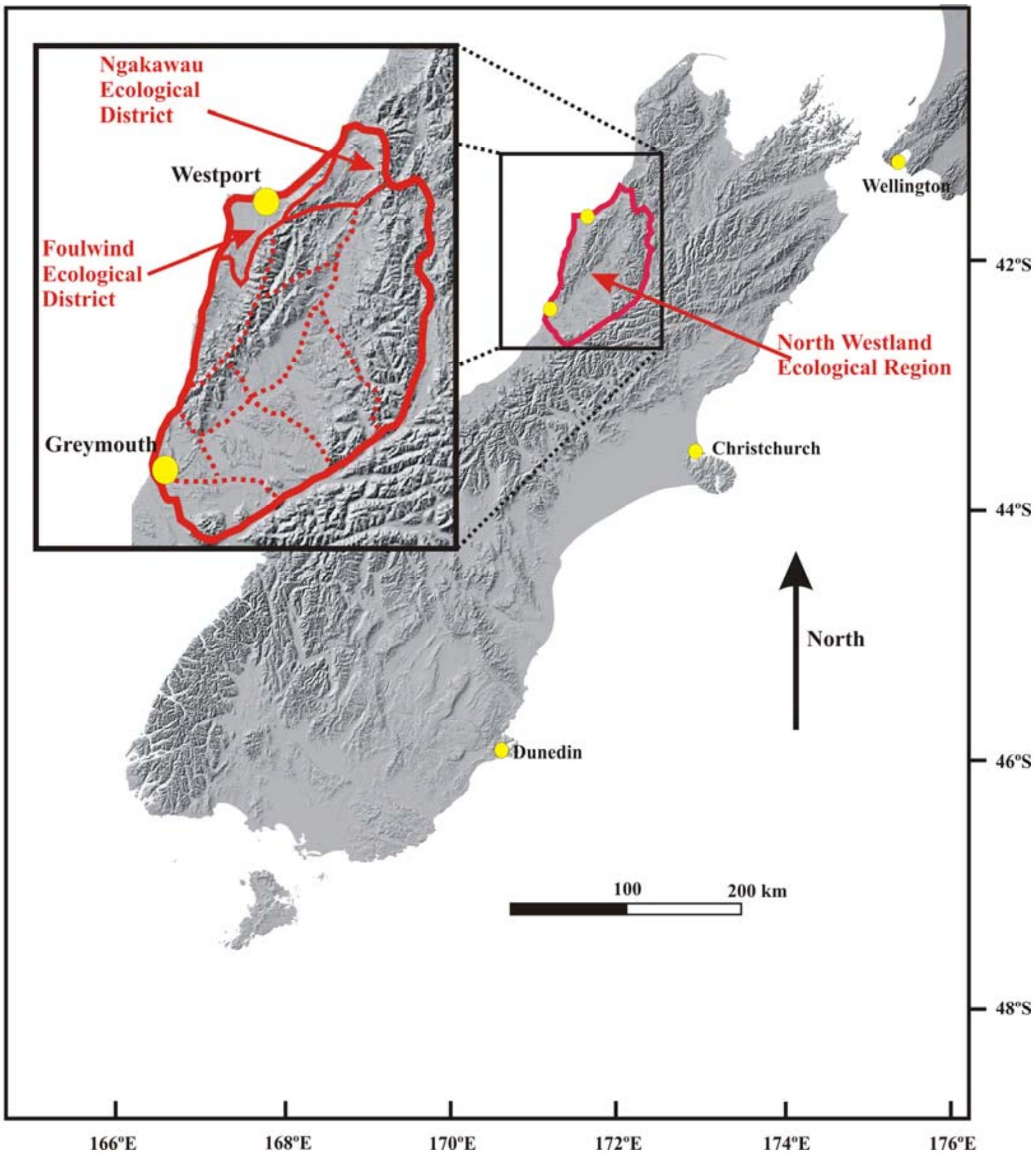
1.3.4 Vegetation

The native vegetation of the Westport region has been largely cleared for pasture but is thought to have consisted of podocarp-hardwood forest (McEwen, 1987). While the actual floristic composition of the region is poorly known extrapolation of the vegetation should be possible from the neighbouring ecological district (Fig. 1.3).

Ecological districts are regions of the country that share a similar climate, geology, topography and vegetation. Human induced modification is also taken into account (McEwen, 1987). Ecological regions are groupings of ecological districts that are very similar in their characteristics to one another (McEwen, 1987). The Westport area falls within the Foulwind ecological district of the North Westland ecological region (McEwen, 1987) and should therefore share ecological characters with the adjacent ecological district of Ngakawau (Fig. 1.3) which is also within the North Westland ecological region (McEwen, 1987).

Extrapolation from the Ngakawau district (McEwen, 1987), and more general records of West Coast vegetation (Wardle, 1991), indicate that coastal areas would be naturally forested by mixed broadleaf taxa including northern rata (*Metrosideros robusta*), kiekie (*Freycinetia banksii*) and the native New Zealand palm (*Rhopalostylis sapida*) (McEwen,

Figure 1.3. Map of South Island, New Zealand showing the North Westland Ecological Region (outlined in red). The inset close-up of the North Westland Ecological Region illustrates the ecological districts that make up the region. Those districts mentioned in the text are labelled and outlined in solid lines. Other districts are outlined in dotted lines.



1987). Bog plants such as manuka (*Leptospermum scoparium*), pakihi rush (Restionaceae), umbrella fern (*Gleichenia* spp.) and mosses dominate in poorly drained areas (McPherson, 1978).

Coastal forest is replaced on the flat plains of the marine terraces by the swamp podocarp kahikatea (*Dacrycarpus dacrydioides*) with rimu (*Dacrydium cupressinum*) and hard beech (*Nothofagus truncata*) forest occupying the poorer soils of the older terraces. Kamahi (*Weinmannia racemosa*) and hard beech forests are dominant on the lower slopes of the Paparua ranges and progressively grade into mixed hard beech, red beech (*Nothfagus fusca*) and silver beech (*Nothofagus menziesii*) forest with increasing altitude (McEwen, 1987). Silver beech is locally dominant near the treeline (approximately 1,300m) (McEwen, 1987). Above the tree line sub-alpine shrubs and grasses, including tussock (*Chionochloa* spp.), *Aciphylla hookeri*, *Celmisia dallii*, and *Gentiana gracifolia* become the dominant vegetation (McEwen, 1987; Wardle, 1991).

1.4 Beetles as palaeoclimatic and palaeoenviromental indicators

With over 350,000 described species in approximately 23,000 genera worldwide (Klimaszewski & Watt, 1997) the beetles (Order Coleoptera) comprise the largest and most diverse group of organisms on the planet (Ashworth & Brophy, 1972; Hutcheson, 1990; Klimaszewski, 1997). They occur in almost every habitat, from deserts to rainforests to the littoral zone (Booth et al., 1990; Ashworth, 2001), with individual species filling a wide variety of specialised ecological roles (Booth et al., 1990; Kuschel, 1990; Hutcheson & Kimberley, 1999). In addition, beetles, like all insects, are ectothermic and thus dependent on climatic conditions during all phases of their life cycle (Ashworth, 2001). This close relationship between beetles and climate means that they are forced to respond rapidly to climatic change. This has been observed in studies of the migration of beetle populations in response to modern fluctuations in temperature (e.g. Hengeveld, 1985). The wide range of environments occupied by beetles, combined with their reliance on temperature, makes beetles excellent proxies for studying climatic and environmental change.

1.4.1 An introduction to the New Zealand beetle fauna

As in the rest of the world, the ecological diversity of beetles is readily apparent in the New Zealand beetle fauna (Leschen et al., 2003). Beetles have been estimated to constitute around 50% of the New Zealand insect fauna (Watt, 1982) and more than 5,220 native species and 350 adventive species (from 1,090 genera in 82 families (Leschen et al., 2003) are currently housed in the New Zealand Arthropod Collection (NZAC) and museums (Klimaszewski & Watt, 1997). This number includes only the formally described taxa and it is probable that the actual number of beetle species in New Zealand is much higher with some estimates in the region of 10,500 (e.g. Kuschel, 1990).

Of the 82 families of beetles occurring in New Zealand (Klimaszewski, 1997; Klimaszewski & Watt, 1997; Leschen et al., 2003) four families, Archeocrypticidae, Gyrinidae, Lycidiae, and Trogidae, contain only adventive species (Klimaszewski et al., 1997). The most common family in New Zealand is the Curculionidae with 1,496 described species (Leschen et al., 2003) followed by the Staphylinidae (936 species), the

Carabidae (424 species), and the Zopheridae (196 species) (Leschen et al., 2003). The proportion of the Curculionidae, Staphylinidae and Carabidae relative to the rest of the fauna is similar to that observed in Australia and the temperate Holarctic Klimaszewski & Watt, 1997). The remaining families generally contain less than 100 species and thus comprise only a minor part of the larger New Zealand fauna. Included in these families are the endemic family Cyclaxyridae and other families representative of a Gondwanan origin (e.g. Chaetosomatidea, Chalcodryidae) (Leschen et al., 2003). The Gondwanan origin, and New Zealand's 80 million years of geographic isolation, has been cited as the primary reason for the high endemism observed at the species (>90% endemism) and genus (>43% endemism) levels of the New Zealand beetle fauna (Klimaszewseki, 1997; Klimaszewski & Watt, 1997).

In addition to the high endemism, New Zealand beetles show other differences to the beetle faunas of elsewhere in the world. Most insects have an *r*-selection breeding strategy, producing high numbers of offspring (Berger, Harper & Townsend, 1996). Some groups of New Zealand insects, however, show an almost *K*-selection breeding strategy producing very few offspring. For example, a study of the endemic New Zealand carabids *Plocamosthetus planiusculus* White and *Megadromous turgidiceps* Broun shows that both species produce around six eggs (Cartellieri & Lövei, 2000). This is ca. 25% of the amount of offspring produced by North American carabids (Marra, 2003).

The New Zealand beetle fauna also shows a distinct lack of adaptation to winter cold (e.g. diapause or freeze tolerance) (Dumbleton, 1967) and are active throughout the year. This year-round activity is confirmed by examination of the seasonal diet of the New Zealand native owl (the morepork, *Ninox novaseelandiae*) (Haw & Clout, 1999) which shows a shift to a primarily beetle-based diet during the winter months when the morepork's primary summer source of food (Leipidoptera) is unavailable. Trap studies examining the seasonal activity of New Zealand invertebrates (e.g. Moeed & Meads, 1992a; 1992b) also indicate that beetles are active in the environment year round although they are less active (i.e. trapped less) during the winter months (e.g. Moeed & Meads, 1992a; 1992b). This year-round activity and lack of adaptation to winter cold is again different to Northern Hemisphere beetles which routinely undergo a winter diapause. This lack of adaptation to winter temperatures suggests that a different group of selection pressures may have acted on the New Zealand beetle fauna during the geological past, perhaps due to the more oceanic setting of New Zealand compared to continental Eurasia and North America.

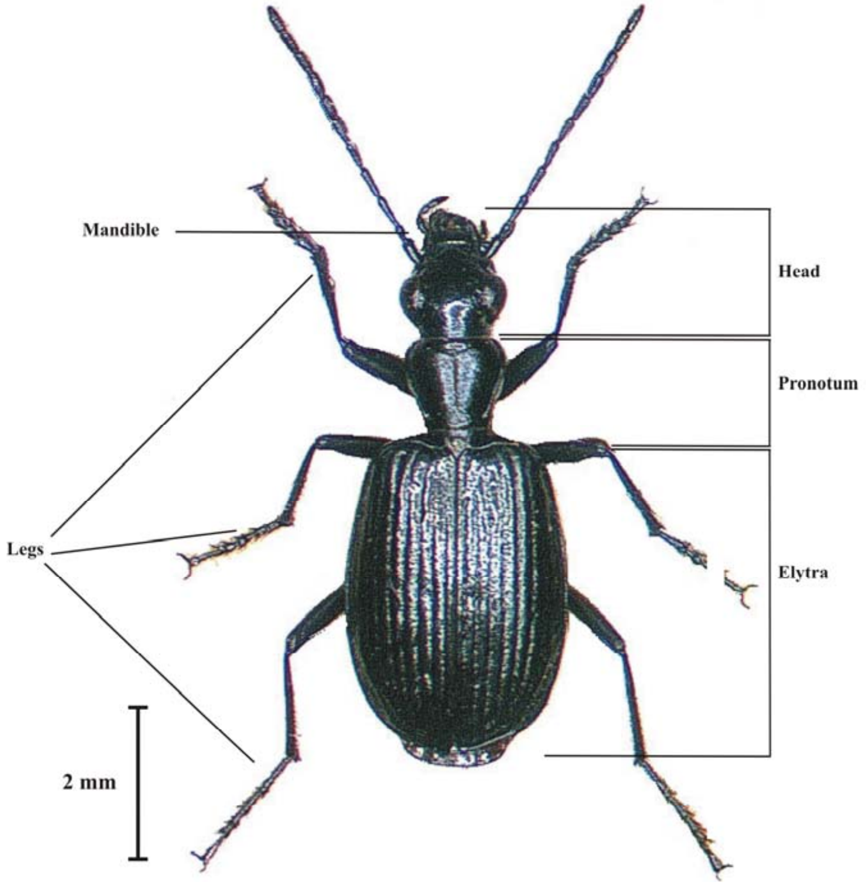
The New Zealand native beetle fauna is primarily associated with the native podocarp-broadleaf and *Nothofagus* beech forests, and the alpine tussock grasslands and herbfelds that covered most of New Zealand during its geological past (Kuschel, 1990; Klimaszewski & Watt, 1997). Introduced taxa tend to restrict themselves to human modified environments (Kuschel, 1990). This association with native habitats means that care must be taken when using New Zealand's native beetle fauna as proxies for palaeoclimatic change as their modern distribution may not reflect their actual climate ranges but rather the modern day distribution of native environments which cover only 23% of New Zealand's land area (Klimaszewski & Watt, 1997). This potential problem is addressed in more detail below.

1.4.2 The evolutionary constancy of beetles

All beetles are characterised by the highly sclerotised plates that make up their exoskeleton and some of these plates, mainly elytra, pronotums, and heads (Fig. 1.4), are often preserved as disarticulated skeletal fragments in organic sediments such as clays, peats, sands and silts (Porch & Elias, 2000). Structural details of these plates can often be distinguished in fossils and, where preserved, key diagnostic characters such as genitalia

Figure 1.4. Illustration of the beetle *Actenonyx bembidioides* White (Carabidae: Harpalinae) showing the commonly preserved skeletal elements. The photograph used in this figure is from Landcare Research, New Zealand, Limited at:

http://www.landcareresearch.co.nz/research/biodiversity/invertebratesprog/carabid/carabidlist/carab_detail.asp?ca_id=175&rec=1.



show a high degree of morphological constancy throughout the Quaternary (Coope, 1977; Morgan & Morgan, 1980). This morphological constancy enables beetle fossils to be identified, often to species level, by comparison to modern specimens and has lead to the conclusion that fossil beetles are representatives of extant species (Coope, 1977; Morgan & Morgan, 1980; Ashworth, 2001)

As the morphology of Northern Hemisphere beetle species appears to have remained constant throughout the Quaternary it is generally assumed that their physiological requirements have also remained stable. The fact that host-specific phytophagus taxa can be sometimes be found in association with macrofossils of their host plant (Coope, 1977) and that the composition of beetle assemblages has remained relatively constant throughout the Quaternary (Coope, 1977) supports this assumption.

Coope (1994; 2004) suggests that one of the reasons for the apparent stability during the Quaternary is that those beetles species that were incapable of surviving fluctuating climates were those that went extinct at the Tertiary-Quaternary boundary ca. 2.4 million years ago when world climates first began to fluctuate. For example, a beetle that was restricted by photoperiod would have been unable to change its latitudinal range, and thus unable to migrate in order to maintain a steady climatic regime (Coope, 1994). Instead the species would probably have gone extinct during the initial period of climatic change at the Tertiary-Quaternary boundary (Coope, 1994). Beetle species that did survive this initial period of climatic change would probably have been able to endure the additional climatic fluctuations that occurred later in the Quaternary (Coope, 1994; Coope, 2004).

Coope (1978; 1994; 2004) and Elias (1991) proposed that the primary mechanism behind the evolutionary constancy of beetle species during the Quaternary was their ability to migrate. Under this hypothesis, as long as beetle populations maintained the ability to change their geographic range in response to climatic change they could effectively maintain a constant climate at the expense of a constant geography (Coope, 1994; Coope, 2004). This migratory behaviour would have the additional effect of continually remixing a species' gene-pool as migrating populations encountered and interbreed with previously isolated populations. This would effectively eliminate any directional selection that had occurred on the populations' gene pools through the introduction of fresh genes (Coope, 1978; Elias, 1991).

Support for this hypothesis is readily apparent in the fossil record where assemblages of beetles appear to have dispersed over hundreds of kilometres in just a few decades (e.g. Atkinson et al. 1987; Schwert et al. 1997). Similar migratory responses have, as previously mentioned, also been observed in modern-day studies of beetles in the Northern Hemisphere (e.g. Hengeveld, 1985).

Bennett (1990) proposed an alternative hypothesis, suggesting that evolutionary constancy of beetle species in the Quaternary could simply be the result of alternating directional selection on populations due to climatic oscillations. For example, during stadial periods, natural selection would act against those genotypes within a population which were poorly adapted to survive cold conditions. Any reduction in the frequency of these cold-intolerant beetles, however, would then be undone by selection for these, presumably, warm-temperature adapted genotypes during interstadials. This alternating sequence of directional selection would effectively result in evolutionary constancy over time (Bennett, 1990).

These hypotheses are not mutually exclusive and may have acted together in order to maintain evolutionary stasis in Quaternary beetle species. However, the apparent evolutionary constancy of beetles from northern and central Europe and North America does not appear to be consistent with some other regions that show high rates of speciation during the Quaternary. Ribera & Volger (2004), for example, created species-level phylogenies of 27 endemic Iberian diving beetles (Coleoptera: Dytiscidae). They determined that 18-19 of the species examined had their origin within the Pleistocene, while 4-6 of those species evolved within the last 100,000 years (Ribera & Vogler, 2004)! These results are similar to other phylogenetic analyses, of both insects and other groups, which also show evidence of rapid Pleistocene radiation (e.g. Vogler et al., 1998; Veith et al., 2003). These studies indicate that *in-situ* speciation was occurring during the Quaternary, probably in response to climatic change (Ribera & Vogler, 2004).

While this evidence of rapid speciation contrasts with the apparent evolutionary stasis exhibited by the fossil beetle fauna of northern and central Europe, Asia and the Americas it may reflect the geographic situation of the taxa. Coope (1979; 1994) hypothesised that the apparent evolutionary stability of beetle species is only likely to occur in *continental* areas where beetle taxa are free to migrate in response to climatic change. Beetle populations that are unable to migrate due to the presence of geographical barriers, such as mountain ranges and oceans, are instead forced to evolve *in-situ* or go extinct (Coope, 1979; 1994). This sort of situation could result in high levels of endemism in regions isolated by geographic barriers. For example the Pyrenees may have effectively isolated the Iberian Peninsula from central and northern Europe during the Quaternary and may therefore be responsible for the ca. 20% endemism observed in the Iberian flora and fauna (e.g. Baletto & Casale, 1991; Greuter, 1991; Blondel & Aronson, 1999 *in* Ribera & Vogler, 2004), and the high incidence of Pleistocene speciation (Ribera & Vogler, 2004). If this hypothesis is correct than it may have grave repercussions for the use of fossil beetles as palaeoclimatic indicators in New Zealand.

New Zealand's flora and fauna exhibit a mix of characteristics similar to those found in continent taxa and those found on an island archipelago (Daugherty et al., 1993). While many of the lineages in New Zealand are from the ancient continent of Gondwana, giving New Zealand's flora and fauna its continental characteristics (Daugherty et al., 1993), the long period of isolation (ca. 80 million years), extensive tectonicism from the late Oligocene on (including extensive mountain building), and periods of sea-level change throughout the Cenozoic (which caused the land area of New Zealand to vary between 122% of modern and 18% of modern) (Cooper & Millener, 1993), has resulted in extensive *in-situ* speciation which appears more characteristic of isolated islands (Daugherty et al., 1993). This high level of speciation is illustrated by the increasing level of endemism observed in the New Zealand flora and fauna throughout the Cenozoic

(Cooper & Millener, 1993), and, as previously mentioned, is particularly apparent in the New Zealand beetle fauna (Klimaszewseki, 1997; Klimaszewski & Watt, 1997).

While this high level of endemism and long period of isolation would seem to indicate that the New Zealand beetle taxa should behave like an isolated island population when it comes to dealing with periods of climatic change (i.e. evolving or going extinct rather than migrating), the existing palaeoenvironmental and palaeoclimatic work on New Zealand beetle fossils (e.g. Marra, 2003; Marra & Leschen, 2004; Marra et al., 2004) does not support this conclusion. Rather this work has shown that beetle fossils can be successfully identified by comparison to the modern fauna (e.g. Marra, 2003; Marra & Leschen, 2004; Marra et al., 2004). This indicates that there has been no morphological change in New Zealand's beetle species throughout the Quaternary, at least amongst those species which have been identified. Unidentified species in fossil assemblages may represent extinct lineages, or may be taxa that have yet to be described from the modern beetle fauna.

While there is currently no published genetic evidence on *when* the species comprising the New Zealand beetle fauna originated, genetic evidence from a study of the New Zealand cicada, *Maoricicada campelli* Myers (Hemiptera: Cicadidae), suggests that evolutionary constancy throughout the Quaternary occurred amongst at least some New Zealand's insects (Buckley et al., 2001). This study indicates that, while there was enough genetic divergence between northern and southern populations of *M. campelli* for a previously unrecognised speciation event to have occurred ca. 2.3 million years ago (around the Tertiary-Quaternary boundary), there is no evidence to suggest any additional speciation events since then, as the remaining genetic variation between populations (within the northern and southern groups) is well within the bounds of a single species (Buckley et al., 2001). This strongly suggests that the last period of speciation in this taxon occurred at the Tertiary-Quaternary boundary. This fits well with the hypothesis of Coope (1994) which proposes that any speciation or extinction amongst those taxa capable of migration in response to climate change would have occurred at the Tertiary-Quaternary boundary. While the findings of Buckley et al. (2001) cannot be directly extrapolated to the New Zealand beetle fauna, when combined with the apparent morphological constancy observed in Quaternary fossils from New Zealand (e.g. Marra, 2003; Marra & Leschen, 2004; Marra et al., 2004) it is considered likely that New Zealand's beetle fauna has, like the beetle taxa used in Northern Hemisphere palaeoentomological studies, remained evolutionary stable throughout the Quaternary. New Zealand beetle fossils should therefore be capable of being used as palaeoclimatic and palaeoenvironmental proxies.

1.4.3 The history of fossil beetles as palaeoenvironmental and palaeoclimatic proxies

Work in the field of palaeoentomology has been undertaken since the 1800s (e.g. Scudder, 1877), however, early studies were consistently based on the false assumption that all fossil specimens, even those found in late Quaternary deposits, were extinct taxa (Elias, 1994). It was not until the mid 20th century that it was determined that many of these fossil specimens were in fact extant taxa (e.g. Lindroth, 1948). This discovery opened the door for the development of 'modern' fossil beetle research.

The first ‘modern’ fossil beetle study was a palaeoenvironmental and palaeoclimatic reconstruction of a late Pleistocene site from Cheshire in the United Kingdom (Coope, 1959). This new method of palaeoenvironmental and palaeoclimatic reconstruction was slow to be taken up by the Quaternary community, however, and initial work on reconstructing Quaternary climates and environments was restricted to the United Kingdom (e.g. Coope et al., 1961; Penny et al., 1969). The discipline was quickly expanded, however, for use at archaeological sites (e.g. Coope & Osborne, 1967). These archaeological-palaeoentomological studies have enabled workers to track the modification of environments by humans (e.g. the clearence of old-growth forests in the British Isles (Whitehouse, 2006)), draw stratigraphic linkages between different sites based on the presence of introduced taxa into different areas (e.g. Coope, 2006), as well as reconstructing the natural and anthropogenic environments occupied by humans (see Elias (1994) for a more detailed discussion of the uses of fossil beetles in archaeology).

Since these early studies the use of fossil beetles as palaeoenvironmental and palaeoclimatic indicators has dramatically increased, spreading to the rest of the Northern Hemisphere (e.g. Matthews, 1974; Coope 1977; Miller & Morgan 1982; Kiselyov & Nazarov, 1984; Guiot et al. 1993; Coope et al. 1997; Lavoie et al. 1997; Motz & Morgan 1997; Whitehouse, 1997; Elias 2000), although the techniques still sees little use compared to palynogical studies (Lavoie & Arseneault, 2001). Most of these palaeoentomological studies have concentrated on producing qualitative reconstructions of environments and quantitative estimates of Quaternary temperatures, however, attempts have also been made to expand the discipline to include reconstructions of precipitation in desert regions (e.g. Elias, 1997).

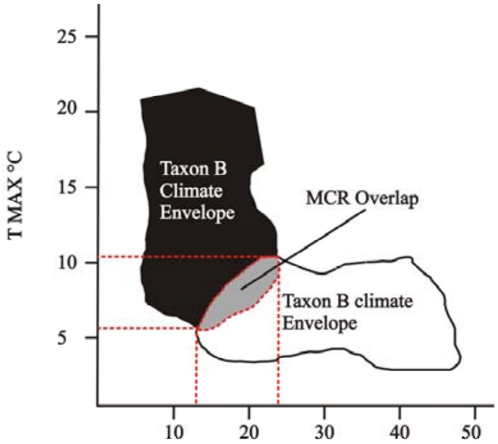
More recently, fossil beetles have seen use as palaeoenvironmental and palaeoclimatic proxies in South America (e.g. Hoganson & Ashworth, 1992; Ashworth & Hoganson, 1993) and work has begun developing them for use in Australia (e.g. Porch & Elias, 2000; Porch, 2007). Fossil beetle research has also spread to New Zealand laying the groundwork for this study. The existing work has been primarily concentrated on developing fossil beetles as proxies for palaeo-temperature (e.g. Marra, 2003; Marra et al., 2004; 2006), although effort has also been put into using them as palaeoenvironmental proxies (e.g Marra & Leschen, 2004).

Paleaoenvironment reconstructions using beetle fossils rely upon the wide range of environments inhabited by beetles (Booth et al., 1990; Ashworth, 2001) and their variety of ecological roles (Booth et al., 1990; Kuschel, 1990; Hutcheson & Kimberley, 1999). As many beetle taxa are associated with specific ecotypes, or even particular host plants, these species can be used to reconstruct the vegetation, substrate and even the type of aquatic environment at a site (Elias, 1994; Porch & Elias, 2000). Palaeoenvironmental reconstructions are typically undertaken by examining the habitat requirements of all the members of a fossil assemblage, including preferred vegetation types (e.g. forest, swamp, grassland), any host plant requirements, the trophic level of the beetles, food preferences etc. These habitat requirements are then combined to produce a composite reconstruction of the palaeoenvironment of the site based on the assemblage. This qualitative reconstructive technique has not changed significantly since Russell Coope originally pioneered fossil beetle research in the 1950s (Coope, 1959), although some workers (e.g. Ashworth & Hoganson, 1993; Cong et al., 1996) have also used cluster analysis in order to quantitatively examine similarities between between different aged assemblages at a site in order to identify the timing of assemblage, and thus environmental, change.

While palaeoenvironmental reconstructions rely on all taxa in an assemblage, palaeoclimatic reconstructions typically rely on only the predators and scavengers as herbivorous beetle may be limited by the distribution of their host plants rather than the climate, and a restricted host plant distribution may therefore result in an inaccurate reconstruction (Coope & Brophy, 1972) The earliest method used to reconstruct palaeoclimate using beetle fossils (e.g. Coope, 1959; Coope et al., 1961) has been termed the 'range overlap method' (Porch & Elias, 2000). This method examines the modern geographic distributions of stenothermic taxa found in the fossil assemblage, inferring information regarding the climate at the time of assemblage formation based on the *geographic* overlap of the taxa's modern distributions. Where climatic data is available from meteorological stations within the overlap of the modern ranges of the taxa, this method can be used to produce quantitative estimates of the temperature (e.g. Cong et al., 1996; Marra, 2003). However, if the modern geographic ranges of the taxa within an assemblage fail to overlap (e.g. due to an anthropomorphically restricted modern distribution) it is impossible to produce a quantitative estimate of the climate at a site (Porch & Elias, 2000). This limitation has resulted in the development of other methods of palaeoclimatic reconstruction which are not reliant upon the overlap of the geographic range.

The most commonly applied method of palaeoclimatic reconstruction is the 'Mutual Climatic Range' (MCR) method of Atkinson et al. (1986). MCR produces quantitative estimates of the palaeoclimate by using the geographic range of a fossil beetle taxon to produce a *climate* envelope. This is measured using a combination of the mean temperature of the warmest month (defined as T MAX) and the range in temperature between the warmest and coldest months (T RANGE) within the area in which the taxon lives (Atkinson et al., 1986). This climate envelope is then graphed as a two dimensional area (Fig. 1.5).

Figure 1.5. An example of a MCR graph with two taxa. The MCR overlap is represented by the grey region and dashed red lines. T MAX is 8.0°C ± 2.5°C and T RANGE is 18.0°C ± 6.0°C.



The climate envelopes of all the taxa within the fossil assemblage are stacked on the same graph and the overlap is the temperature range within which all the taxa could co-habit. This is termed the Mutual Climatic Range (MCR) (Fig. 1.5) and the palaeoclimate at the site, at the time the assemblage was formed, is taken to lie somewhere within the overlap

(Atkinson et al., 1986). MCR can also be used to calculate the temperature of the coldest month (T MIN) (Atkinson et al., 1986).

The MCR method of palaeoclimatic reconstruction requires an extensive knowledge of the ecology and distribution of the beetle taxa in a fossil assemblage. While such information is available for Western Europe (e.g Atkinson et. al., 1987), where MCR was pioneered, it is less readily available for other locations, especially in Australasia, and new techniques have, or are currently being, developed.

One of these techniques is the bioclimatic prediction system BIOCLIM (Busby, 1991). This system examines the constituent species within a fossil assemblage and, working on the assumption that the climate range occupred by each species fits a normal distribution, uses the overlap between the species climate ranges to predict the climate at a site. The development of this system as a method of palaeoclimatic reconstruction using beetle fossils is currently being undertaken in Australia (Porch & Elias, 2000) where it has already being used to reconstruct past climates from Australian pollen records (e.g. McKenzie & Busby, 1992; Lloyd & Kershaw, 1997). It is considered to be more robust than MCR for Australian reconstructions as it is not reliant upon the seasonal difference between winter and summer temperatures, which is less extreme than in the Northern Hemisphere, and thus less likely to be limiting. BIOCLIM instead examines each climatic variable separately, enabling the variables controlling beetle distribution in Australia to be more accurately identified (Porch & Elias, 2000).

Recent work in New Zealand has produced a fourth method of palaeoclimatic reconstruction called the Maximum Likelihood Envelope (MLE) method (Marra et al., 2004). Like BIOCLIM, this method treats each climatic variable separately, with existing studies producing estimates of mean summer temperature (MST) and mean daily minimum winter temperature (MMWT) (Marra et al., 2004). The MLE method adds a statistical error, based on the number of collection locations and the coherency of the data set, to temperature ranges derived from the known distribution of beetle taxa to account for the fact that the full distribution of a beetle taxon is unlikely to be knonw. The addition of a statistical error has traditionally been missing from the other methods of beetle based palaeoclimatic reconstruction although linear regression calculations based on differences between expected and observed values in modern beetle assemblages (e.g. Atkinson et al., 1987) hve been used to 'correct' temperature reconstructions from fossil assemblages. More recently Bray et al. (2006) have undertaken some preliminary work on adding statistical errors to MCR reconstructions using ubiquity analysis.

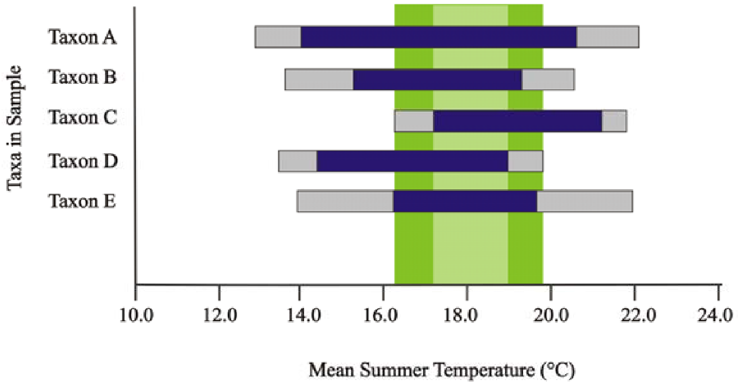
The addition of a statistical error is extremely important in New Zealand studies as the knowledge regarding New Zealand's native beetle distribution is extremely patchy. This is because of the fact that the collection has been undertaken by many different workers using multiple techniques (e.g. malaise traps, (Hutcheson, 1990), pit traps (Watts & Gibbs, 2000)) and that systematic collection studies have been generally been concentrated around urban areas (e.g. Kuschel, 1990). While this type of collection is a common problem world-wide it is particularly problematic in New Zealand as most collection will have occured in the mere ca. 170 years since European settlement. In fact the majority of the New Zealand fauna was collected by Thomas Broun between 1880 and 1923 (Leschen et al., 2003). Establishing an accurate estimate of the distribution of the New Zealand beetle fauna has been further hampered by the fact that most native vegetation was cleared soon after European arrival effectively limiting the natural distribution of native beetle species to the remaining remnants of native vegetation (Kuschel, 1990; Klimaszeski & Watt, 1997).

As previously mentioned, the MLE method treats each temperature variable separately (i.e. separate climate ranges exist for MST and MMWT for each taxon) in a similar manner to BIOCLIM (Busby, 1991). However, while MLE methods typically use a Gaussian distribution to produce an error at the end of a known climate range, the temperature range within which a beetle lives is potentially finite and the MLE method of Marra et al. (2004) therefore uses a sine curve, which has finite end points, to calculate the errors. Like MCR, the climate envelopes for each taxon within an assemblage are then graphed against one another and the overlap in the climate envelopes treated as the range within which the climate variable fell at the time of assemblage deposition (Fig. 1.6).

1.4.4 Potential problems with beetles as palaeoclimatic indicators

While the different methods of palaeoclimatic reconstruction using beetle fossil have been shown to produce accurate estimates of climate by reconstructing the climate of modern assemblages (e.g. Atkinson et. al., 1996; 1997; Coope & Lemdahl, 1996), and by

Figure 1.6. An example of a MLE reconstruction with five taxa. The blue bars represent the known climate envelope occupied by a taxon. The grey tails represent the MLE errors. The pale green region of the figure represents the reconstructed MST for the known ranges while the darker green represents the reconstructed MST taking the MLE errors into account. It indicates an MST of between 16.2°C and 19.9°C.



agreement with other quantitative temperature proxies (e.g. Marra et. al., 2004), some questions have been raised regarding the reliability of fossil beetles as palaeoclimatic indicators (e.g. Andersen, 1993). While these criticisms have typically been levelled at the MCR method, they apply equally to all of the methods of palaeoclimatic reconstruction using beetle fossils.

While some collection studies of modern beetles have obtained distributional data with correlated information on taxon abundance this is by no means standard (Bray et al., 2006), and one of the largest criticisms of palaeoclimatic reconstruction techniques using fossil beetles (e.g. MCR, MLE) is that they typically rely on presence/absence data to establish the climatic range occupied by a beetle taxon (Bray et al., 2006). This is a world wide problem and may result in large errors in the accuracy of a climate reconstruction even when it is based on well known data sets like those of Europe or North America (Huppert & Solow, 2004).

The only way to resolve this problem is extensive sampling of modern beetle populations with recording of species abundance at each collection site. Such work will take decades, and even then will be hampered by anthropogenic modification of the landscape as this will further restrict beetle distribution. In the meantime the development of methods which take into account the incomplete knowledge of species distribution (e.g. MLE (Marra et al., 2004)), and the modification of old methods to include error terms (e.g. Huppert & Solow, 1993; Bray et al., 2006), are improving the accuracy of palaeoclimatic reconstructions based on fossil beetles. The MLE method of Marra et al. (2004) in particular, appears to have good potential at improving the accuracy, if not the precision, of palaeoclimatic reconstuctions, as it was specifically designed around the assumption that the modern distribution of a beetle does not represent its entire climate range.

The MLE method is not without it flaws as it assumes that the climate range occupied by a beetle species has a unimodal distribution. Unfortunately, this may not be the case in all, or even most, beetle species which often show bimodal (or even trimodal) distributions in climate space (Bray et al., 2006). Until quantitative frequency data is available, however, further development and refinement of methods of palaeoclimatic reconstruction such as the MLE method (Marra et al., 2004) or MCR ubiquity analysis (Bray et al., 2006)) are the best way to improve beetle based palaeoclimatic reconstructions.

A second criticism levelled at the reliability of beetle based palaeoclimatic reconstructions is that the macroclimatic zones to which beetles are assigned do not accurately reflect the actual climatic tolerance of the species. This is because individual beetles actually inhabit *microclimates* that differ from the surrounding *macroclimate* (Andersen, 1993; Bray et al., 2006). For example, high-altitude ground dwelling or burrowing beetles may enjoy a warmer microclimate than indicated by the surrounding air temperature due to the fact that soil temperatures decrease more slowly with altitude than do air temperatures (Andersen, 1993). This criticism has not gone unrecognised by the palaeoentomological community, however, and is already acccounted for in the way that MCR and MLE reconstructions are created.

Both MCR and MLE methods use a 'broad-brush' approach to reconstructing palaeoclimate using the entire known geographic range of a species to construct its climate envelope (Atkinson et al., 1986; Coope & Lemdahl, 1996; Marra et al., 2004; Bray et al., 2006). While it is possible that taxa may inhabit a particular of microclimate within the broad climate envelope indicated by its geographic range, this microclimate will, to a large extent, be determined by the overall macroclimate (Coope & Lemdahl, 1996; Bray et al., 2006). If this was not the case then thermophilous species would not be geographically restricted to lower, warmer latitudes, and cold-adapted taxa would not be limited to high latitudes and altitudes, as stenothermic species would be able to find suitable microclimates in a much wider variety of macroclimates (Coope & Lemdahl, 1996). Thus, while the exact microclimatic tolerance of a beetle species may be unknown, the broad macroclimatic patterns that give rise to that microclimate can be reconstructed using a broad-brush approach like MCR or MLE. This is confirmed by studies which use modern beetle assemblages from sites with known climate to test whether those modern assemblages can accurately estimate known temperatures (e.g. Atkinson et al., 1987; Coope & Lemdahl, 1996). Typically the results of these studies are close approximations of the known temperature (e.g. Atkinson et al., 1987; Coope & Lemdahl, 1996), clearly validating these ‘broad-brush’ methods of palaeoclimatic reconstruction.

While the preferred microclimate of a beetle taxon does not appear to impact broad scale reconstructions of palaeo-macroclimate (Coope & Lemdahl, 1996), the point that beetles tend to occupy a microclimate (Andersen, 1993; Bray et al., 2006) highlights the fact that beetles are constrained in their distribution by more than macroclimatic effects. This means that any palaeoclimatic reconstruction is therefore subject to some degree of error. It is for this reason, as mentioned above, that phytophagus taxa are typically excluded from palaeoclimatic reconstructions (Atkinson et al., 1987; Elias, 1991; Bray et al., 2006). The exception to the exclusion of photophagous taxa has been the MLE reconstructions undertaken in New Zealand which use as many taxa in the assemblage as possible.

There are two main reasons for the inclusion of phytophagus taxa in New Zealand studies. Firstly, New Zealand fossil assemblages are routinely dominated by herbivourous weevils (Curculionidae) and include few predatory ground beetles (Carabidae) (Marra, 2003; 2007). The lack of ground beetles differs dramatically from fossil assemblages obtained from other parts of the world. These fossils assemblages typically include many species of ground beetle (e.g. Cong & Ashworth, 1996) and they comprise a substantial proportion of the taxa used in palaeoclimatic reconstructions. The reason for the lack of carabid beetles in New Zealand's fossil assemblages has been related to two factors. Firstly, as previously mentioned, carabid beetles occur in extremely low densities in the New Zealand fauna (Marra, 2003), and secondly New Zealand lacks carabid beetles associated with swamps and peats where most fossil beetle assemblages form (Marra, 2003; 2007).

In addition to the lack of carabids and the dominance of weevils, the New Zealand beetle fauna is also particularly poorly understood and many taxa lack good distributional data (pers. observation). Excluding phytophagus taxa, therefore, leaves few species left in an assemblage to reconstruct the climate. It has therefore been necessary to include all taxa with available distributional data, regardless of which tropic level they occupy, in order to produce palaeoclimatic reconstructions from New Zealand fossil assemblages.

The inclusion of phytophagus species in palaeoclimatic reconstructions from New Zealand does, however, raise the question of whether the climatic reconstructions produced reflect the climate at the time of assemblage formation, or the modern day distribution of New Zealand's native vegetation. While there is no way to be completely sure of the answer to this question, the fact that every climate envelope produced using the MLE method adds a statistical error to the climate range, in order to account for the fact that the full distribution of the beetle is unknown (Marra et al., 2004), may help to alleviate any problems associated with the restricted distribution of New Zealand's native vegetation.

Furthermore, the MLE method has been shown to produce estimates of temperature (e.g. Marra et al., 2004) that agree with temperature estimates from other quantitative proxies such as sea-surface temperatures (e.g. Barrows & Juggins, 2005), equilibrium line estimates (ELAs) for glaciers (e.g. Porter, 1975) and from transfer function results from chironomids (Woodward & Shulmeister, 2007) suggesting that it is a robust method of measuring the New Zealand palaeoclimate. The reconstructions presented in this thesis therefore continue to use the MLE method of Marra et al. (2004).

1.5 Vegetation history of the West Coast since the penultimate (Waimea) glaciation

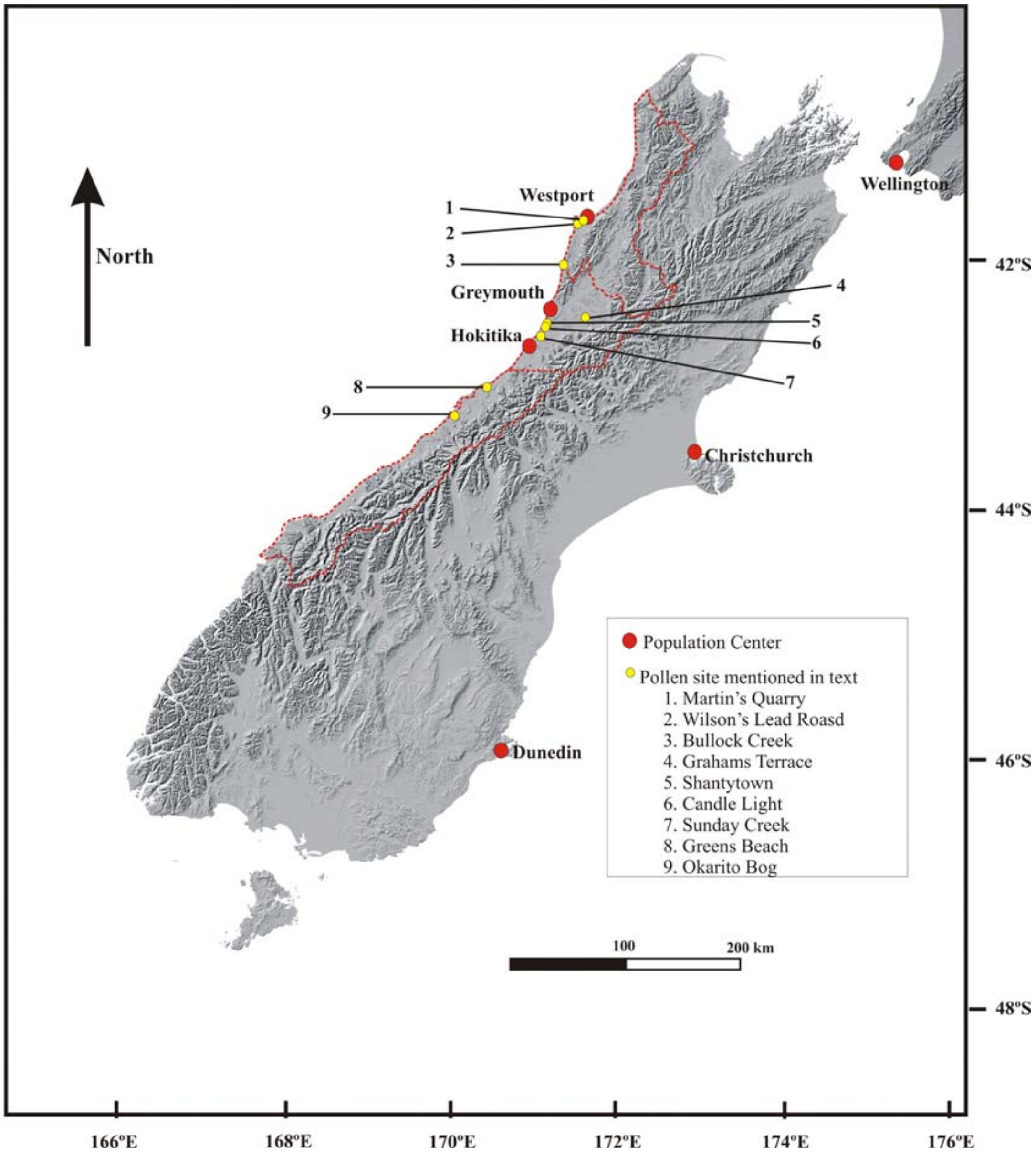
Pollen records indicate that the vegetation of the West Coast of the South Island has undergone transitions from forest to shrubland to grassland and back. These changes have been used to infer periods of climatic change which have been matched to the Oxygen Isotope Stages (OIS) recognised in marine cores (Table 1.1).

The later part of the penultimate (Waimea) glaciation (OIS 6) (ca. 189.6 – 129.8 ka BP (Martinson et al., 1987)) is known from few West Coast records. Those that do cover this period (e.g. Chesterfield Road (42°38’S, 171°07’E) (Moar & Suggate, 1996), Greens Beach (43°01’S, 170°32’E) (Moar & McKellar, 2001) and Okarito Bog (43°13’S, 170°13’E) (Vandergoes et al., 2005), Fig. 1.7) indicate that the vegetation was characterised by a mixture of grassland and shrubland (Table 1.1). This has been

Table 1.1 Palaeoenvironmental History of the West Coast, South Island New Zealand with qualitative climate inferences. Based on the summary of Moar & Suggate (1996) with South Westland information from Almond (1996), Almond et al. (2001), Moar & McKellar (2001) and Vandergoes et al. (2005). New Zealand nomenclature of the events is given along with the associated Oxygen Isotope Stage. Approximate ages for the beginning of the events are from Martinson et al. (1987).

Stratigraphic Nomenclature	**OIS**	**Age (ka BP)**	**Qualitative Climate Inferences**	**South Westland**	**North Westland**	**Bullock Creek, Punakiaki**	**Westport**
Aranui Interglaciation	1	12.1	Warm	Podocarp forest	*Dacrydium cupressinum* forest OR *Weinmannia*/*Metrosideros* (hardwood) forest OR Shrubland		*Dacrydium cupressinum* forest
Late Otira Glaciation	2	24.1	Cold	Shrubland/Grassland	Grassland OR Grassland/Shrubland		Grassland
Mid Otira Glaciation	3	59.0	Cool	Shrubland	Open *Nothofagus menziesii* forest		*Halocarpus*/*Phyllocladus* shrubland
Early Otira Glaciation	4	79.3	Cold	Grassland OR Shrubland	Grassland		
Kaihinu Interglaciation	5a	91.0	Warm	Podocarp forest and shrubland	Various combinations of *Nothofagus fusca*-type and *Nothofagus menziesii* forest	*Metrosideros*/Shrubland	
	5b	99.4	Cool	Podocarp forest and shrubland	Various combinations of *Nothofagus fusca*-type and *Nothofagus menziesii* forest with some *Dacrydium cupressinum*	*Nothofagus* forest	
	5c	110.8	Warm	*Dacrydium cupressinum* forest OR Podocarp forest	Various combinations of *Nothofagus fusca*-type and *Nothofagus menziesii* forest with some *Dacrydium cupressinum*	*Metrosideros*/*Nestigis* forest and shrubland	Mixed *Nothofagus*/*Dacrycarpus* forest
	5d	122.6	Cool	Heath forest OR Heath-shrubland OR Podocarp forest & shrubland	Various combinations of *Nothofagus fusca*-type and *Nothofagus menziesii* forest		*Nothofagus* forest
	5e	129.8	Warm	*Dacrydium cupressinum*/*Weinmannia* forest	*Dacrydium cupressinum*/*Metrosideros*/*Weinmannia* forest		*Dacrydium cupressinum forest*
Waimea Glaciation	6	189.6	Cold	Grassland and *Coprosma*/*Myrsine* shrubland OR Grassland, shrubland and *Nothofagus* forest	Grassland and *Coprosma*/*Myrsine* shrubland		

Figure 1.7. Map of the South Island, New Zealand indicating the location of the pollen records mentioned in the text.



interpreted as representative of a cold, moist climate (Vandergoes et al., 2005). The shrub flora appears to have consisted of *Coprosma* and *Myrsine* and is inferred to have occupied areas with poorly drained soils (Moar & Suggate, 1996; Moar & McKellar, 2001). The Okarito Bog record (Vandergoes et al., 2005) also indicates significant *Nothofagus* pollen at this time. While it is posited that this is from long distance dispersal Vandergoes et al. (Vandergoes et al., 2005) acknowledge that *Nothofagus* forest may also have been a significant component of the vegetation.

The transition from the penultimate glaciation to the last (Kaihinu) interglaciation (OIS 5e) (ca. 129.8 ka BP (Martinson et al., 1987)) is recorded in a number of sites along the West Coast (e.g. Martins Quarry (41°45'E, 171°35'E) (Moar & Suggate, 1979) Candle Light (42°34'S, 171°10'E), Chesterfield Road (Moar & Suggate, 1996), Greens Beach, (Moar & McKellar, 2001) and Okarito Bog (Vandergoes et al., 2005), Fig. 1.7) and saw the disappearance of the grass and shrub dominated flora and its replacement with podocarp rainforest (Table 1.1). The pollen records indicate that this podocarp rain forest comprised a similar assemblage of trees and shrubs to those found on the West Coast today (see Section 1.3 above) with *Dacrydium cupressinum* (rimu), *Metrosideros* and *Weinmannia* dominant (Moar & Suggate, 1996; Moar & McKellar, 2001). This pollen flora has been interpreted as representing a warm climate (Moar & Suggate, 1996). While the initial phase (OIS 5e) (ca. 129.8 – 110.8 ka BP (Martinson et al., 1987)) of the Kaihinu interglaciation was warm the pollen records show that shifts in the composition of the vegetation occurred on the West Coast during OIS 5. This has been interpretated as indicating that the climate of the last interglaciation fluctuated between warm and cool phases (Table 1.1) (Moar & Suggate, 1996). *Nothofagus* (southern beech) forest became dominant in both North Westland (e.g. Candle Light (Moar & Suggate, 1996), Sunday Creek (42°38'S, 171°07'E) (Dickson, 1972; Moar & Suggate, 1996), Fig. 1.7) and

Westport regions (e.g. Martins Quarry (Moar & Suggate, 1979)) in OIS 5d (ca. 110.8 – 99.4 ka BP (Martinson et al., 1987)) but was replaced during OIS 5c (ca. 99.4 – 91.0 ka BP (Martinson et al., 1987)) by podocarp or mixed podocarp-beech forest indicative of a transition back to a warmer phase (Table 1.1). The Bullock Creek pollen record (42°06'S, 171°21'E) differs from other northern West Coast sites indicating *Metrosideros* shrubland dominant during the OIS 5c and OIS 5a (ca. 79.3 – 74.0 ka BP (Martinson et al., 1987)) warm phases and *Nothofagus* forest dominant during the cooler OIS 5b (ca. 91.0 – 79.3 ka BP (Martinson et al., 1987)) phase (Moar & Suggate, 1996). Unlike the North Westland and Westport regions South Westland appears to have remained free of significant beech forest throughout the last interglaciation (Moar & McKellar, 2001; Vandergoes et al., 2005). The cool phases of the last interglaciation are still represented in the pollen record however. The Greens Beach record (Moar & McKellar, 2001) correlates a replacement of podocarp rainforest taxa by heath forest (or heath shrubland) taxa in the OIS 5d cool phase (Table 1.1). The Okarito Bog record indicates two peaks in shrub and grass pollen relative to tree pollen prior to the apparent transition to the last glaciation. These are interpreted as corresponding to the OIS 5d and OIS 5b cool phases (Vandergoes et al., 2005).

Palaeoenvironmental information about the early part of the last (Otira) glaciation (OIS 4) (ca. 73.9 – 59.0 ka BP (Martinson et al., 1987)) is limited outside of South Westland. Only the Sunday Creek site in North Westland (Fig. 1.7) covers the transition and indicates a shift from *Nothofagus* dominated forest to open grassland (Dickson, 1972; Moar & Suggate, 1996). Records from South Westland also indicate the decline of forest vegetation during OIS 4 (Table 1.1). Okarito Bog shows the virtual elimination of all tree pollen coinciding with a peak in grass pollen (Vandergoes et al., 2005) although shrubs remain the dominant source of pollen (Vandergoes et al., 2005). The Opuku record from Greens Beach (Moar & McKellar, 2001) indicates that forest was replaced by grassland during OIS 4. These records indicate that South Westland was dominated by a combination of montane-subalpine shrubs and grasses during OIS 4 (Table 1.1).

The presence of *Phyllocladus*/*Halocarpus* shrubland is indicated for the Westport region (the Wilson's Lead Road sites (Moar & Suggate, 1979)) during OIS 3 (ca. 59.0 – 24.1 ka BP (Martinson et al., 1987)) and this is in keeping with records from Okarito Bog in South Westland (Vandergoes et al., 2005). Records from North Westland contrast with this reconstruction and instead indicate an open forest of *Nothofagus menzieseii* (e.g. Shantytown (42°32'S, 171°10'E) (Moar & Suggate, 1996), Fig. 1.7). The Westport region continues to differ from more southerly areas during OIS 2 (ca. 24.1 – 12.1 ka BP (Martinson et al., 1987)) (Table 1.1) with evidence for a widespread grassland in the region at this time (Wilson's Lead Road (Moar & Suggate, 1979)). This agrees with inland sites (e.g. Grahams Terrace (42°29'S, 171°34'E) (Mew et al., 1986) however it differs from both North (Moar & Suggate, 1996) and South Westland (Okarito Bog (Vandergoes et al., 2005)) records which indicate a mixture of both shrub and grassland during this period. The differences between North Westland and the Westport region are thought to be the result of strong winds and differing soil conditions (Moar & Suggate, 1996) although increased frostiness has also been proposed (Moar & Suggate, 1979).

The end of the Otira Glaciation (ca. 12,050 yrs BP (Martinson et al., 1987)) sees a shift from grassland or grass-shrubland dominated pollen assemblages to assemblages dominated by *Dacrydium cupressinum* indicating widespread podocarp forest dominating low elevations across the entire West Coast during OIS 1 (Moar & Suggate, 1996; Vandergoes et al., 2005). This is consistent with modern records of vegetation (see section 1.3 above) from the West Coast which indicate the dominance of podocarp-broadleaf vegetation in lowland areas.

1.6 Thesis Layout

This thesis follows a standard format but was initially developed as a series of papers. Papers based on Chapter 5 and part of Chapter 6 are currently in press (Burge & Shulmeister, In Press-a, Burge & Shulmeister, In Press-b).

Chapter 2 describes the methods of fossil beetle sampling and palaeoenviromental and palaeoclimatic reconstruction used in this study.

Chapter 3 presents a statistical test of the environmental factors controlling beetle distribution in New Zealand. This chapter was undertaken with the statistical assistance of Mr. Craig Woodward.

Chapters 4 through 6 address a series of individual sites and provide a chronological transect of palaeoclimatic and palaeoenvironmental change on the West Coast.

Chapter 4 presents a palaeoenvironmental and palaeoclimatic reconstruction from a mid-Holocene site in the Westport region. This chapter tests the reliability of beetle fossils as palaeoclimatic proxies for this region by comparing fossil beetle reconstructions to the known climate and environment of the Holocene. This chapter also produces the first estimates of palaeoprecipitation in New Zealand using beetle fossils.

Chapter 5 presents a palaeoenvironmental and palaeoclimatic reconstruction from OIS 4. No palaeoenvironmental or palaeoclimatic data exists for this period in the Westport region and this study provides a fossil beetle record supported by spot pollen samples.

Chapter 6 presents a record of palaeoenvironment and palaeoclimatic change in the Westport region over the OIS 3/OIS 2 transition. This record is the core of this thesis and comprises the longest continuous fossil beetle record undertaken in New Zealand. The record consists of 18 samples from a single unit and covers the 16,000 year period between ca. 37 and 21 ka BP. The record is compared to the existing pollen based record from the same site.

Chapter 7 places the regional studies in the wider context of global climate and environmental change during the last glacial cycle.

Chapter 8 reiterates the problems with palaeoentomological research in New Zealand, suggestes directions for future research and summarises the major findings of this thesis.

Chapter 2

Methods for palaeoclimatic and palaeoenvironmental reconstruction

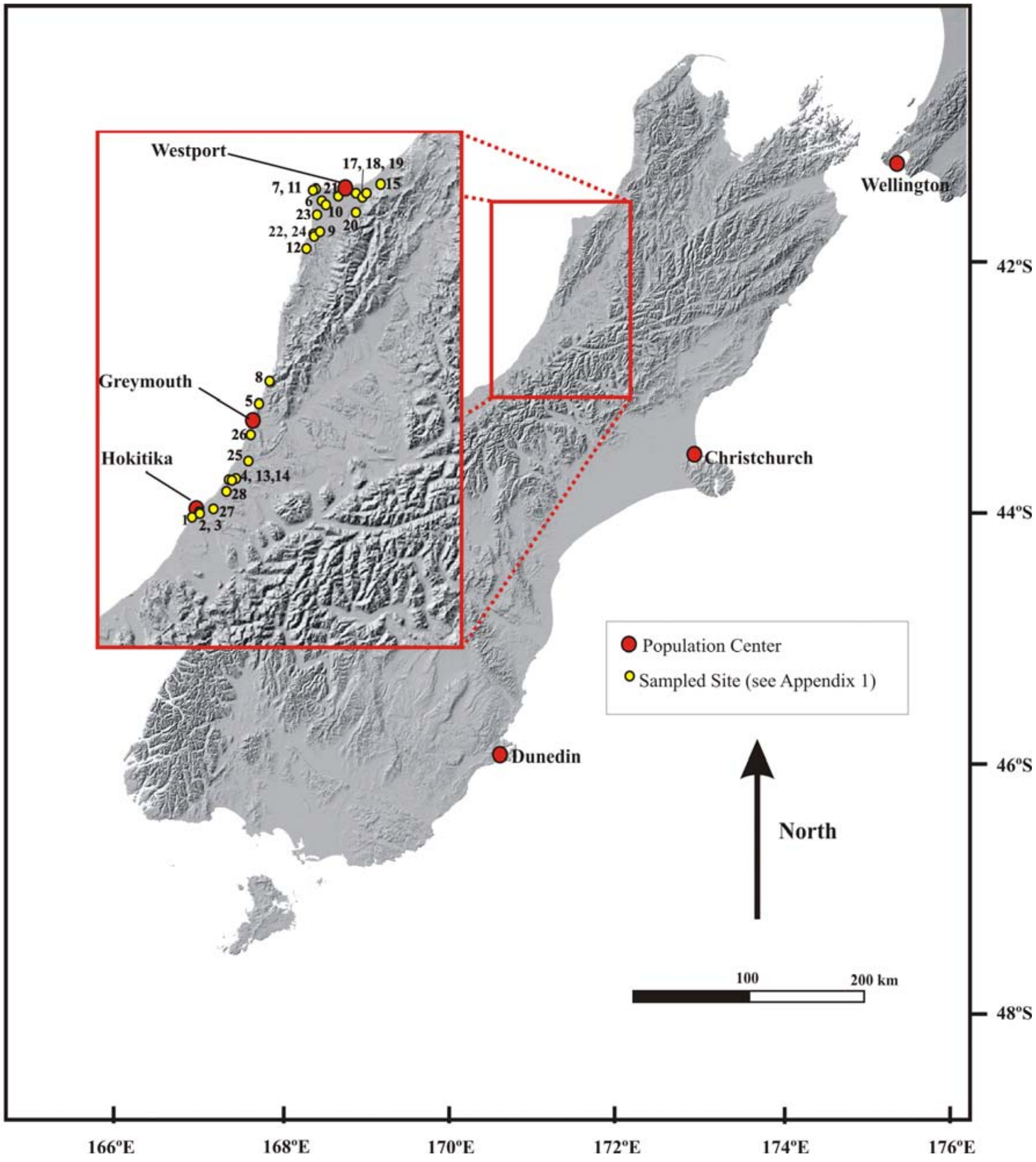
2.1 Site selection

Water-lain sediments such as those deposited in lakes, ponds and overbank peat deposits have been determined to be prime targets to look for beetle fossils as they help provide the rapid burial (Marra et al., 2004) and anoxic conditions that encourage the preservation of beetle remains (Elias, 1994). Particularly good sediments are silts and peats that are rich in organic matter such as plant macrofossils (Elias, 1994). Unlike pollen, which requires small samples for analysis, fossil beetle studies generally require the collection of samples which are substantially more than a litre in volume (Elias, 1994). Consequently most samples are collected from exposed outcrops found in road-cuttings and in river banks (Elias, 1994).

The depositional environments required for the preservation of beetle fossils are similar to those required for the preservation of fossil pollen (Macphail & McQueen, 1983). West coast sites known to have existing palynological records were therefore the first sites sampled as being most likely to contain beetle samples. Additionally many of these sites are either numerically dated, or at least correlated to the marine oxygen isotope record, enabling sites within the targeted time period of this study to be actively selected. Additional sites, predominantly road cuttings and coastal and river exposures, were also sampled where sediments appeared appropriate for the preservation of fossil beetles.

Potential beetle-bearing units were identified at each site and bulk sampled. In total, 71 pilot samples were processed from 28 different sites (see Appendix 1). Eleven of these sites were in the Greymouth/Hokitika region of Westland and the remaining 17 were in the region around Westport (Fig. 2.1).

Figure 2.1. Map of the South Island, New Zealand with enlargement of the West Coast showing the location of sites sampled for beetle fossils in the course of this thesis. A breakdown of these sites is provided in Appendix 1.



Most of these pilot samples did not contain adequete numbers of beetle fossils to warrent futher examination and they were discarded from the study. In order to enable future workers to avoid pointless re-sampling of these sites, however, a brief description, and the grid reference, for each site are provided in Appendix 1.

Six sites contained sufficient numbers of beetle remains to be considered worth re-sampling (Appendix 1). After re-examination of these six sites only three sites, all in the Westport region, were deemed suitable for use in this study. These sites are Alma Road (Chapter 4), Keoghan's Road (Chapter 5) and Wilson's Lead Road (Chapter 6). These sites contained both the best preserved and greatest numbers of identifiable beetle taxa, and also appeared to span the target time period of this study.

2.2 Sample collection, processing and identification

Bulk samples generally consisted of at least ca. 5 kilograms of sediment from a single stratigraphic unit. They were collected from cleaned-off outcrops using a spade. Samples were kept in the dark in sealed plastic bags prior to processing. Processing of the samples generally followed the process outlined in Elias (1994). A summary of the process used, along with the minor modifications made to the standard method, is provided below.

Water was added to a bulk sample and the sample was brought to the boil so as to gently break up the sediment without damaging the beetle fossils (Maureen Marra, pers. comm. 2003). In cases of samples that were difficult to disaggregate calgon (Sodium hexametaphosphate, $Na_6O_{18}P_6$) was also added. Once the material was disaggregated it was washed through a 297μm sieve to remove the silt and clay particles while retaining organic materials on the mesh. Excess water was gently pressed from the retained material before it was moved to a plastic bowl. As oil adheres primarily to chitin rather than plant material it enables beetle fossils to float when water is added (Elias, 1994). Lamp oil (following Marra, 2002), being more pleasant to use than the more typical kerosene (Elias, 1994), was therefore massaged through the retained material before cold water was rapidly added to the sample. The addition of water in this way stirred up the organic material and enabled the coated insect remains to float to the surface (Elias, 1994). The water was then left to settle allowing any non-coated material to sink to the bottom of the bowl. The floating insect remains were then decanted off. This process was repeated multiple times until no more material floated to the surface.

Once the floating organic material had been decanted it was first rinsed with detergent, to remove the oil, and then ethanol, to remove the detergent. The material was then examined under a microscope and the beetle fossils picked out using forceps. These remains were stored in ethanol and later mounted onto palaeontology slides using gum tragacanth (Elias, 1994) for identification.

Identification of beetle fossils was undertaken at the New Zealand Arthropod Collection (NZAC) in Auckland, New Zealand. Identifications were made by morphological comparison of the preserved fossil elements to the same elements in modern specimens. Consultation with experts at NZAC was also used to help identify some fossils.

In many cases it was not possible to identify fossils to species level due to a combination of poor fossil preservation and a lack of modern specimens in the NZAC. This problem was often exacabated by the fact that some of the older specimens within the NZAC were mounted in such a way as to obscure the surface detail of the skeletal elements of the beetle. While it was therefore impossible to confidently ascribe some fossils to species level it was generally possible to narrow these fossils down to a group of species or a genus.

2.3 Age control

Methods of age control varied between each site due to differences in available dating targets and the presence of existing age data. The age control at each site is therefore discussed separately in each chapter. Radiocarbon (^{14}C) ages were the most common method of dating used, however, and ages were calibrated using the OXCAL programme (Bronk Ramsey, 2001) using the INTCAL 04 calibration curve. Ages under 11,000 years in age were corrected by -27 years due to the offset between the Northern and Southern Hemispheres (McCormack et al., 1998). Ages beyond the INTCAL 04 calibration curve were calibrated using CALPAL (Weninger et al., 2006).

2.4 Palaeoclimatic and palaeoenvironmental reconstructions

Data on the present-day habitat preferences (e.g. closed canopy, swamp, tussock grassland, aquatic, riparian etc.) of the identified beetle taxa were collated from the literature, the NZAC and the Lincoln University Entomology Museum (LUNZ), Christchurch, New Zealand. This information was then compiled for the beetle assemblages at each site to provide a reconstruction of the environment at the site at the time of deposition. When a beetle taxon was known to be host-specific to a particular plant taxon this was taken to be evidence of the occurrence of that plant taxon at, or close to, the deposition site, as, unlike pollen, beetle fossils are typically derived from the area immediately around the deposition site due to the necessity of rapid burial for fossil preservation to occur (Marra & Leschen, 2004).

Modern distributional data for each of the identified beetle taxa was compiled from specimen label information at NZAC and LUNZ. Estimates of the palaeoclimate were then produced using the Maximum Likelihood Envelope (MLE) method of Marra et al. (2004). MLE is a non-gaussian approach to reconstructing bioclimatic envelopes for taxon ranges. Each taxon is assigned a known range in climate space based on its modern geographic distribution. This is done by assigning each collection location a set of climate variables derived from the New Zealand climate surfaces (Leathwick et al., 1998). These climate surfaces are based on a 100m grid digital elevation model derived from 20m contour data from the New Zealand 1:50,000 topographic map series. The climate surface estimates are produced from thin-plate splines (smooth interpolators) surfaces using ANUSPLIN (v. 4.1) from the climate data collected from 346 New Zealand climate stations over a period of 30 years (Leathwick et al., 1998). For each of the locations at which a beetle taxon was collected the value of the climate variable in the appropriate grid cell (climate surface) is placed into the MLE model (Marra et al., 2004). The MLE model then uses a sine curve to calculate a box error for each end of the climate distribution based on the number of observations (collection sites) and the similarity of the data set (Marra et al., 2004). The less coherent the data or the fewer the number of data points, the larger the error term.

For those taxa which could not be identified to species level the collection locations of all species within the genus or species group were used to produce the MLE envelope. Ironically this inability to identify fossils to species level actually improves the *accuracy* of the MLE reconstructions, due to the poor collection data available for New Zealand beetle species. Using the larger distribution data set available for a species group or genus helps eliminate this problem by providing more data points on which to calculate the MLE reconstruction. The resulting MLE envelope is less precise, i.e. wider, than if based on a single taxon, but is a more accurate estimate of the climate range within which the fossil taxon is likely to have lived.

The MLE climate ranges created for each taxon are then compared against one another with the overlap of these climate envelopes producing the estimated range of the climate variable at the time that the assemblage was formed. This is plotted against the modern mean value of the reconstructed variable at the sample site to determine the change in climate from today (Marra et al., 2004). During the course of this study the MLE approach was also applied to precipitation data.

Chapter 3

Environmental and climatic factors controlling the distribution of the New Zealand beetle fauna: A test of the assumptions underlying the use of fossil beetles as palaeoclimatic proxies

3.1 Introduction

The application of fossil beetles as quantitative palaeoclimatic proxies in New Zealand (e.g. Marra et al., 2004) builds on fossil beetle studies in the Northern Hemisphere which routinely produce quantitative estimates of temperature (e.g. Atkinson et al., 1987; Elias, 1999). An assumption of these studies is that due to the ecothermic nature of beetles temperature controls their distribution. While this assumption has been validated for Northern Hemisphere beetle taxa, which show temperature controlled distribution limits (e.g. Ungerer et al, 1999) and migrational responses to temperature change (e.g. Hengeveld, 1985), it has not been validated for the New Zealand beetle fauna and its application is based upon anecdotal evidence (e.g. Dumbleton, 1969).

The New Zealand beetle fauna has been geographically isolated from the rest of the world for the last 80 million years (Klimaszewski, 1997) resulting in 90% endemism of the beetle fauna at the species level and a high level of endemism at the generic level (Klimaszewski & Watt, 1997). This isolation means that assumptions regarding the New Zealand beetle fauna based on the traits of Northern Hemisphere taxa may be naive. For example, Northern Hemisphere beetle taxa commonly exhibit strong freeze tolerance and diapause as a means of surviving the cold winters in continental parts of the Northern Hemisphere. Both of these traits are rare in Southern Hemisphere taxa (Dumbleton, 1967;

Sinclair et al., 2003b), which, particularly in oceanic settings like New Zealand, are subject to more maritime climates. These differences in climate are important considerations as different ecological pressures may have been emphasised over the past 80 million years of isolation. Variables such as moisture levels, previously suggested as one of the major factors affecting the New Zealand beetle fauna (e.g. Dumbleton, 1969; Hurnard, 1978), may be just as important as temperature in controlling beetle distribution.

In addition to the New Zealand specific issues there are some general problems with beetle distribution data. While intensive sampling has been undertaken in some areas, such as the 15 year long Lynfield Project in Auckland (Kuschel, 1990), other areas have seen little in the way of systematic collection and a large proportion of beetle distributional data is the result of chance collection. This means that the distribution of many taxa is poorly understood. Furthermore while abundance data is available from some studies collectors have used a variety of collection techniques (e.g. malaise traps, (Hutcheson, 1990) and pit traps (Watts & Gibbs, 2000)). This makes it difficult to compare between different studies and makes statistical analysis based on abundance data (e.g. Lotter et al., 1997) difficult to apply. Instead any studies of beetle distribution must rely on presence/absence data.

This chapter presents a series of numerical analyses using the available presence/absence data to explore the influence of a suite of environmental and climatic factors on the distribution of New Zealand beetle taxa preserved as fossils. The statistical analysis was undertaken with the assistance of Mr. Craig Woodward.

3.2 Methods

The purpose of this chapter is to test whether fossil beetles can be used as reliable indicators of environmental and climatic change. The initial data set used in this study comprised modern presence/absence collection data, from 1,443 sites in the North and South Islands of New Zealand, for 82 taxa (from 14 families) (see Appendix 2). These taxa were chosen as they were observed to occur in the fossil assemblages examined in this thesis. Distributional and ecological data for these taxa were compiled as described in Chapter 2.

In order to determine which environmental parameter(s) explain the greatest amount of variation in the distribution of New Zealand beetle species a series of ordinations were performed using the following environmental parameters:

1. Latitude (Lat.)
2. Longitude (Long.)
3. Mean Summer (February) Temperature (MST) (ºC)
4. Mean daily Minimum Winter (July) Temperature (MMWT) (ºC)
5. Mean Annual Precipitation (MAP) (cm year^{-1})
6. Ratio of Precipitation to Evaporation (P:E)
7. Mean Annual Solar Radiation budget (MAS) (MJ m^{-2} day^{-1})

8. Vegetation Habitat Index (VI) (0.0: open vegetation (e.g. grassland), 0.5: half-closed vegetation (e.g. shrubland), 1.0: closed vegetation (e.g. forest))
9. Water Habitat Index (WI) (0.0: dominantly dry, 0.5: riparian/swamp, 1.0: open water)

Latitude (variable 1) and longitude (variable 2) were included to account for geographic influences on beetle distribution. The climate variables (variables 3 through 7) were those available from the New Zealand climate surfaces (Leathwick et al. 1998) (see Chapter 2) and include the major climatic controls.

A method of measuring the influence of the habitat on beetle distribution was also required and two arbitrary habitat variables, a vegetation index (variable 8) and a water index (variable 9), were created based on the ecological affinities of each taxon. Taxa were scored based on their preferences for different types of vegetation coverage with 1 representing closed canopy vegetation such as forest, 0.5 representing shrubland/forest edge environments and 0 representing open environments such as grassland and herbfeld. Taxa which were known to inhabit more than one of the three environments (e.g. forest and shrubland) were given an intermediate score between the value of the different vegetation types (e.g. 0.75). A composite value for each collection site was then created by taking the average of the scores for each taxon occurring at the site to minimise any effect from inaccurate environment assignations. The composite water index was constructed in the same manner with fully aquatic taxa being scored as 1, riparian and swampland taxa being scored as 0.5 and fully terrestrial taxa being scored as 0. All of the environmental variables were tested for normality using SPSS® statistical software (SPSS Inc., 2002). Log_{10} transformations were required to normalise MAP and P:E. As P:E values were sometimes zero Log_{10} transformation was undertaken using (P:E +1) to avoid taking the Log_{10} of zero which results in a mathematical error.

Two methods of ordination analysis were considered for examining the relationship between the environment and species data. Both methods examine the relationship between a set of independent variables (in this case the environmental variables) and a set of dependent variables (the taxa). The first method, Redundancy Analysis (RDA), works under the assumption that the relationship between the variables is linear while the second method, Canonical Correspondence Analysis (CCA), assumes that the relationship between the two variables is unimodal (i.e. a bell curve). To determine which ordination technique was most suitable for exploring the environmental controls on beetle distribution a detrended correspondence analysis (DCA) with detrending-by-segments and downweighting of the rare species was undertaken (ter Braak, 1995). DCA examines the pattern of compositional variation within the data set, i.e. the variation in the taxon composition of the assemblages between sites and the turnover of RTUs (the rate of change in site taxon composition) while ignoring the role of the environmental variables. The results of DCA are given in terms of the number of standard deviations from the centroid of the first axis (which explains the most variation) assuming a normal distribution. Results (gradient lengths) of < 2 SD suggests the use of RDA and gradient-lengths > 4 SD suggest the use of CCA (ter Braak, 1995).

Both RDA and CCA analyses were undertaken for the reduced data set using CANOCO version 4.5 (ter Braak & Šmilauer, 2002). In order to determine the explanatory power of all the environmental variables together and individually the multiple ordinations were undertaken with both the full suite of all nine environmental variables (fully constrained ordination) and with subsets of the variables (partially constrained ordination). Rare species were down weighted using the analysis option in CANOCO version 4.5 (ter Braak & Šmilauer, 2002). The statistical significance of each environmental variable was tested by using a Monte Carlo permutation test with 999 unrestricted permutations under the full model. The partially constrained CCAs were then used to calculate variance partitioning of those environmental variables with a significant ($p \leq 0.05$) relationship to variation in the dataset.

3.3 Results

Systematic sampling of an area is required to provide an accurate indication of the taxonomic composition at a particular site however most of the sites in the original dataset appear to represent the chance collection of an individual specimen. As the presence of a single taxon at a site implies that all other 81 taxa are absent, a highly improbably occurrence, the inclusion of these sites is likely to introduce unwanted and un-necessary noise into the dataset. This was evidenced by an initial canonical correspondence analysis (CCA, see below for more details) of the original dataset (82 taxa from 1443 sites) which, when constrained to all nine environmental variables, explained only 3% of the variance in the taxon distribution data (Table 3.1).

Table 3.1. Results of initial CCA analysis of all 82 taxa from 1443 sites

Axes	**1**	**2**	**3**	**4**	**Total inertia**
Eigenvalues :	0.222	0.162	0.09	0.056	21.448
Species-environment correlations :	0.628	0.533	0.437	0.374	
Cumulative percentage variance					
of species data:	1	1.8	2.2	2.5	
of species-environment relation:	37.6	65.1	80.3	89.8	
Sum of all eigenvalues:					21.448
Sum of all canonical eigenvalues:					0.59
Variance Explained					0.03

In an effort to minimise this noise, a minimum of 10 taxa at a site was set as an arbitrary cut-off for the inclusion of a site in the final dataset. Furthermore taxa that were present from less than 5 sites were excluded to minimise the noise caused by species that have been rarely collected. This left a data set comprising 44 taxa (listed in Appendix 3) and 50 sites.

The DCA of the examined beetle taxa produce a gradient length for its first axis of 2.6 standard deviations (SD) (Table 3.2). As this falls between a gradient-length of < 2 SD, suggesting the use of linear ordination (RDA) (ter Braak, 1995), and a gradient-length of > 4 SD, suggesting the use of unimodal ordination (CCA) (ter Braak, 1995), either technique could be applied to this data set. Both CCA and RDA ordinations were therefore performed (Table 3.3). As CCA explained a higher percentage of the total species variation (Table 3.3) all further ordinations were undertaken using this technique.

A full CCA constrained to all nine of the environmental variables indicates that two axes are primarily responsible for explaining the distribution of the beetle taxa (Table 3.4, Fig. 3.1). Axis 1 is primarily associated with MMWT (Fig. 3.1) which has a correlation

Table. 3.2. Results of DCA ordination to determine whether CCA or RDA ordination is more appropriate for use in analysising the data

Axes	**1**	**2**	**3**	**4**	**Total inertia**
Eigenvalues:	0.281	0.227	0.169	0.1	2.702
Lengths of gradient :	2.647	2.649	2.282	2.034	
Cumulative percentage variance of species data:	10.4	18.8	25.1	28.8	
Sum of all eigenvalues					2.702

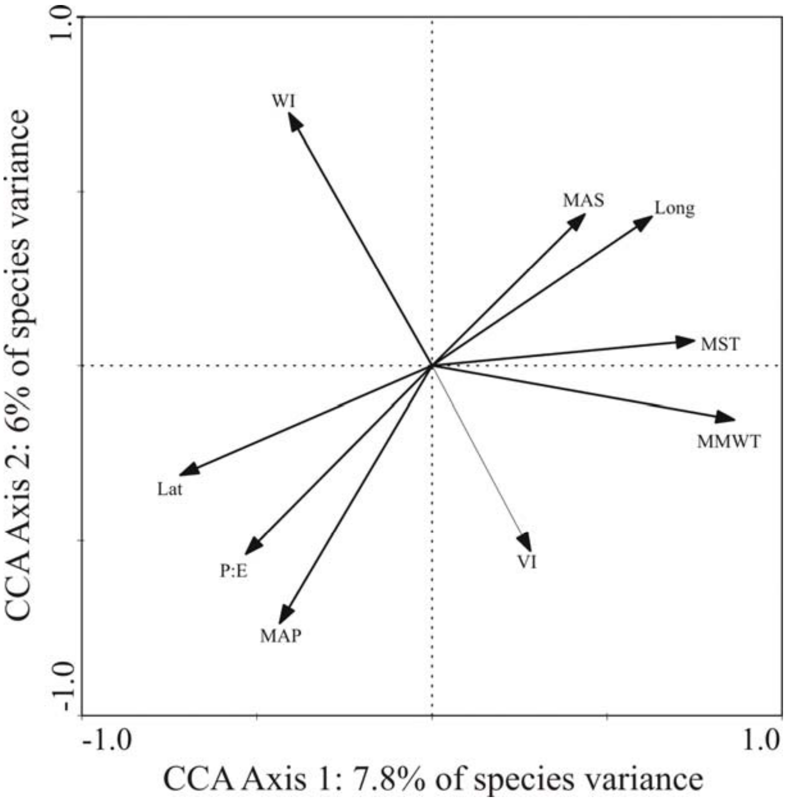
Table. 3.3. Comparison of amount of total species variation explained by CCA and RDA methods of ordination. Total explained variance is highlighted in grey.

	CCA					**RDA**				
Axes	**1**	**2**	**3**	**4**	**Total inertia**	**1**	**2**	**3**	**4**	**Total variance**
Eigenvalues:	0.211	0.162	0.150	0.093	2.702	0.088	0.068	0.039	0.028	1.000
Species-environment correlations:	0.885	0.869	0.894	0.815		0.904	0.857	0.706	0.715	
Cumulative percentage variance -										
- of species data:	7.800	13.800	19.400	22.800		8.800	15.600	19.500	22.300	
- of species-environment relation:	24.500	43.200	60.700	71.500		32.000	56.700	71.000	81.300	
Sum of all eigenvalues					2.702					1.000
Sum of all canonical eigenvalues					0.862					0.274
Variance Explained					**0.319**					**0.274**

Table 3.4. Results of the CCA including all nine environmental variables. The varience explained is highlighted in grey.

Axes	**1**	**2**	**3**	**4**	**Total inertia**
Eigenvalues :	0.211	0.162	0.15	0.093	2.702
Species-environment correlations:	0.885	0.869	0.894	0.811	0.815
Cumulative percentage variance					
of species data :	7.8	13.8	19.4	22.8	
of species-environment relation:	24.5	43.2	60.7	71.5	
Sum of all eigenvalues:					2.702
Sum of all canonical eigenvalues:					0.862
Variance Explained					0.319

Figure 3.1. CCA plot of the nine significant ($P< 0.05$) environmental variables with respect to CCA axis 1 and 2. The amount of species variation explained by each axis is also provided. Abbreviations for the environmental parameters are provided in the body of the text.



coefficient of 0.76. MST (correlation coefficient = 0.66) and Latitude (correlation coefficient = -0.63) also show high degrees of correlation with this axis (Fig. 3.1). The second axis appears less well constrained to any one variable (Fig. 3.1) but precipitation (MAP) (correlation coefficient = -0.64) and WI (correlation coefficient = 0.62) show the strongest correlations. The vegetation index (VI) is also correlated to this axis (correlation coefficient = -0.46).

There is a propensity for taxa and sites associated with high precipitation and closed-canopy vegetation to fall near the negative end of axis 2 while aquatic taxa and sites associated with open vegetation and lower precipitation fall at the positive end. While this appears to indicate some relationship between closed-canopy environments and high rainfall (and inversely open vegetation, open water and low precipitation) it is probably an artefact resulting from the taxa used in this study rather than an actual trend. The taxa used in this study were those recorded in the fossil assemblages used for the palaeoenvironmental and palaeoclimatic reconstructions presented in Chapters 4 through 6. These assemblages are all from the West Coast of South Island, New Zealand and therefore there is a bias in the collection data towards this region (Fig. 3.2) which retains much of its forest cover and is also a region of high rainfall (e.g. Hessell, 1982). Collection sites are therefore more likely to be associated with both high precipitation and closed canopy vegetation(Hessell, 1982). A wider selection of taxa from across New Zealand is required to establish the reality of this apparent relationship.

Variation partitioning based on the CCA indicates that the nine environmental variables explain 31.9% of the variation in the species data (Fig. 3.3). Of this explained variation 5.7% relates to the interaction between all the environmental variables (Fig. 3.3) although most of the explained variation (13.9%) can be attributed to the temperature and precipitation variables (Fig. 3.3). Most of this is due to the combination of MMWT and MST (5.9%) while MAP and P:E explain slightly less (4.9%). The interaction between precipitation and temperature explains 2.4% of the total variation in taxon distribution.

After the effects of temperature, precipitation and the interaction between all the environmental variables is removed, the remaining explained variation can be attributed

Figure 3.2. Location of the 50 collection sites at which the beetle taxa used in this study are known to occur and from where the climatic data tested in this study was obtained. The location of Wesport (fossil locality is also shown).

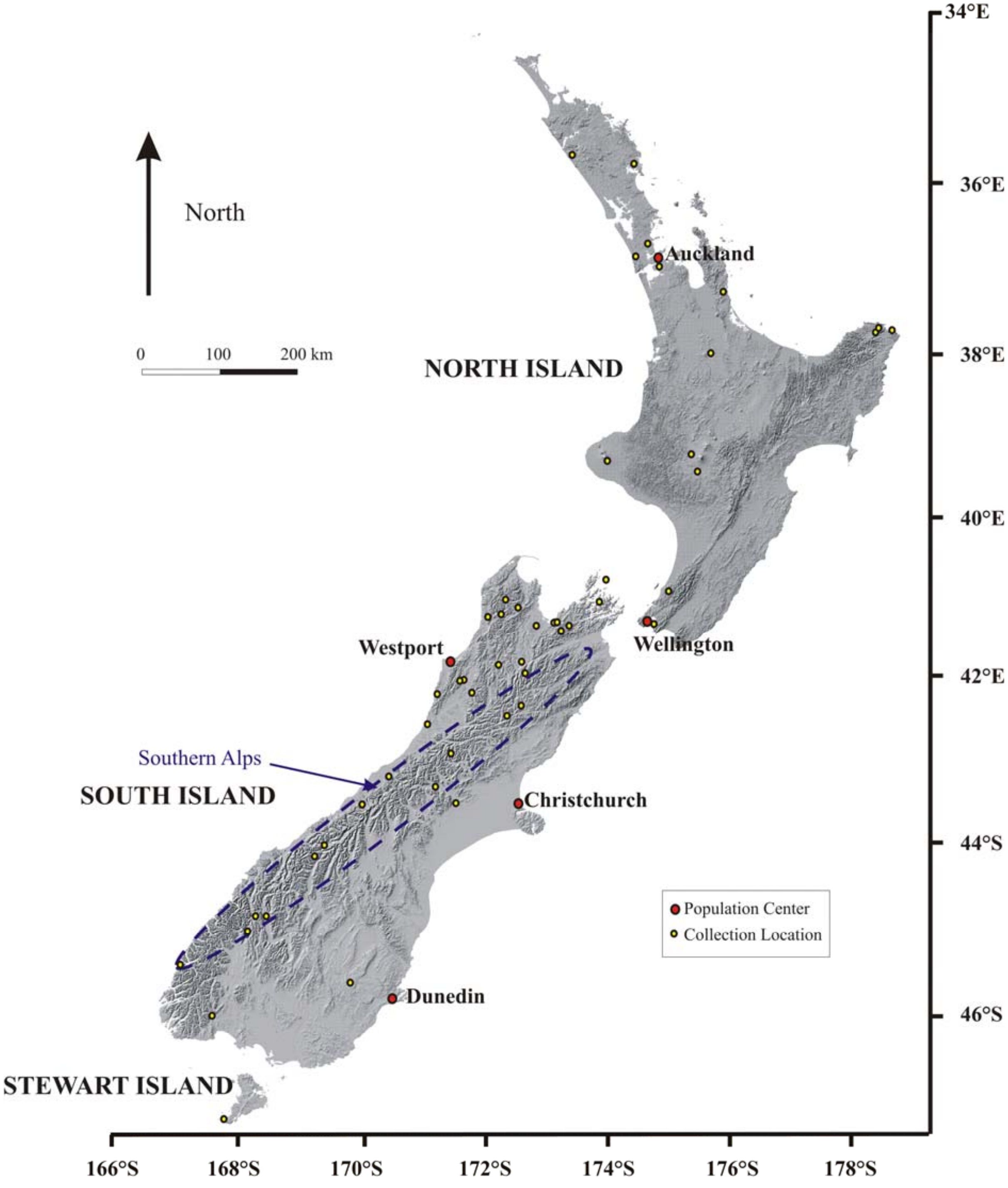
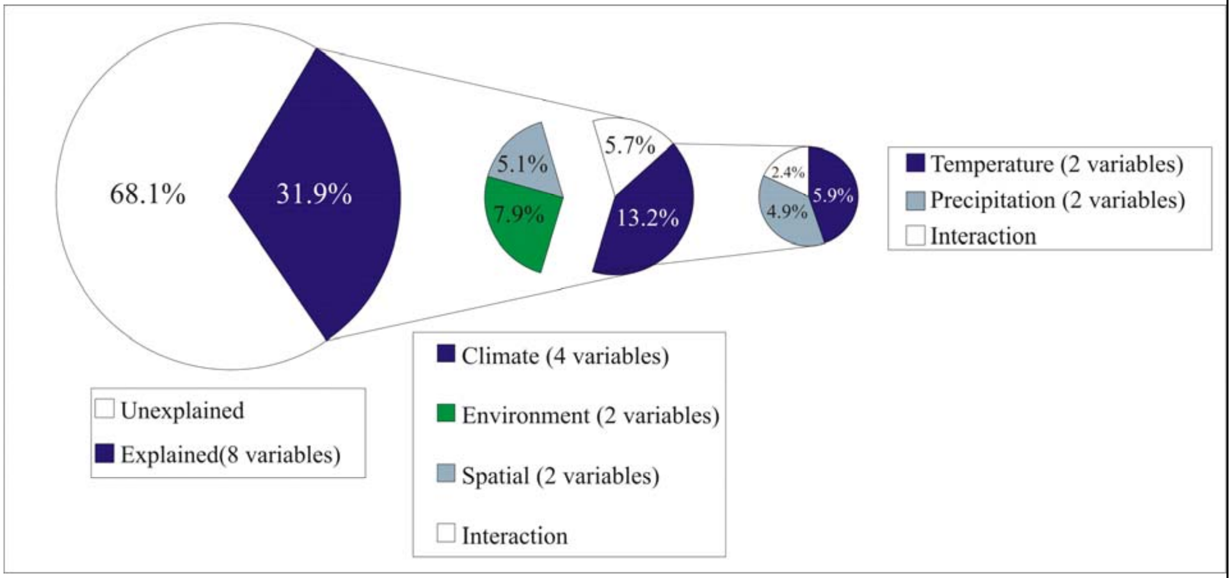


Figure 3.3. Variance partitioning: Pie graphs depict the amount of the total variation of the beetle taxonomic data independently explained by all nine environmental variables and their interactions.



to a combination of the habitat (WI and VI) (7.9%, Fig. 3.3) and the spatial variables (latitude and longitude) (5.1%, Fig. 3.3). MAS does not appear to make an important contribution to explaining variation in taxon distribution even though when the environmental variables were tested with a series of partial CCAs without co-variables (i.e. without the influence of the other environmental variables) all indicated a significant relationship ($p \leq 0.05$) to beetle distribution (Table 3.5).

This apparent dichotomy between the variation partitioning and the partial CCA is explained by the relationship between MAS and the other climate variables. When the effects of the other climate variables are partialled out (Table 3.5) MAS is no longer significant ($p = 0.09$) indicating that its apparent influence is actually a function of the other climatic variables. MAS has no significant effect in and of itself.

Table 3.5. Results of partial CCAs for all variables individually and with other variables partialled out. Results highlighted in grey are not significant (P> 0.05). Abbreviations for environmental parameters are provided in the text.

CLIMATE VARIABLES

Variable	Co-var	λ1/λ2	P	F	Cum %
MST	None	0.66	0.001	3.04	6.0
	Lat	0.45	0.002	2.11	4.3
	Long	0.53	0.001	2.50	5.0
	MMWT	0.41	0.002	1.94	4.0
	MAP	0.60	0.001	2.82	5.7
	P:E	0.56	0.001	2.63	5.3
	Solar	0.60	0.001	2.81	5.6
	Water	0.67	0.001	3.16	6.3
	Veg	0.65	0.001	3.04	6.1
	ENV	0.68	0.001	3.21	6.5
	Climate	0.46	0.004	1.88	4.1
MMWT	None	0.74	0.001	3.45	6.7
	Lat	0.57	0.001	2.61	5.3
	Long	0.66	0.001	2.96	5.9
	MST	0.50	0.001	2.33	4.7
	MAP	0.76	0.001	3.38	6.7
	P:E	0.70	0.001	3.05	6.1
	Solar	0.73	0.001	3.20	6.4
	Water	0.71	0.001	3.25	6.5
	Veg	0.74	0.001	3.44	6.8
	ENV	0.72	0.001	3.41	6.9
	Climate	0.53	0.001	2.18	4.7
MAP	None	0.53	0.001	2.76	5.4
	Lat	0.59	0.001	2.33	4.7
	Long	0.45	0.001	2.18	4.4
	MST	0.54	0.001	2.54	5.1
	MMWT	0.61	0.001	2.71	5.4
	P:E	0.27	0.122	1.30	2.7
	Solar	0.42	0.001	2.13	4.3
	Water	0.64	0.001	2.86	5.7
	Veg	0.56	0.001	2.83	5.7
	ENV	0.64	0.001	2.99	6.1
	Climate	0.31	0.187	1.24	2.7
P:E	None	0.47	0.001	2.32	4.6
	Lat	0.35	0.02	1.63	3.3
	Long	0.31	0.03	1.52	3.1
	MST	0.41	0.001	1.93	3.9
	MMWT	0.45	0.003	1.96	4.0
	MAP	0.18	0.648	0.88	1.8
	Solar	0.32	0.027	1.57	3.3
	Water	0.55	0.001	2.45	5.0
	Veg	0.50	0.001	2.40	4.9
	ENV	0.56	0.002	2.53	5.2
	Climate	0.14	0.966	0.57	1.3
Solar	None	0.38	0.006	1.91	3.8
	Lat	0.26	0.248	1.17	2.4
	Long	0.23	0.345	1.09	2.3
	MST	0.37	0.012	1.70	3.5
	MMWT	0.39	0.014	1.70	3.5
	MAP	0.26	0.12	1.31	2.7
	P:E	0.24	0.198	1.19	2.5
	Water	0.47	0.003	2.06	4.2
	Veg	0.42	0.003	2.03	4.1
	ENV	0.47	0.004	2.13	4.4
	Climate	0.33	0.09	1.36	3.0

HABITAT AND GEOGRAPHICAL VARIABLES

Variable	Co-var	λ1/λ2	P	F	Cum %
Lat	None	0.61	0.001	2.88	5.7
	Long	0.32	0.053	1.48	3.1
	MST	0.42	0.005	1.96	4.0
	MMWT	0.46	0.001	2.07	4.2
	MAP	0.53	0.001	2.45	5.0
	P:E	0.46	0.001	2.17	4.4
	Solar	0.47	0.001	2.11	4.3
	Water	0.68	0.001	3.05	6.1
	Veg	0.64	0.001	3.00	6.0
	ENV	0.71	0.001	3.17	6.4
	Climate	0.38	0.023	1.53	3.4
Long	None	0.55	0.001	2.64	5.2
	Lat	0.27	0.162	1.25	2.6
	MST	0.45	0.001	2.11	4.3
	MMWT	0.48	0.001	2.17	4.4
	MAP	0.43	0.002	2.06	4.2
	P:E	0.38	0.005	1.82	3.7
	Solar	0.38	0.008	1.79	3.7
	Water	0.62	0.001	2.77	5.6
	Veg	0.58	0.001	2.75	5.5
	ENV	0.65	0.001	2.88	5.9
	Climate	0.40	0.021	1.62	3.6
WI	None	0.55	0.001	2.77	5.5
	Lat	0.65	0.001	2.94	5.9
	Long	0.65	0.001	2.91	5.8
	MST	0.61	0.001	2.89	5.8
	MMWT	0.57	0.001	2.60	5.2
	MAP	0.64	0.001	2.88	5.8
	P:E	0.66	0.001	2.89	5.8
	Solar	0.66	0.001	2.91	5.8
	Veg	0.57	0.001	2.96	5.9
	Climate	0.56	0.001	2.30	5.1
Veg	None	0.47	0.001	2.45	4.9
	Lat	0.55	0.001	2.58	5.2
	Long	0.55	0.001	2.57	5.2
	MST	0.53	0.001	2.47	5.0
	MMWT	0.53	0.001	2.46	5.0
	MAP	0.50	0.001	2.52	5.1
	P:E	0.53	0.001	2.53	5.1
	Solar	0.53	0.001	2.56	5.2
	Water	0.51	0.001	2.64	5.3
	Climate	0.58	0.001	2.41	5.3

When partial CCAs were applied to the habitat variables (VI and WI) it became apparent that the other environmental variables had minimal effect on the significance and explanatory power of either the vegetation index (VI) or water index (WI) (Table 3.5). This was not the case with the climatic variables (MMWT, MST, MAP and P:E).

When the other environmental variables were partialled out of the CCA analysis of the temperature variables both MST and MMWT remained significant although the explanatory power of both was reduced (Table 3.5). While partialling out of MST had the greatest negative influence on MMWT's explanatory power both MMWT and Latitude (which is itself negatively correlated to MST (Table 3.6, Fig. 3.1)) considerably reduced the explanatory power of MST. Of the two temperature variables, MMWT was least effected by the partialling out of the other temperature variable (MST).

Table 3.6. Intra-set correlation matrix for all nine environmental variables

	Lat	**Long**	**MST**	**MMWT**	**MAP**	**P:E**	**MAS**	**WI**	**VI**
Lat	1								
Long	-0.8449	1							
MST	-0.6102	0.5356	1						
MMWT	-0.5852	0.4415	0.8319	1					
MAP	0.3081	-0.3908	-0.4026	-0.2984	1				
P:E	0.47	-0.5581	-0.3935	-0.3712	0.7329	1			
MAS	-0.7447	0.7986	0.4445	0.308	-0.4765	-0.6453	1		
WI	-0.053	0.0529	-0.004	-0.219	-0.3096	-0.1495	0.1822	1	
VI	0.0301	-0.0609	0.0661	0.0932	0.1912	0.1381	-0.1562	-0.7865	1

While both precipitation proxies (MAP and P:E) became insignificant when the effect of all the climatic variables were partialled out (Table 3.5) both remained significant when the effects of the environmental variables, other than the other precipitation variable, were partialled out individually. The insignificance of the precipitation variables when all of the climate variables were partialled out appears to be an artefact of the close relationship between the two precipitation proxies (Table 3.6, Fig. 3.1).

While the partialling out of the habitat variables had little effect on the explanatory power or significance of the spatial variables (latitude and longitude) (Table 3.5) the partialling out of the climate variables (MST, MMWT, MAP and P:E) reduced their explanatory power (Table 3.5), although both remained significant. When the effects of one spatial variable on the other were partialled out it became apparent that latitude had more of a detrimental effect on the significance of longitude than vice-versa.

3.4 Discussion

3.4.1 Weaknesses in the data-set

Beetle collections in New Zealand have been compiled over a period of decades by numerous different collectors. They have used a wide variety of techniques at thousands of different sites. This lack of standardised collection makes statistical analysis of beetle distribution difficult as only presence/absence data can be used. Presence/absence data gives equal statistical weighting to every collection site whether it is at the optimum or extreme limit of a species range and climatic distribution. Furthermore, the lack of detailed information regarding the vegetation at the collection sites means that indices of vegetation structure and standing water for a site must be based on the known ecological preferences of the taxa found there.

These inherent weaknesses in the data set make drawing unqualified conclusions difficult however the exclusion of sites with less than 10 taxa and the exclusion of taxa known from less than 5 localities minimises the ability of any one taxa to unduly influence the statistics. The overall trends indicated by the results are therefore likely to be robust.

In standard statistical fashion the limit for statistical relevance was set at $p = 0.05$ but given the limitations of the data this cut off is arbitrary. Variables are therefore identified as simply more ($p < 0.05$) or less ($p > 0.05$) significant, i.e. those variables which are significant ($p < 0.05$) are interpreted as having a strong effect on the distribution of beetle taxa while those variables that are insignificant ($p > 0.05$) are interpreted as having a weaker effect.

3.4.2 The factors controlling beetle distribution

The distribution of the beetle taxa used in this study appears to be controlled by a combination of factors with those tested in this study explaining almost 32% of the variance in beetle distributions (Fig. 3.3). Other organisms used as biological proxies in New Zealand, such as diatoms (Reid, 2005) and chironomids (Woodward & Shulmeister, 2006), show a similar level of explained distributional variance (31% in both cases) . This indicates that fossil beetles are equally robust palaeoclimatic indicators. The variables responsible for the remaining 68% of the variance in beetle distribution are unknown but probably include biotic factors, such as interspecific competition and predation, as well as abiotic factors such as soil texture, soil moisture and sampling bias (amongst others).

Many of the environmental parameters are correlated (especially temperature) and almost 20% of the explained variation in the species data results from these interactions (Fig. 3.3). However all the variables, except MAS, also remain significant when the other variables are partialled out. This indicates that while the interaction between the variables plays a substantial role each variable also acts independently to affect beetle distribution.

Temperature and spatial variables

The primary axis (CCA axis 1, $\lambda 1/\lambda 2 = 1.24$) explaining the distribution of the beetle taxa used in this study is associated with the temperature and geographic variables. The temperature variables (Table 3.5, Fig. 3.3) are the most important factors controlling beetle distribution in this dataset suggesting that temperature estimates from fossil beetles can be validated. This is not surprising as beetles, like all insects, are poikilothermic. Ambient temperature therefore affects their metabolism, development, behaviour and activity (Gillot, 1991). Furthermore different insects show different temperature preferences (Hurnard, 1978; Gillot, 1991) and this translates into diverse thermal distributions for different taxa.

MMWT appears to be the primary temperature variable controlling beetle distribution in New Zealand i.e. the explanatory power ($\lambda 1/\lambda 2$) and significance (p) remained higher than MST after partial CCAs (Table 3.5). The mean percentage variance explained after partialling out co-variables for MMWT was 6.1%, and MST 5.4%. The reasons why MMWT is the controlling variable are unclear but may be related to the thermal tolerance ranges of the beetle taxa. Southern hemisphere insects generally have a lower thermal tolerance somewhere between ca. 0ºC and -40ºC and upper thermal tolerances between ca. 40ºC and 60ºC (Addo-Bediako et al., 2000). As minimum winter temperatures, especially in inland and mountainous areas of the South Island, are more likely to fall within these lower thermal limits than summer temperatures are likely to fall within the upper thermal limits (Anonymous, 1983), New Zealand beetles may tend to distribute themselves primarily by their resistance to low temperatures. This makes sense as, as previously discussed in Chapter 1, Southern Hemisphere beetles generally lack physiological adaptations for dealing with extremely low temperatures (e.g. diapause or freeze tolerance) (Dumbleton, 1967; Sinclair et al., 2003b) and remain active throughout the year (e.g. Moeed & Meads, 1992a; 1992b). It should be noted, however, that the lower thermal limits presented by Addo-Bediako et al. (2000) for Southern Hemisphere insects are generalised lethal restrictions. It has long been recognised that insect species have preferred thermal ranges within these tolerance limits (e.g. Deal, 1941, Buse et al., 2001) and the distribution of the beetle fauna examined in this chapter are more likely to reflect these preferred temperature ranges rather than a lethal limit.

The geographic variables of latitude and longitude explain 5.1% of the distributional variance even when the effects of climate were partialled out (Fig. 3.3). While the exact nature of this spatial signal cannot be identified, two sources are likely. Penev (1996) argued that large scale (i.e. continental scale) variation in the distribution of Northern Hemisphere carabid (ground) beetles is in response to combination of climatic factors, such as temperature, and historical factors, such as the presence of glacial ice-sheets. Due to the focus of this project all the fossil taxa used in this study are from fossil sites located in the Westport region of the northwest South Island and the modern collection sites of these taxa are also predominantly clustered in and around this region (Fig. 3.2). Prior observations have determined that this region is populated by a large number of regionally endemic insect and plant taxa (Dumbleton, 1969; Wardle, 1991) and it has been proposed that this may be result of the restriction of flora and fauna to this region by the effects of Pleistocene glaciation (Wardle, 1988). The apparent geographical effect observed in this study may therefore relate to regional endemism and reflect a historical influence.

The presence of the Southern Alps has also acted, and probably continues to act, at least partially, to limit the distribution of the beetle taxa examined in this study. Mountain ranges are acknowledged barriers to gene flow, especially during glacial periods (e.g. Swenson & Howard, 2005), and are capable of stopping the movement of even flying insects (e.g. the fly *Anopheles punctipennis* Say (Fairley et al., 2000)), although some migration across mountains is likely to be possible via low passes. The Southern Alps, which reach ca. 3,750 metres at their maximum elevation (Aoraki/Mt. Cook), run the entire length of the South Island following a northwest to southeast trend creating both a longitudinal and latitudinal trend in this dataset which is predominantly constructed from South Island sites (Fig. 3.2).

If the Southern Alps are acting to limit the distribution of the beetle taxa examined in this study it also explains why both the precipitation (MAP and P:E) and geographic variables trend along the same line in the ordination diagram (Fig. 3.1). Latitude and the precipitation variables show a positive correlation. This is due to the general trend of increasing precipitation with increasing latitude. Longitude and precipitation on the other hand fall in opposite directions. This is because the Southern Alps (Fig. 3.2) block the westerly movement of weather systems in the New Zealand region (Sturman & Tapper, 1996) with resulting lower precipitation on the east coast and a trend of decreasing rainfall with increasing longitude. The relationship between the geographic and precipitation variables does not fully explain the effects of precipitation on the beetle distribution and a strong correlation exists between beetle distribution and axis 2.

Precipitation and habitat variables

The importance of moisture as a climate variable affecting insects has long been recognised (Yazdani & Agarwal, 1997; Schowalter, 2000). The small size of insects means that they have a large surface area relative to their volume and are therefore subject to increased water loss proportional to their size (Edney, 1977; Hadley, 1994) potentially leading to water stress in moisture poor environments. As it is the overall moisture level, rather than any particular link to preciptation, that affects the rate of water loss of a beetle to the environment it is likely that beetles will inhabit microclimates where the precipitation, hydrology, and evaporation levels (amongst other factors), all combine to provide an appropriate relative humidity (Elias, 1997). It would be expected, therefore, that the best climate variable to model the distribution between beetle taxa and mositure levels would be P:E, the ratio between preciptation and evaporation, as this is more likely to reflect the combination of factors that create the humidity levels experienced by the beetles. This is not the case, however, with both precipitation variables instead explaining similar amounts of the variance. This relates to the fact that the two variables are so closely correlated that they become insignificant when the other is partialled out (Table 3.5). As estimates of P:E from climate stations will be calculated from measurements of precipitation, and in some instances zonally estimated values for evaporation, the interaction between P:E and MAP is predictable and reflects the importance of precipitation in establishing overall moisture levels in an environment.

While the precipitation variables explain 4.9% of the distributional variance by themselves they also interact with temperature to explain an additional 2.4% (Fig. 3.3). This is again probably related to water stress and the large surface area to volume ratio of insects. As ambient temperature increases, insect body temperature also increases exacerbating the problem of water retention as water loss generally increases along with body temperature (Hadley, 1994). This interaction is exemplified by a study of the New Zealand weevil *Euophyrum confine* Broun (Green & Pitman, 2003) where mortality at high temperatures (33ºC) was not noticeably different from lower temperatures (23ºC and 28ºC) except when relative humidity was below 30% (Green & Pitman, 2003). This relationship between precipitation and temperature again highlights the fact that beetles are likely to be occupying a microclimate whose *overall* moisture level is suitable for their survival and that MAP is only one of a suite of variables acting to produce the moisture regime occupied by the beetles.

Other than an apparent correlation to precipitation the environmental variables (VI and WI) show little relationship to the rest of the climatic variables (Fig. 3.1, Table 3.6). They do however make a significant contribution to controlling the distribution of the beetle taxa. This relationship is an intuitive one as taxa will obviously be restricted to the environment that they are best adapted to exploit. Eyre et al. (2005) previously noted this relationship in a study of the distribution of British ground (Carabid) beetles where taxa in the highly modified and variable environments of the modern-day British lowlands were dominantly distributed by the availability of the appropriate habitat types (Eyre et al., 2005). In the more homogeneous moors of the British highlands however temperature played a larger role (Eyre et al. 2005). Studies of beetle distributions in the Finnish taiga (e.g. Niemelä et al. 1994) observed a similar relationship.

The results of this study appear to follow the general theory regarding environmental controls on beetle distribution. Large scale variations in beetle assemblages can be explained by variations in macro-climatic variables, such as temperature and precipitation, historical factors and geographic barriers, such as mountain ranges. These variables act to constrain the general pool of beetle species available in any given region (Penev, 1996). This regional pool of species is then modified on a local scale into site specific assemblages based on factors such as the available habitat type (Penev, 1996). Thus, from this study, it is temperature, precipitation and topography that control which taxa occur in a particular region of New Zealand while it is the local habitat (e.g. open or closed vegetation, open pools of water versus no standing water) surrounding a particular site that controls what actual subset of that pool of beetle taxa occurs at a particular site.

3.5 Conclusions

It is apparent from the results of the statistical analysis that while there are multiple variables interacting to control the distribution of the beetles examined in this study the assumptions underlying palaeoclimatic reconstructions from New Zealand beetles are sound. The amount of variation explained by the climate variables is similar to the amount explained for other biological proxies used in quantitative inference models and consequently fossil beetle studies are a good tool for palaeoclimatic work in New Zealand. Internationally, the demonstration that fossil beetles are suitable as palaeoclimatic proxies in New Zealand has implications for their use in other Southern Hemisphere locations and in regions with oceanic, rather than continental climates, although regional studies should be still carried out to confirm the suitability of beetles in these regions.

This study also indicates that it is minimum daily minimum winter temperature rather than mean summer temperature that is the most significant limiting factor on beetle distribution for the West Coast beetle fauna examined in this study. The probable reason why MMWT is more significant is because it is more likely to be physiological limiting in a New Zealand context than MST. Ths does not mean that estimates of MST are useless however. Mean summer temperature remains a significant controlling variable on beetle distribution and reconstructions of MST probably relate to the preferred thermal range occupied by beetles during the summer months. Estimates of MST are therefore still likely to accurately represent summer temperatures although more weight should be applied to estimates of MMWT in fossil beetle reconstructions.

Finally the explanatory power of the precipitation variables, in particular MAP, indicates that beetles may be used as *indirect* proxies for precipitation. The use of beetle fossils as proxies for palaeoprecipitation has been previously attempted using MCR (e.g Elias, 1997), although its use appears to have been restricted to desert environments (Elias, 1997). Knowledge of past precipitation patterns in New Zealand is currently sparse but is vital to answering some of the outstanding questions about the palaeoclimate of New Zealand such as whether westerly atmospheric circulation was strengthened (e.g. Shulmeister et al., 2004) or weakened (e.g. Hope et al., 2004) at the Last Glacial Maximum and whether New Zealand glacial advances are primarily controlled by precipitation (e.g. Rother & Shulmeister, 2006) or temperature (e.g. Anderson & MacIntosh, 2006).

A potential complicating factor in the use of beetles as proxies for palaeoprecipitation, however, is that fossil assembalges form, by their very nature, in wet places such as ponds and bogs (Elias, 1994). The presence of a bog or pond at a site will affect the microclimate occupied by the beetles, and thus, due to the indirect nature of beetles as proxies of palaeoprecipiation, may affect the results of the reconstruction. While this situation may indeed cause a problem when dealing with aquatic taxa it is considered unlikely to be a problem for those taxa without a particular association with standing water. These taxa are likely to inhabit a specific microclimatic range but not all of the collection sites for those taxa will be associated with ponds and bogs. The microclimate of those sites is likely to be driven, at least in part, by the broad-scale macroclimatic pattern of precipitation. The overlap of the macroclimatic preciptiation ranges of the non-aquatic beetles in an assemblage is still, therefore, likely to reflect the level the precipitation at a site. Care should still be taken, however, to ensure that precipitation estimates are not limited by aquatic taxa. An application of the MLE model of Marra et al. (2004) to producing estimates of mean annual precipitation is presented in Chapter 4.

Chapter 4

The palaeoclimate and palaeoenvironment of the Westport region during the mid-Holocene (ca. 5.8ka BP): Evidence from Alma Road

4.1 Introduction

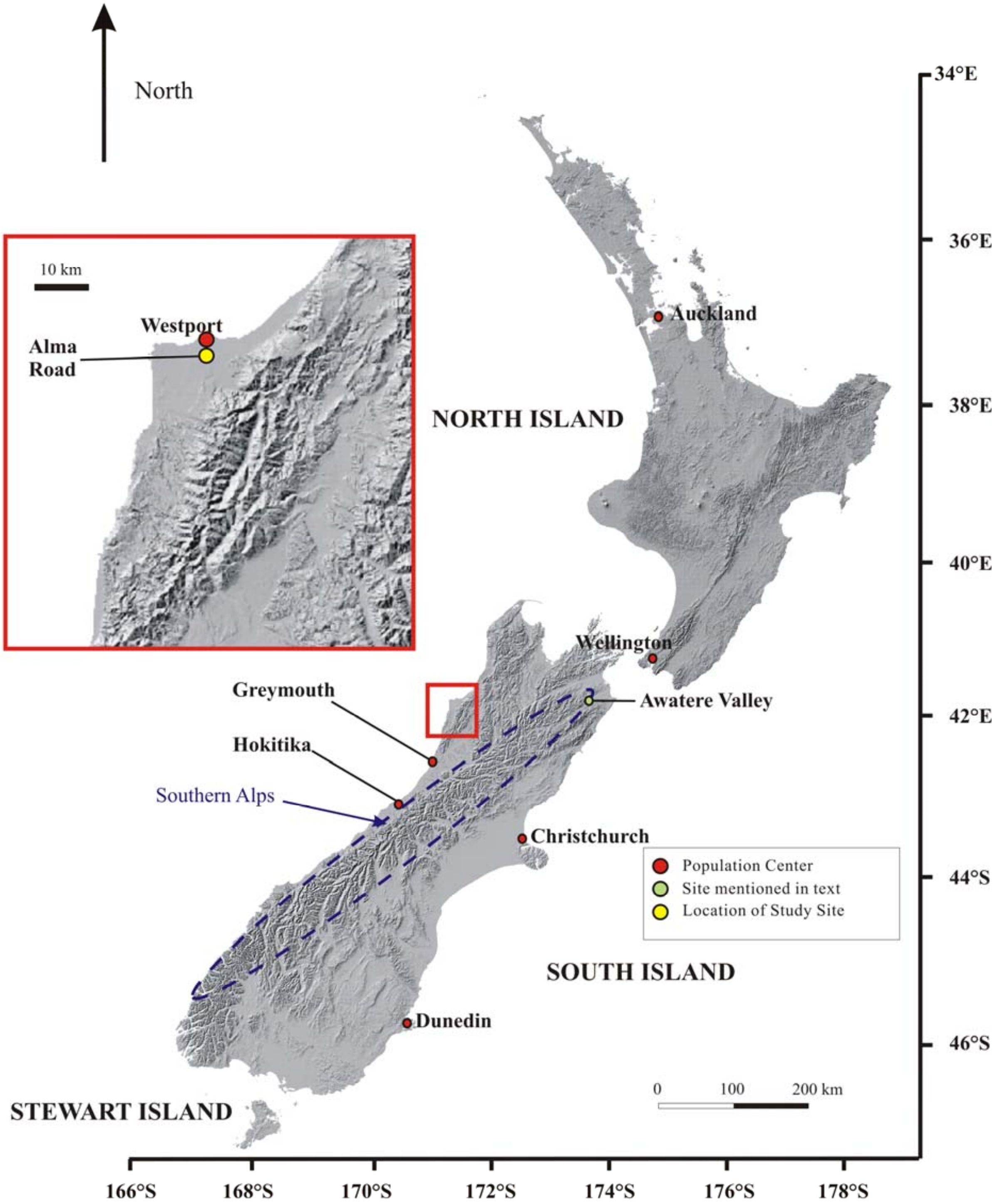
The West Coast of the South Island is one of the least well sampled areas of New Zealand for modern beetles. As geographical barriers such as the Southern Alps play a role in restricting beetle distributions (see Chapter 3) it is possible that the lack of data regarding the modern-day beetle fauna of the West Coast may impact on the ability of the MLE model of Marra et al. (2004) to accurately reconstruct past climates.

This chapter examines a mid-Holocene site in order to test the robustness of beetle based reconstructions in this poorly collected area. As the climate of the mid-Holocene does not appear to have been significantly different to the present day the reconstructed temperature estimates should straddle, or fall very close to, the modern day values at the site. Chapter 3 indicated that beetles are suitable proxies for estimating palaeopreciptiation and this chapter also applies the MLE method of Marra et al. (2004) to precipitation data to produce estimates of mean annual precipitation. A palaeoenvironmental reconstruction is also provided.

4.1.1 Modern physiography

The site examined in this chapter (41°46’S, 171°35’E, NZMS E2391500, N5936500) is a south facing road cutting on Alma Road situated two kilometres southeast of Westport (Fig. 4.1) at approximately 40 metres above sea-level. The modern values for mean

Figure 4.1 Locality map showing the major New Zealand population centres, West Coast towns and sites mentioned in the text. An inset enlargement of the Westport region shows the locations of the study site relative to Westport.



summer temperature (MST, 16.4°C), mean daily minimum winter temperature (MMWT, 3.8°C) and mean annual precipitation (MAP, 2,300mm yr^{-1}) for the Alma road site were derived from the climate surfaces of Leathwick et al. (1998). The closest climate station to Alma Road is at the Westport Airport (41°44'S, 171°35'E, NZMS E2391930, N5939940, 4m a.m.s.l.) ca. 4 km distant so the values are likely to be very similar.

Like most of the Westport region the native vegetation at the site has been cleared and the modern vegetation immediately above the outcrop is dominated by introduced trees (*Pinus* spp.). Information on the native vegetation is meagre beyond the fact that it probably consisted of mixed podocarp-beech forest (McEwen, 1987). Extrapolation regarding its composition must be made from neighbouring areas. Rimu (*Dacrydium cupressinum*) and hard beech (*Nothofagus truncata*) probably dominated the local podocarp-beech forest (McEwen, 1987; Wardle, 1991) although kahikatea (*Dacrycarpus dacrydioides*) was probably the most important arboreal species in wet areas (McEwen, 1987; Wardle, 1991). Kaikawaka (*Libocedrus bidwillii*), kamahi (*Weinmannia racemosa*), matai (*Prumnopitys taxifolia*), miro (*Prumnopitys ferruginea*) and northern rata (*Metrosideros robusta*) would also have formed an important part of the canopy. Smaller tree taxa including haumakaroa (*Raukaua simplex*), mapau (*Myrsine australis*), pigeonwood (*Hedycarya arborea*) and silver pine (*Manoao colensoi*) plus the tree ferns *Cyathea smithii* and *Dicksonia squarrosa* (Wardle, 1991) likely formed a sub-canopy layer. Lianas including supplejack (*Ripogonum scandens*) and the ratas *Metrosideros fulgens* and *M. diffusa* would have been common (Wardle, 1991). A shrub flora comprising stinkwood (*Coprosma foetidissima*), karapapa (*Alseuosmia macrophylla*) and

D. squarrosa would have overlain a ground layer of ferns dominated by *Blechnum discolor* (Wardle, 1991).

4.2. Methods

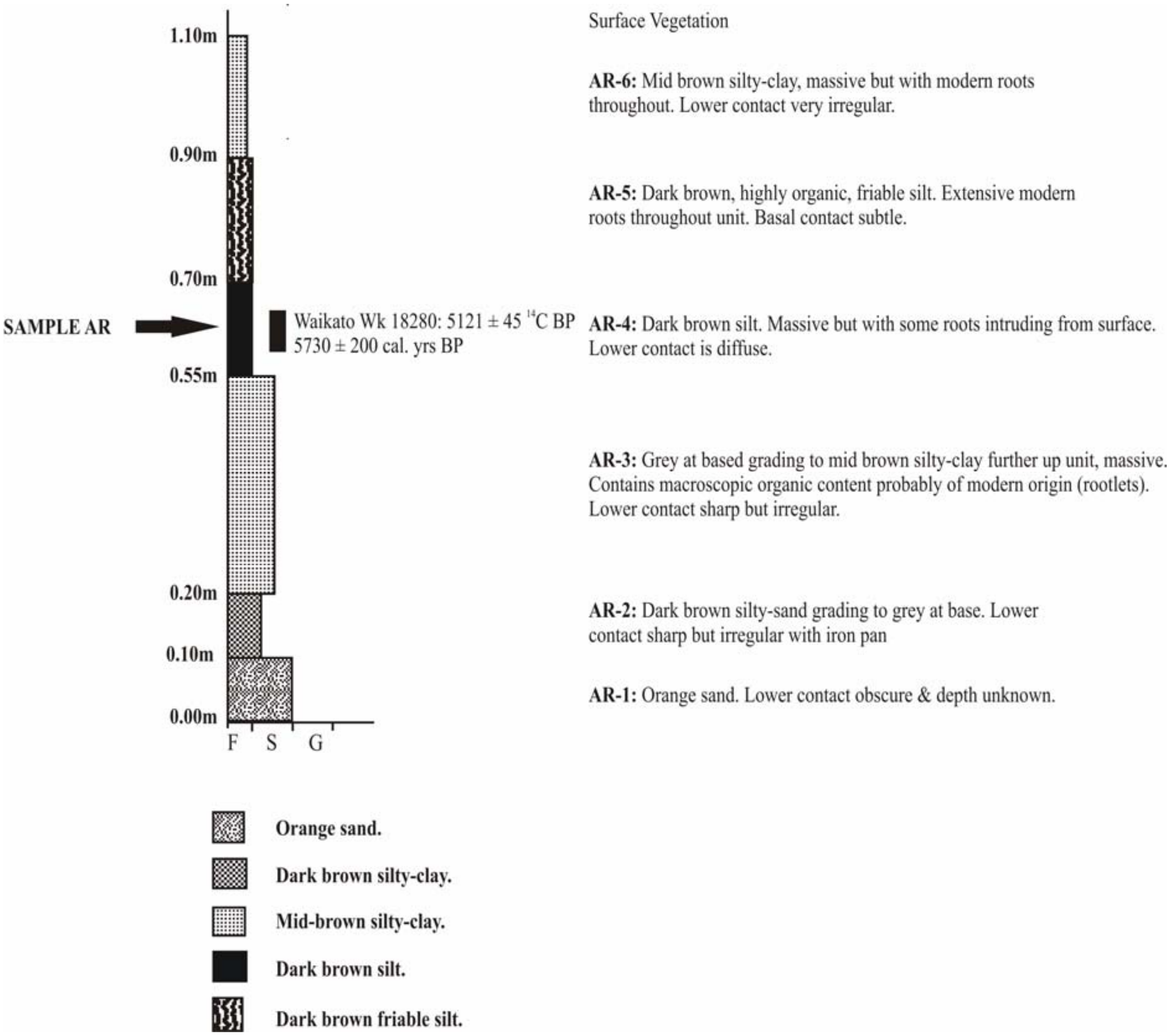
While all units, except the orange sand unit (Unit AR-1, Fig. 4.2), of this outcrop were bulk sampled identifiable beetle fossils were only retrieved from the dark brown silt unit designated AR-4. This bulk sample comprised approximately 10kg of material and was then processed according to the methods detailed in Chapter 2. Sediment from the same unit as that sampled for beetles was also collected for ^{14}C dating. Due to potential problems with contamination from modern rootlets, root-like material was removed from the sediment prior to drying at 60°C for in excess of 72 hours. A sample of ca. 400g was then submitted to the University of Waikato Radiocarbon Dating Laboratory, New Zealand. Following standard pre-treatment techniques ca. 300g of material remained. 76g of sample was combusted and a ^{14}C age obtained using the gas scintillation technique. The radiocarbon age was calibrated with the OXCAL programme (Bronk Ramsey, 2001) using INTCAL 04. As INTCAL 04 is a Northern Hemisphere calibration curve the ca. 27 year interhemispheric offset (McCormack et al., 1998) was subtracted from the ^{14}C age prior to calibration.

4.3 Results

4.3.1. Summary stratigraphy & chronology

A stratigraphic summary of the outcrop can be seen in Figure 4.2. The base of the outcrop consists of orange sands that have accumulated on what has been mapped as an OIS 7

Figure 4.2. Stratigraphy of Alma Road Site describing and illustrating the position of the different units. The sampled unit and location of the ^{14}C age are also indicated. The ^{14}C age was corrected by -27 years prior to calibration to account for the interhemispheric offset effect (McCormack et al., 1998).



terrace (Nathan et al., 2002). The sands are separated from a metre of overlying sediments by a sharp, undulating iron pan. Five different silty-sand and silty-clay units can be observed above the sands (Fig. 4.2). These units are massive but have been infiltrated with roots from the vegetation above the outcrop. The infiltration is dominantly in the upper two units although larger roots and some rootlets make it furtherdown the profile. The radiocarbon age (Wk 18280) obtained from the Waikato Radiocarbon Dating Laboratory for the unit sampled for beetle fossils (AR-4) indicates that the deposit is 5,730 ± 200 cal. yrs BP (5,121 ± 45 ^{14}C yrs BP) in age. This places the unit as mid-Holocene in age.

4.3.2 Palaeoenvironmental reconstruction

Seventeen taxa were identified in the Alma Road fossil beetle fauna and are dominantly associated with forest environments (Table 4.1). The presence of Cryptorynchini weevils (Family Curculionidae), known to be endophytic on dead woody plants (Lyal, 1993) and *Pycnomerus latitans* Sharp (Family Zopheridae), a member of a genus associated with loose and rotten bark on the forest floor (NZAC label information), indicate the presence of a thick layer of litter on the ground while *Rystheus* indet. sp. (Family Curculionidae), a genus known to live on and in ferns (May, 1987; May, 1993), implies the presence of ferns in the understory. The terrestrial water scavenger beetle (Family Hydrophilidae) *Tormus nitidulus* Broun, associated with damp, decaying matter, the presence of the rove beetle (Family Staphylinidae) *Hyperomma* indet. sp. (Kuschel, 1990; NZAC label information)(Kuschel, 1990) and indeterminate marsh beetles (Family Scirtidae) (Klimaszewski & Watt, 1997), generally associated with vegetation near sources of water, implies that conditions at the site were moist.

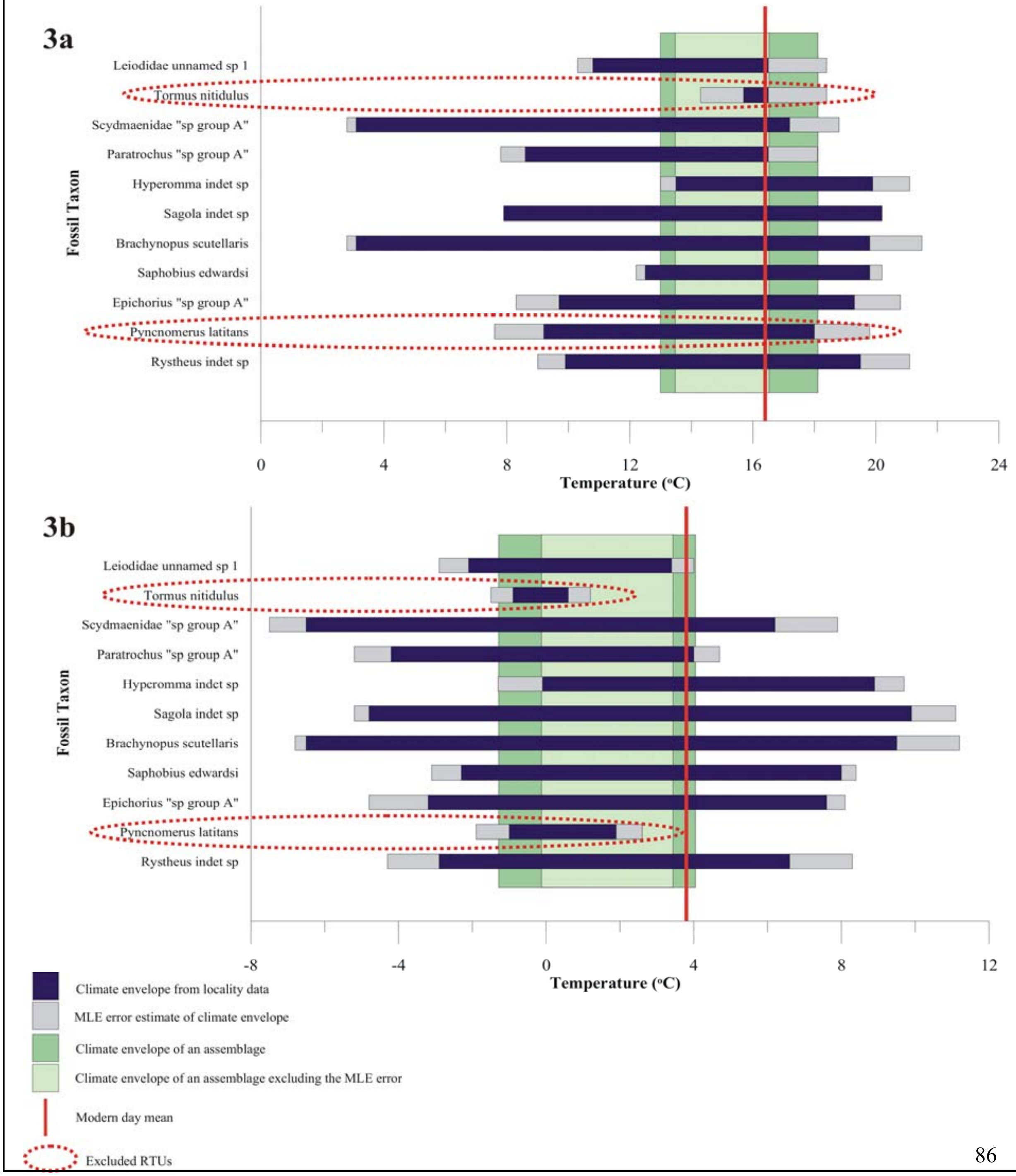
Table 4.1. Taxonomic list of fossil beetle taxa and their associated environments from the Alma Road site, Westport. Fossil elements are given a letter designation e = elytron, p = pronotum, h = head. Environmental information was collated from [1]Barratt & Patrick (1987), [2]Booth et al. (1990), [3]Chandler (2001), [4]Chandler & Peck (1992), [5]Emberson & Matthews (1973), [6]Hansen (1997), [7]Klimaszewski et al. (1996), [8]Klimaszewski & Watt (1997), [9]Kuschel (1990), [10]Löbl & Leschen (2003), [11]Lyal, (1993), [12]Marra (2003), [13]May (1987), [14]May (1993), [15]McColl (1982), [16]Newton (1984), [17]Slipinski & Lawrence (1997), [18]NZAC specimen label data and [19]LUNZ specimen label data

Family	**Taxon**	**Fossil Element**	**Associated Environment**
Hydrophilidae	*Tormus* cf. *nitidulus* Broun	e, p, h	Forest [6, 8, 18]
Leiodidae	Leiodidae unnamed sp.	e	Forest, open grassland [4, 9, 17]
Scydmaenidae	Scydmaenidae “sp. group A”	e	Forest, grassland, shrubland [8, 9, 16, 18]
Staphylinidae	*Paratrochus* “sp. group A”	h, p	Forest [7, 15, 18]
	Dalma gigantea Broun	e	Forest [3, 7]
	Eupines “sp. group A”	e	Forest [3, 7, 8, 9, 18]
	Sagola indet. sp.	e	Wide range of habitats [3, 8, 9, 18]
	Brachynopus scutellaris Klimaszewski	e	Forest [7, 10]
	Hyperomma indet sp.	h	Forest, waters edge [7, 8, 9, 18]
Scarabidae	*Saphobius edwardsi* Sharp	e, h	Forest [2, 5, 8, 18, 19]
	Saphobius indet. sp.	p	Forest [2, 5, 8, 18, 19]
Scirtidae	Scirtidae indet spp.	e, p, h	Vegetation nr water, forest [8]
Byrrhidae	*Epichorius* “sp. group A”	h	Wide range of habitats [1, 8, 18]
	Epichorius indet. sp.	e, p	Wide range of habitats [1, 8, 18]
Zopheridae	*Pycnomerus* cf. *latitans*	p	Forest [8, 18, 19]
Curculionidae	Cryptorynchini indet spp.	e, p, h	Forest [11, 12, 14]
	Rystheus indet sp.	e	Forest & swamps, lives on ferns [13, 14]

4.3.3 Palaeoclimatic reconstruction

Of the seventeen taxa found in the fossil beetle assemblage collection location data was available for eleven. These 11 taxa were used to calculate MLE envelopes as detailed in Chapter 2. Figure 4.3a illustrates that prediced summer temperatures were similar to the present falling between 13.0°C and 18.1°C and straddling the present day MST of 16.4°C (Leathwick et al., 1998). The modern mean summer temperature falls near the upper limt of the reconstructed temperature range (Fig. 4.3a) and the mean of the reconstructed temperature range (15.6°C) indicates that MST may have been slightly lower than at

Figure 4.3 Alma Road climatic reconstructions: **3a.** Mean Summer (February) Temperature Reconstruction; **3b**. Mean Daily Minimum Winter (July) Temperature Reconstruction. The blue bars indicate the range of the variable within which the taxon is known to inhabit. The grey ends of the bars represent the error to these known ranges as calculated by the MLE model. The darker green box indicates the reconstructed range of the variable including the MLE error while the light green box illustrates the reconstructed range without the MLE error term. The solid red vertical line represents the present day mean value of the variable at the site as derived from the climate surfaces of Leathwick et al. (Leathwick et al., 1998). Taxa treated as outliers in the reconstruction are highlighted by red dashed ovals and discussed in the text.



present. The mean daily minimum winter temperature estimates (Fig. 4.3b) indicates that minimum winter temperatures fell between -1.3°C and 4.0°C (mean 1.35°C). Like the MST reconstruction this range straddles the present day mean (3.8°C) but it again falls near the upper limit of the reconstructed temperature range (Fig. 4.3b) implying that winter temperatures may also have been cooler than present or that fossil beetles slightly under predict mean daily minimum winter temperatures. The precipitation reconstruction (Fig. 4.4) indicates that precipitation levels fell between 1,460mm yr^{-1} and 2,450mm yr^{-1} (mean 1,955mm yr^{-1}), straddling the present day mean annual precipitation of 2,300mm yr^{-1}. Like the temperature variables the modern mean falls at the upper end of the reconstructed precipitation range (Fig. 4.4) implying a possible slight decrease in precipitation.

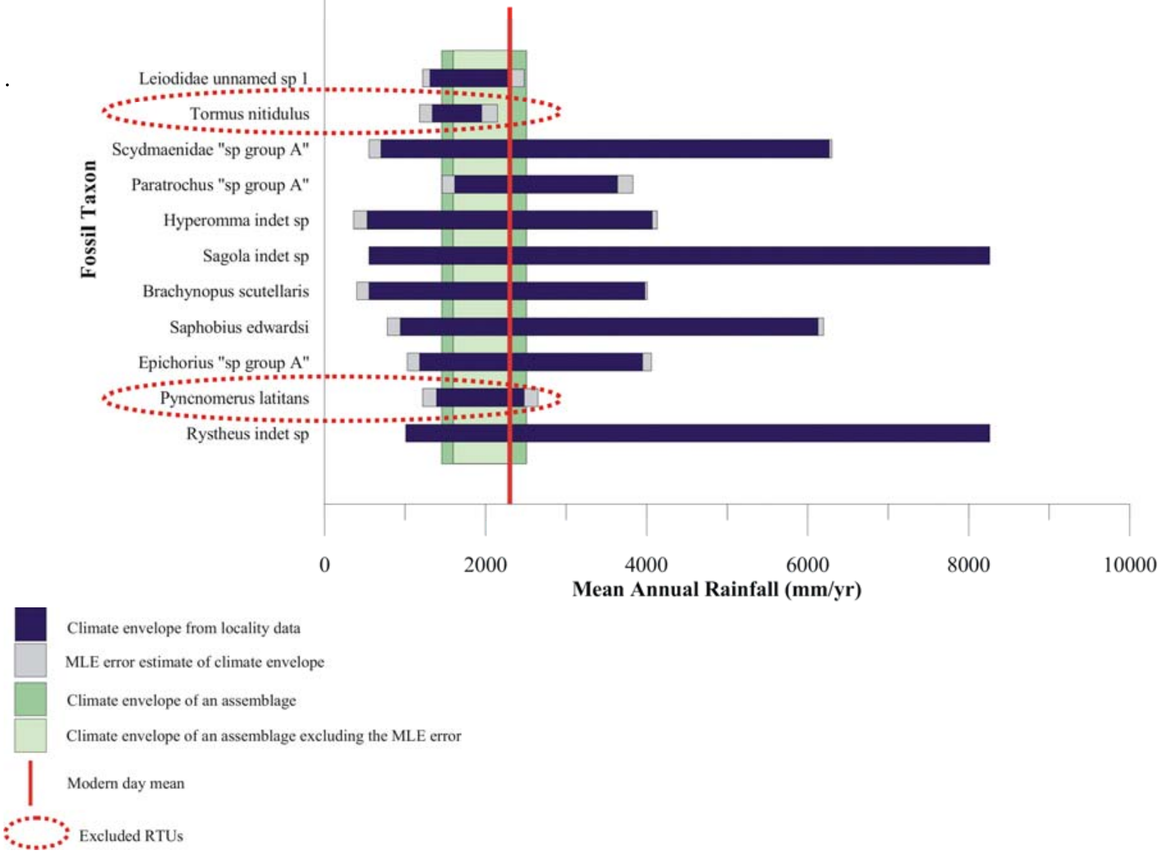
4.4 Discussion

4.4.1 Stratigraphic interpretation

This outcrop is located upon the remains of an uplifted marine terrace related to OIS 7 age (ca. 244.2 - 189.6 ka BP (Martinson et al., 1987)) (Nathan et al., 2002). The orange sands at the base of the outcrop (Fig. 4.2) are interpreted as dune sands. There is no age control for these dunes. The overlying sequence of silts and clays (Fig. 4.2) are interpreted as having formed in a swampy environment during the Holocene. This is supported by the ca. 5,800 yrs BP ^{14}C age obtained from unit AR-4 at 0.55 – 0.70m (Fig. 4.2).

4.4.2 Outlying taxa

Figure 4.4 Alma Road climatic reconstruction of Mean Annual Precipitation (MAP). The blue bars indicate the range of MAP within which the taxon is known to inhabit. The grey ends of the bars represent the error to these known ranges as calculated by the MLE model. The darker green box indicates the reconstructed range of the variable including the MLE error while the light green box illustrates the reconstructed range without the MLE error term. The solid red vertical line represents the present day mean value of MAP at the site as derived from the climate surfaces of Leathwick et al. (Leathwick et al., 1998). Taxa treated as outliers in the reconstruction are highlighted by red dashed ovals and discussed in the text.

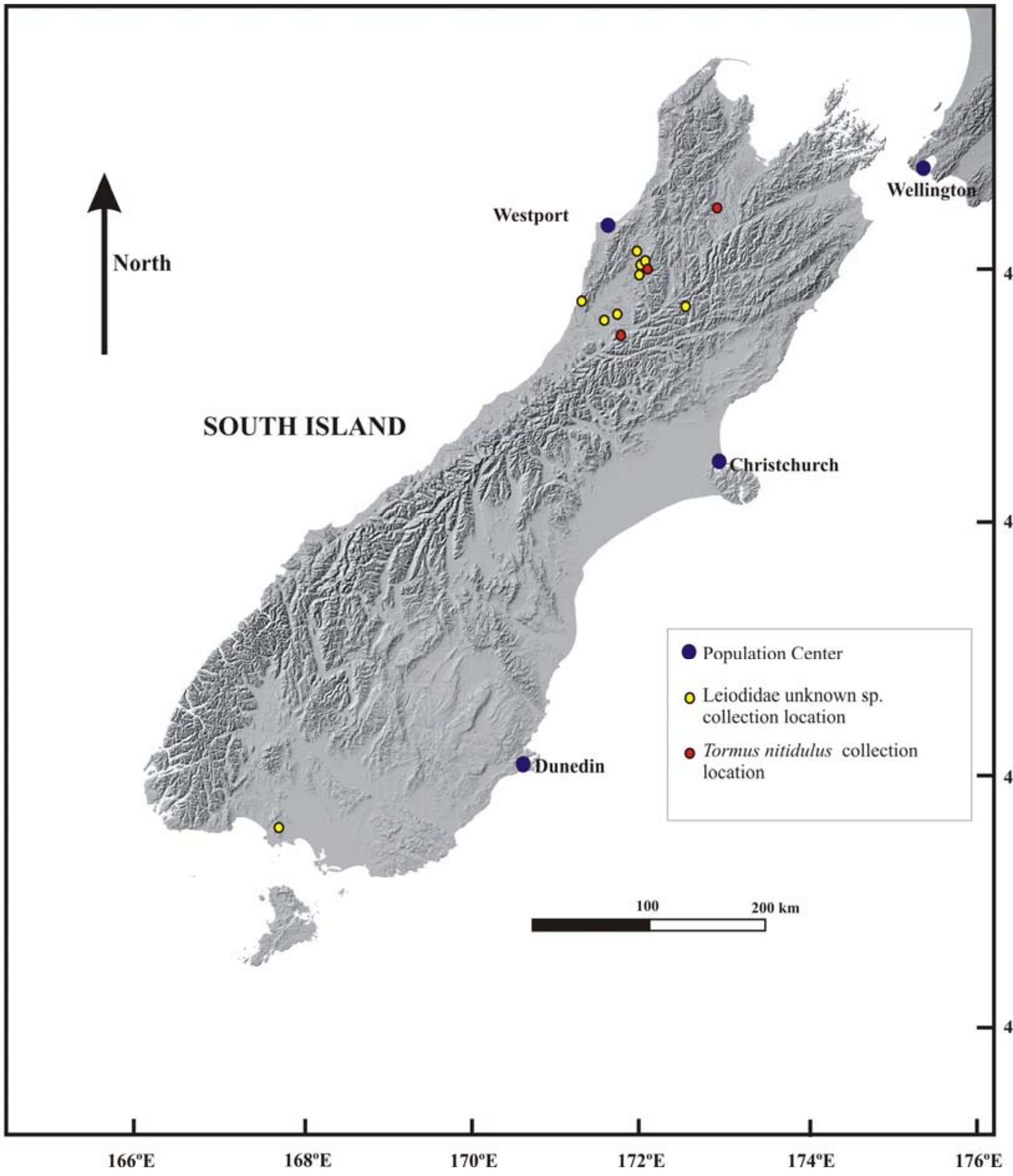


The MLE reconstructions treat two taxa, *Tormus nitidulus* Broun and *Pycnomerus latitans* Sharp as outliers (Fig. 4.3a-b, Fig. 4.4). The reason for the exclusion of these taxa is that their inclusion would have resulted in a MMWT reconstruction ca. 3-6°C (mean 4.5°C) colder than the present day (Fig. 4.3b). This is similar to estimates of full glacial temperature depression (e.g. Porter, 1975; Barrows & Juggins, 2005) and while there is some evidence of a possible slight cooling in the mid Holocene (e.g. McGlone & Topping 1983; Williams et al. 2004; Williams et al. 2005) there is no evidence to indicate that temperatures reached stadial levels of cooling. The reconstructed MMWT climate range of these taxa is therefore unreasonable considering what is already known about mid-Holocene cooling.

While the current distribution of these species may, at least in part, be due to habitat loss caused by forest clearance examination of the distribution data for these two taxa indicates that they have been extremely rarely collected. While the MLE model of Marra et al. (2004) is designed to produce climate ranges from limited distribution data sets where distribution data is inadequate it will still produce inaccurate reconstructions and this appears to be the reason for the unacceptably low climate envelopes produced from these taxa.

Tormus nitidulus is known from only three collection locations (Fig. 4.5) and four specimens. All of these sites are at the base of inland ranges of the South Island, one inland from the Westport region (42º04'S, 171º55'E), one south in Westland (42º36'S, 171º40'E) and the last from the Nelson region to the northeast (41º39', 172º39'E) (NZAC label information) (Fig. 4.5). This is much the same geographic area from which Leiodidae unnamed sp. 1 is known (Fig. 4.5) however unlike *T. nitidulus* this taxon is known from ten collection localities and has a significantly broader MLE envelope. As both Leodidae unnamed sp. 1 and *T. nitidulus* occur within the same general region during the mid-Holocene it is likely that *T. nitidulus* shares a similar distribution today and the degree of cooling indicated by its MLE envelope is due to the limited knowledge of its distribution.

Figure 4.5 Map of the South Island of New Zealand illustrating the distribution of the outlying taxon *Tormus nitidulus* (red dots) and the similar distribution of Leiodidae unknown sp. 1 (yellow dots).



Pyncnomerus latitans is also known from only three collection locations and while these are far more widespread, occurring in the central North Island (39°12’S, 175°08’E), the north of the South Island (40°56’S, 172°37’E) and the far south of the South Island (46°08’S, 167°19’E) (NZAC label information), they again appear to over estimate the magnitude of winter cooling. While such a widespread distribution of collection locations should, in theory, have broadened the reconstructed climate range it appears likely that in this case the limited number of data points remains inadequate to accurate reflect the true climate range of this taxon and it is therefore excluded from the reconstructions.

4.4.3 Palaeoenvironment

The beetle fauna obtained from this site (Table 4.1) indicates a moist forest environment characterised by leaf litter and dead wood beetles (e.g. the Curculionidae weevils) and includes taxa closely associated with ferns (e.g. *Rystheus* indet. sp.). This is consistent with the podocarp forest expected to have occupied this site during the Holocene based on West Coast pollen records (e.g. Moar & Suggate 1973; Moar & Suggate 1979; Moar & Suggate 1996; Vandergoes et al. 2005) and is also consistent with extrapolation of local forest composition from the surviving native flora in nearby regions (McEwen, 1987; Wardle, 1991).

4.4.4 Palaeoclimate

The beetle based reconstructions of mean summer temperature (Fig. 4.3a), mean daily minimum winter temperature (Fig. 4.3b) and mean annual precipitation (Fig. 4.4) all straddle the modern day mean values at the Alma Road site. As there is little evidence in New Zealand that Holocene climates varied significantly from the present day this is what would be expected if the beetle fossils are accurately reconstructing the palaeoclimate. Interestingly however the present day means all fall in the upper error range of the climate variable reconstructions (Fig. 4.3a-b, Fig. 4.4). While this is not conclusive evidence of cooling or drying at this time (as the reconstructed ranges straddle the modern mean variables) this implies that either the beetles are systematically underestimating temperature and precipitation or both temperature and precipitation may have been slightly lower in the mid-Holocene than at the present day.

Only one other Holocene palaoeclimatic reconstruction has been undertaken in New Zealand using beetle fossils (Marra et al., 2004). This study, from the Awatere Valley in Marlborough (Fig. 4.1), produced mid-Holocene temperature reconstructions straddling the present day mean indicating that temperatures were indistinguishable from the present day (Marra et al., 2004). Although some taxa in the Awatere Valley study did fall outside the reconstructed Holocene temperature range they fell on the warmer side of the reconstruction and are currently restricted to North Island forests, primarily north of 37°S. As they occur in a Holocene site it is probable that they were more widespread in the past and are restricted to their current distribution due to habitat loss (Marra et al., 2004) although one of the taxa (being flightless) may also have been from a now extinct population with different physiological requirements to the modern populations (Marra et al., 2004). Regardless, the Awatere Valley study indicates that beetle based reconstructions do not automatically show a bias towards overestimation of winter cooling and therefore the implied cooling may be real.

Evidence supporting a cooling event at this time can be found in other New Zealand proxy records from the mid-Holocene. Speleothem records from both the North and South Islands indicate a period of cooling between ca. 6,000 and ca. 3,000 years BP (Williams et al., 2004; Williams et al., 2005). Pollen records also indicate a shift to cooler, and on the West Coast, drier conditions at ca. 7,000 years BP (McGlone, 1988; McGlone et al., 1993) although there is disagreement about the exact timing of the onset of these conditions. For example Horrocks & Ogden (1998) place the onset of cooling and drying in the central North Island at ca. 7,500 ka BP while McGlone & Topping (1983) put the transition at ca. 5,000 years BP. It should noted that while the cooler and drier conditions indicated by pollen records after ca. 7,000 years BP are obviously different from the climate of the early Holocene (McGlone, 1988) they are generally indistinguishable from the modern day although McGlone & Topping (1983) acknowledge that there have been "cooler, drier intervals" than at the present day during the late Holocene (Table 2 *in* McGlone & Topping, 1983). It is possible that the cooling implied by this beetle record is representative of one of these intervals. The advance of the Franz Josef glacier on the western side of the Southern Alps at 5,455 ± 145 cal. yrs. BP (4,730 ± 75 ^{14}C yrs BP (Wardle, 1973) is possibly the best support for the inferred cooling in this record as the errors of the calibrated age from this study (5,730 ± 200 cal. yrs BP) and that of the glacial advance (5,455 ± 145 cal. yrs. BP) overlap by 70 years.

While there is disagreement about the exact timing of mid Holocene cooling the fact that multiple proxies indicate cooling and drying of the climate somewhere between ca. 6,000 and 3,000 years BP indicates that the implied cooling observed in this beetle record is probably robust.

4.5 Conclusions

The palaeoenvironmental reconstruction indicates that moist forest vegetation with a ground layer of ferns dominated this site during the mid-Holocene. This is consistent with what is expected for this site from regional pollen records and from extrapolation from modern floras in neighbouring ecological districts (McEwen, 1987). The palaeoclimatic reconstructions in this study straddle the modern day climatic variables at this site but appear to fall on the lower side of the modern day temperature and precipitation levels. While it is possible that fossil beetle based palaeoclimate reconstuctions overestimate cooling (and drying) other Holocene beetle studies appear to accurate reconstruct expected Holocene temperatures. Furthermore the slight cooling and drying indicated in this beetle record is in keeping with other New Zealand proxies from the same period of time which indicate that temperatures and precipitation levels were slightly reduced. This indicates fossil beetle based palaeoclimatic reconstructions can be successfully applied to the poorly collected beetle fauna of the West Coast, South Island although outliers in the data set emphasis the need to carefully evaluate the palaeoclimatic ranges estimated from poorly known taxa. Additionally this study shows, as indicated by the statistical analysis in Chapter 3, that fossil beetles can be used as proxies to produce robust estimates of palaeoprecipitation.

Chapter 5

The palaeoclimate and palaeoenvironment of the Westport region between 74 and 40ka BP: Evidence from Keoghan's Road

5.1 Introduction

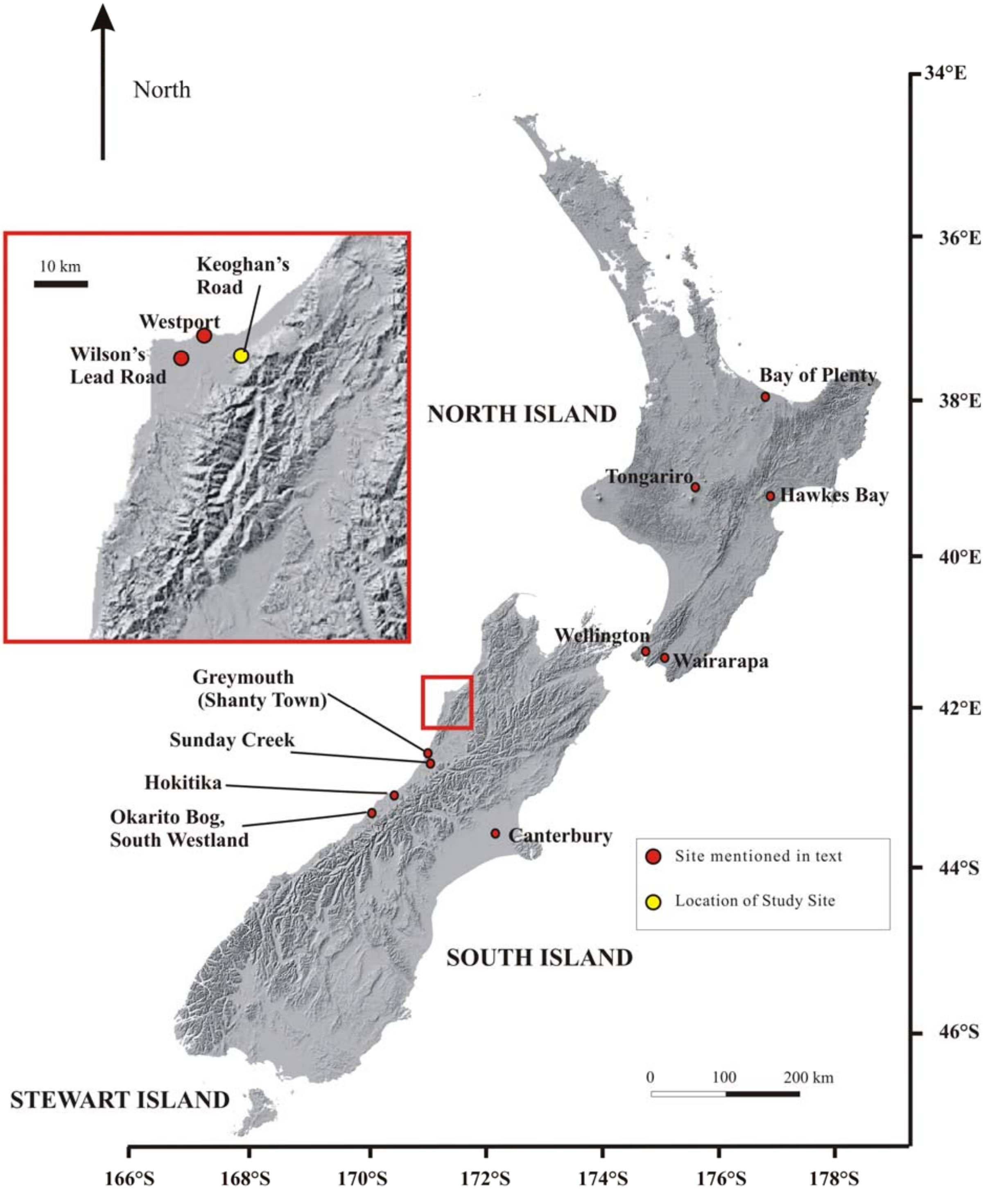
While palynological records from the West Coast of the South Island have provided a relatively comprehensive record of palaeoenvironmental change for Westland out to the penultimate glaciation (see Chapter 1), the palaeoenvironmental history of the Westport region has a gap in the record for the late last Interglacial (OIS 5b and OIS 5a) and the early part of the last Glacial (OIS 4). There is also a lack of quantitative climate estimates for this period.

This chapter uses the MLE model of Marra et al. (2004) to provide the first quantitative palaeoclimatic information, and also the first palaeoenvironmental information, about time period between 74 and 40ka BP in the Westport region. Pollen records are also presented. This site has been worked up for publication and a modifed version of this chapter is currently in press (Burge & Shulmeister, In Press-a).

5.1.1 Modern Physiography

The site examined in this chapter is an outcrop beside Keoghan's Road, four kilometres east of Westport (41°46'S, 171°40'E, NZMS E2399000, N5936400) and ca. 40 metres above sea-level (Fig. 5.1). The outcrop consists of a 60 metre long exposure in the south bank of the Orowaiti River at the base of the so-called "German Terrace" (McPherson,

Figure 5.1 Locality map showing sites and regions mentioned in the text with an inset enlargement of the Westport region showing the area around the study site.



1978). German Terrace is one of the suite of terraces that characterise the northwest coastal margin of South Island, New Zealand as explained in Chapter 1.

The closest climate station to Keoghan's Road is ca. 8 km away at the Westport Airport (41°44'S, 171°35'E, NZMS E2391930, N5939940, 4m a.m.s.l.). The modern values for mean summer temperature (MST, 16.5°C), mean daily minimum winter temperature (MMWT, 3.4°C) and mean annual precipitation (MAP, 2711mm yr^{-1}) for the Keoghan's Road site were therefore obtained using the climate surfaces of Leathwick et al. (1998).

The vegetation immediately surrounding the site has been cleared for pasture but probably consisted of mixed podocarp-beech forest comprising mainly rimu (*Dacrydium cupressinum*) and hard beech (*Nothofagus truncata*) with kahikatea (*Dacrycarpus dacrydioides*) in wet areas (McEwen, 1987; Wardle, 1991). Other tree taxa probably included kaikawaka (*Libocedrus bidwillii*), kamahi (*Weinmannia racemosa*), matai (*Prumnopitys taxifolia*), miro (*Prumnopitys ferruginea*) and northern rata (*Metrosideros robusta*) in the canopy with a sub-canopy of smaller trees including haumakaroa (*Raukaua simplex*), mapau (*Myrsine australis*), pigeonwood (*Hedycarya arborea*), silver pine (*Manoao colensoi*) and the tree ferns *Cyathea smithii* and *Dicksonia squarrosa* likely (Wardle, 1991). The ratas *Metrosideros fulgens* and *M. diffusa* and supplejack (*Ripogonum scandens*) would have been common lianas hanging down from the canopy (Wardle, 1991) while *D. squarrosa*, karapapa (*Alseuosmia macrophylla*) and stinkwood (*Coprosma foetidissima*) would have formed an intermediate shrub-layer above a ground flora of ferns probably dominated by *Blechnum discolor* (Wardle, 1991).

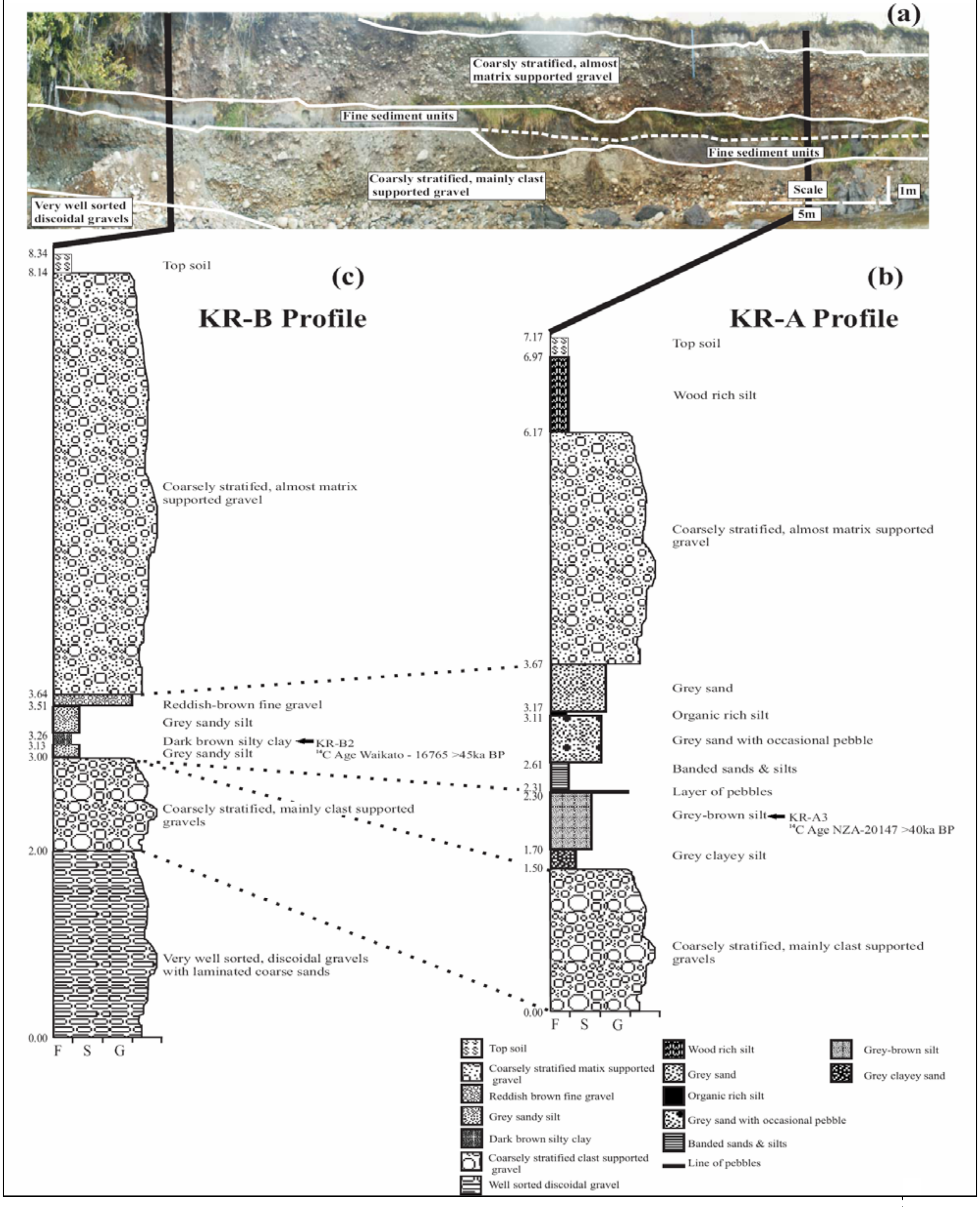
5.2 Methods

Five units inferred to be overbank deposits (Fig. 5.2) were bulk sampled using the methods outlined in Chapter 2. Of the five samples only two contained enough fossil material to merit further examination. Sample KR-A3 was collected from a brownish-grey silty-sand unit (Fig. 5.2) while KR-B2 was obtained from a dark brown silty-clay unit. These two units are located in different parts of the outcrop (Fig. 5.2) and were initially considered to be from the same stratigraphic level. KR-B2 was re-sampled with ca. 15kg of material processed. A later re-examination of the site revealed that unit KR-B2 is actually situated stratigraphically immediately above unit KR-A3 (Fig. 5.2) from which ca. 5kg of material was processed. All beetle fossil samples were processed and identified according to the standard methods outlined in Chapter 2. Palaeoclimate reconstructions were undertaken using the MLE method of Marra et al. (2004).

Both KR-A3 and KR-B2 were sub-sampled for pollen. Sample preparation followed the standard technique of Moore et al. (1991). Samples were mounted in glycerol and identified using a ZEISS transmitted light microscope at 400x magnification using the published photographs and keys of Large and Braggins (1991), Moar (1993) and Pocknall (1981) as guides. For each sample a minimum of 300 terrestrial pollen grains were counted (Appendix 4).

Samples for Infrared Stimulated Luminescence (IRSL) dating were obtained by driving 500 ml steel tubes into the sediment faces of each unit. These were then wrapped in aluminium foil and sealed with packing tape to preserve water content and retain

Figure 5.2 Simplified stratigraphy of Keoghan's Road Site. Photograph (a) indicates the relative positions of the major units and the sections. (b) shows a summary log of profile KR-A with sample KR-A3 at 1.70-2.33m and (c) displays a summary log of profile KR-B with sample KR-B2 marked at 3.13-3.26m. A break in deposition between the different groups of fine sediment units is marked with a dashed line on the photograph.



cohesion. The samples were analysed at the Luminescence Dating Laboratory at the School of Earth Sciences, Victoria University of Wellington. *In situ* wood was also obtained from the units and dried for in excess of 72 hours at 60°C prior to being submitted to the University of Waikato Radiocarbon Dating Laboratory, New Zealand. Following pre-treatment only 0.17g of holocellulose was available for dating from the KR-A3 sample and it was sent for AMS dating at the Rafter Radiocarbon Laboratory in Petone, Wellington, New Zealand. 6.95g of holocellulose from the KR-B2 sample remained following pre-treatment and this was dated using the gas scintillation technique at the University of Waikato Radiocarbon Dating Laboratory.

5.3 Results

5.3.1 Summary stratigraphy

Figure 5.2 provides a simplified lithographic-stratigraphic diagram of the Keoghan's Road outcrop and illustrates the position of the two sampled profiles (KR-A and KR-B) relative to one another. A more detailed lithographic-stratigraphic description of the individual units is provided in Table 5.1 and summarised below.

The outcrop sits on a unit of clast supported, discoidal gravels of a dominantly phyllitic (70%) nature. These gravels are inter-bedded with laminated, mica-rich sands. This unit is only visible at the east end of the exposure (Profile KR-B, Fig. 5.2, Table 5.1) and is overlain by another gravel unit. This gravel unit is poorly sorted, coarsely stratified and comprised of a mix of phyllitic (50%) and granitic clasts (50%) (Fig. 5.2, Table 5.1). The unit is dominantly clast supported but does contain within it an area which is matrix

Table 5.1 Summary of the stratigraphy of the two sampled profiles in the Keoghan's Road outcrop, West Coast, South Island, New Zealand. Location of samples and ages are marked in bold text.

Profile KR-A

6.97-7.17 m	top soil
6.17-6.97 m	wood rich silt
3.67-6.17 m	coarsely stratified, marginally matrix supported gravel. Clasts of up to 0.5 m diameter; dominantly granitic (80%) with low-grade serpentinite. Matrix consisting of coarse sand to granule sized particles. Lower contact sharp and undulating.
3.17-3.67 m	well sorted, coarse grey sand. Thickness of unit varies across outcrop between 0.20 and 0.50 m. Sharp basal contact.
3.11-3.17 m	organic rich silt band containing wood macrofossils in growth position. Thickness of unit varies across outcrop between 0.02-0.50 m. Sharp basal contact.
2.61-3.11 m	relatively poorly sorted brown-grey, quartz rich, coarse sand; sub-angular to sub-rounded with pebbles. Sharp undulating basal contact.
2.31-2.61 m	banded sands and silts (cm scale) with some organic lenses and macroscopic wood and leaves. Contains tree stumps in growth position.
2.30-2.31 m	break in deposition marked by intermittent line of pebbles across outcrop.
1.70-2.30 m	grey-brown silt, browning towards base. Macroscopic wood in growth position in basal 0.10 m. **Sample KR-A3. IRSL Age (WLL452) 36.2 ± 9.8 ka. ^{14}C Age (NZA-20147) >40 ka**.
1.50-1.70 m	grey clayey sand with no visible organics. Lower contact sharp and undulating.
<0.00-1.50 m	coarsely stratified, mainly clast supported, gravel. Clasts of up to 0.5m diameter; 50% granitic/50% phyllitic. Proportion of granitic clasts rises up profile from 30% at base to 70% at top. Lower contact obscured.

Profile KR-B

8.14-8.34 m	top soil
3.64-8.14 m	coarsely stratified, marginally matrix supported gravel. Clasts of up to 0.5 m diameter; dominantly granitic (80%) with low-grade serpentinite. Matrix consisting of coarse sand to granule sized particles. Lower contact undulating and sharp.
3.51-3.64 m	fine reddish brown gravel with sand and silt matrix. Iron pan at sharp, undulating basal contact.
3.26-3.51 m	grey sandy silt containing occasional pebbles in matrix. Unit darkens towards base. Sharp, undulating basal contact.
3.13-3.26 m	dark brown silty clay containing occasional pebbles in matrix as well as macroscopic wood. Unit lightens towards base. Lower contact undulating but sharp, unit thins towards edges. **Sample KR-A2, IRSL Age (WLL451) 28.4 ± 5.8 ka. ^{14}C Age (Waikato – 16765) >45 ka**.
3.00-3.13 m	grey sandy silt iron stained at upper and lower contacts. Sharp and undulating basal contact with iron pan.
2.00-3.00 m	coarsely stratified, mainly clast supported, gravel. Clasts of up to 0.5m diameter; 50% granitic/50% phyllitic. Proportion of granitic clasts rises up profile from 30% at base to 70% at top.
<0.00-2.00 m	very well sorted largely discoidal clasts of pebble to cobble size with very well sorted, laminated, coarse sands interbedded amongst gravels. Gravel clasts are dominantly phyllitic (70%) with granitic clasts strongly represented (30%). Sands are mica rich. Lower contact obscured.

supported. This unit can be traced across the entire outcrop and is the basal unit observed in the KR-A profile (Fig. 5.2, Table 5.1).

The poorly sorted gravel unit is topped by a sequence of finer sediments (Fig. 5.2, Table 5.1). These deposits vary in thickness along the outcrop and some pinch out entirely. Macroscopic wood is obvious in some horizons and is often in growth position (Table 5.1). This group of fine sediment units is only observed in the KR-A profile and a thin intermittent layer of pebbles across part of the face (profile KR-A, Table 5.1) divides this lower group of units from a second group (Fig. 5.2). While the individual units within this second group again vary in thickness and lateral extent the group can be traced across most of the outcrop and is found in both KR-A and KR-B profiles (Fig. 5.2).

The second grouping of fine sediment deposits are covered by another layer of coarsely stratified gravels (Fig. 5.2). These gravels are almost matrix supported and dominantly granitic (80%) in origin (Table 5.1). These gravels are in turn topped by a soil unit which varies in thickness across the outcrop (Table 5.1).

5.3.2. Chronology of the Keoghan's Road site

The position of IRSL and ^{14}C ages obtained for the two samples are indicated in Figure 5.2. The IRSL ages are 36.2 ± 9.8ka (2σ) for unit KR-A3 (WLL452) and 28.4 ± 4.8ka (2σ) for KR-B2 (WLL451) (Table 5.2a-b), and place both units within OIS 3. However while the stratigraphic relationship between the ages is correct, the IRSL ages disagree with the infinite radiocarbon ages of >40k ^{14}C years BP for KR-A3 (NZ-20147) and >45k k ^{14}C years BP for KR-B2 (Waikato – 16765) which imply a much older age for the sediments. A discussion of the age discrepancies is given in section 5.4.1.

5.3.3 Palaeoenvironment and palaeoclimate of unit KR-A3

Palaeoenvironment - pollen

Table 5.3 shows that *Nothofagus fusca*-type pollen makes up more than 90% of pollen from this unit. *Podocarpus* and *Coprosma* spp. are present in small amounts at 2% along with *N. menziesii* (1%). *Griselinia*, *Halocarpus*, *Muehlenbeckia*, and *Leptospermum* pollen all occur at trace levels, along with rare *Dacrydium* sp., *Genistoma*, Apiaceae,

Table 5.2a: Radionuclide and water contents

Sample	Unit Code	Depth below surface (m)	dD_c/dt (Gy/ka)[1]	Water content δ^2	U (µg/g) from ^{234}Th,	U (µg/g)[3] from ^{226}Ra, ^{214}Pb, ^{214}Bi	U (µg/g) from ^{210}Pb	Th (µg/g)[3] from ^{208}Tl, ^{212}Pb, ^{228}Ac	K%
WLL451	KR-B2	3.5	0.1300±0.0065	1.357	**5.23±0.33**	**3.98±0.06**	**5.29±0.30**	14.91±0.17	2.15±0.05
WLL452	KR-A3	4.7	0.1121±0.0056	1.252	**6.57±0.46**	**4.70±0.07**	5.49±0.39	16.68±0.21	3.21±0.07

[1] Contribution of cosmic radiation to the total doserate, calculated as proposed by Prescott & Hutton (Prescott & Hutton, 1994).

[2] Ratio wet sample to dry sample weight. Errors assumed 50% of (δ-1).

[3] U and Th-content is calculated from the error weighted mean of the isotope equivalent contents.

All numbers marked in bold: Minor radioactive disequilibrium (significant on 2σ-level), either between ^{234}Th and ^{226}Ra (probably due to Radium migration associated with water flow), or between ^{226}Ra and ^{210}Pb (probably due to influx of Radon).

Table 5.2b: Measured a-value and equivalent dose, doserate and luminescence age

Sample	a-value	D^e (Gy)	dD/dt (Gy/ka)	OSL-age (Ka)	Unit Code
*WLL451	0.069±0.005	126±3.3	4.46±0.38 (4.14±0.38)	28.4±2.9 30.6±2.9)	KR-B2
*WLL452	0.076±0.008	226±23.5	6.25±0.45 (5.90±0.45)	36.2±4.9 (38.4±4.9)	KR-A3

* These samples showed a radioactive disequilibrium (see Table 2b), and the given age was corrected accordingly. As the level of disequilibrium over time is unknown, this age is only a better estimate and cannot be seen as the true age. In brackets the uncorrected doserates and ages are given, calculated under the invalid assumption that the samples were in radioactive equilibrium (^{226}Ra contents used for calculation)

Table 5.3. Percentage composition of spot pollen samples from the Keoghan's Road Site. Actual pollen counts are provided in Appendix 4.

Taxon	**Type**	**KR-A3**	**KR-B2**
Terrestrial Taxa			
Nothofagus fusca-type	tree	91.1	93.2
Nothofagus menziesii	tree	0.8	3.4
Prumnopitys taxifolia	tree		0.3
Podocarpus	prostrate shrubs/tall trees	1.4	
Metrosideros	lianes/shrubs/small to tall trees	0.3	
Quintinia	small tree		0.3
Dacrydium sp.	shrub/tree	0.3	
Halocarpus	shrub/tree	0.6	
Leptospermum	shrub/medium tree	0.6	
Ascarina lucida	shrub/small tree	0.3	
Coprosma spp.	shrub/small tree	2.0	2.1
Grisellinia	shrub/small tree	0.6	
Phyllocladus	shrub/small tree		0.3
Epiaecridaceae	prostrate & erect shrubs	0.3	
Genistoma	tall shrub	0.3	
Mulenbeckia	laines/shrubs	0.3	
Solanum	shrub		0.3
Phormium	tall tussock	0.3	
Gramineae	grass	0.3	
Apiaceae	herb	0.3	
Gentiana	herb		0.3
Rumex	herb	0.3	
Aquatic Taxa			
Cyperaceae	herb	5.7	5.3
Monolete Fern	fern	2.2	1.5
Trilete Fern	fern	3.2	1.5

Gramineae, Epacridaceae and *Ascarina*. The tree and shrub pollen clearly indicates a closed canopy Fuscaspora beech forest with scattered silver beech (Macphail & McQueen, 1983). Podocarp pollen occurs in such low amounts that it is probably derived from elsewhere (Macphail & McQueen, 1983). Broadleafs and shrubs are typically under-represented in pollen diagrams and may indicate either long distance dispersal or rare local occurrence. Coprosmas in particular occur in beech forests and are well enough represented to suggest local occurrence (Macphail & McQueen, 1983). The understorey consists of a mix of mono- and trilete ferns and sedges, the relative abundance of

Cyperaceae pollen (5.7%) indicates a moist environment such as would be found on a flood plain.

Palaeoenvironment - beetles

A total of 12 beetle taxa from seven families were collected from the KR-A3 unit. All taxa are associated with forests or are eurytopic (Table 5.4) indicating that the site was forested at the time KR-A3 was deposited. In particular members of the genus *Nestrius* (weevils, family Curculionidae) are known for being flightless, leaf-litter inhabiting taxa (Kuschel, 1964) indicating the presence of forest litter at the site.

Table 5.4. Taxonomic list of fossil beetle taxa and their associated environments from Keoghan's Road Sample KR-A3. Fossil parts are given a letter designation e= elytron, p = pronotum and h = head. Environmental information was collated from [1]Kuschel 1964; [2]Emberson & Matthews 1973; [3]McColl 1982; [4]Newton 1984; [5]Barratt & Patrick 1987; [6]Booth et al. 1990; [7]Lyal 1993; [8]May 1993; [9]Klimaszewski et al. 1996; [10]Hansen 1997; [11]Klimaszewski & Watt 1997; [12]Marra 2003; [13]NZAC specimen label information and [14]LUNZ specimen label information

Family	**taxon**	**Fossil Element**	**Environment**
Hydrophilidae	*Tormus* c.f. *nitidulus* Broun	e	Forest [10, 11, 13]
Staphylinidae	*Paratrochus* "sp. group A"	e, p	Eurytopic [3, 4, 6, 9, 11]
Scarabidae	*Saphobius edwardsi* Sharp	h	Forest [2, 6, 11, 13, 14]
Byrrhidae	*Epichorius* "sp. group A"	p	Eurytopic [5, 11, 13]
Bothrididae	*Ascetoderes* indet. sp.	p	Forest [11, 13]
Zopheridae	*Pycnomerus marginalis* Broun	p	Forest [11, 13, 14]
	Pycnomerus rufficolis Broun	p	Forest [11, 13, 14]
	Pycnomerus "sp. group A"	e	Forest [11, 13, 14]
	Pycnomerus "sp. group B"	e	Forest [11, 13, 14]
Curculionidae	Cryptorynchini indet spp.	e	Forest [7, 8, 12]
	"*Metacalles* genus group" sp.	h	Forest [7, 8, 12]
	Nestrius "sp. group A"	e	Forest [1]

The Cryptorhynchini species, a tribe of weevils known to be endophytic on dead woody plants, (Lyal, 1993) and the presence of the genus *Pycnomerus* (family Zopheridae), found predominantly in loose and rotten bark or under litter and stones in podocarp/broadleaf or *Nothofagus* forest (NZAC label information), also strongly support the interpretation of this fauna as representing a forest environment. The presence of the hydrophiliel water beetle (family Hydrophilidae) *Tormus nitidulus* Broun, a member of subfamily Sphaeridiinae, a group known for their habitation of damp, decaying matter (Booth et al., 1990) indicates that the environment was also moist.

Palaeoclimate

Collection location data, required for the construction of climate envelopes, was available for ten of the twelve taxa identified from this unit. Data was unavailable for the distribution of the unknown Cryptorynchini weevils and the weevils of the "*Metacalles* genus group". The results of the climatic reconstructions from these taxa are presented in Fig. 5.3a-b and Fig. 5.4.

Figure 5.3a illustrates a mean summer temperature range of between 15.1ºC and 18.2ºC. This straddles the modern mean summer temperature at this site (16.5ºC (Leathwick et al., 1998)) giving a median value of 16.7ºC which suggests no discernable change from modern conditions. The winter mean daily minimum temperature reconstruction (Fig. 5.3b) also straddles the modern mean for Keoghan's Road with a range of -0.3ºC to 4.3ºC, a mean drop of 1.1ºC from the present day mean minimum winter temperature of 3.4ºC (Leathwick et al., 1998). This variance in the difference between modern and reconstructed temperatures during summer and winter may indicate increased seasonality over the present day.

Figure 5.3. Keoghan's Road (Unit KR-A3) climatic reconstructions: **3a**. Mean Summer (February) Temperature Reconstruction; **3b**. Keoghan Road (Unit KR-A3) Minimum Winter (July) Temperature Reconstruction. The blue horizontal bars in these figures indicate the range of the variable within which the taxon is known to inhabit. The grey ends of the bars represent the error to these known ranges as calculated by the MLE models. The darker green box indicates the reconstructed range of the variable including the MLE error while the light green box illustrates the reconstructed range without the MLE error term. The solid red vertical line represents the present day mean value of the variable at the site as derived from the climate surfaces of Leathwick et al. (1998). Taxa considered to be outliers are indicated by dashed red circles and are discussed in the text.

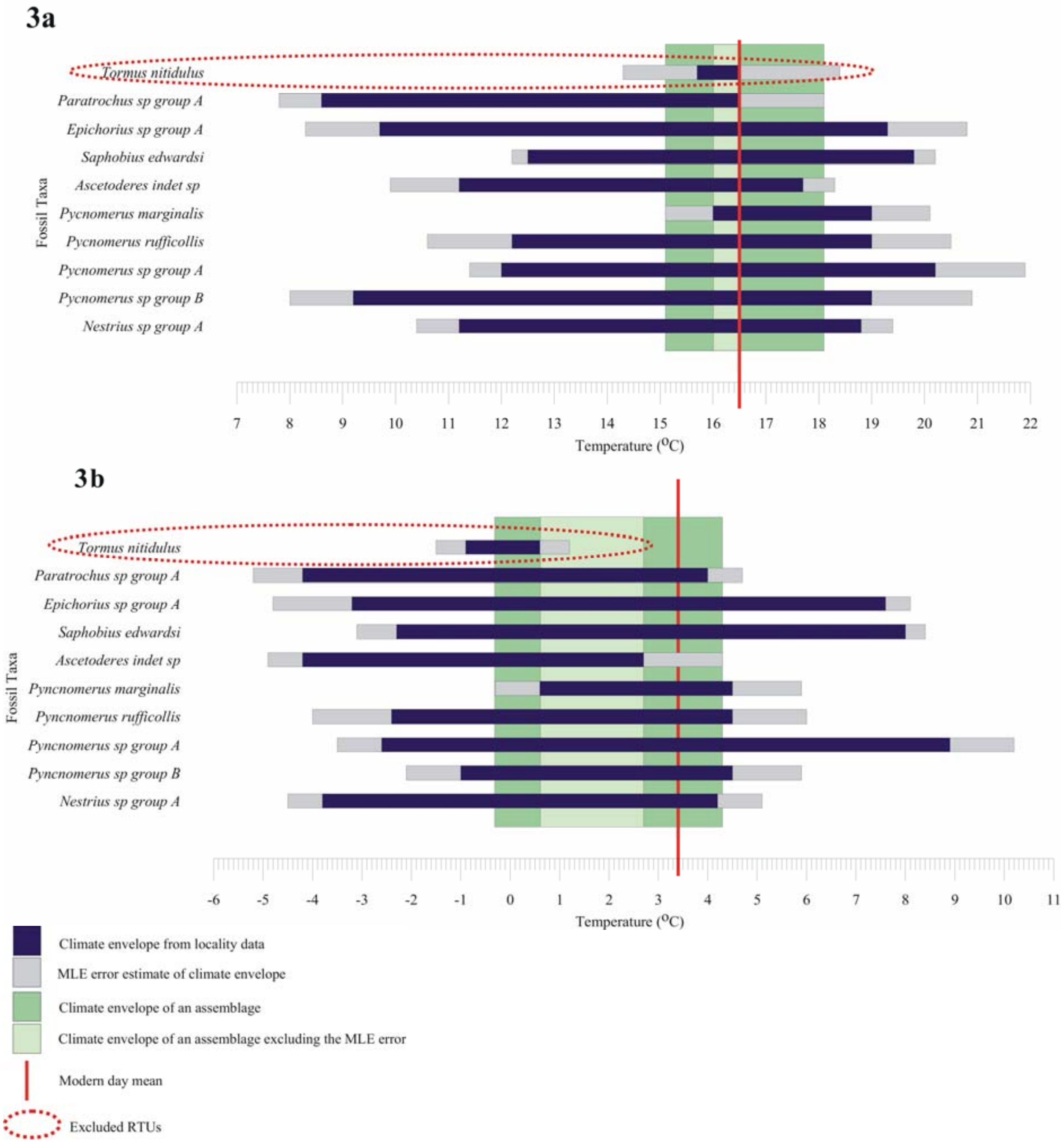


Figure 5.4. Keoghan Road (Unit KR-A3) Mean Annual Precipitation Reconstruction. The blue horizontal bars in these figures indicate the range of mean annual precipitation within which the taxon is known to inhabit. The grey ends of the bars represent the error to these known ranges as calculated by the MLE models. The darker green box indicates the reconstructed ra nge of the variable including the MLE error while the light green box illustrates the reconstructed range without the MLE error term. The solid red vertical line represents the present day mean value of the variable at the site as derived from the climate surfaces of Leathwick et al. (1998). Taxa considered to be outliers are indicated by dashed red circles and are discussed in the text.

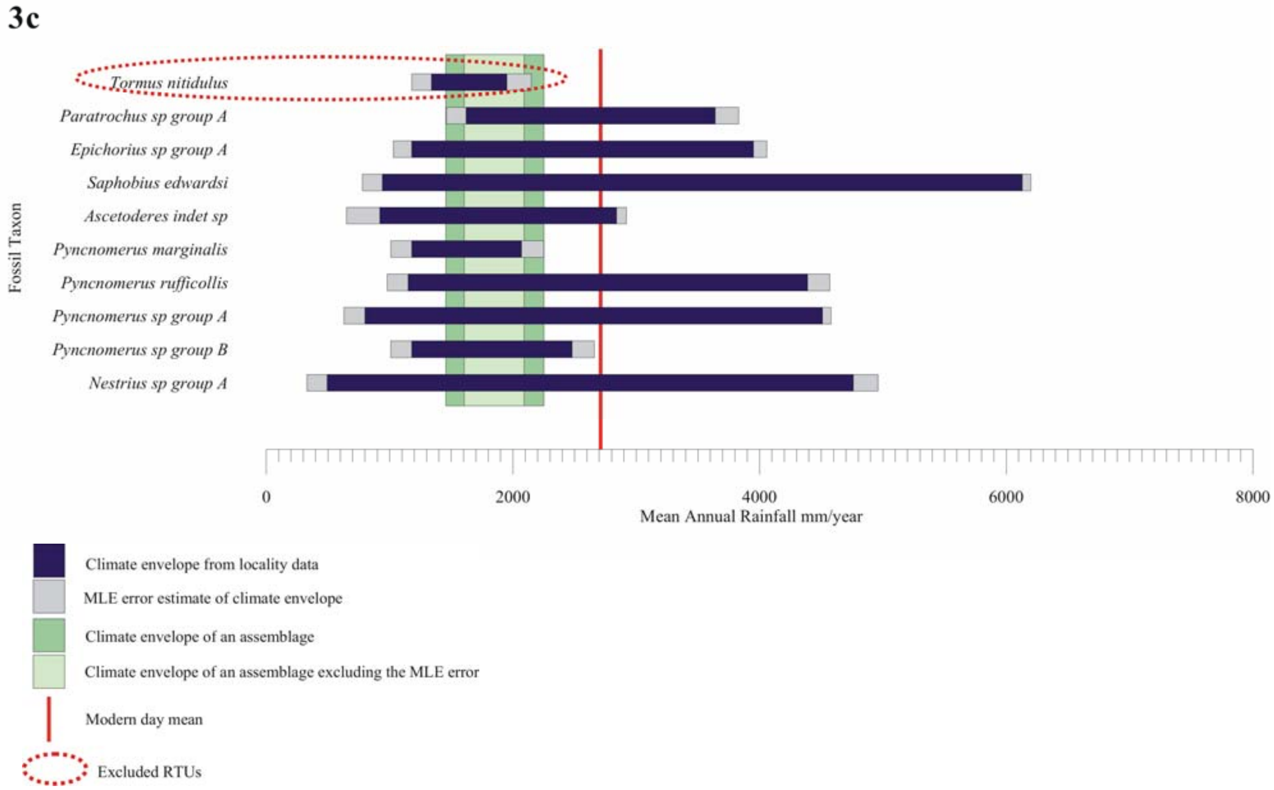


Figure 5.4 examines mean annual rainfall from KR-A3 and indicates that in addition to possible seasonal cooling at this time the environment was also drier, with mean annual precipitation (MAP) of between 1,460mm and 2,250mm per year. This is a reduction of 461mm to 1251mm from the current mean of 2,711mm per year (Leathwick et al., 1998), or a reduction in MAP of between 17-46% lower than present day.

5.3.4 Palaeoenvironment and palaeoclimate of unit KR-B2

Palaeoenvironment - pollen

Table 5.3 illustrates the composition of the spot pollen sample taken from KR-B2. Again the pollen from this unit is greater than 90% *Nothofagus fusca*-type with some *N. menziesii* (3.4%) and *Coprosma* spp. (2.1%). Other pollen types occur in extremely low amounts (< 1.0%). The high proportion of *N. fusca*-type pollen indicates a closed canopy beech forest with coprosmas in the understorey. *N. menziesii* is notoriously under represented in pollen diagrams (Macphail & McQueen, 1983) and the beech forest probably contains a significant proportion of *N. menziesii*. Fuscaspora beech forest is difficult to key to individual taxa but the beetle information (below) strongly suggests the larger, more lowland, red (*N. fusca*) or hard beech (*N. truncata*) types over mountain beech (*N. solandri* var. *cliffortioides*). The trace amounts of matai (*Prumnopitys taxifolia*) are probably wind derived (Macphail & McQueen, 1983). The ground cover remains a mix of trilete and monolete ferns and sedges. All indicate a moist environment.

Palaeoenvironment - beetles

A total of 33 taxa from 12 families were obtained from unit KR-B2 (Table 5.5). Most of the taxa are known to inhabit forest litter (e.g. *Cyloma* “sp. group A”, *Dalma pubescens* Sharp, *Zelandis* indet. sp., *Nestrius* “sp. group A”.), dead wood (e.g. *Pycnomerus* and the Cryptorynchinae weevil species) and fallen branches (e.g. *Zolus* indet. sp.). The presence of the hygrophilous forest-dwelling ground beetle (Carabidae) *Zeopoecilus putus* Broun (Larochelle & Larivière, 2001), the weevil *Euophryum confine* Broun (Green & Pitman, 2003) and an unidentified member of the Scirtidae (a family of beetles colloquially

Table 5.5. Taxonomic list of fossil beetle taxa and their associated environments from Keoghan's Road Sample KR-B2. Fossil parts are given a letter designation e= elytron, p = pronotum and h = head. Environmental information was collated from [1]Kuschel, 1964; [2]Emberson & Matthews 1973; [3]McColl 1982; [4]Newton 1984; [5]Barratt & Patrick 1987; [6]Thompson, 1989; [7]Booth et al. 1990; [8]Kuschel 1990; [9]Lyal 1993; [10]May 1993; [11]Newton & Thayer 1995; [12]Klimaszewski et al. 1996; [13]Hansen 1997; [14]Klimaszewski & Watt 1997; [15]Chandler 2001; [16]Larochelle & Larivière 2001; [17]Green & Pitman, 2003 [18]Löbl & Leschen 2003; [19]Marra 2003; [20]NZAC specimen label information and [21]LUNZ specimen label information.

Family	**taxon**	**Fossil Element**	**Environment**
Carabidae	*Zolus* indet sp.	e	Forest [16, 20]
	Zeopoecilus putus Broun	e	Forest? [16, 20]
Hydrophilidae	*Tormus* cf. *nitidulus* Broun	e	Forest [13, 14, 20]
Leiodidae	*Paracatops* "sp. group A"	e	Forest [8, 14, 20]
	Paracatops "sp. group B"	e	Forest [8, 14, 20]
Scydmaenidae	Scydmaenidae indet. sp.	e	Forest, grassland, shrubland [4, 8, 14, 20]
Staphylinidae	*Stenomalium cognatum* Broun	e	Forest [11, 20]
	Dalma pubescens Sharp	e	Forest [14, 20]
	Sagola indet. sp.	e	Eurytopic [8, 14, 15, 20]
	Zelandius indet. sp.	e	Forest [8, 12, 14, 15, 20]
	Brachynopus scutellaris Redtenbacher	e	Forest [12, 18]
	Paratrochus "sp. group A"	p	Eurytopic [3, 4, 7, 12, 14]
	Philonthus rectangulus Sharp	e	Forest? [12]
Scarabidae	*Saphobius edwardsi* Sharp	e, h	Forest [2, 7, 14, 20, 21]
	Saphobius indet. sp.	e	Forest [2, 7, 14, 20, 21]
Scirtidae	Scirtidae indet spp.	e	Vegetation nr water, forest [14]
Byrrhidae	*Epichorius* "sp. group A"	h	Eurytopic [5, 14, 20]
	Epichorius sp. 3	p	Forest [20]
	Epichorius sp. 26	p	Forest [20]
	Liochoria sp. 1	p	Tussock grassland [20]
Ciidae	*Orthocis undulates* Broun	e	Forest margin, shrubland [20]
Zopheridae	*Pycnomerus* "sp. group A"	e	Forest [14, 20, 21]
	Pycnomerus "sp. group B"	e	Forest [14, 20, 21]
Chrysomelidae	Chrysomelidae indet. sp.	e	Unknown but low vegetation [10, 14]
Curculionidae	*Euophryum confine* Broun	e, h	Forest [6, 17, 20]
	Cryptorynchini indet. spp.	e, h	Forest [9, 10, 19]
	"*Metacalles* genus group" sp.	h	Forest [9, 10, 19]
	cf. *Trindicalles* indet. sp.	e	Forest [9, 10, 19, 20]
	Alloprocas niger Broun	e	Forest, generally *Nothofagus* [20]
	Nestrius "sp. group A"	e	Forest [1, 19]

known as marsh beetles) (Klimaszewski & Watt, 1997), provide evidence that the site was also moist and probably near a body of water. The presence of fungi at the site is confirmed by the presence of the mycophagus rove beetle (family Staphylinidae) *Brachynopus scutellaris* Redtenbacher (Löbl & Leschen, 2003) and the Ciidid *Orthocis undulates* Broun.

The >90% *N. fusca* type pollen (Table 5.3), the *in-situ* macrofossil wood and the dominance of forest taxa amongst the beetle fossils appears to indicate a closed canopy beech forest occupied this site. While it is possible that this forest was one of montane mountain beech (*N. solandri* var. *cliffortioides*), as proposed by Okuda et al. (2002) for Hawkes Bay at these times, the dominance of forest litter and dead wood inhabiting species (Table 5.5) amongst the beetle taxa indicate a substantial ground cover of litter and fallen branches, something far more common in lowland beech forests of *N. fusca* (red beech), *N. truncata* (hard beech) or *N. solandri* var. *solandri* (black beech) forests than in mountain beech forests (Wardle, 1984). Furthermore, montane mountain beech forests tend to have open canopies and an understory containing grasses and other montane herbs (J. Shulmeister pers. comm., 2006; pers. observation). This sort of ground flora is far less common in lowland beech forests (J. Shulmeister pers. comm., 2006; pers. observation). Pollen from these taxa is extremely rare in the pollen assemblages from these samples (Table 5.3) even though grasses, in particular, produce significant amounts of pollen (Macphail & McQueen, 1983). The lack of grass and herb pollen indicates that they were not present in the immediate vicinity again implying a lowland beech forest. In summary, most of the beetles and ancillary evidence are consistent with a closed canopy beech forest with dead wood and deep litter on the forest floor.

One taxon, *Liochoria* sp. 1, is recorded as being found exclusively on or above the treeline amongst tussock and spear-grass species in the eastern ranges of South Island, New Zealand (NZAC label information). No other species present in this assemblage is restricted in their distribution to subalpine environments although the Ciidid *O.*

undulates, which also occurs in KR-B2, is thought to be representative of forest margin or shrubland environments. The presence of these taxa therefore indicates that the surroundings, at the time of deposition of KR-B2, were a wet *Nothofagus* forest environment containing moist litter, decaying wood and fungi at, or near, the forest margin bordering an area of tussock grassland.

Palaeoclimate

Data regarding the modern range of 23 of the 33 taxa were obtained for the reconstruction of climate envelopes. Most of those taxa excluded were those that could not be identified to a lower taxonomic group than family. As previously discussed in Chapter 2, genus and species group collection data was considered to be usable in the palaeoclimatic reconstructions as the data set enscapulates the entire range of its component species. This much larger data set is likely to provide a much broader climate range for a taxon producing an accurate, if not very precise, measure of a taxon's climate range.

Analysis of the mean summer temperature (Fig. 5.5) indicates a range of between 13.4ºC and 13.6ºC which is a reduction of approximately 3.0ºC. The mean daily minimum winter temperature reconstruction (Fig. 5.6) indicates a range of temperatures from -2.1ºC to -1.4ºC, a drop of between 4.8ºC and 5.5ºC from the present day mean daily minimum winter temperature of 3.4ºC.

Reconstruction of the mean annual precipitation (Fig. 5.7, above) also indicates drier conditions at this time with MAP of between 1,500 and 1,800mm compared to the

Figure 5.5 Keoghan's Road (Unit KR-B2) Mean Summer (February) Temperature Reconstruction. The blue horizontal bars indicate the range of mean summer temperature within which the taxon is known to inhabit. The grey ends of the bars represent the error to these known ranges as calculated by the MLE model. The darker green box indicates the reconstructed range of the variable including the MLE error while the light green box illustrates the reconstructed range without the MLE error. The solid red vertical line represents the present day mean value of the variable as derived from the climate surfaces of Leathwick et al. (1998). Taxa considered to be outliers are indicated by dashed red circles and are discussed in the text.

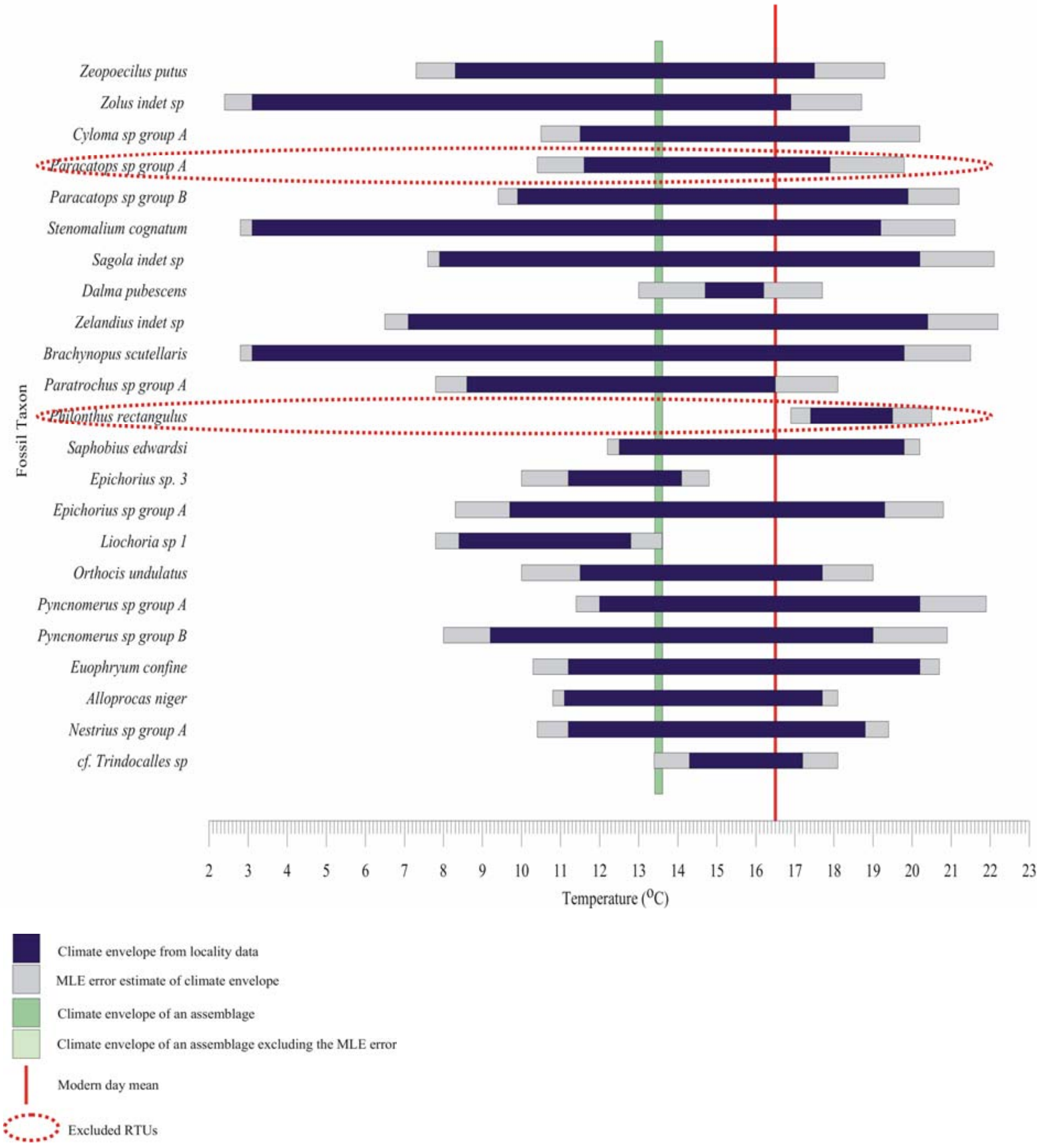


Figure 5.6 Keoghan's Road (Unit KR-B2) Mean daily Minimum Winter (July) Temperature Reconstruction. The blue horizontal bars indicate the range of mean daily minimum winter temperature within which the taxon is known to inhabit. The grey ends of the bars represent the error to these known ranges as calculated by the MLE model. The darker green box indicates the reconstructed range of the variable including the MLE error while the light green box illustrates the reconstructed range without the MLE error. The solid red vertical line represents the present day mean value of the variable as derived from the climate surfaces of Leathwick et al. (1998). Taxa considered to be outliers are indicated by dashed red circles and are discussed in the text.

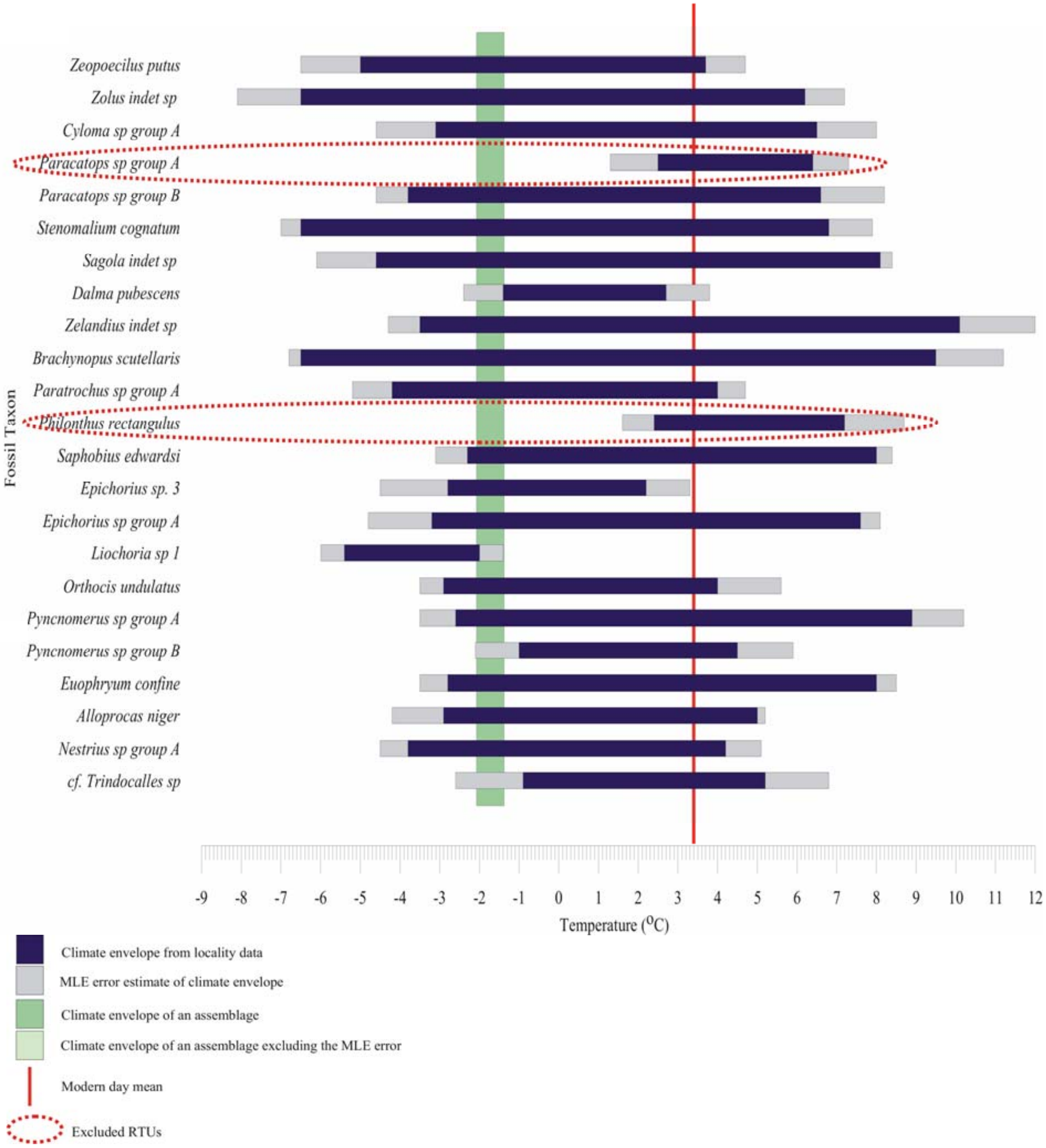
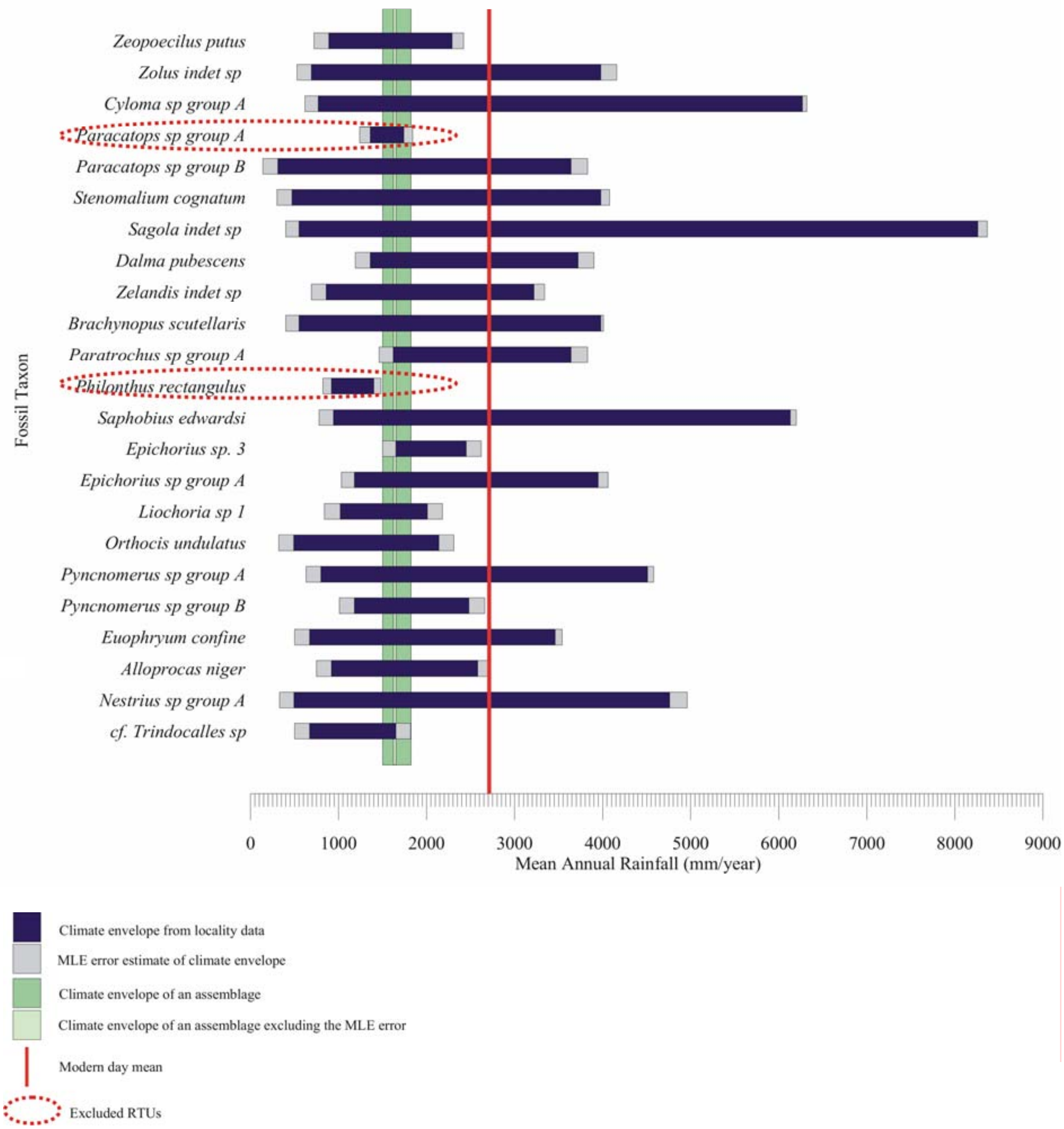


Figure 5.7 Keoghan's Road (Unit KR-B2) Mean Annual Precipitation Reconstruction. The blue horizontal bars indicate the range of mean annual precipitation within which the taxon is known to inhabit. The grey ends of the bars represent the error to these known ranges as calculated by the MLE model. The darker green box indicates the reconstructed range of the variable including the MLE error while the light green box illustrates the reconstructed range without the MLE error. The solid red vertical line represents the present day mean value of the variable as derived from the climate surfaces of Leathwick et al. (1998). Taxa considered to be outliers are indicated by dashed red circles and are discussed in the text.



modern value of 2711mm per year. This is a reduction in rainfall of between 30-40% annually.

5.4 Discussion

5.4.1 Stratigraphic interpretation

The clast support, discoidal shape and well sorted nature of the basal gravels in Profile KR-B (Table 5.1) indicates that they are of marine origin. These gravels underlie "Grahams Terrace" and are mapped by Nathan et al. (2002) as OIS 5a (ca. 91-74ka BP (Martinson et al., 1987)) in age. The overlying gravel unit (Fig. 5.2, Table 5.1) appears to be of alluvial origin and the sequence of finer sediments that overlie the alluvial gravel unit are inferred to be overbank deposits lying within an abandoned river channel (Fig. 5.2, Table 5.1). The thin intermittent layer of pebbles observed in Profile KR-A (Table 5.1) indicates that there was a break in deposition between the formation of the lower group of overbank deposits observed in Profile KR-A (Fig. 5.2) and a younger, overlying, set of overbank deposits that are also present in Profile KR-B (Fig. 5.2). Each overbank deposit is likely to relate to a single event and, while the age control is poor (see below), the fossil beetle assemblages from unit KR-B and KR-A (Fig 5.2) represent unique points in time. The bed of gravel overlying the second group of overbank deposits again appears to be alluvial in origin.

The site is interpreted as the preserved remains of a river floodplain overlying an old beach surface. Current mapping places the marine gravels as OIS 5a in age (Nathan et al., 2002) and the change from marine to alluvial gravels could have occurred as soon as the marine platform was above sea-level. This may have occurred either late in OIS 5a or within OIS 4. The shift from alluvial gravels to finer sediments indicates that the river shifted its bed and the fine sediments are interpreted as representing overbank deposits at its edges. The further unit of alluvial gravel indicates that the river shifted its course back prior to its final abandonment of the site.

5.4.2 Age control

The most significant problem encountered in this chapter is the disagreement between the two dating techniques used. In short, the radiocarbon ages are at or beyond the range or radiocarbon (early OIS 3 or older) whereas the luminescence ages suggest a mid- to late-OIS 3 age. Both radiocarbon and luminescence dating have encountered problems in the hyper-humid environment of the West Coast of the South Island of New Zealand. Many radiocarbon ages have been discarded on the basis of contamination with younger carbon due to movement of carbon through sediments (e.g. Grant-Taylor & Rafter, 1971; Dickson 1972; Hammond et al., 1991) and luminescence ages sometimes give ages either too old or too young due to issues of zeroing and possibly weathering or the provenance of the dated material (e.g. Almond et al, 2001; Berger et al., 2001a). However both techniques are known to work where samples are suitable (e.g. Hormes et al., 2003; Preusser et al., 2005).

In this case the radiocarbon ages are preferred for the following reasons. Firstly the samples used to obtain the ages are very good targets. Both samples are cellulose from wood taken from small tree stumps in growth position within the outcrop. This means that there is no chance that the wood has been recycled from older deposits. Additionally the wood was in structurally good condition which suggests that contamination is a low probability. Furthermore while in many locations along the West Coast contamination from old carbon derived from limestone and calcareous sandstone could be an issue the local lithologies at this site are not carbon yielding (granites and phyllites).

In contrast, the dose rates determined from the luminescence samples are very high, being about twice those typical of samples from the eastern side of New Zealand (e.g. Berger et al., 2001b). Furthermore the dose rates are remarkably variable for samples recovered from similar lithologies only a few metres apart. Minor secular disequilibrium and a down face increase in uranium content were also observed (see Table 5.2a). There is therefore a strong suspicion that radioactive elements may be moving vertically through the profile via soil processes or horizontally though percolation, or both. This means that modern dose rates may not be a good indication of long term averages and substantial age variations are possible. If uranium or radium is concentrating in the organic rich layers from which the beetles come from, the IRSL ages must be minimum ages only. The total doses received by the samples at 126 and 226 Gy (Table 5.2b) are exceptionally high for samples of these young apparent ages. For example, Wang et al (2006) treat samples with more than 50 Gy total doses as ‘old’ in IRSL dating terms. The samples should be close to saturation and with these dose rates, it is highly improbable that pre-OIS 5 samples would remain unsaturated. It is therefore probable that the samples are likely to be OIS 5 or younger.

Additionally the samples are taken from above marine gravels mapped as OIS 5a in age (Nathan et al., 2002). Although there is no direct age control on this terrace at this site the terraces are well mapped and the age assignations have been published and generally accepted as correct. Furthermore initial luminescence chronologies from the Westland coast south of this study support the younger part of the regional terrace chronology (out to OIS 5) (Preusser et al., 2005). On the basis of the current mapping of the marine unit as OIS 5a, the stratigraphically younger position of the sampled sediments, and the constraints of the ^{14}C ages as being >40ka BP, the true age of the samples appears to lie between ca. 74ka BP (end of OIS 5a (Martinson et al., 1987)) and ca. 40ka BP. The preferred age for the older of the two samples (KR-A3) is near the OIS 5a/OIS 4 transition (ca. 74ka BP (Martinson et al., 1987)) as the palaeotemperature reconstuctions indicate that temperatures were similar to today (Fig. 5.3a-b). The age of the younger unit (KR-B2) is likely to be somewhere within OIS 4 (74-59ka BP (Martinson et al., 1987)) in age as the palaeotemperature reconstructions indicate stadial scale cooling (Fig. 5.5, Fig. 5.6).

5.4.3 Outlying taxa

In the KR-A3 sample the species *Tormus nitidulus* Broun is treated as an outlier. The reasons for excluding *T. nitidulus* from MLE reconstructions have been previously discussed in Chapter 4. Two other taxa, *Philonthus rectangulus* Sharp and *Paracatops* sp. group A, are considered outliers in the KR-B2 reconstructions. *Philonthus rectangulus* is an obvious outlier in all three reconstructed climate variables while

Paracatops sp. group A is only an obvious outlier in the mean daily minimum winter temperature reconstruction (MMWT).

Philonthus rectangulus is a member of an extremely widespread genus yet this particular species is known from only five collection locations. Of these collection locations only one is found outside the Auckland metropolitan area (ca. 36º56’S, 174º43’E) in the Nelson region (41º16’S, 173º01’E) of the South Island (NZAC label information). While it is possible that some factor other than temperature and precipitation (see Chapter 3) limits *P. rectangulus* to the area around Auckland and Nelson it is more likely that this taxon has a far more widespread distribution than is currently known and that the concentration in Auckland is due to the higher intensity of collection around the city. This means that the warm temperature and high precipitation reconstructions are likely to be biased towards levels found in the Auckland region rather than resembling the actual climate range occupied by this taxon.

Examination of the distributional data of *Paracatops* sp. group A indicates that it is a collection of three species (Appendix 2) which, from the fossil fragment obtained, are indistinguishable from one another. Unfortunately the three species are known from only one, or in the case of *Paracatops luxbris* Sharp, two collection locations. These locations are widespread with *P. luxbris* occurring both in the far north (35º12’S, 173º27’E) and in the East Cape region (38º29’S, 178º04’E) of New Zealand. *Paracatops* sp. 3 also inhabits the East Coast region (38º27’S, 178º03’E) while the third species, *P. triangulum* Geamuel, is found in the far south of New Zealand (47º14’S, 167º24’E) (NZAC label information). This small number of collection localities and their extremely widespread distribution indicates that the distribution of this taxon is far more widespread than indicated by the limited data set. Unlike *P. rectangulus*, *Paracatops* sp. group A is only an outlier in Fig. 5.6 and it is possible to fit an overlap to include this taxon. However doing so excludes *Liochoria* sp. 1. This taxon provides the upper limit on the MMWT reconstruction illustrated in Fig. 5.6 and is known from six collection locations all of which are above the treeline in the South Island ranges (NZAC label information). The MMWT reconstruction for this taxon is consistent with its known habitat and considering the poorly defined distribution of *Paracatops* sp. group A it is more reasonable to accept a climate range based on *Liochoria* sp. 1 and treat *Paracatops* sp. group A as an outlier.

5.4.4 Palaeoclimate, palaeoenvironments and the presence of refugia between 74-40ka BP

This site indicates the continuation of a Fuscaspora beech forest in the Westport region for the period between 74-40ka. This finding contrasts strongly with the current palaeoenvironmental reconstruction for this period although data on the palaeoenvironment of the West Coast during this period is extremely limited with only two pollen sites from the West Coast covering the time period between 74 and 40ka BP.

The first site is Okarito Bog from South Westland approximately 200km to the south of Westport (Fig. 5.1). The record from this site indicates that the early part of this period was one of transition from a podocarp-hardwood dominated flora to one dominated by montane and subalpine shrubs (Vandergoes et al., 2005). The second site, Sunday Creek

(Dickson, 1972; Moar & Suggate, 1996) near Greymouth (Fig. 5.1), indicates that the transition from late OIS 5 to early OIS 4 is a period of rapid change from a *Nothofagus fusca*-type forest to grassland. This is similar to examples of the OIS 5a/OIS 4 transition from elsewhere in the country such as the Canterbury region of South Island (Moar & Gage, 1973) and the Wellington (Mildenhall, 1994; Mildenhall, 1995), Wairarapa (Harper, 1989; McGlone, 1989; Carter & Lian, 2000), Tongariro (McGlone & Topping, 1983) and Hawkes Bay (Okuda et al., 2002) regions of the North Island (Fig. 5.1). In all these cases, environments dominated by *Nothofagus fusca*-type forests underwent a transition to either grassland or grass/shrubland.

The Sunday Creek record ends during early OIS 4 but the Okarito Bog record indicates that following the transition to a shrub/grassland environment open vegetation continued for the entire 74-40ka period (Vandergoes et al., 2005). To the north, records from Wellington (Mildenhall, 1994) also indicate the continuance of a shrub/grassland dominated flora through OIS 4 and OIS 3 but with stands of *N. menziesii* (silver beech) becoming more significant during the latter part of this period. OIS 3 records from south of Greymouth (e.g. Shanty Town (Moar & Suggate, 1996), Fig. 5.1) indicate that open *Nothofagus menziesii* forest was the dominant vegetation during this time in North Westland, however a record from Wilson's Lead Road, 10km south of Westport (Moar & Suggate, 1979; Moar & Suggate, 1996) (Fig. 5.1) indicate *Halocarpus*/*Phyllocladus* shrubland was dominant in the Westport region at the same time (Moar & Suggate, 1996).

The MLE temperature reconstructions indicate a shift between the samples from a period with similar temperatures to the present (Fig. 5.3a-b) to a period of more severe cold (Fig. 5.5, Fig. 5.6). This 3-5°C reduction in temperatures is consistent with other estimates of stadial cooling from pollen (e.g. McGlone & Topping, 1983; Mildenhall, 1994; Okuda et al., 2002), sea surface temperatures (e.g. Barrows & Juggins, 2005) and equilibrium line altitudes for glaciers (e.g. Porter, 1975). This degree of temperature reduction is not enough to have excluded forest from lowland areas (McGlone, 1985; McGlone et al., 1993) and the apparent restriction of forest from the West Coast of the South Island has been attributed to a combination of decreased precipitation and/or increased windiness (Moar & Suggate, 1996) or increased frostiness (Moar & Suggate, 1979).

While generally interpreted as indicating a significant reduction of tree taxa the pollen diagrams from this period show a continuous low incidence of pollen from forest taxa (e.g Dickson, 1972; Moar & Suggate, 1996). When combined with the rapid re-forestation of the region following the end of the last glacial (McGlone, 1988) this suggests that forest vegetation must have survived locally, even if only in small stands (McGlone et al., 1993). Wardle (1963) noted that the northwest of the South Island may have acted as a refugium for much of the present flora, probably due to the wide variety of available habitats (Wardle, 1988). This low elevation site, sheltered to the east, distal to any glaciers, set back from the coast but close enough to the coast to be relatively mild, is a perfect candidate for such a refugium. Based on the combination of the beetle fossil and pollen assemblages this site could be the first stadial refugium for tall beech forest identified on the West Coast of the South Island.

5.4.5 Moisture

The MAP reconstructions indicate a transition from a somewhat drier period than present (Fig. 5.4) to a period of definately drier, although still moist, conditions (Fig. 5.7). The scale of this reduction (30-40%) is large enough that the decline is probably real. The impact of this moisture reduction is much less apparent. Both sets of samples indicate moist beech forest environments with ferns and sedges on the forest floor, thick leaf litter, and extensive amounts of dead wood. Given that the larger reduction is associated with a clearly cooler climate the more important relative humidity parameter is probably little affected and with the reconstructed mean annual precipitation still between 1,500-1,700mm, the environment remained humid. The implications of reduced rainfall at this site are potentially more significant for eastern regions of the South Island. If the reduced precipitation is due to drier air masses moving onto the West Coast then this would aid in the creation of semi-arid (or possibly even arid) environments on the Canterbury Plains during the early part of the last glaciation. In contrast, if the reduction in mean annual precipitation is due to a weakening of westerly atmospheric circulation (e.g. Dodson, 1998; Shulmeister et al., 2004) this will have an opposite effect on the eastern South Island as reduced westerly airflows would result in fewer föhn winds east of the Southern Alps. This may permit an increase in easterly or southerly air flows and a resulting increase in rainfall along the east coast. The strength of westerly atmospheric circulation during OIS 4 and OIS 3 is currently unknown (Shulmeister et al., 2004) and it is impossible to confidently conclude which of these two models is correct. A precipitation reconstruction from an east coast OIS 4/OIS 3 site would help resolve this issue.

5.4.6 Seasonality

Denton et al. (2005) recently highlighted the importance of seasonality in understanding climate change and an important aspect of these data is that they give insight into seasonal variations. Rather than providing measures of annual temperature change the beetle data instead indicates that winter cooling in sample KR-B2 was ca. 2ºC greater than summer cooling. There are two likely reasons for this seasonal signal.

The first possibility is that the seasonal signal is the result of orbital forcing of insolation. The obliquity of the Earth to the Sun controls the ratio of summer to winter insolation. At 30ºS peak seasonal variation is about 290 W m^{-2} (Berger, 1992) while minimal seasonal variation is ca. 240 W m^{-2} (Berger, 1992). While the difference in insolation varies by only ca. 50 W m^{-2} this variation directly increases or decreases seasonal temperatures. Vandergoes et al. (2005) have invoked orbital forcing as an explanation for the onset of New Zealand glaciations and the seasonal signal apparent in our data may indicate that the younger unit is representative of stadial cooling. If this is the case it is apparent that conditions, while cooler, were not particularly harsh.

A second possible reason for the observed seasonal variation in temperature depression may be the consequence of seasonal expansion of Antarctic sea-ice. The extent of OIS 4/OIS 3 sea-ice is poorly constrained although evidence does exist to indicate a seasonal expansion during these times (Crosta et al., 2004). The effects of increased sea-ice are varied (Gersonde et al., 2005) however, an important seasonal effect is that increased sea-ice would allow polar air masses to move further north from the Southern Ocean without modification by passage over warmer seas during winter. The magnitude of these modifications is extreme. A modern example is the change in energy flux over the Greenland Sea. During open water years air masses over the sea are warmed by more than 250 W m^{-2} (Deser et al., 2000) This regional effect is enormous and much larger than changes associated with insolation forcing. Because the sea-ice was seasonal the cooling would be concentrated in winter. During summer, circulation patterns would be more similar to modern conditions. Both sea-ice and insolation forcing of seasonality are possible and they are not mutually exclusive.

5.5 Conclusions

The data implies enhanced seasonality at this site, particularly in the younger of the two units. While the reasons for this seasonal shift are probably related to variation in seasonal insolation levels, sea-ice growth or some combination of these factors any conclusions as to the exact cause are impossible to make due to the discrepancies between the age outcomes from the luminescence and radiocarbon dating. While these discrepancies make a conclusive age assignation impossible the stratigraphic setting suggests an age between 74-40ka BP for the deposits and the temperature reconstructions indicate that the older sample likely dates to the older end of this range (late OIS 5a, ca. 74ka BP (Martinson et al., 1987)) while the younger sample could be from anywhere within OIS 4 (ca. 74-59ka BP (Martinson et al., 1987)).

While no conclusions can be drawn about the enhanced seasonality at this site, like other recent studies (e.g. Marra & Leschen, 2004) this chapter highlights the persistence of tall forest in areas of New Zealand previously thought to be deforested during the last glacial cycle. The beetles (and pollen) indicate the persistence of lowland beech (i.e. *N. fusca*, *N. truncata* and/or *N. solandri* var. *solandri*) forest through a period previously thought to be characterised by the replacement of *N. fusca*-type beech forest with shrub/grasslands or dominated by *N. menziesii* (silver beech) forest. The presence of lowland beech at this site during a stadial suggests that closed canpoy forest may be more extensive during glacial periods than previously considered.

Chapter 6

The palaeoclimate and palaeoenvironment of the Westport region between 37 and 21ka BP: Evidence from Wilson's Lead Road

6.1 Introduction

The current palaeoenvironmental reconstruction of the Westport region through the period between ca. 37 and ca. 21ka BP (late OIS 3 and OIS 2) is based primarily on a pollen diagram from an outcrop colloquially known as "The Hill", found on Wilson's Lead Road Westport (Moar & Suggate, 1979). This pollen-based reconstruction indicates that the palaeovegetation of the region comprised a shrubland of *Halocarpus* and *Phyllocladus* during late OIS 3 and a wide spread swampy grassland during OIS 2 (Moar & Suggate, 1979). The glacial period vegetation differs from elsewhere on the West Coast which indicates shrub-grassland during OIS 2 (see Chapter 1, Table 1.1) and has been attributed to harsh frosts (Moar & Suggate, 1979) or increased windiness and differing soil conditions (Moar & Suggate, 1996). These discrepancies have never been closely examined even though the site has been revisited in other publications (e.g. Moar & Suggate 1996; Suggate & Almond 2005). Furthermore, no quantitative reconstruction of the climate of the Westport region for this time interval has been attempted.

This chapter examines the Wilson's Lead Road site using beetle fossils to produce the first quantitative estimates of palaeoclimate from the Westport region at this time. This chapter also presents a beetle-based reconstruction of the palaeoenvironment at the site and compares and reconciles it with the current pollen-based interpretation in order to determine why this region differs from elsewhere on the West Coast, South Island, New

Zealand. Finally, the fossil beetle record presented in this is the longest continuous (ca. 16,000 year using 18 samples) fossil beetle record in New Zealand and one of the longest in the southern hemisphere.

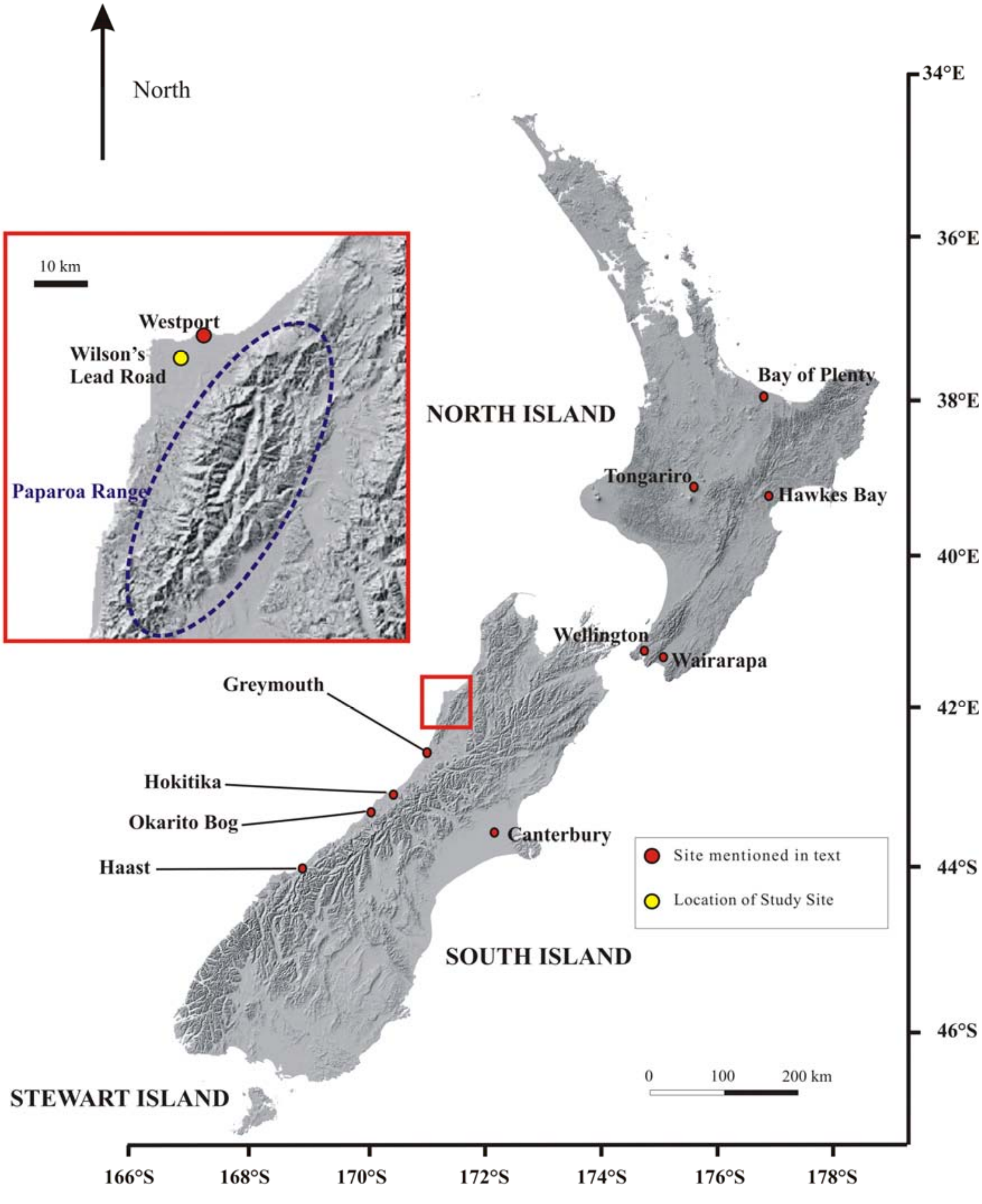
6.1.1 Modern physiography

The site examined in this chapter is an outcrop exposed in a road cutting approximately 9 km west of Westport on the northeast side of Wilson's Lead Road (41°47'S, 171°30'E NZMS E2385410, N5935067) (Fig. 6.1). The outcrop is situated within a dune field that accumulated on the surface of an abandoned marine terrace. Based on the altitude of the site (ca. 35 m.a.s.l.) and estimated rates of uplift the terrace is inferred to be last interglacial (80-125ka BP (Martinson et al., 1987)) in age (Moar & Suggate, 1979)).

The closest climate station to the site is ca. 8 km away at Westport Airport (41°44'S, 171°35'E, NZMS E2391930, N5939940, 4m a.m.s.l). Modern day values for mean daily minimum winter temperature (MMWT, 3.9°C), mean summer temperature (MST, 16.3°C) and mean annual precipitation (MAP, 2190mm yr^{-1}) were therefore obtained from the mathematically derived climate surfaces of Leathwick et al. (1998).

As described for the previous sites of Alma Road and Keoghan's Road, the native regional vegetation at Wilson's Lead Road has been cleared for pasture and information on its former composition is sparse. Like at the previous sites this outcrop is situated on a marine terrace, however, unlike Alma Road or Keoghan's Road, it is the remnant of in-filled depression within a dune field (Moar & Suggate, 1979). It appears that this dune field stabilised during the Holocene and the local vegetation at the site was probably a

Figure 6.1. Locality map showing sites and regions mentioned in the text. An enlargement of the study area near Westport is provided.



podocarp-broadleaf forest similar to that described for Alma Road (see Chapter 4). If the dune field remained active, however, the vegetation probably had a similar structure, if not composition, to that observed at the active dune field near Haast in South Westland (Dickinson & Mark, 1994). In that case, lowland forest, similar to that observed at Alma Road (Chapter 4), would most likely have occupied the dune peaks while a community of swamp vegetation including manuka (*Leptospermum scoparium*), pakihi rush (Restionaceae) and umbrella fern (*Gleichenia* spp.) would have dominated the dune swales as seen in poorly drained parts of the Westport region today (McPherson, 1978).

6.2 Methods

Eighteen samples were collected at 50mm continous intervals from a 0.95m thick organic silt unit (Fig. 6.2). Each sample consisted of ca. 5kg of sediment. The samples were designated H1 at the top of the silt unit (1.85m) and H18 at the base (0.95m). The other units in the face were sand rich and non beetle bearing. The samples were processed and beetle fossils identified according to the standard methods presented in Chapter 2.

In addition to the general methods outlined in Chapter 2 the environmental affinities of each beetle taxon found in the samples obtained in this study was used to determine assemblage zones that could be compared to the pollen zones of Moar & Suggate (1979). This was done by giving each taxon occuring in a sample assemblage worth a score of '1'. This score was then divided between four general environmental categories, open environments (e.g. grassland), shrubland/forest edge, closed canopy forest and aquatic/riparian. Thus if a taxon appeared in only one category then it was worth a value of ‘1’ for that category and ‘0’ in the other three. If a taxon occurred in more than one environment category its score of ‘1’ was divided evenly between them. For example the Staphylinidae *Aleochara hammondi* Klimazeswki is only found in tussock grasslands. It therefore scores ‘1’ in the open environment category and ‘0’ in the other three. The eurytopic taxon *Sagola* indet sp., on the other hand, scored ‘0.25’ in each of the four categories. Thus the presence of taxa associated with particular ecotones played a greater role in determining the type of environment present in each assemblage zone.

6.3 Results

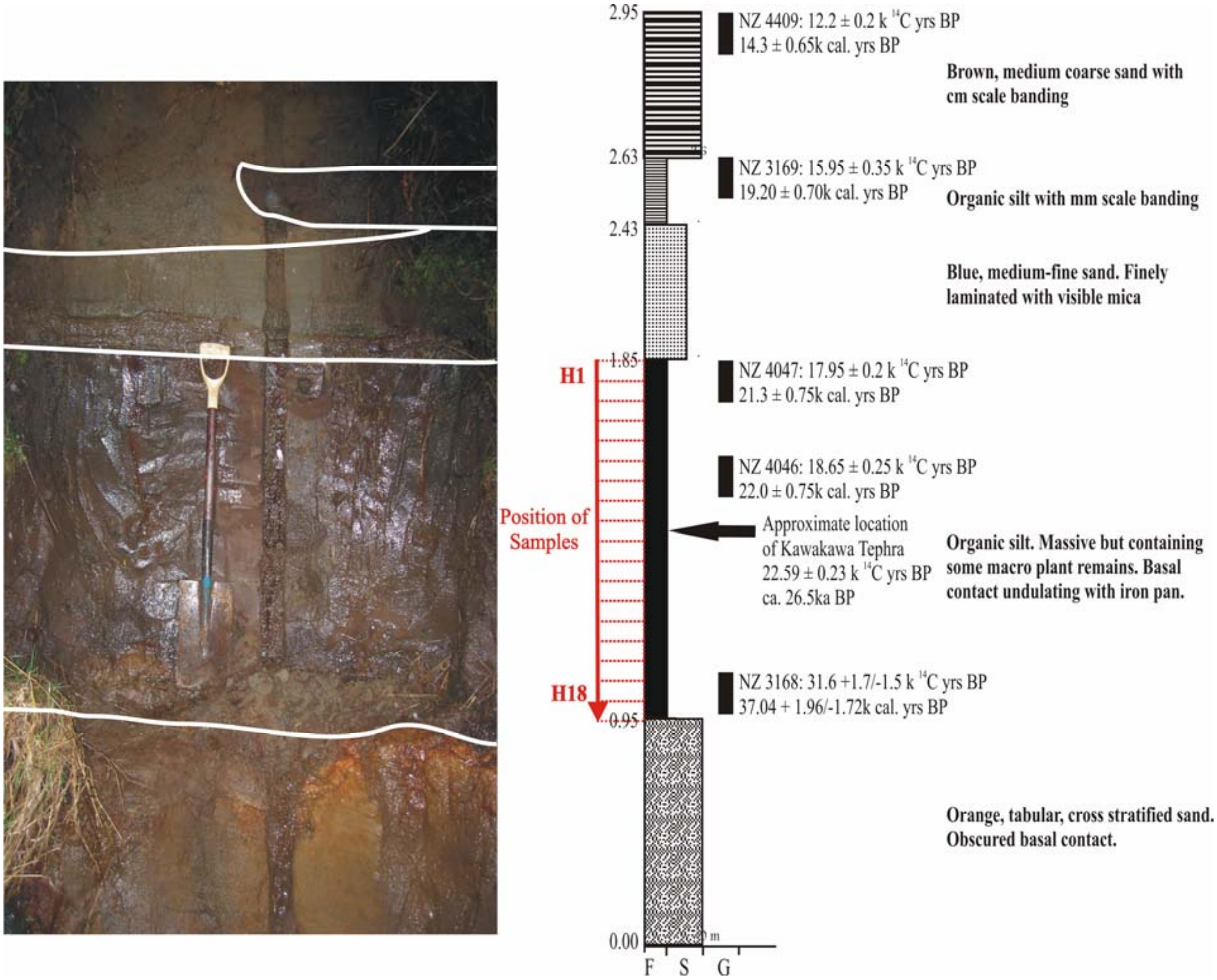
6.3.1 Summary Stratigraphy

The basal unit of the outcrop (Fig. 6.2) consists of tabular, coarsely stratified orange sand. The contact between this sand unit and the overlying unit is marked by an iron pan. The overlying unit comprises a massive, dark brown, organic silt unit and is the unit containing beetle fossils. A sharp contact between the organic silt and an overlying 600mm of finely laminated bluish sand containing visible mica indicates an abrupt termination to silt deposition. The blue sand also shows a sharp transition to a unit of banded, medium to coarse brown sand which rises to the upper limit of the outcrop (Fig. 6.2). Finely laminated organic silt intrudes into the brown sand unit at the east end of the outcrop.

6.3.2 Chronology of “The Hill”, Wilson’s Lead Road

Age control for this outcrop is derived from Moar & Suggate (1979) and Suggate & Almond (2005). The original outcrop examined by Moar and Suggate (1979) was

Figure 6.2. Stratigraphy of the Wilson's Lead Road site indicating the position and description of the different units. The position of the ^{14}C ages are inferred from those previously published by Moar & Suggate (1979) and the position of the Kawakawa tephra is inferred from Suggate & Almond (2005).. Ages were calibrated using the INTCAL 04 calibration curve. Exceptions include the Kawakawa tephra, which has an accepted calendar age of 26.5ka BP (Froggatt & Lowe, 1990), and NZ 3168 which was beyond the calibration range of INTCAL 04 and was therefore re-calibrated using CalPal (Weninger et al., 2006). The position of the 18 samples obtained from this outcrop are indicated in red. Samples were numbered H1 at the top of the unit and H18 at the base.



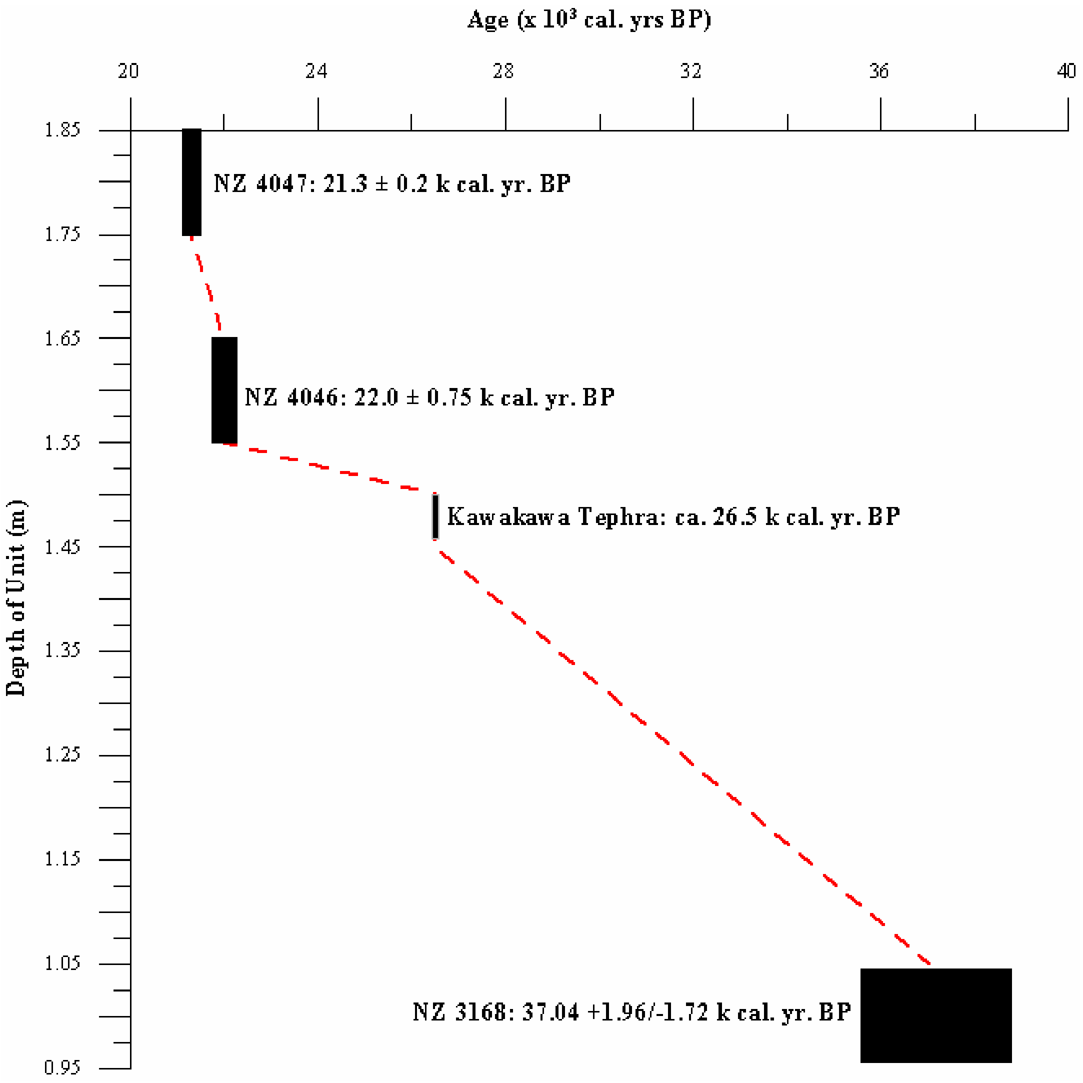
destroyed by road widening since its initial sampling in 1974 however Suggate and Almond (2005) determined that the modern outcrop is stratigraphically extremely similar to that originally sampled. Based on this recent re-examination of the outcrop the results and ages from the original pollen study can be confidently matched to this new record

(Suggate & Almond, 2005). Calibration of radiocarbon ages was undertaken using OXCAL (Bronk Ramsey, 2001) and using the INTCAL04 calibration curve except where the ages were beyond the calibration age of INTCAL04. In those cases, CALPAL (http://www.calpal-online.de/) (Weninger et al., 2006) was used instead. Conventional ages and lab numbers are provided alongside the stratigraphy in Figure 6.2 and only calendar ages are reported in the text.

Based on the position of the outcrop Moar & Suggate (1979) placed the accumulation of the basal sand unit on an abandoned OIS 5 (125 – 80ka BP (Martinson et al., 1987)) terrace. The dark brown organic silt unit began accumulating at 37.043 + 1.961/-1.724k cal. yrs. BP (NZ 3168) and ended at 21.3 ± 0.75k cal. yrs. BP (NZ 4047) (Fig. 6.2). Suggate & Almond (2005) found traces of the Kawakawa tephra, an important marker tephra generally accepted to be 26.5ka BP, at ca. 1.45m (beetle sample H8) (Fig. 6.2). A date from the finely laminated organic silt that intrudes into the brown sand unit indicates that this unit is 19.25 ± 0.70k cal. yrs. BP (NZ 3169) (Fig. 6.2). A final age from the top of the original outcrop indicates that outcrop formation ended at 14.3 ± 0.65k cal. yrs. BP (NZ 4409) (Fig. 6.2).

The ages obtained for this outcrop indicate that the accumulation rate of the organic unit was quite variable as indicated in the age-depth diagram (Fig. 6.3). The section of the unit between the basal age (ca. 0.95m, ca. 37ka. BP) and the Kawakawa tephra (ca. 1.45-1.50m, 26.5ka BP) has an average deposition rate of 0.05 mm/year or about 1,000 years per sample (Fig. 6.3). Between the Kawakawa tephra (ca. 26.5ka BP) and the older of the

Figure 6.3. Age-depth diagram showing the accumulation rate of sediment in the organic silt unit sampled for beetle fossils (Fig. 6.2) from Wilson's Lead Road. The red dashed line represents the accumulation rate. The black boxes represent the inferred position of the bulk ^{14}C ages of Moar & Suggate (1979) and the inferred position of the Kawakawa Tephra from Suggate & Almond (2005) The width of the black box on the x-axis represents the error of the calibrated age. Note that the Kawakawa tephra has been generally accepted by the New Zealand Quaternary community as ca. 26.5 ka BP in age and does not appear to have an associated error with this accepted age.



two upper ^{14}C ages (ca. 22ka. BP) (ca. 1.55-1.65m) the average deposition rate drops to 0.03 mm/year giving an average resolution of 1,500 years per sample (Fig. 6.3). The section of the unit between the upper two ^{14}C ages (ca. 22ka and 21.3ka BP) (ca. 1.75-1.85m) (Fig. 6.2) has an average deposition rate of approximately 0.36 mm/year giving an average resolution of 140 years per sample (Fig. 6.3).

6.3.3 Palaeoenvironment

Table 6.1 contains environmental data for the 76 taxa, from 12 families, identified at the WLR site. Sample H18, at the bottom of the sequence, contained only two poorly preserved fossils and as these could only be identified to the Family level so this sample is excluded from the environmental reconstructions. Using the environmental affinities of the beetles (see section 6.2 above) the assemblages of the remaining samples were used to determine two assemblage zones, one divided in two sub-zones. These zones are designated E1, E2a and E2b (Fig. 6.4).

Zone E1 – Samples H17 to H15 (1.00-1.15m)

Figure 6.4 indicates that Zone E1 is primarily dominated by a closed canopy assemblage with some taxa associated with riparian environments. An examination of the individual taxa (Table 6.1) indicates that the forest taxa comprise the rove beetles (Family Staphylinidae) *Brachynopus scutellaris* Redtenbacher (Klimaszewski et al., 1996; Löbl & Leschen, 2003; NZAC label information), *Vidamus* indet. sp. (Klimaszewski et al., 1996;

Table 6.1. Fossils beetles retrieved from the first seventeen samples from Wilson's Lead Road and their associated environments. A * indicates the presence of a particular taxon in a sample. The 18th sample is not included as it contained no identifiable beetle remains. Environmental information was collated from [1]Linsey 1959; [2]Winterbourn 1970; [3]Emberson & Matthews 1973; [4]Lindroth 1976; [5]McColl 1982; [6]Newton 1984; [7]Barratt & Patrick 1987; [8]Thompson 1989; [9]Booth et al. 1990; [10]Kuschel 1990; [11]Chandler & Peck 1992; [12]Lyal 1993; [13]May 1993; [14]Newton & Thayer 1995; [15]Klimaszewski et al. 1996; [16]Hansen 1997; [17]Klimaszewski & Crosby 1997; [18]Klimaszewski & Watt 1997; [19]Slipinski & Lawrence 1997; [20]Hansen 2000; [21]Leschen 2000; [22]Lawrence et al. 2000 onwards; [23]Chandler 2001; [24]Larochelle & Larivière 2001; [25]Löbl & Leschen 2003; [26]Marra 2003; [27]Archangelsky 2004; [28]Marra & Leschen 2004, [29]NZAC specimen label data and [30]LUNZ specimen label data

Sample	**H1**	**H2**	**H3**	**H4**	**H5**	**H6**	**H7**	**H8**	**H9**	**H10**	**H11**	**H12**	**H13**	**H14**	**H15**	**H16**	**H17**	
Depth (m)	**1.85-1.80**	**1.80-1.75**	**1.75-1.70**	**1.70-1.65**	**1.65-1.60**	**1.60-1.55**	**1.55-1.50**	**1.50-1.45**	**1.45-1.40**	**1.40-1.35**	**1.35-1.30**	**1.30-1.25**	**1.25-1.20**	**1.20-1.15**	**1.15-1.10**	**1.10-1.05**	**1.05-1.00**	
Taxon																		**Environment**
CARABIDAE																		
Bembidion indet. sp.										*								Riparian [4, 18, 24]
Bembidion maorinum maorinum Bates											*		*					Riparian, open ground [9, 18, 24]
Bembidion tekapoense Broun											*	*						Riparian, open ground [9, 18, 24]
Bembidion wanakense Lindroth				*														Riparian, open ground [4, 18, 24]
Oopterus indet. sp.						*	*		*	*	*							Forest, open vegetation [18, 24, 29, 30]
Oopterus pallidipes Broun		*	*				*	*	*									Fell fields, forest [18, 24, 29]

Sample	**H1**	**H2**	**H3**	**H4**	**H5**	**H6**	**H7**	**H8**	**H9**	**H10**	**H11**	**H12**	**H13**	**H14**	**H15**	**H16**	**H17**	
Depth (m)	**1.85-1.80**	**1.80-1.75**	**1.75-1.70**	**1.70-1.65**	**1.65-1.60**	**1.60-1.55**	**1.55-1.50**	**1.50-1.45**	**1.45-1.40**	**1.40-1.35**	**1.35-1.30**	**1.30-1.25**	**1.25-1.20**	**1.20-1.15**	**1.15-1.10**	**1.10-1.05**	**1.05-1.00**	
Taxon																		**Environment**
Dierochile flavipes	*																	Forest [18, 24, 29]
Notagonium feredayi Bates	*	*	*	*	*			*	*									Open vegetation, swamps [18, 24, 29]
Notogonium indet. sp.									*	*	*	*	*					Hygrophilous [18, 24]
Scopodes "sp. group A"		*		*	*	*		*	*	*								Eurytopic [18, 24, 29]
Scopodes indet. sp.											*							Eurytopic [18, 24, 29]
HYDROPHILIDAE																		
Enochrus tritus Broun			*															Pond or swamp [10, 18, 27]
Paracymus pygmaeus Macleay				*				*										Slow or still water [2, 18, 20, 27, 28]
Adolopus helmsi Sharp		*	*	*	*			*	*	*	*							Moist forest [16, 18, 28, 29]
Adolopus indet. sp.		*	*	*	*	*	*	*	*	*	*	*	*	*				Moist forest [10, 16, 18, 28, 29]
Cyloma "sp group B"		*	*		*	*	*	*	*	*	*							Moist forest [16, 18, 29]

Sample	**H1**	**H2**	**H3**	**H4**	**H5**	**H6**	**H7**	**H8**	**H9**	**H10**	**H11**	**H12**	**H13**	**H14**	**H15**	**H16**	**H17**	
Depth (m)	**1.85-1.80**	**1.80-1.75**	**1.75-1.70**	**1.70-1.65**	**1.65-1.60**	**1.60-1.55**	**1.55-1.50**	**1.50-1.45**	**1.45-1.40**	**1.40-1.35**	**1.35-1.30**	**1.30-1.25**	**1.25-1.20**	**1.20-1.15**	**1.15-1.10**	**1.10-1.05**	**1.05-1.00**	
Taxon																		**Environment**
Cyloma indet. sp.	*																	Moist forest [16, 18, 29]
Sphaeridiinae indet. sp.										*	*							Moist terrestrial [16, 18, 27, 29]
Tormus nitidulus Broun	*	*	*	*	*	*	*	*	*	*	*	*	*			*		Moist forest [16, 18, 29]
LEIODIDAE																		
Isocolon modestum Broun		*	*	*				*										Forest, swamp [10, 29]
Leiodidae unnamed sp.									*	*		*		*				Forest, open grassland [10, 11, 21]
SCYDMAENIDAE																		
Adrastia nelsoni Franz						*	*				*							Montane grassland, shrubland [6, 10, 18, 29]
Scydmaenidae "sp group A"	*				*		*	*	*	*	*	*	*					Forest, grassland, shrubland [6, 10, 18, 29]
Scydmaenidae indet. spp.										*								Forest, grassland, shrubland [6, 10, 18, 29]

Sample	**H1**	**H2**	**H3**	**H4**	**H5**	**H6**	**H7**	**H8**	**H9**	**H10**	**H11**	**H12**	**H13**	**H14**	**H15**	**H16**	**H17**	
Depth (m)	**1.85-1.80**	**1.80-1.75**	**1.75-1.70**	**1.70-1.65**	**1.65-1.60**	**1.60-1.55**	**1.55-1.50**	**1.50-1.45**	**1.45-1.40**	**1.40-1.35**	**1.35-1.30**	**1.30-1.25**	**1.25-1.20**	**1.20-1.15**	**1.15-1.10**	**1.10-1.05**	**1.05-1.00**	
Taxon																		**Environment**
STAPHYLINIDAE																		
Corneolabium mandibulare Steel				*				*	*	*	*	*	*	*				Forest $^{14, 15, 18}$
Ischnoderus curtipennis Broun			*															Forest $^{10, 14, 28}$
Stenomalium cognatum Broun			*															Forest $^{14, 29}$
Stenomalium indet. sp.			*			*	*		*	*								Forest, beaches $^{14, 29}$
Dalma pubescens Sharp								*				*	*					Forest $^{18, 29}$
Eupines "sp group A"	*			*		*	*	*	*	*	*	*	*	*	*	*		Forest $^{10, 15, 18, 23, 29}$
Eupines "sp group B"		*																Forest $^{15, 18, 23, 29}$
Eupines indet. spp.					*		*	*			*							Forest $^{10, 15, 18, 23, 29}$
Eupines monstrosa Reitter									*									Forest $^{25, 23, 29}$
Eupines rudicornis Broun			*				*	*		*	*							Forest $^{15, 23, 29}$

Sample	**H1**	**H2**	**H3**	**H4**	**H5**	**H6**	**H7**	**H8**	**H9**	**H10**	**H11**	**H12**	**H13**	**H14**	**H15**	**H16**	**H17**	
Depth (m)	**1.85-1.80**	**1.80-1.75**	**1.75-1.70**	**1.70-1.65**	**1.65-1.60**	**1.60-1.55**	**1.55-1.50**	**1.50-1.45**	**1.45-1.40**	**1.40-1.35**	**1.35-1.30**	**1.30-1.25**	**1.25-1.20**	**1.20-1.15**	**1.15-1.10**	**1.10-1.05**	**1.05-1.00**	
Taxon																		**Environment**
Pselaphinae indet. spp.									*	*	*	*	*					Forest [18, 23]
Pselaphus indet. sp.									*	*	*	*	*	*				Forest, grassland [10, 18, 23, 29]
Sagola indet. sp.						*		*			*							Euytopic [10, 18, 23, 29]
Vidamus indet. sp.								*		*	*	*			*		*	Forest [9, 15, 18, 23, 29]
Zelandius indet. sp.							*	*		*	*							Forest [10, 15, 18, 23, 29]
Aleocharinae indet. sp.										*								Eurytopic [15, 18]
Aleochara hammondi Klimaszewski		*	*			*												Montane tussock grassland [15, 17]
Brachynopus scutellaris Redtenbacher	*	*	*	*	*	*	*	*	*	*	*	*	*				*	Forest [15, 25]
Paratrochus "sp group A"														*	*	*	*	Eurytopic [5, 6, 9, 15, 18]
Agnosthaetus indet. sp.										*	*							Forest, grassland [15, 18, 29]
Hyperomma indet. sp.							*	*	*	*			*					Forest, waters edge [10, 15, 18, 29]

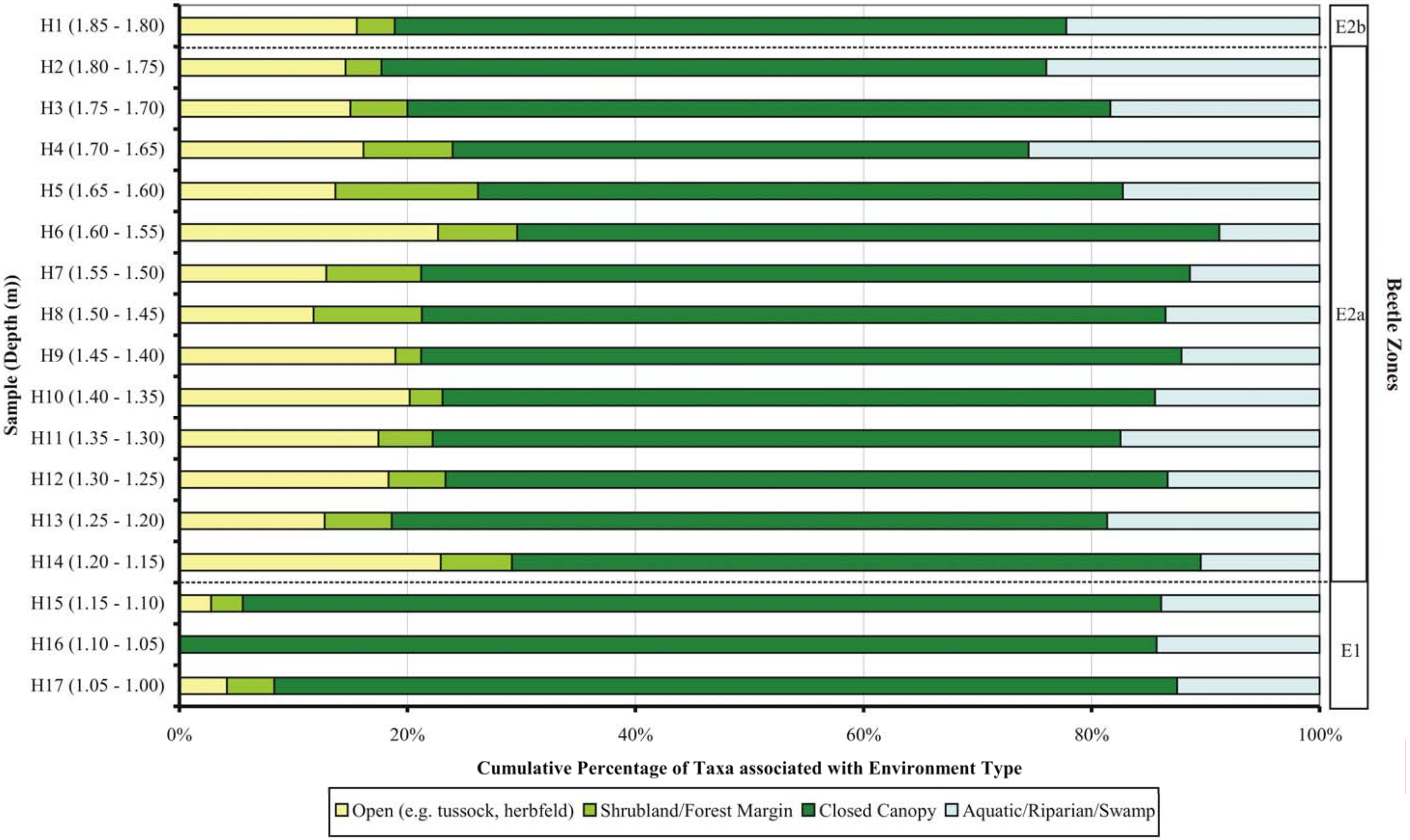
Sample	**H1**	**H2**	**H3**	**H4**	**H5**	**H6**	**H7**	**H8**	**H9**	**H10**	**H11**	**H12**	**H13**	**H14**	**H15**	**H16**	**H17**	
Depth (m)	**1.85-1.80**	**1.80-1.75**	**1.75-1.70**	**1.70-1.65**	**1.65-1.60**	**1.60-1.55**	**1.55-1.50**	**1.50-1.45**	**1.45-1.40**	**1.40-1.35**	**1.35-1.30**	**1.30-1.25**	**1.25-1.20**	**1.20-1.15**	**1.15-1.10**	**1.10-1.05**	**1.05-1.00**	
Taxon																		**Environment**
Philonthus indet. sp.	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*		*	Eurytopic ^{15}
Staphylinidae indet. spp.									*	*	*		*					Eurytopic ^{15}
SCARABIDAE																		
Saphobius edwardsi Sharp						*	*	*	*	*		*			*			Forest $^{3, 9, 18, 29, 30}$
Saphobius indet. sp.							*		*									Forest $^{3, 9, 18, 29, 30}$
SCIRTIDAE																		
Scirtidae indet. spp.	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	Vegetation nr water, forest ^{18}
BYRRHIDAE																		
Curimus "sp group A"	*																	Swamp $^{18, 22, 29}$
Curimus squamiger Broun		*																Swamp $^{18, 22, 29}$
Curimus zeelandicus Redtenbacher							*											Near swampy ponds $^{18, 22, 29}$

Sample	**H1**	**H2**	**H3**	**H4**	**H5**	**H6**	**H7**	**H8**	**H9**	**H10**	**H11**	**H12**	**H13**	**H14**	**H15**	**H16**	**H17**	
Depth (m)	**1.85-1.80**	**1.80-1.75**	**1.75-1.70**	**1.70-1.65**	**1.65-1.60**	**1.60-1.55**	**1.55-1.50**	**1.50-1.45**	**1.45-1.40**	**1.40-1.35**	**1.35-1.30**	**1.30-1.25**	**1.25-1.20**	**1.20-1.15**	**1.15-1.10**	**1.10-1.05**	**1.05-1.00**	
Taxon																		**Environment**
Epichorius "sp group A"				*		*	*	*	*	*	*	*	*					Eurytopic [7, 18, 29]
Epichorius indet. sp.	*	*		*	*		*	*	*	*	*	*	*	*	*	*		Eurytopic [7, 18, 29]
Epichorius sp. 26							*											Insufficent habitat information [29]
PHYCOSECIDAE																		
Phycosecis limbata Fabricius	*																	Beach, dune field [18, 29]
ZOPHERIDAE																		
Coxelus indet. sp.							*											Forest, shrubland, open vegetation [10, 18, 19, 29]
Pycnomerus "sp group B"															*			Forest, dead wood [18, 29, 30]
Pycnomerus latitans Sharp															*			Forest, dead wood [18, 29, 30]
CERAMBYCIDAE																		

Sample	**H1**	**H2**	**H3**	**H4**	**H5**	**H6**	**H7**	**H8**	**H9**	**H10**	**H11**	**H12**	**H13**	**H14**	**H15**	**H16**	**H17**	
Depth (m)	**1.85-1.80**	**1.80-1.75**	**1.75-1.70**	**1.70-1.65**	**1.65-1.60**	**1.60-1.55**	**1.55-1.50**	**1.50-1.45**	**1.45-1.40**	**1.40-1.35**	**1.35-1.30**	**1.30-1.25**	**1.25-1.20**	**1.20-1.15**	**1.15-1.10**	**1.10-1.05**	**1.05-1.00**	
Taxon																		**Environment**
Hybolasius "sp group A"								*										Eurytopic [1, 9, 28, 29]
CHRYSOMELIDAE																		
Adoxia indet. sp.	*	*		*														Swamp, forest, shrubs [9, 10, 18, 29]
Chrysomelidae indet. sp. 1	*	*	*	*	*	*	*	*	*	*	*	*						Low vegetation [9, 18]
Chrysomelidae indet. sp. 2		*		*			*				*							Low vegetation [9, 18]
Caccomolpus cinctiger Broun				*														Eurytopic [9, 18, 29]
CURCULIONIDAE																		
Areocryptus indet. sp.																*		Specific to *Rhopalostylis sapida* = coastal forest [13, 29]
Cryptorynchini indet. spp.	*	*			*	*	*	*	*	*	*	*	*	*	*	*	*	Forest [12, 13, 26]
Areoscapsus indet. sp.										*								Unknown (probably forest) [29]

Sample	**H1**	**H2**	**H3**	**H4**	**H5**	**H6**	**H7**	**H8**	**H9**	**H10**	**H11**	**H12**	**H13**	**H14**	**H15**	**H16**	**H17**	
Depth (m)	**1.85-1.80**	**1.80-1.75**	**1.75-1.70**	**1.70-1.65**	**1.65-1.60**	**1.60-1.55**	**1.55-1.50**	**1.50-1.45**	**1.45-1.40**	**1.40-1.35**	**1.35-1.30**	**1.30-1.25**	**1.25-1.20**	**1.20-1.15**	**1.15-1.10**	**1.10-1.05**	**1.05-1.00**	
Taxon																		**Environment**
Areoscapus estriatus Broun	*																	Forest [29]
Areoscapus subcostatus Broun							*	*										Forest [29]
Bryocatus amplus Broun										*								Moss, sea-level to 1400m [13, 29]
Oreocalus latipennis Broun					*													Specific to *Hebe* = open vegetation or forest margin [13, 18]
Phemus indet. sp.				*		*	*	*	*		*	*	*					Forest [29]
Gromilus indet. sp.						*	*	*	*	*	*	*		*				Forest, grassland [10, 13, 18, 29]
Irenimus indet. sp.			*	*	*		*	*				*	*	*				Forest edge, grassland [13, 18, 26, 28]

Figure 6.4. Comparison of the percentage composition of samples by habitat type. Depth measurements are the same as those illustrated in Figure 6.2. Also shown is the division of the samples into the assemblage zones E1, E2a and E2b.



Chandler, 2001; NZAC label information) and *Eupines* "sp. group A", the scarab beetle (Family Scarabidae) *Saphobius edwardsi* Sharp (Emberson & Matthews, 1973; Klimaszewski & Watt, 1997; LUNZ label information; NZAC label information), the Zopheridid *Pyncnomerus latitans* Sharp (Klimaszewski & Watt, 1997; LUNZ label information; NZAC label information) and a suite of indeterminate Cryptorynchini weevils (Family Curculionidae) (Lyal, 1993; May, 1993). These taxa are all associated with forests where they inhabit forest litter and dead vegetation (Table 6.1). The presence of the water scavenger beetle (Family Hydrophilidae) *Tormus nitidulus* Broun (Table 6.1), also an inhabitant of forest, indicates that conditions were moist (Klimaszewski & Watt, 1997; Archangelsky, 2004) while a fossil elytron from the weevil *Arecocryptus* indet. sp. (Table 6.1), a genus whose larvae are restricted to the native New Zealand palm (*Rhopalostylis sapida*) (May, 1993), indicates the presence of this palm at, or in close proximity to, this site. Indeterminate species of marsh beetles (Family Scirtidae), inhabitants of vegetation near water, indicate that the site was moist (Klimaszewski & Watt, 1997).

Zone E2a – Samples H14 to H2 (1.15-1.80m)

The proportion of taxa associated with riparian and aquatic environments remains relatively constant in Zone E2a which is again dominated by beetle taxa representative of a closed canopy environment (Fig. 6.4). The proportion of taxa associated with open environments increases in this zone (Fig. 6.4) indicating a change in the composition of the environment to a mosaic environment including elements of both closed and open vegetation types.

The closed canopy taxa include beetles previously observed in zone E1 including the Cryptorynchini weevils, *B. scutellaris*, and *S. edwardsi*. Additional taxa associated with closed canopy environments include the Staphylinidids *Corneolabrium mandibulare* Steel (Newton & Thayer, 1995; Klimaszewski et al., 1996), *Dalma pubescens* Sharp (Klimaszewski et al., 1996; Chandler, 2001; NZAC label information) and *Eupines rudicornis* Broun (Klimaszewski et al., 1996; Chandler, 2001; NZAC label information) (Table 1). Terrestrial Hydrophilidae taxa (sub-family Sphaeridinae) (e.g. *T. nitidulus*, *Adolopus helmsi* Sharp) indicate that conditions under the canopy remained moist (Hansen, 1997; Klimaszewski & Watt, 1997; Marra & Leschen, 2004).

The area contained still open water, indicated by the presence of the aquatic water scavenger beetles (Hydrophilidae: Hydrophilinae) *Enochrus tritus* Broun (Kuschel, 1990; Klimaszewski & Watt, 1997; Archangelsky, 2002; Archangelsky, 2004) and *Paracymus pygmaeus* Macleay (Winterbourn, 1970; Hansen, 2000; Marra & Leschen, 2004; NZAC label information). Marshy conditions are indicated by the moss beetles (Family Byrrhidae) *Curimus zeelandicus* Redtenbacher and *Curimus squamiger* Broun (Klimaszewski & Watt, 1997; Lawrence et al., 2000 onwards) and the ground beetle (Family Carabidae) *Notogonium feredayi* Bates (Larochelle & Larivière, 2001).

Notogonium feredayi is also found in tussock areas (Larochelle & Larivière, 2001) and along with the stone beetle (Family Scydmaenidae) *Adrastia nelsoni* Franz, found in alpine areas above 1,200m (NZAC label information), and the rove beetle *Aleochara hammondi* Klimaszewski, found in tussock grasslands between 850 and 1,500m (Klimaszewski et al., 1996; Klimaszewski & Crosby, 1997) is representative of the presence of a more open subalpine grassland type environment. Open environment taxa also include the weevil genus *Irenimus* which is generally associated with open and forest edge environments (May, 1993 Marra, 2003; Marra & Leschen, 2004). The weevil *Oreocalus latipennis* Broun (Table 1) is restricted to the plant genus *Hebe* in its larval stage (May, 1993) and is also indicative of open, forest-margin type vegetation as *Hebe* is typically found in such habitats (Dawson & Lucas, 2000).

Zone E2b – Sample H1 (1.80-1.85m)

The final assemblage zone in Fig. 6.4 is in most ways similar to the previous assemblage zone E2a (Table 6.1). It is differentiated from zone E2a by the presence of the beach beetle (Family Phycosecidae) *Phycosecis limbata* Fabricius (Table 6.1) which is associated with sandy environments (Klimaszewski & Watt, 1997).

6.3.4 Palaeoclimate

While a total of 76 taxa were obtained from the Wilson's Lead Road site (Table 6.1) the collection location data required for the palaeoclimatic reconstructions was only available for 61 (Table 6.2). The presence of outliers in the MLE reconstructions in Chapters 4 and 5 also raises questions regarding the reliability of the MLE reconstructions based on poorly known taxa. In an effort to avoid misleading reconstructions due to rare taxa conservative MLE reconstructions were produced excluding any taxon known from less than five collection localities. A summary diagram of the trends is presented in Fig. 6.5

Table 6.2. List of all taxa used in the palaeoclimatic reconstructions and those taxa known from 5 or less collection locations. Those taxa known from less than 5 collection locations are excluded from the palaeoclimatic reconstructions presented in Fig. 6.5.

Taxa used in Palaeoclimatic Reconstruction

CARABIDAE
Bembidion indet. sp.
Bembidion maorinum maorinum Bates
Bembidion tekapoense Broun
Bembidion wanakense Lindroth
Dierochile flavipes
Notagonium feredayi Bates
Oopterus indet. sp.
Oopterus pallidipes Broun
Scopodes "sp. group A"
Scopodes indet. sp.
HYDROPHILIDAE
Adolopus helmsi Sharp
Adolopus indet. sp.
Cyloma "sp group B"
Cyloma indet. sp.
Enochrus tritus Broun
Paracymus pygmaeus Macleay
Tormus nitidulus Broun
LEIODIDAE
Isocolon modestum Broun
SCYDMAENIDAE
Adrastia nelsoni Franz
Scydmaenidae "sp group A"
STAPHYLINIDAE
Agnosthaetus indet. sp.
Aleochara hammondi Klimaszewski
Brachynopus scutellaris Redtenbacher
Corneolabium mandibulare Steel
Dalma pubescens Sharp
Eupines "sp group A"
Eupines monstrosa Reitter
Eupines rudicornis Broun
Hyperomma indet. sp.
Paratrochus "sp group A"
Pselaphus indet. sp.
Sagola indet. sp.
Stenomalium cognatum Broun
Stenomalium indet. sp.
Vidamus indet. sp.
Zelandius indet. sp.
SCARABIDAE
Saphobius edwardsi Sharp
BYRRHIDAE
Curimus "sp group A"
Curimus squamiger Broun
Curimus zeelandicus Redtenbacher
Epichorius "sp group A"
Epichorius indet. sp.
PHYCOSECIDAE
Phycosecis limbata Fabricius

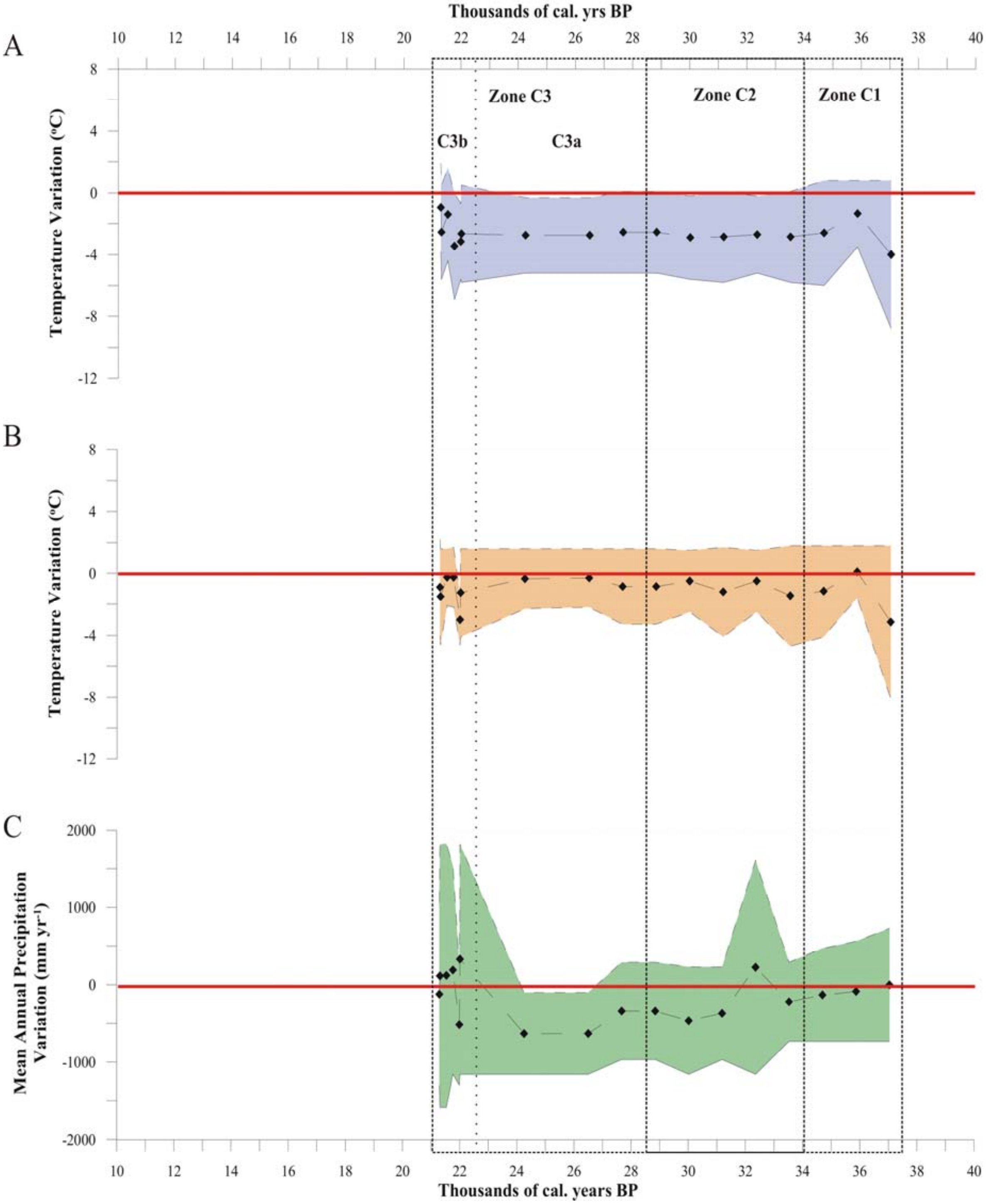
Taxa used in Palaeoclimatic Reconstruction (continued from previous column)

ZOPHERIDAE
Coxelus indet. sp.
Pycnomerus "sp group B"
Pycnomerus latitans Sharp
CERAMBYCIDAE
Hybolasius "sp group A"
CHRYSOMELIDAE
Adoxia indet. sp.
Caccomolpus cinctiger Broun
CURCULIONIDAE
Areocryptus indet. sp.
Areoscapsus indet. sp.
Areoscapus estriatus Broun
Areoscapus subcostatus Broun
Bryocatus amplus Broun
Gromilus indet. sp.
Irenimus indet. sp.
Oreocalus latipennis Broun
Phemus indet. sp.

Taxa known from 5 or less collection locations

CARABIDAE
Bembidion wanakense Lindroth
Oopterus pallidipes Broun
HYDROPHILIDAE
Tormus nitidulus Broun
SCYDMAENIDAE
Adrastia nelsoni Franz
STAPHYLINIDAE
Aleochara hammondi Klimaszewski
Corneolabium mandibulare Steel
Dalma pubescens Sharp
Eupines monstrosa Reitter
BYRRHIDAE
Curimus squamiger Broun
ZOPHERIDAE
Pycnomerus latitans Sharp
CURCULIONIDAE
Areoscapus estriatus Broun

Figure 6.5. Conservative reconstructed climate estimates excluding any taxa known from less than five collection localities. Reconstructions are **A**. Mean Minimum Winter Temperature; **B**. Mean Summer Temperature and **C**. Mean Annual Precipitation, from the Wilson's Lead Road site. Age scale is in thousands of calendar years BP. The red lines represent the present day mean value of the climate variable at the site. Also indicated are the three climate zones (C1 to C3) discussed in section 6.5.4.



Only two trends are apparent in Fig. 6.5. The first trend is enhanced winter cooling relative to summer and the second is decreasing winter temperatures ca. 34 ka BP. Fig. 6.5 shows no finer scale variability in climate as the removal of rare taxa left only eurythermic taxa with which to reconstruct the palaeoclimate. Eurythermic taxa inhabit a wide climatic range and, while the results are probably accurate, the reconstructed climate estimates are imprecise and lack the ability to distinguish short term climatic change. In order to produce more precise estimates of climatic change it was therefore decided to include all taxa except known outliers (*Tormus nitidulus* Broun and *Pyncnomerus latitans* Sharp) in the reconstructions for the final analysis.

Figures 6.6a-c, 6.7a-c and 6.8a-c illustrate the MLE envelopes used for the final palaeoclimatic reconstructions of mean daily minimum winter temperature (MMWT), mean summer temperature (MST) and mean annual precipitation (MAP) respectively. Reconstructions were only possible for 17 of the 18 samples as sample H18 was fossil poor. The climatic variation from modern levels is illustrated in Figure 6.9a-c.

The MMWT reconstruction (Fig. 6.6a-c, Fig. 6.9a) indicates an initial cooling of ca. 2-3ºC below the present day in the first three samples (samples H17-H15). At about 34-33ka BP (sample H14) winter temperatures drop to between 4.5-5.5ºC cooler than present and remain at this level for ca. 6,000 years. Winter temperatures rise to a peak of ca. 3.0ºC below modern levels at 28-27ka BP (sample H9) before briefly returning to ca. 5.0ºC below present at ca. 26.5ka BP (sample H8). The reconstructed climate range then broadens at ca. 25-24ka BP (sample H7) to between 2.5-5.5ºC below present indicating a slight amelioration of the climate (Fig. 6.9a). This broadening of the reconstructed

Figure 6.6a Wilson's Lead Road Mean Minimum Winter (July) Temperature Reconstruction for samples H1 to H6. The blue horizontal bars in these figures indicate the range of the variable within which the taxon is known to inhabit. The lighter ends of the bars represent the error to these known ranges as calculated by the MLE models. Green boxes represent a reconciled range for all taxa within the sample. Samples containing multiple possible ranges have pink boxes for the warmer ranges and blue boxes for the cooler ranges. Darker boxes illustrate the reconstructed range including the MLE error term. Lighter boxes illustrate the range without the MLE error term. The solid red vertical line represents the present day mean value of the variable at the site as derived from the climate surfaces of Leathwick et al. (1998). Black lines on the y-axis represent the position of ^{14}C ages of Moar & Suggate (1979) relative to the samples.

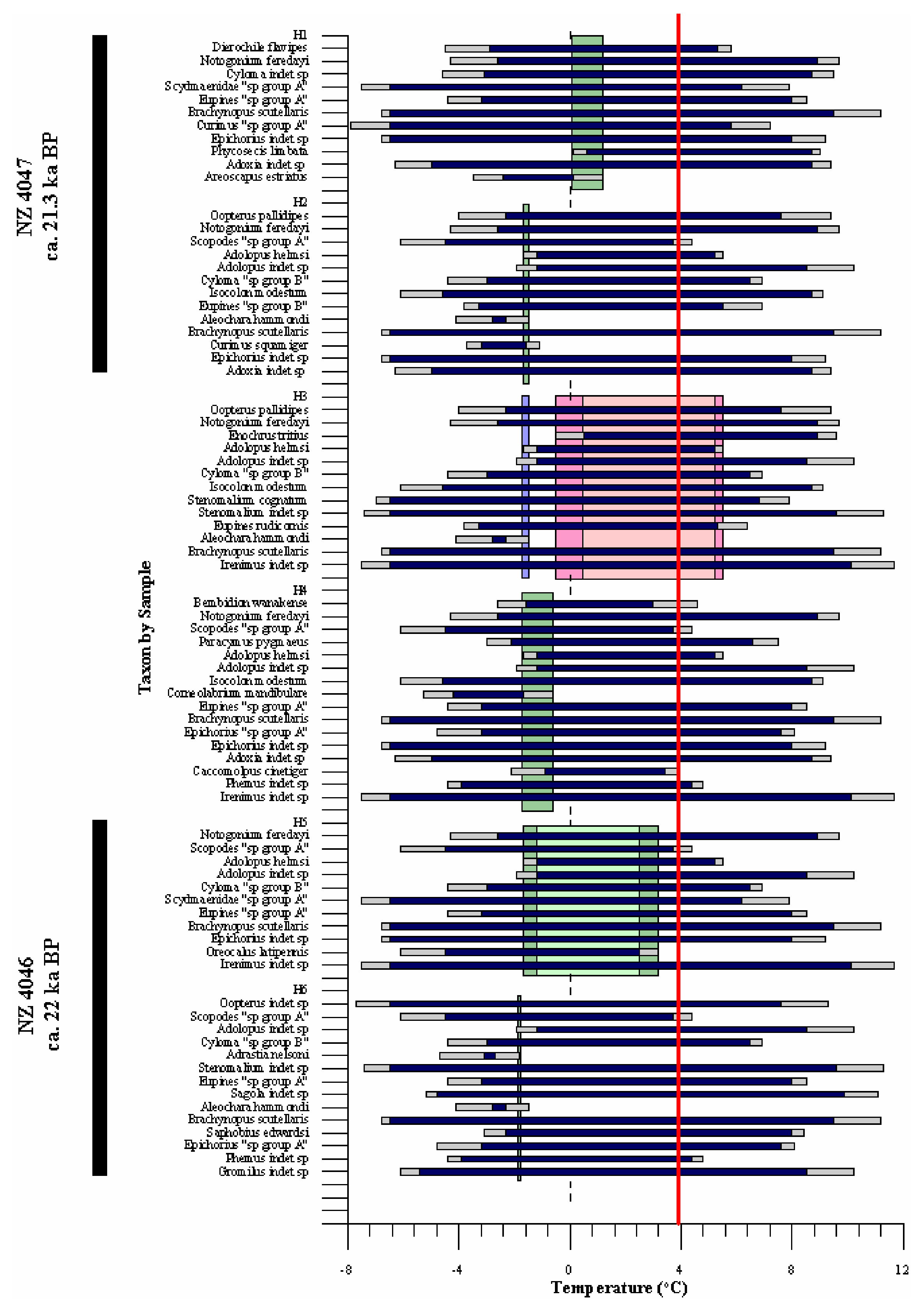

NZ 4047
ca. 21.3 ka BP
NZ 4046
ca. 22 ka BP
Taxon by Sample
H1
Dierochile flavipes
Notogonium feredayi
Cyloma indet sp
Scydmaenidae "sp group A"
Eupines "sp group A"
Brachynopus scutellaris
Curimus "sp group A"
Epichorius indet sp
Phycosecis limbata
Adoxia indet sp
Areoscapus estriatus
H2
Oopterus pallidipes
Notogonium feredayi
Scopodes "sp group A"
Adolopus helmsi
Adolopus indet sp
Cyloma "sp group B"
Isocolon modestum
Eupines "sp group B"
Aleochara hammondi
Brachynopus scutellaris
Curimus squamiger
Epichorius indet sp
Adoxia indet sp
H3
Oopterus pallidipes
Notogonium feredayi
Enochrus tritus
Adolopus helmsi
Adolopus indet sp
Cyloma "sp group B"
Isocolon modestum
Stenomalium cognatum
Stenomalium indet sp
Eupines rudicornis
Aleochara hammondi
Brachynopus scutellaris
Irenimus indet sp
H4
Bembidion wanakense
Notogonium feredayi
Scopodes "sp group A"
Paracymus pygmaeus
Adolopus helmsi
Adolopus indet sp
Isocolon modestum
Corneolabrium mandibulare
Eupines "sp group A"
Brachynopus scutellaris
Epichorius "sp group A"
Epichorius indet sp
Adoxia indet sp
Caccomolpus cinctiger
Phemus indet sp
Irenimus indet sp
H5
Notogonium feredayi
Scopodes "sp group A"
Adolopus helmsi
Adolopus indet sp
Cyloma "sp group B"
Scydmaenidae "sp group A"
Eupines "sp group A"
Brachynopus scutellaris
Epichorius indet sp
Oreocalus latipennis
Irenimus indet sp
H6
Oopterus indet sp
Scopodes "sp group A"
Adolopus indet sp
Cyloma "sp group B"
Adrastia nelsoni
Stenomalium indet sp
Eupines "sp group A"
Sagola indet sp
Aleochara hammondi
Brachynopus scutellaris
Saphobius edwardsi
Epichorius "sp group A"
Phemus indet sp
Gromilus indet sp
-8
-4
0
4
8
12
Temperature (°C)

Figure 6.6b Wilson's Lead Road Mean Minimum Winter (July) Temperature Reconstruction for samples H7 to H11. The blue horizontal bars in these figures indicate the range of the variable within which the taxon is known to inhabit. The lighter ends of the bars represent the error to these known ranges as calculated by the MLE models. Green boxes represent a reconciled range for all taxa within the sample. Samples containing multiple possible ranges have pink boxes for the warmer ranges and blue boxes for the cooler ranges. Darker boxes illustrate the reconstructed range including the MLE error term. Lighter boxes illustrate the range without the MLE error term. The solid red vertical line represents the present day mean value of the variable at the site as derived from the climate surfaces of Leathwick et al. (1998). Black lines on the y-axis represent the position of ^{14}C ages of Moar & Suggate (1979) relative to the samples.

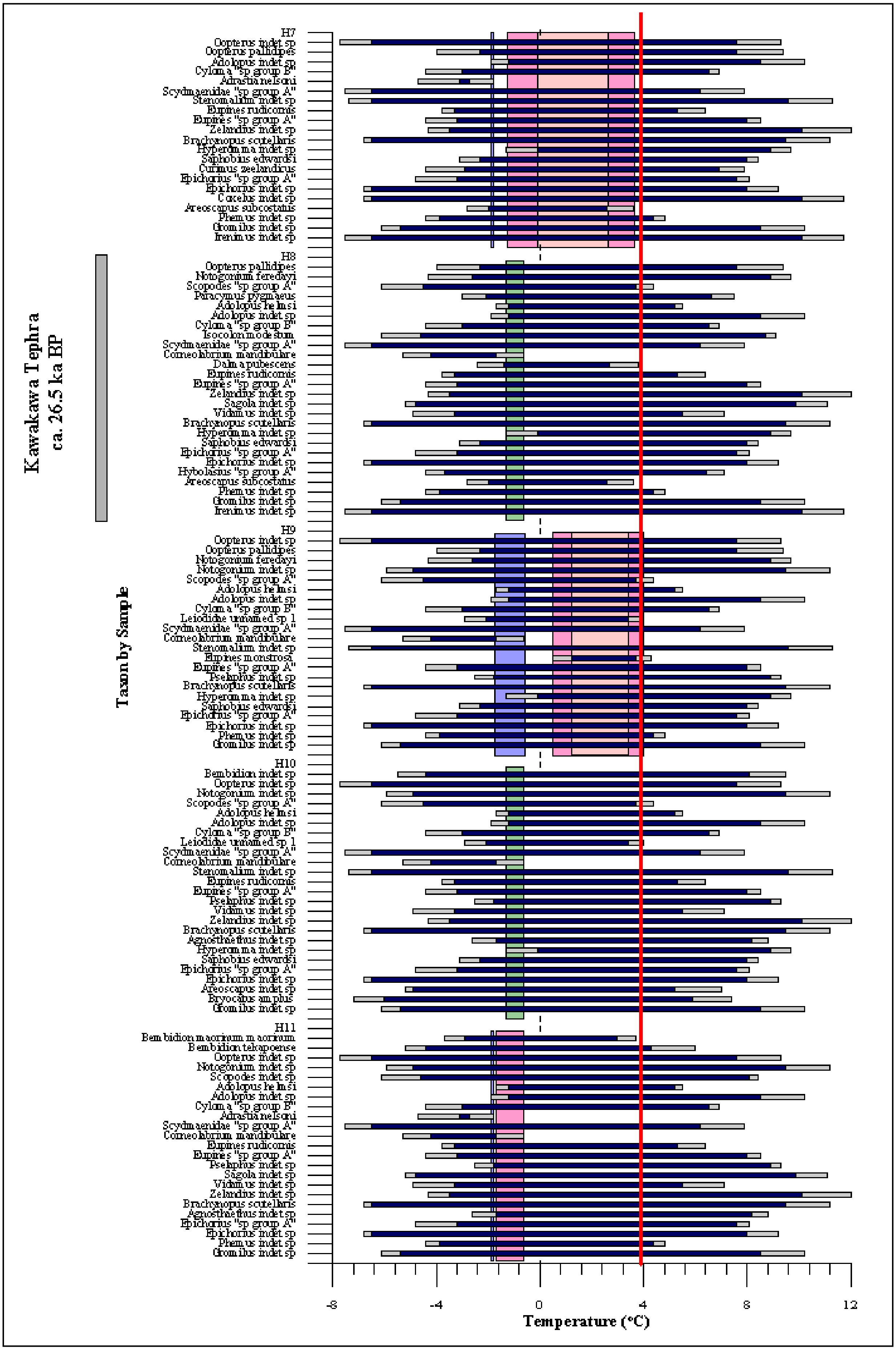

Kawakawa Tephra
ca. 26.5 ka BP
Taxon by Sample
H7
Oopterus indet sp
Oopterus pallidipes
Adolopus indet sp
Cyloma "sp group B"
Adrastia nelsoni
Scydmaenidae "sp group A"
Stenomalium indet sp
Eupines rudicornis
Eupines "sp group A"
Zelandius indet sp
Brachynopus scutellaris
Hyperomma indet sp
Saphobius edwardsi
Curimus zeelandicus
Epicharius "sp group A"
Epichorius indet sp
Coxelus indet sp
Areoscapus subcostatus
Phemus indet sp
Gromilus indet sp
Irenimus indet sp
H8
Oopterus pallidipes
Notogonium feredayi
Scopodes "sp group A"
Paracymus pygmaeus
Adolopus helmsi
Adolopus indet sp
Cyloma "sp group B"
Isocolon modestum
Scydmaenidae "sp group A"
Corneolabrium mandibulare
Dalma pubescens
Eupines rudicornis
Eupines "sp group A"
Zelandius indet sp
Sagola indet sp
Vidamus indet sp
Brachynopus scutellaris
Hyperomma indet sp
Saphobius edwardsi
Epicharius "sp group A"
Epichorius indet sp
Hybolasius "sp group A"
Areoscapus subcostatus
Phemus indet sp
Gromilus indet sp
Irenimus indet sp
H9
Oopterus indet sp
Oopterus pallidipes
Notogonium feredayi
Notogonium indet sp
Scopodes "sp group A"
Adolopus helmsi
Adolopus indet sp
Cyloma "sp group B"
Leiodidae unnamed sp 1
Scydmaenidae "sp group A"
Corneolabrium mandibulare
Stenomalium indet sp
Eupines monstrosa
Eupines "sp group A"
Pselaphus indet sp
Brachynopus scutellaris
Hyperomma indet sp
Saphobius edwardsi
Epicharius "sp group A"
Epichorius indet sp
Phemus indet sp
Gromilus indet sp
H10
Bembidion indet sp
Oopterus indet sp
Notogonium indet sp
Scopodes "sp group A"
Adolopus helmsi
Adolopus indet sp
Cyloma "sp group B"
Leiodidae unnamed sp 1
Scydmaenidae "sp group A"
Corneolabrium mandibulare
Stenomalium indet sp
Eupines rudicornis
Eupines "sp group A"
Pselaphus indet sp
Vidamus indet sp
Zelandius indet sp
Brachynopus scutellaris
Agnosthaetus indet sp
Hyperomma indet sp
Saphobius edwardsi
Epicharius "sp group A"
Epichorius indet sp
Areoscapus indet sp
Bryocatus amplus
Gromilus indet sp
H11
Bembidion maorinum maorinum
Bembidion tekapoense
Oopterus indet sp
Notogonium indet sp
Scopodes indet sp
Adolopus helmsi
Adolopus indet sp
Cyloma "sp group B"
Adrastia nelsoni
Scydmaenidae "sp group A"
Corneolabrium mandibulare
Eupines rudicornis
Eupines "sp group A"
Pselaphus indet sp
Sagola indet sp
Vidamus indet sp
Zelandius indet sp
Brachynopus scutellaris
Agnosthaetus indet sp
Epicharius "sp group A"
Epichorius indet sp
Phemus indet sp
Gromilus indet sp
-8
-4
0
4
8
12
Temperature (°C)

Figure 6.6c Wilson's Lead Road Mean Minimum Winter (July) Temperature Reconstruction for samples H12 to H17. The blue horizontal bars in these figures indicate the range of the variable within which the taxon is known to inhabit. The lighter ends of the bars represent the error to these known ranges as calculated by the MLE models. Green boxes represent a reconciled range for all taxa within the sample. Samples containing multiple possible ranges have pink boxes for the warmer ranges and blue boxes for the cooler ranges. Darker boxes illustrate the reconstructed range including the MLE error term. Lighter boxes illustrate the range without the MLE error term. The solid red vertical line represents the present day mean value of the variable at the site as derived from the climate surfaces of Leathwick et al. (1998). Black lines on the y-axis represent the position of ^{14}C ages of Moar & Suggate (1979) relative to the samples.

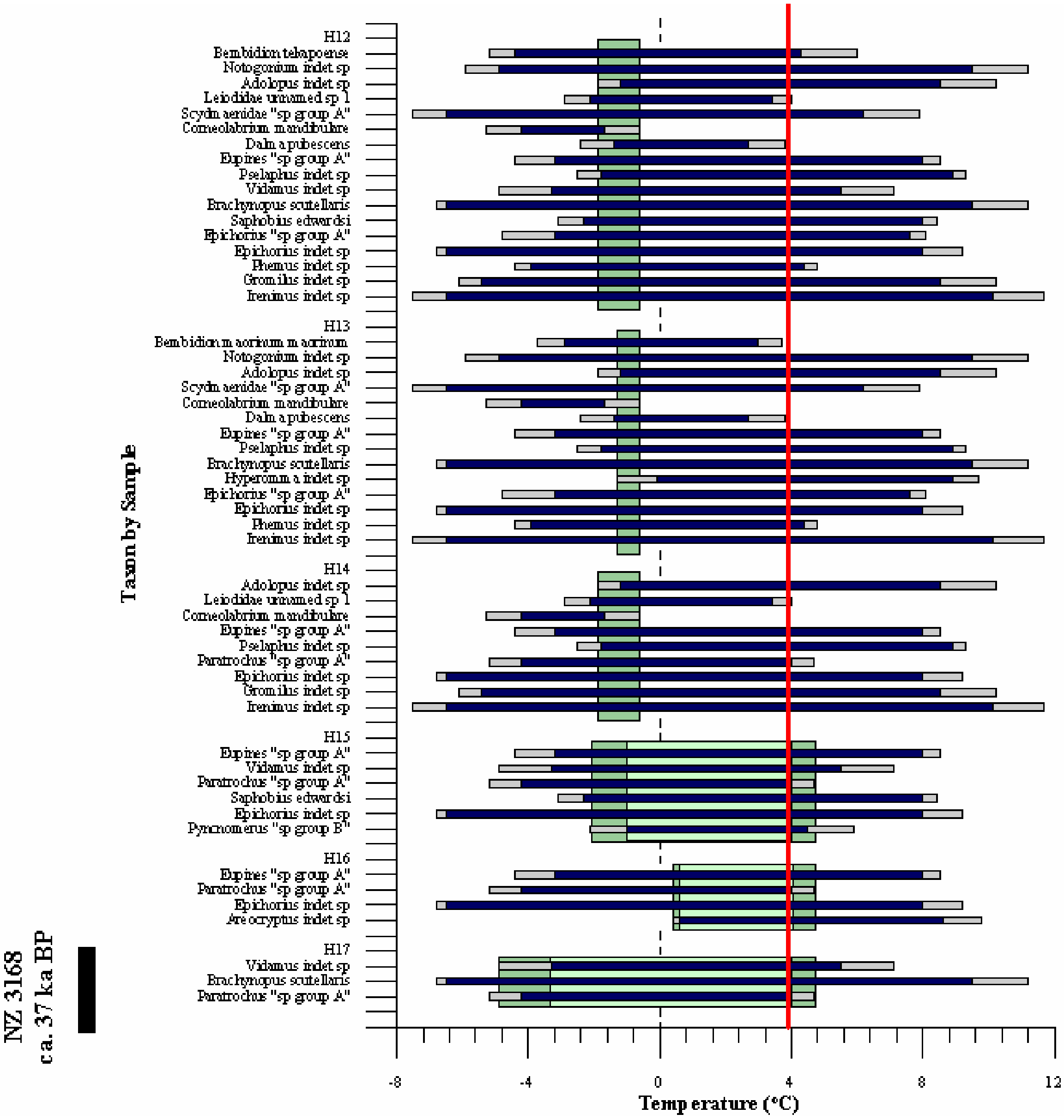


Figure 6.7a. Wilson's Lead Road Mean Summer (Feburary) Temperature Reconstruction for samples H1 to H6. The blue horizontal bars in these figures indicate the range of the variable within which the taxon is known to inhabit. The lighter ends of the bars represent the error to these known ranges as calculated by the MLE models. Green boxes represent a reconciled range for all taxa within the sample. Samples containing multiple possible ranges have pink boxes for the warmer ranges and blue boxes for the cooler ranges. Darker boxes illustrate the reconstructed range including the MLE error term. Lighter boxes illustrate the range without the MLE error term. The solid red vertical line represents the present day mean value of the variable at the site as derived rom the climate surfaces of Leathwick et al.(1998). Black lines on the y-axis represent the position of ^{14}C ages of Moar & Suggate (1979) relative to the samples.

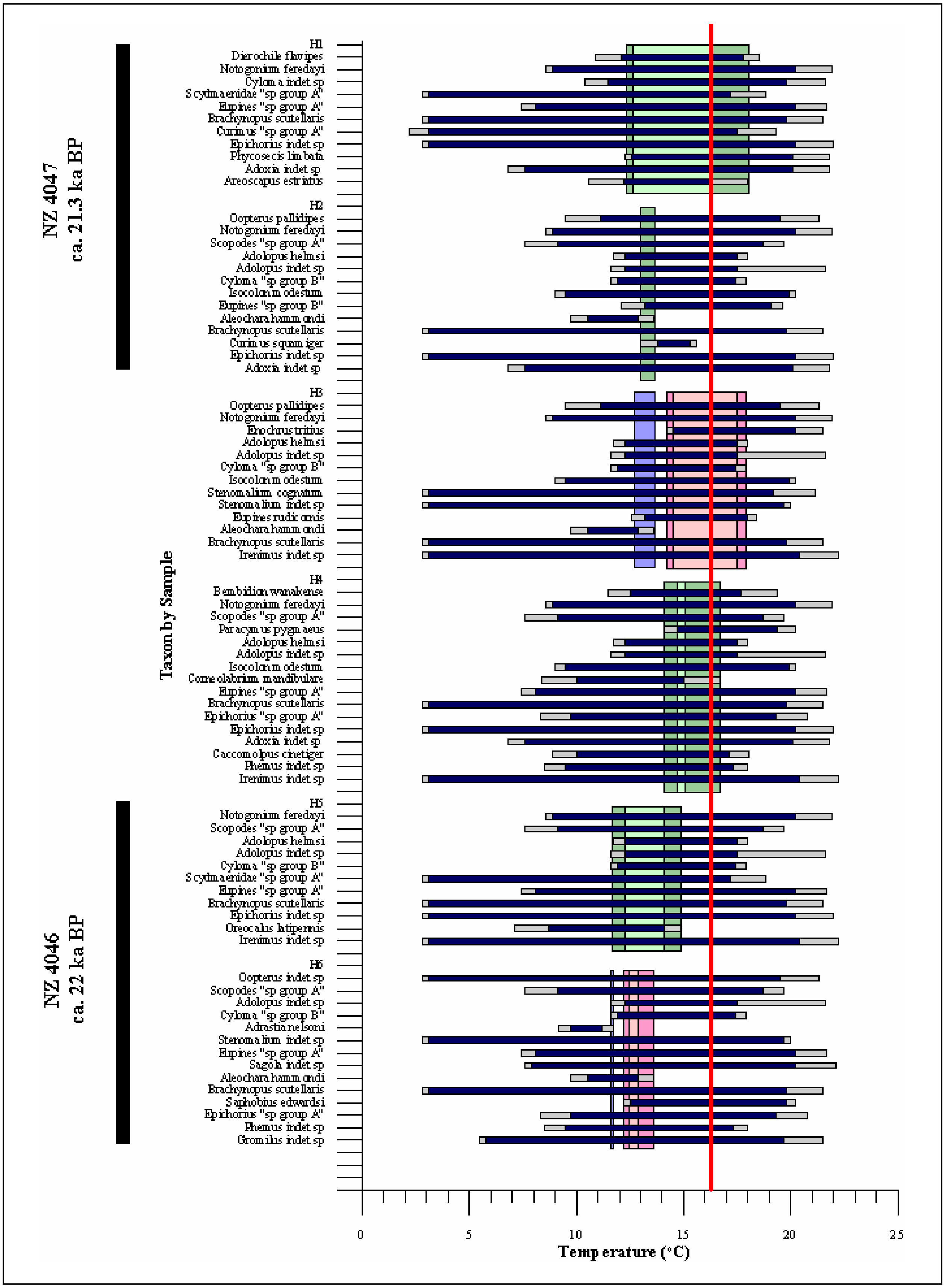

NZ 4047
ca. 21.3 ka BP
NZ 4046
ca. 22 ka BP
Taxon by Sample
H1
Dierochile flavipes
Notogonium feredayi
Cyloma indet sp
Scydmaenidae "sp group A"
Eupines "sp group A"
Brachynopus scutellaris
Curimus "sp group A"
Epichorius indet sp
Phycosecis limbata
Adoxia indet sp
Areoscapus estriatus
H2
Oopterus pallidipes
Notogonium feredayi
Scopodes "sp group A"
Adolopus helmsi
Adolopus indet sp
Cyloma "sp group B"
Isocolon modestum
Eupines "sp group B"
Aleochara hammondi
Brachynopus scutellaris
Curimus squamiger
Epichorius indet sp
Adoxia indet sp
H3
Oopterus pallidipes
Notogonium feredayi
Enochrus tritius
Adolopus helmsi
Adolopus indet sp
Cyloma "sp group B"
Isocolon modestum
Stenomalium cognatum
Stenomalium indet sp
Eupines rudicornis
Aleochara hammondi
Brachynopus scutellaris
Irenimus indet sp
H4
Bembidion wanakense
Notogonium feredayi
Scopodes "sp group A"
Paracymus pygmaeus
Adolopus helmsi
Adolopus indet sp
Isocolon modestum
Corneolabrium mandibulare
Eupines "sp group A"
Brachynopus scutellaris
Epichorius "sp group A"
Epichorius indet sp
Adoxia indet sp
Caccomolpus cinctiger
Phemus indet sp
Irenimus indet sp
H5
Notogonium feredayi
Scopodes "sp group A"
Adolopus helmsi
Adolopus indet sp
Cyloma "sp group B"
Scydmaenidae "sp group A"
Eupines "sp group A"
Brachynopus scutellaris
Epichorius indet sp
Oreocalus latipennis
Irenimus indet sp
H6
Oopterus indet sp
Scopodes "sp group A"
Adolopus indet sp
Cyloma "sp group B"
Adrastia nelsoni
Stenomalium indet sp
Eupines "sp group A"
Sagola indet sp
Aleochara hammondi
Brachynopus scutellaris
Saphobius edwardsi
Epichorius "sp group A"
Phemus indet sp
Gromilus indet sp
0
5
10
15
20
25
Temperature (°C)

Figure 6.7b. Wilson's Lead Road Mean Summer (Feburary) Temperature Reconstruction for samples H7 to H11. The blue horizontal bars in these figures indicate the range of the variable within which the taxon is known to inhabit. The lighter ends of the bars represent the error to these known ranges as calculated by the MLE models. Green boxes represent a reconciled range for all taxa within the sample. Samples containing multiple possible ranges have pink boxes for the warmer ranges and blue boxes for the cooler ranges. Darker boxes illustrate the reconstructed range including the MLE error term. Lighter boxes illustrate the range without the MLE error term. The solid red vertical line represents the present day mean value of the variable at the site as derived rom the climate surfaces of Leathwick et al.(1998). Black lines on the y-axis represent the position of ^{14}C ages of Moar & Suggate (1979) relative to the samples.

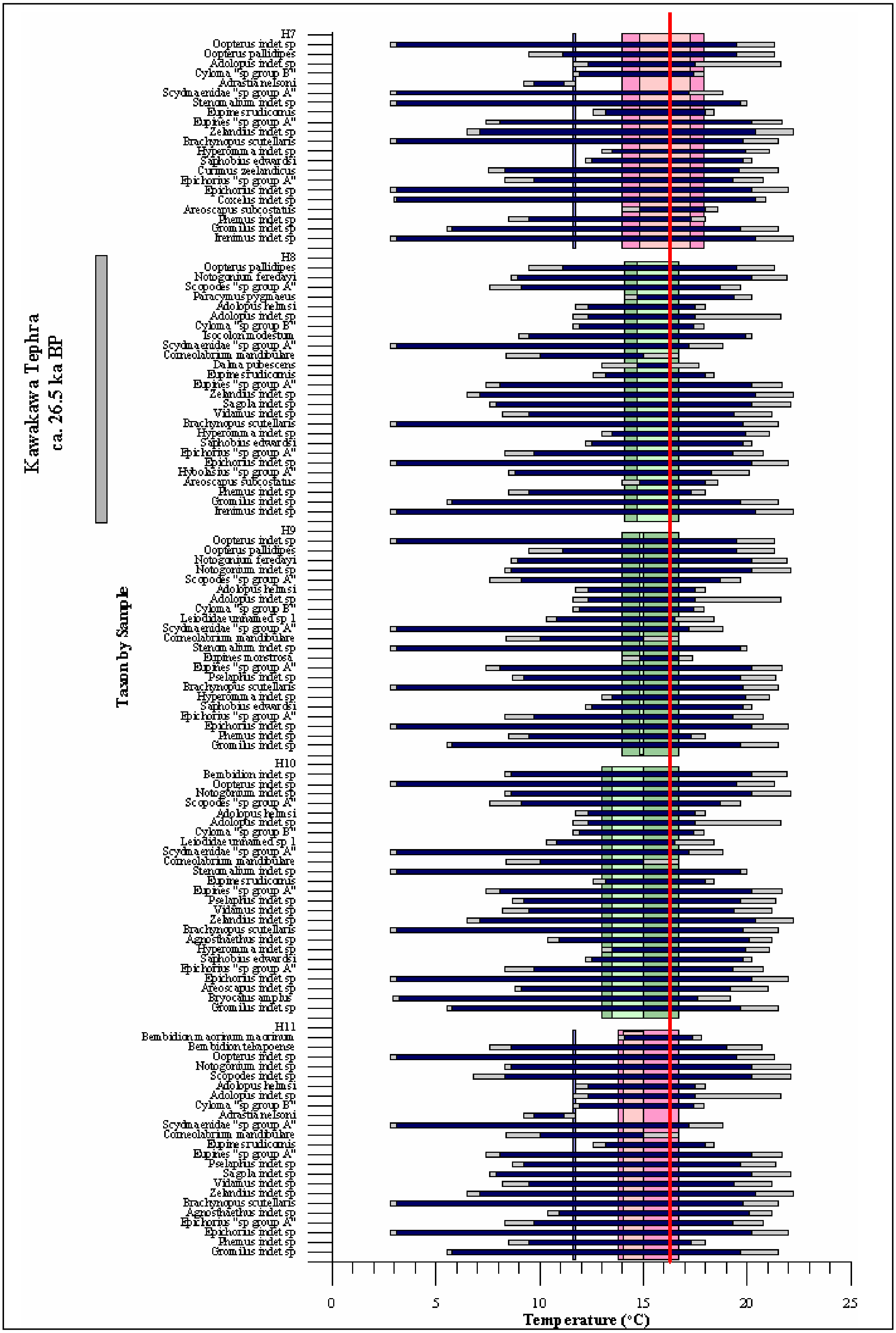

Kawakawa Tephra
ca. 26.5 ka BP
Taxon by Sample
H7
Oopterus indet sp
Oopterus pallidipes
Adolopus indet sp
Cyloma "sp group B"
Adrastia nelsoni
Scydmaenidae "sp group A"
Stenomalium indet sp
Eupines rudicornis
Eupines "sp group A"
Zelandius indet sp
Brachynopus scutellaris
Hyperomma indet sp
Saphobius edwardsi
Curimus zeelandicus
Epichorius "sp group A"
Epichorius indet sp
Coxelus indet sp
Areoscapus subcostatus
Phemus indet sp
Gromilus indet sp
Irenimus indet sp
H8
Oopterus pallidipes
Notogonium feredayi
Scopodes "sp group A"
Paracymus pygmaeus
Adolopus helmsi
Adolopus indet sp
Cyloma "sp group B"
Isocolon modestum
Scydmaenidae "sp group A"
Corneolabrium mandibulare
Dalma pubescens
Eupines rudicornis
Eupines "sp group A"
Zelandius indet sp
Sagola indet sp
Vidamus indet sp
Brachynopus scutellaris
Hyperomma indet sp
Saphobius edwardsi
Epichorius "sp group A"
Epichorius indet sp
Hybolasius "sp group A"
Areoscapus subcostatus
Phemus indet sp
Gromilus indet sp
Irenimus indet sp
H9
Oopterus indet sp
Oopterus pallidipes
Notogonium feredayi
Notogonium indet sp
Scopodes "sp group A"
Adolopus helmsi
Adolopus indet sp
Cyloma "sp group B"
Leiodidae unnamed sp 1
Scydmaenidae "sp group A"
Corneolabrium mandibulare
Stenomalium indet sp
Eupines monstrosa
Eupines "sp group A"
Pselaphus indet sp
Brachynopus scutellaris
Hyperomma indet sp
Saphobius edwardsi
Epichorius "sp group A"
Epichorius indet sp
Phemus indet sp
Gromilus indet sp
H10
Bembidion indet sp
Oopterus indet sp
Notogonium indet sp
Scopodes "sp group A"
Adolopus helmsi
Adolopus indet sp
Cyloma "sp group B"
Leiodidae unnamed sp 1
Scydmaenidae "sp group A"
Corneolabrium mandibulare
Stenomalium indet sp
Eupines rudicornis
Eupines "sp group A"
Pselaphus indet sp
Vidamus indet sp
Zelandius indet sp
Brachynopus scutellaris
Agrosthaethus indet sp
Hyperomma indet sp
Saphobius edwardsi
Epichorius "sp group A"
Epichorius indet sp
Areoscapus indet sp
Bryocatus amplus
Gromilus indet sp
H11
Bembidion maorinum maorinum
Bembidion tekapoense
Oopterus indet sp
Notogonium indet sp
Scopodes indet sp
Adolopus helmsi
Adolopus indet sp
Cyloma "sp group B"
Adrastia nelsoni
Scydmaenidae "sp group A"
Corneolabrium mandibulare
Eupines rudicornis
Eupines "sp group A"
Pselaphus indet sp
Sagola indet sp
Vidamus indet sp
Zelandius indet sp
Brachynopus scutellaris
Agrosthaethus indet sp
Epichorius "sp group A"
Epichorius indet sp
Phemus indet sp
Gromilus indet sp
0
5
10
15
20
25
Temperature (°C)

Figure 6.7c. Wilson's Lead Road Mean Summer (Feburary) Temperature Reconstruction for samples H12 to H17. The blue horizontal bars in these figures indicate the range of the variable within which the taxon is known to inhabit. The lighter ends of the bars represent the error to these known ranges as calculated by the MLE models. Green boxes represent a reconciled range for all taxa within the sample. Samples containing multiple possible ranges have pink boxes for the warmer ranges and blue boxes for the cooler ranges. Darker boxes illustrate the reconstructed range including the MLE error term. Lighter boxes illustrate the range without the MLE error term. The solid red vertical line represents the present day mean value of the variable at the site as derived rom the climate surfaces of Leathwick et al.(1998). Black lines on the y-axis represent the position of ^{14}C ages of Moar & Suggate (1979) relative to the samples.

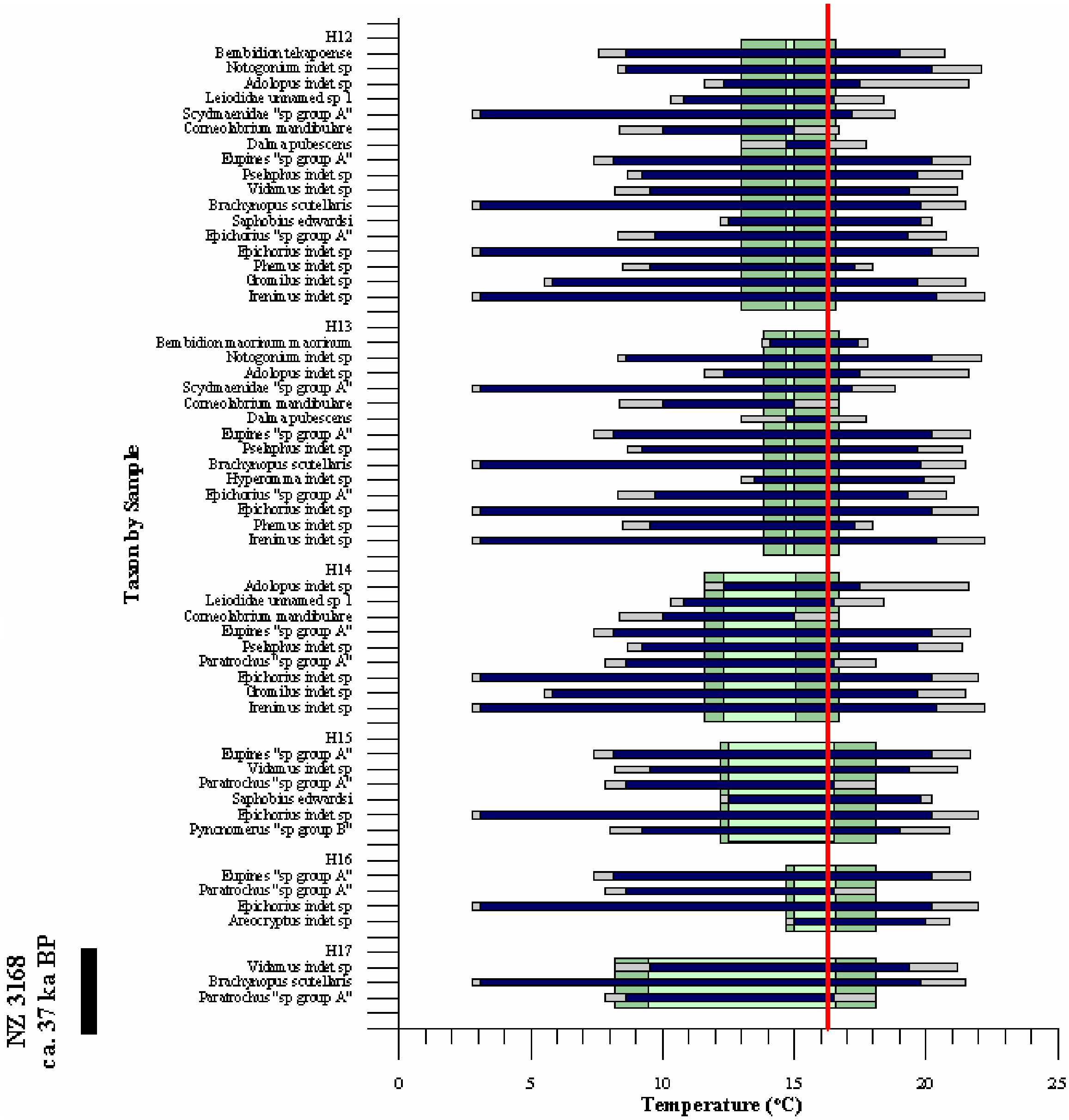


Figure 6.8a Wilson's Lead Road Mean Annual Precipitation Reconstruction for samples H1 to H6. The blue horizontal bars in these figures indicate the range of the variable within which the taxon is known to inhabit. The lighter ends of the bars represent the error to these known ranges as calculated by the MLE models. Green boxes represent a reconciled range for all taxa within the sample. Samples containing multiple possible ranges have pink boxes for the warmer ranges and blue boxes for the cooler ranges. Darker boxes illustrate the reconstructed range including the MLE error term. Lighter boxes illustrate the range without the MLE error term. The solid red vertical line represents the present day mean value of the variable at the site as derived from the climate surfaces of Leathwick et al. (1998). Exclusively montane taxa, which are not used in the MAP reconstruction, are indicated by dashed red circles. Black lines on the y-axis represent the position of ^{14}C ages of Moar & Suggate (1979) relative to the samples.

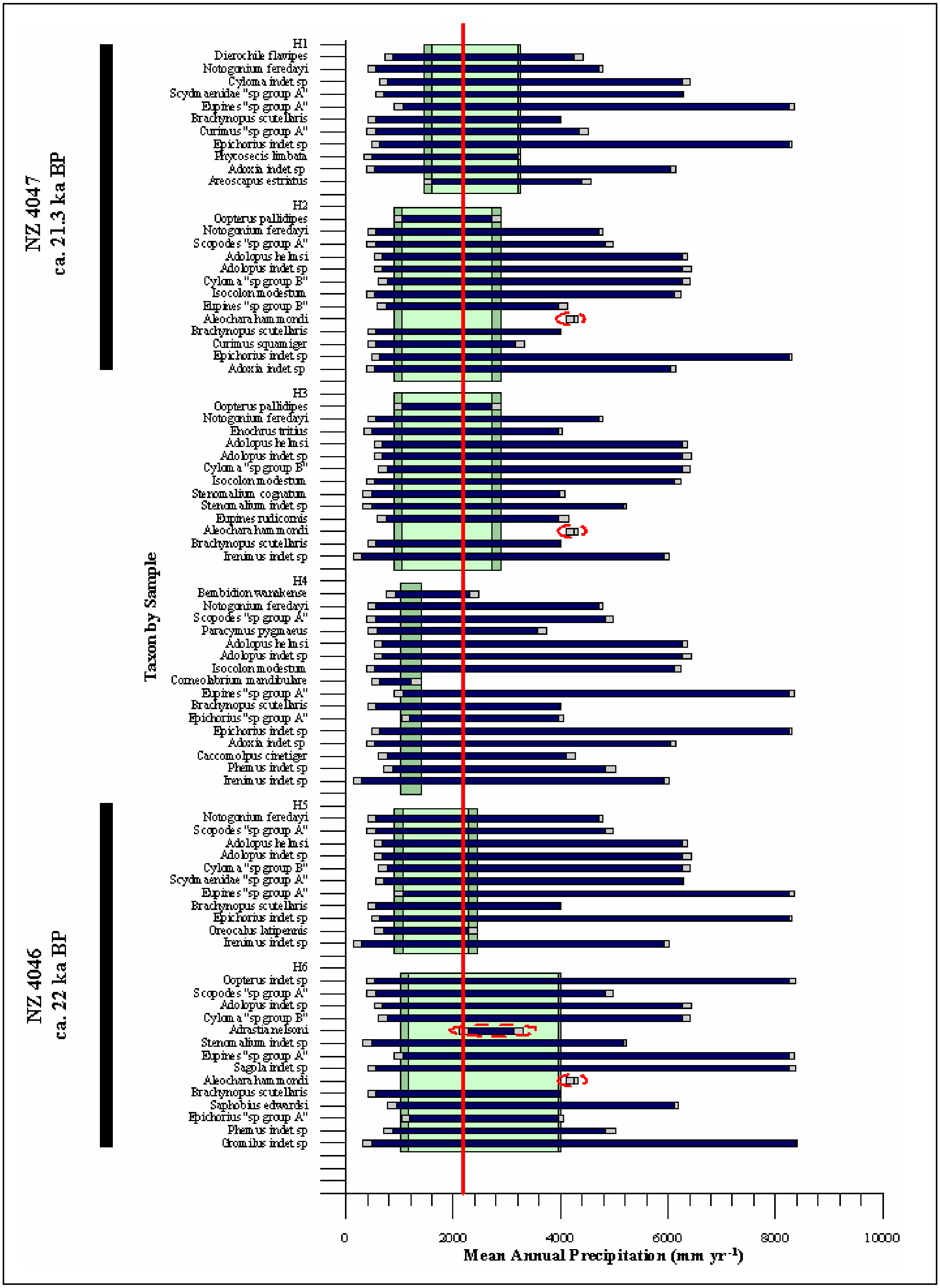

NZ 4047
ca. 21.3 ka BP
NZ 4046
ca. 22 ka BP
Taxon by Sample
H1
Dierochile flavipes
Notogonium feredayi
Cyloma indet sp
Scydmaenidae "sp group A"
Eupines "sp group A"
Brachynopus scutellaris
Curimus "sp group A"
Epichorius indet sp
Phycosecis limbata
Adoxia indet sp
Areoscapus estriatus
H2
Oopterus pallidipes
Notogonium feredayi
Scopodes "sp group A"
Adolopus helmsi
Adolopus indet sp
Cyloma "sp group B"
Isocolon modestum
Eupines "sp group B"
Aleochara hammondi
Brachynopus scutellaris
Curimus squamiger
Epichorius indet sp
Adoxia indet sp
H3
Oopterus pallidipes
Notogonium feredayi
Enochrus tritus
Adolopus helmsi
Adolopus indet sp
Cyloma "sp group B"
Isocolon modestum
Stenomalium cognatum
Stenomalium indet sp
Eupines ruficornis
Aleochara hammondi
Brachynopus scutellaris
Irenimus indet sp
H4
Bembidion warakense
Notogonium feredayi
Scopodes "sp group A"
Paracymus pygmaeus
Adolopus helmsi
Adolopus indet sp
Isocolon modestum
Corneolabium mandibulare
Eupines "sp group A"
Brachynopus scutellaris
Epichorius "sp group A"
Epichorius indet sp
Adoxia indet sp
Caccomolpus cinetiger
Phemus indet sp
Irenimus indet sp
H5
Notogonium feredayi
Scopodes "sp group A"
Adolopus helmsi
Adolopus indet sp
Cyloma "sp group B"
Scydmaenidae "sp group A"
Eupines "sp group A"
Brachynopus scutellaris
Epichorius indet sp
Oreocalus latipennis
Irenimus indet sp
H6
Oopterus indet sp
Scopodes "sp group A"
Adolopus indet sp
Cyloma "sp group B"
Adrastia nelsoni
Stenomalium indet sp
Eupines "sp group A"
Sagola indet sp
Aleochara hammondi
Brachynopus scutellaris
Saphobius edwardsi
Epichorius "sp group A"
Phemus indet sp
Gromilus indet sp
0
2000
4000
6000
8000
10000
Mean Annual Precipitation (mm yr⁻¹)

Figure 6.8b Wilson's Lead Road Mean Annual Precipitation Reconstruction for samples H7 to H11. The blue horizontal bars in these figures indicate the range of the variable within which the taxon is known to inhabit. The lighter ends of the bars represent the error to these known ranges as calculated by the MLE models. Green boxes represent a reconciled range for all taxa within the sample. Samples containing multiple possible ranges have pink boxes for the warmer ranges and blue boxes for the cooler ranges. Darker boxes illustrate the reconstructed range including the MLE error term. Lighter boxes illustrate the range without the MLE error term. The solid red vertical line represents the present day mean value of the variable at the site as derived from the climate surfaces of Leathwick et al. (1998). Exclusively montane taxa, which are not used in the MAP reconstruction, are indicated by dashed red circles. Black lines on the y-axis represent the position of ^{14}C ages of Moar & Suggate (1979) relative to the samples.

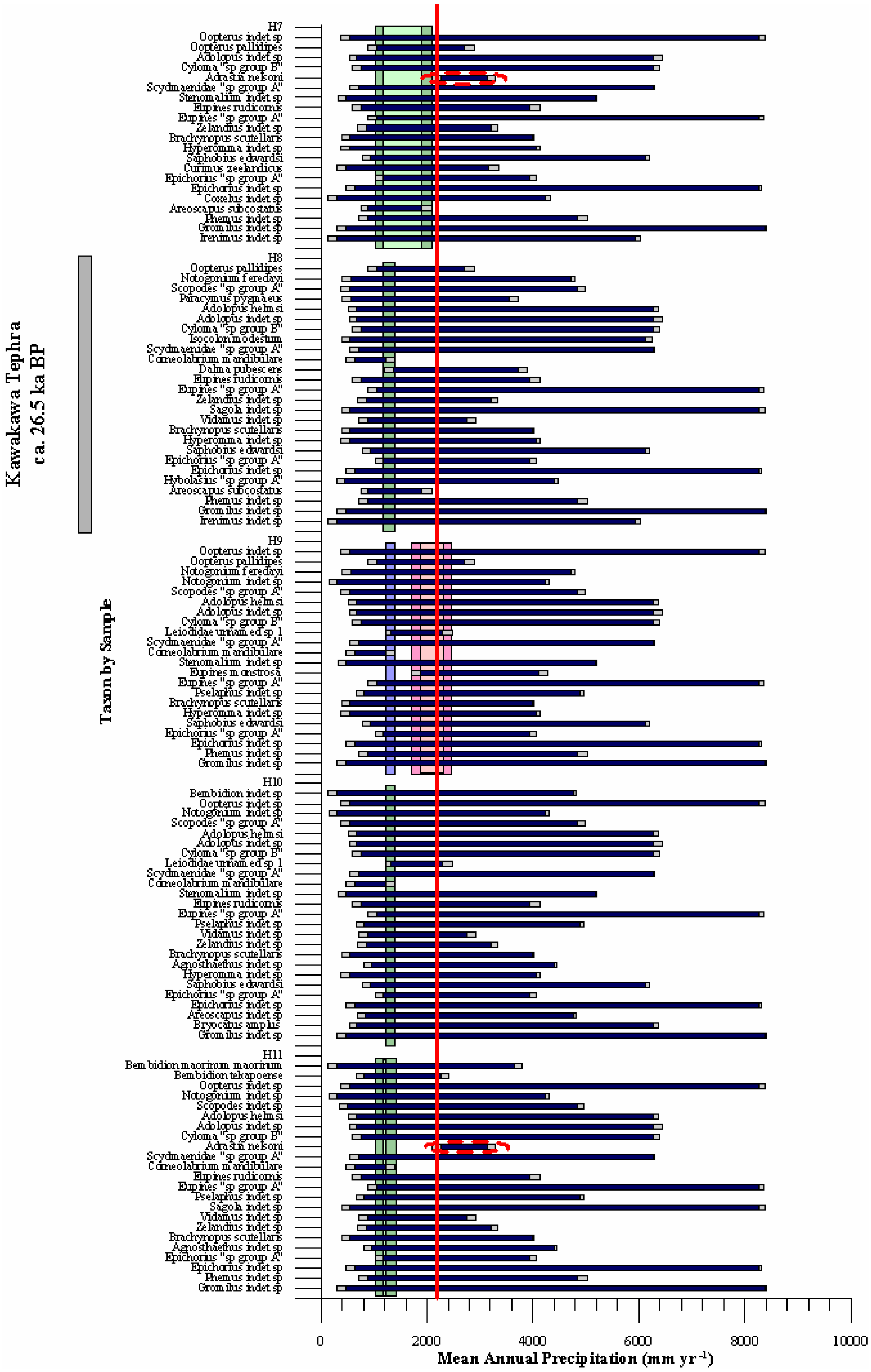

Kawakawa Tephra
ca. 26.5 ka BP
Taxon by Sample
H7
Oopterus indet sp
Oopterus pallidipes
Adolopus indet sp
Cyloma "sp group B"
Adrastia nelsoni
Scydmaenidae "sp group A"
Stenomalium indet sp
Eupines rudicornis
Eupines "sp group A"
Zelandius indet sp
Brachynopus scutellaris
Hyperomma indet sp
Saphobius edwardsi
Curimus zeelandicus
Epichorius "sp group A"
Epichorius indet sp
Coxelus indet sp
Areoscapus subcostatus
Phemus indet sp
Gromilus indet sp
Irenimus indet sp
H8
Oopterus pallidipes
Notogonium feredayi
Scopodes "sp group A"
Paracymus pygmaeus
Adolopus helmsi
Adolopus indet sp
Cyloma "sp group B"
Isocolon modestum
Scydmaenidae "sp group A"
Cameolabrium mandibulare
Dalma pubescens
Eupines rudicornis
Eupines "sp group A"
Zelandius indet sp
Sagola indet sp
Vidamus indet sp
Brachynopus scutellaris
Hyperomma indet sp
Saphobius edwardsi
Epichorius "sp group A"
Epichorius indet sp
Hybolasius "sp group A"
Areoscapus subcostatus
Phemus indet sp
Gromilus indet sp
Irenimus indet sp
H9
Oopterus indet sp
Oopterus pallidipes
Notogonium feredayi
Notogonium indet sp
Scopodes "sp group A"
Adolopus helmsi
Adolopus indet sp
Cyloma "sp group B"
Leiodidae unnamed sp 1
Scydmaenidae "sp group A"
Cameolabrium mandibulare
Stenomalium indet sp
Eupines monstrosa
Eupines "sp group A"
Pselaphus indet sp
Brachynopus scutellaris
Hyperomma indet sp
Saphobius edwardsi
Epichorius "sp group A"
Epichorius indet sp
Phemus indet sp
Gromilus indet sp
H10
Bembidion indet sp
Oopterus indet sp
Notogonium indet sp
Scopodes "sp group A"
Adolopus helmsi
Adolopus indet sp
Cyloma "sp group B"
Leiodidae unnamed sp 1
Scydmaenidae "sp group A"
Cameolabrium mandibulare
Stenomalium indet sp
Eupines rudicornis
Eupines "sp group A"
Pselaphus indet sp
Vidamus indet sp
Zelandius indet sp
Brachynopus scutellaris
Agnosthaetus indet sp
Hyperomma indet sp
Saphobius edwardsi
Epichorius "sp group A"
Epichorius indet sp
Areoscapus indet sp
Bryocatus amplus
Gromilus indet sp
H11
Bembidion maorinum maorinum
Bembidion tekapoense
Oopterus indet sp
Notogonium indet sp
Scopodes indet sp
Adolopus helmsi
Adolopus indet sp
Cyloma "sp group B"
Adrastia nelsoni
Scydmaenidae "sp group A"
Cameolabrium mandibulare
Eupines rudicornis
Eupines "sp group A"
Pselaphus indet sp
Sagola indet sp
Vidamus indet sp
Zelandius indet sp
Brachynopus scutellaris
Agnosthaetus indet sp
Epichorius "sp group A"
Epichorius indet sp
Phemus indet sp
Gromilus indet sp
0
2000
4000
6000
8000
10000
Mean Annual Precipitation (mm yr^{-1})

Figure 6.8c Wilson's Lead Road Mean Annual Precipitation Reconstruction for samples H12 to H17. The blue horizontal bars in these figures indicate the range of the variable within which the taxon is known to inhabit. The lighter ends of the bars represent the error to these known ranges as calculated by the MLE models. Green boxes represent a reconciled range for all taxa within the sample. Samples containing multiple possible ranges have pink boxes for the warmer ranges and blue boxes for the cooler ranges. Darker boxes illustrate the reconstructed range including the MLE error term. Lighter boxes illustrate the range without the MLE error term. The solid red vertical line represents the present day mean value of the variable at the site as derived from the climate surfaces of Leathwick et al. (1998). Exclusively montane taxa, which are not used in the MAP reconstruction, are indicated by dashed red circles. Black lines on the y-axis represent the position of ^{14}C ages of Moar & Suggate (1979) relative to the samples.

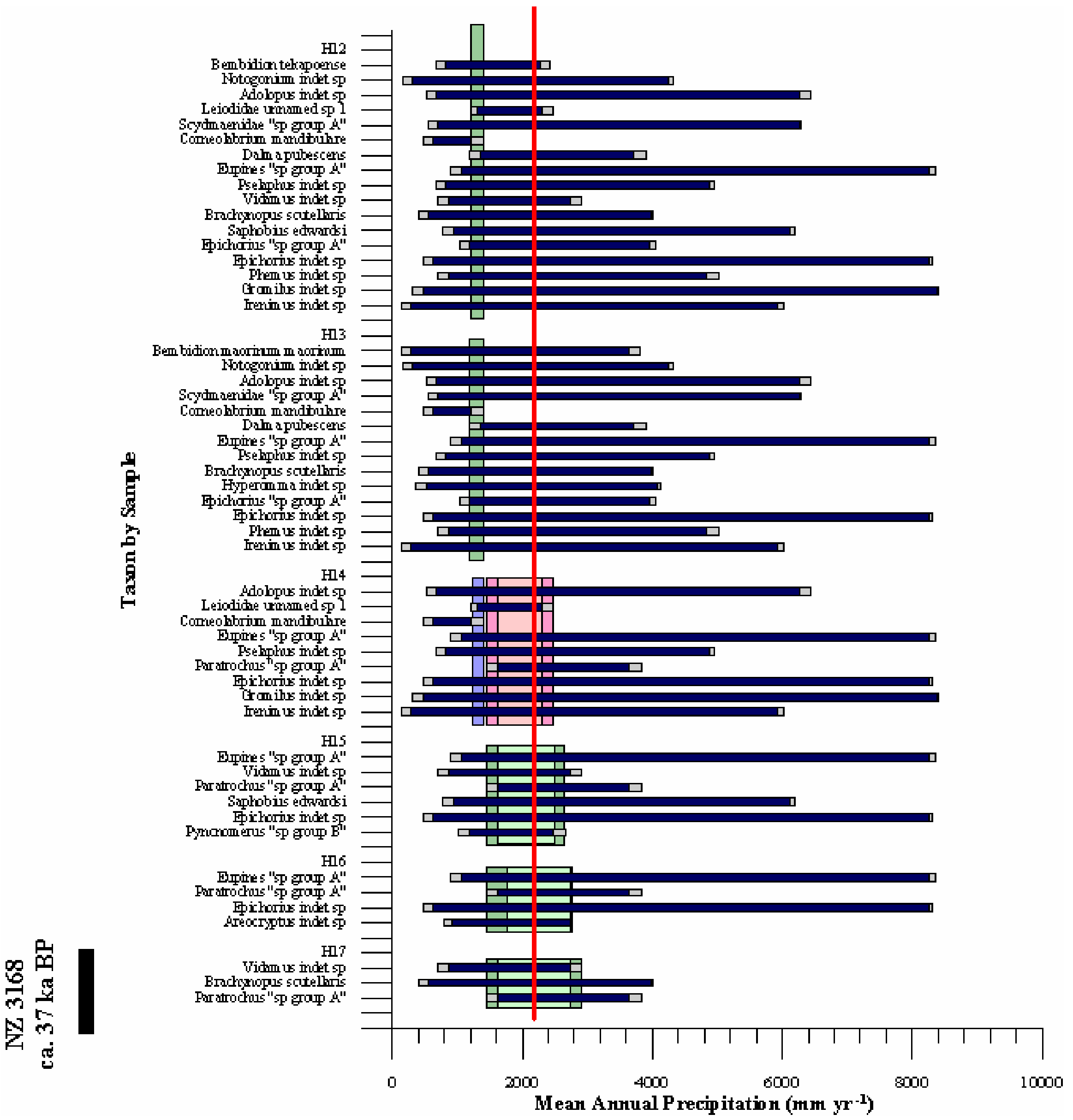
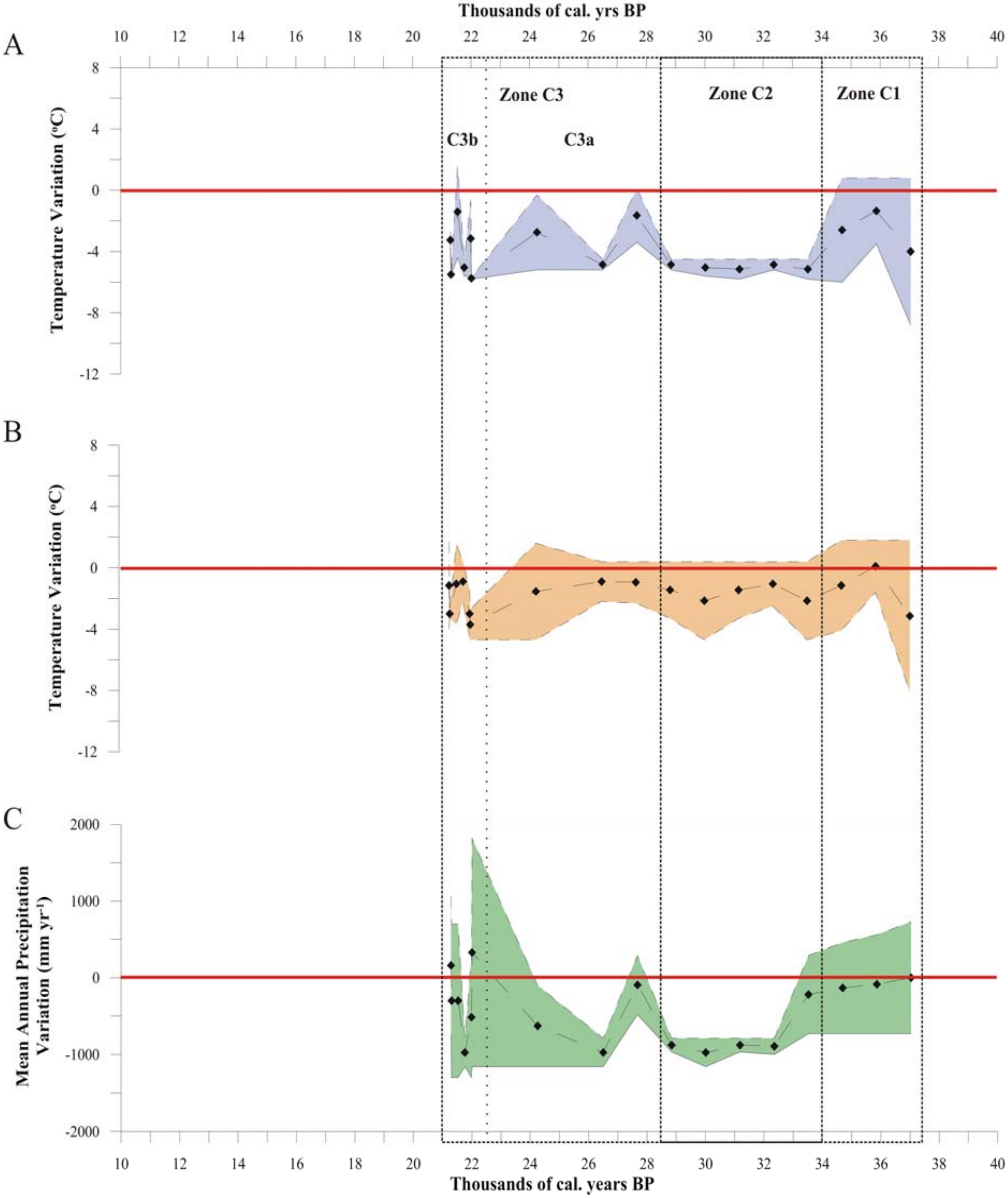


Figure 6.9. Reconstructed climate estimates of: **A**. Mean Minimum Winter Temperature; **B**. Mean Summer Temperature and **C**. Mean Annual Precipitation, from the Wilson's Lead Road site. Age scale is in thousands of calendar years BP. The red lines represent the present day mean value of the climate variable at the site. Also indicated are the three climate zones (C1 to C3) discussed in section 6.5.4.



climate range continues until ca. 22 ka (samples H5 and H6) when fluctuations in the climate envelope between ca. 3.0ºC and ca. 5.0ºC cooler than present become apparent (Fig. 6.6a, Fig. 6.9a). These fluctuations continue until the record ends at 21.3 ka BP.

The MST reconstruction initially (samples H17-H15 Fig. 6.7c, Fig. 6.9b) straddles the present day mean summer temperature (16.3ºC) at the site indicating that summer temperatures fell between ca. 1.5ºC warmer and ca. 4.ºC cooler (Fig. 6.9b). At 34-33ka BP (Sample H14) the upper limit of the summer temperature reconstruction drops to ca. 0.5ºC warmer than present probably, although not conclusively, indicating slight cooling.

This is coincidental with the cooling observed in the MMWT reconstruction (Fig. 6.6a-c, Fig. 6.9a). This apparently slight cooling lasts for ca. 8,000 years until the MST envelope broadens to straddle the present day mean with the summer temperature falling between ca. 1.5ºC warmer and ca. 5.0ºC cooler then today at 25-24ka BP (sample H7). Summer temperatures continue at this level until ca. 22ka BP (sample H5 and H6) when fluctuations between ca. 1.5ºC warmer and ca. 3.5ºC cooler than present become apparent.

Like the temperature reconstrucitons the MAP estimates (Fig. 6.8a-c, Fig. 6.9c) initially (samples H17-H15) straddle the present day mean annual preciptation with a lower estimate consistently ca. 750mm below present levels (2,190mm yr^{-1}) and an upper estimate varying between ca. 750mm and ca. 450mm above present (Fig. 6.9c). The precipitation record indicates a sharp reduction at 34-33ka BP (sample H14) with estimates of the mean annual precipitation falling between 800 and 1000mm below present levels. Precipitation remains at this decreased level until ca. 28ka BP (sample H9) (Fig. 6.9c) when precipitation increases to between ca. 500mm below the modern mean annual precipitation and the present value. This increase is short-lived but coincides with the warming indicated in the winter temperature reconstruction. Precipitation estimates return to between 800 and 1000mm below present levels at ca. 26.5ka BP (sample H8) prior to broadening of the envelope at ca. 25-24ka BP (sample H7) to between 1000 mm below present levels and near modern day levels (Fig. 6.9c). The timing of this broadening is consistent with the warming indicated in both temperature records and while no conclusive estimate of increased precipitation can be made it suggests a real increase in mean annual precipitation. This broadening of the precipitation envelope continues up to ca. 22ka BP (Sample H6) after which the upper precipitation limit drops sharply to ca. 1,000mm below modern levels (Fig. 6.9c). The upper limit of the precipitation envelope then shows a rapid return to near modern levels (Fig. 6.9c).

6.4 Discussion

6.4.1 Age control

This study applies the ^{14}C ages from a previous study conducted at the same location by Moar & Suggate (1979). While the outcrop originally dated by Moar & Suggate (1979) has been destroyed the modern stratigraphy of the outcrop is similar enough that a recent re-examination of the site by Suggate & Almond (2005) concluded that the original ^{14}C ages could be matched to the current outcrop. This conclusion is supported by the position of the Kawakawa tephra in the outcrop (Suggate & Almond, 2005) whose age of ca. 26.5ka BP (22,590 ± 230 ^{14}C yrs. BP (Froggatt & Lowe, 1990)) is consistent with the ages of Moar & Suggate (1979). I accept the age attributions of Suggate and Almond (2005).

The age of the upper portion of the beetle rich unit is controlled by two ^{14}C ages and the Kawakawa tephra. Ages in the lower half of the unit are less well constrained with only the position of the Kawakawa tephra and a basal age (calibrated as 37.043 + 1.961/-1.724k cal. yrs. BP) (Fig. 6.2) providing limits.

6.4.2 Environmental reconstruction and comparison to the pollen record from WLR

This study recognised three types of fossil beetle assemblage representative of different environments. These assemblages were used to designate three zones E1, E2a and E2b (Fig. 6.4). While the previous palynological study of "the Hill" (Moar & Suggate, 1979) also recognised three different zones (H1, H2a and H2b, Fig. 6.10) within the same section of the outcrop, the environmental reconstructions differ quite markedly from one another.

Zone E1 (ca. 37 – 34ka BP)

The assemblage zone E1 correlates to Pollen Zone H1 in the original pollen study of Moar and Suggate (1979) (Fig. 6.10 and Fig. 6.11). The deposition of this unit began at ca. 37.1ka BP and was interpreted as ending at the transition between a somewhat warmer period (interstadial) into a period of full glacial conditions (Moar & Suggate, 1979). This interpretation agrees with the beetle based palaeoclimatic reconstruction (this

Figure 6.10. Pollen diagram from "The Hill", Wilson's Lead Road. The position of the stratigraphic unit sampled for beetles is highlight with a red dashed box on the figure. Some of the plant taxa shown in the figure have undergone taxonomic revision since the original publication of the figure and of particular relevance is the change of name of the shrub taxa identified here as *Dacrydium bidwillii-biforme* to *Halocarpus bidwillii*. This figure is a reproduction of Fig. 8, Moar & Suggate (1979)

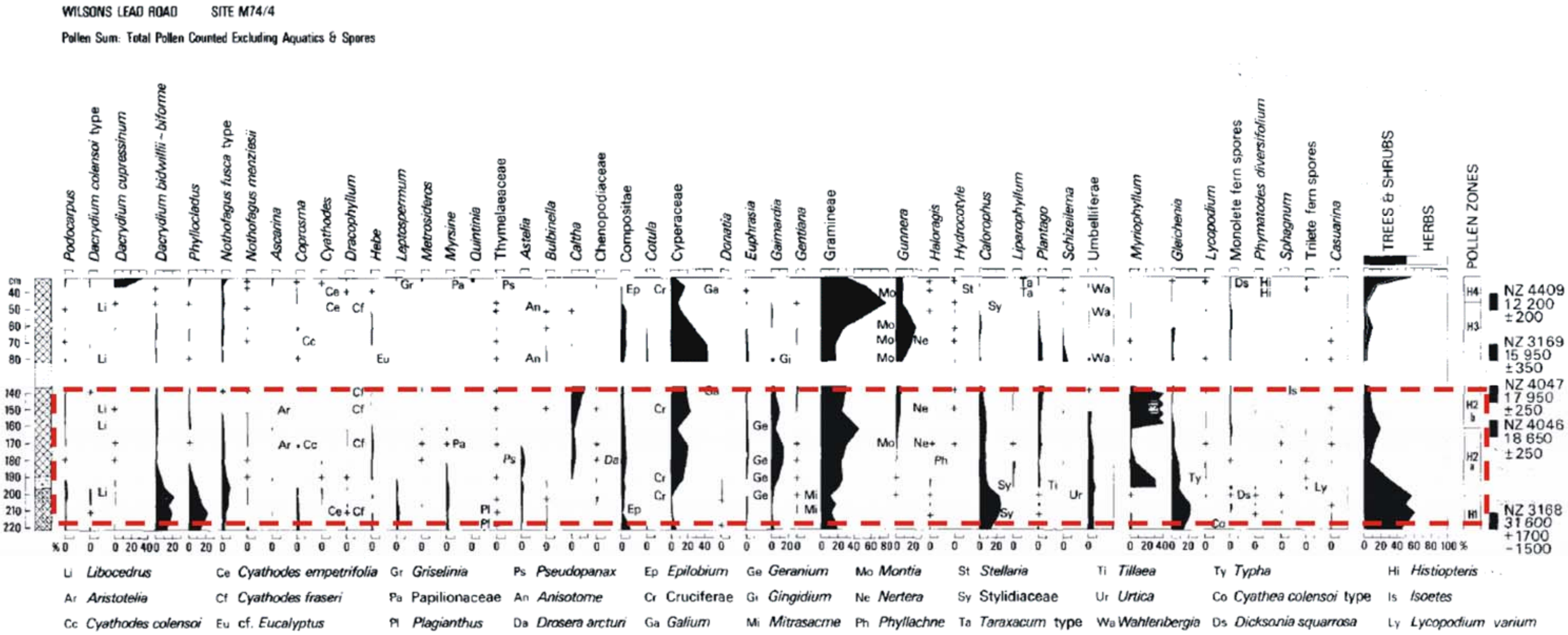
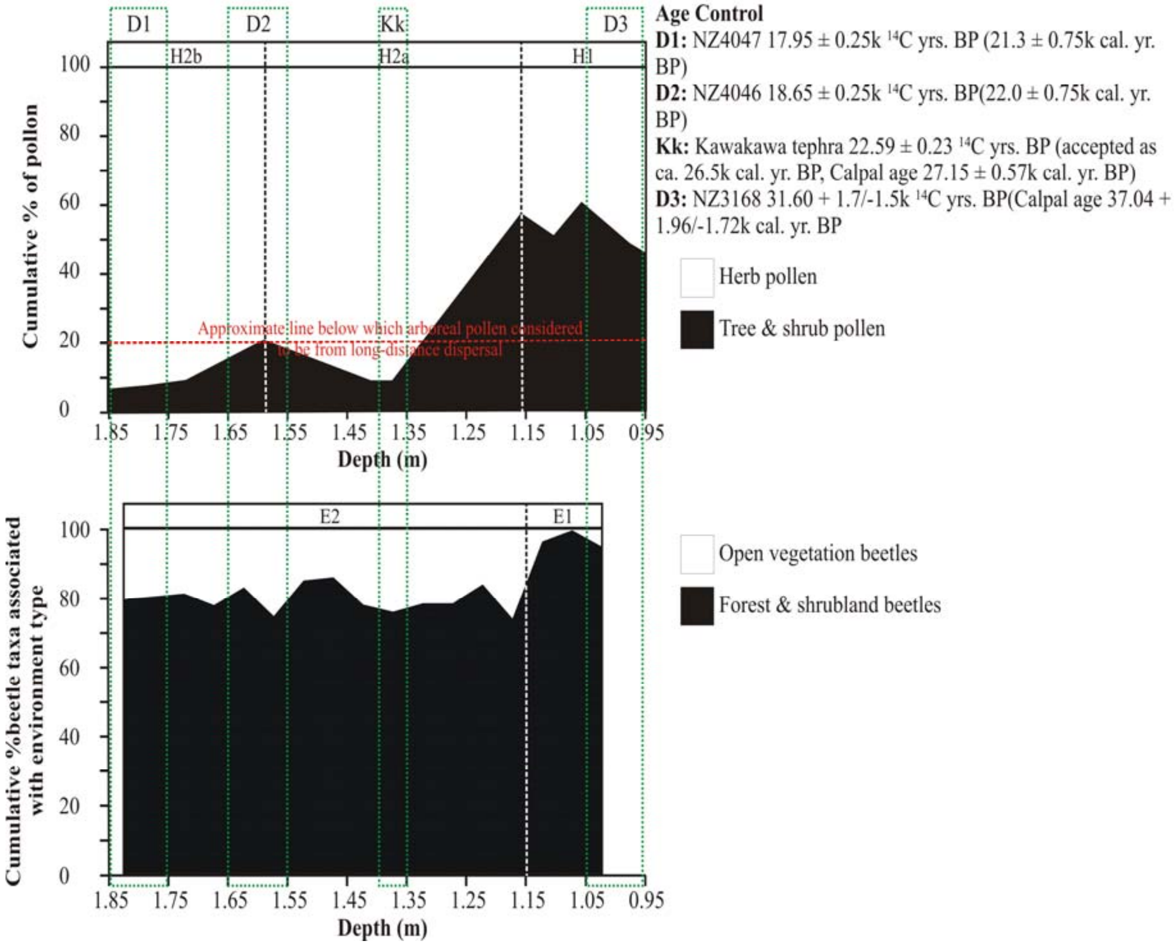


Figure 6.11. Comparison of the summary pollen diagram (top, (Suggate & Almond, 2005)) and summary beetle record (bottom) from "The Hill" Wilson's Lead Road Westport. The pollen diagram has been re-plotted on the depth scale used in this study (Fig. 6.2). The figure shows the discrepancy between the proportion of pollen and beetles associated with forest-shrub vegetation as well as the generally accepted cut off below which arboreal pollen is associated with long distance dispersal.



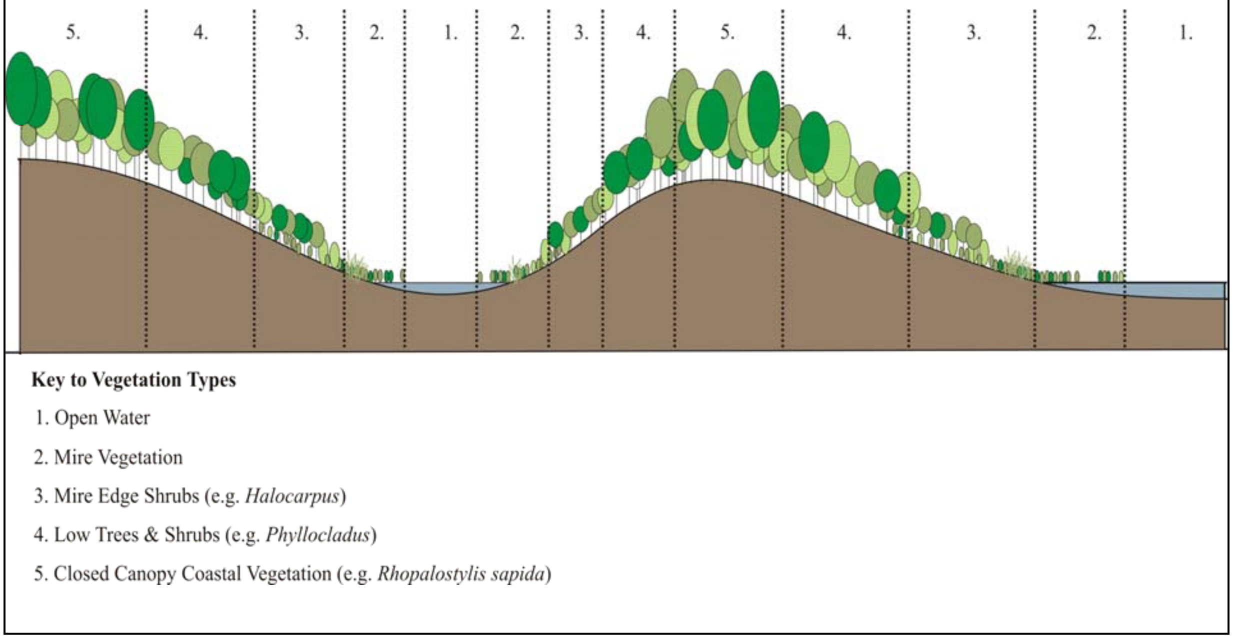
chapter) which indicates decreasing temperatures in the same sample as the end of the E1 zone ca. 34ka BP (Fig. 6.9). The beetle fossils indicate a moist closed canopy, forest environment (Fig. 6.4, Table 6.1) in close proximity to a water source with the beetle *Areocryptus* indet. sp. indicating the presence of nikau palm (*R. sapida*) near the site. Modern South Island instances of *R. sapida* are found only in coastal-lowland sites north of 43º45'S (Enright & Watson, 1992) indicating nikau palm was near its modern southern limit during OIS 3 and that the local vegetation had coastal-lowland affinities (Dawson & Lucas, 2000).

The reconstruction of coastal closed canopy vegetation contrasts with the interpretation of the corresponding zone from Moar and Suggate (1979) (Fig. 6.10, Fig. 6.11). That zone, H1, was correlated with other pollen diagrams from WLR (Moar & Suggate, 1979) and interpreted as representing a regional environment of wet peaty hollows and shallow ponds dominated by a *Phyllocladus* and *Halocarpus* shrub/grassland with scattered patches of *Nothofagus* in sheltered locations (Moar & Suggate, 1979). *Halocarpus* and *Phyllocladus* are generally considered to represent montane-subalpine vegetation (Macphail & McQueen, 1983; Wardle, 1991) and Moar and Suggate (1979) initially argued that as *Nothofagus menziesii* forest survived near Hokitika during this time period the Westport region must have been subjected to a regime of harsh frosts (Moar & Suggate, 1979). Moar and Suggate (1996) later revised this hypothesis arguing instead different soil development and increased windiness to explain the lack of forest in the area.

While the beetle and pollen reconstructions appear incompatible they can be reconciled. Examination of the pollen record from Moar and Suggate (1979) (Fig. 6.10) shows similarities, although not complete correspondence, to the taxonomic makeup of the lowland bogs and forest-heaths found in the Westland region near Greymouth (e.g. Mark & Smith, 1975; Wardle, 1977; Norton, 1989). This region is also known to contain areas of coastal-lowland vegetation containing *R. sapida* (Moore & Edgar, 1970; Enright &

Watson, 1992). Dickinson and Mark (1994) examined the vegetation of a modern dune-slack sequence near Haast in South Westland observing a pattern of herbaceous wetland taxa in poorly drained dune swales progressing through shrub-land/low forest to tall mixed lowland rainforest on the dune crests. While the taxonomic composition observed at the WLR sites differs from that seen in the South Westland dune-slack sequence (Dickinson & Mark, 1994) it is possible that the *Halocarpus*/*Phyllocladus* shrubland indicated by the pollen (Moar & Suggate, 1979) and the closed canopy coastal vegetation indicated by the beetles could have coexisted in a similar manner (Fig. 6.12).

Figure 6.12 Idealised transect of the environment structure of the dunefield at Wilson's Lead Road, Westport during interstadial conditions. The environment shifts from open water in the dune swales through mire shrubs and low tree trees to closed canopy vegetation on the dune peaks..



All the WLR sites examined by Moar and Suggate (Moar & Suggate, 1979) occurred in "hollows in deeply eroded sands" (Moar & Suggate, 1979) and these wet, swampy areas would have been dominated by swampy herb taxa including wire brush (*Calorophus*)

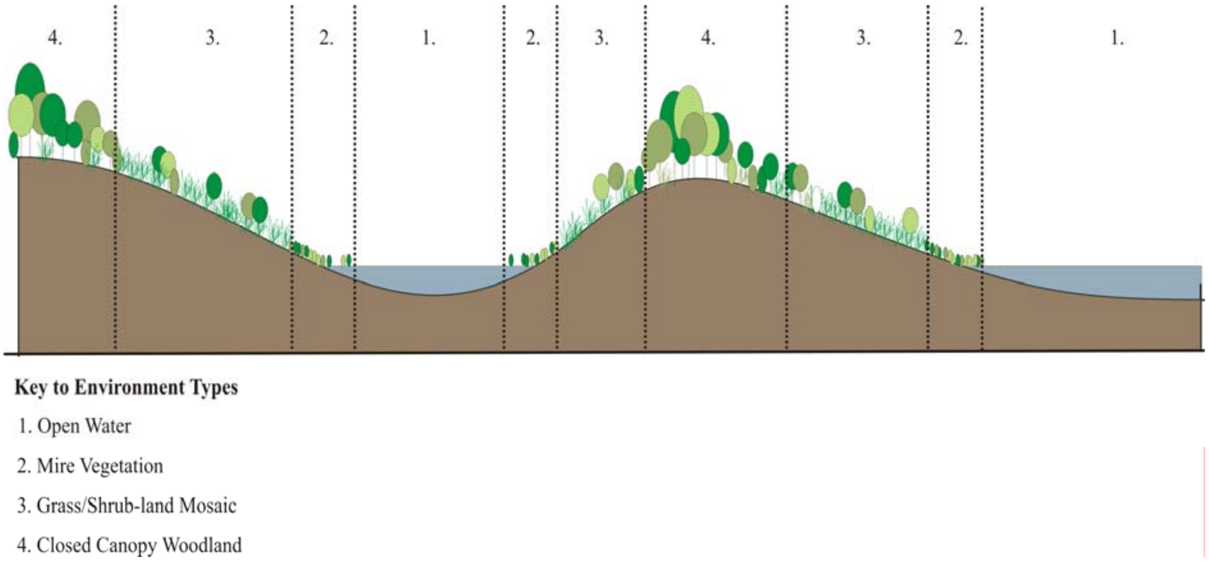
(Mark & Smith, 1975) which is well represented in the local pollen (Fig. 6.10) (Moar & Suggate, 1979).

Further from the centre of these swampy areas the herbaceous vegetation would give way to woody forest-mires, similar to those seen in Westland today (Mark & Smith, 1975), consisting of a combination of *Halocarpus* and other shrubby bog taxa near the bog edge and progressively grading into a forest of *Phyllocladus* and other low tree species (Norton, 1989). Closed canopy coastal vegetation including taxa such as *Metrosideros*, *R. sapida* and *Plagianthus* would have occupied better drained areas, such as atop dune ridges (Fig. 6.10). *R. sapida* is a poor pollen producer (Macphail & McQueen, 1983) and the pollen rain into small (< 1 ha) shrub covered bogs is dominated by the pollen from the local shrubs even when surrounded by forest (Jacobson & Bradshaw 1981; Macphail & McQueen 1983). The lack of *R. sapida* pollen is therefore to be expected if the local shrub (e.g. *Halocarpus* and *Phyllocladus*) and swamp (e.g. *Calorophus*) vegetation dominates the pollen rain. Trace amounts of *Metrosideros* and *Plagianthus*-type pollen, taxa also known to occur in lowland and coastal forests (Allan, 1961; Macphail & McQueen, 1983), does occur in some of the WLR pollen diagrams (e.g. Fig. 6.10) (Moar & Suggate, 1979) and may represent input from the local stands of coastal vegetation on the dune peaks rather than being derived via long distance dispersal.

Zones E2a & E2b (ca. 34 – 21ka BP)

The transition between assemblage zone E1 and E2a is marked by an opening up of the environment (Fig. 6.4, Table 6.1) with areas of open water indicated by the occurrence of aquatic beetle taxa such as *Paracymus pygmaeus* (Winterbourn, 1970; Hansen, 2000) and *Enochrus tritus* (Archangelsky, 2002; Archangelsky, 2004). The increase in open water is also accompanied by the spread of tussock grassland, indicated by the presence of taxa associated with high altitude tussock grassland (e.g. *Aleochara hammondi* (Klimaszewski & Crosby, 1997)) and shrubby vegetation such as *Hebe* (e.g. *Oreocalus latipennis* (May, 1993)). The dominant environmental signal from the beetles is still one of closed canopy vegetation, however, and the beetle assemblage is interpreted as representing a mosaic environment of woodland, tussock grassland and swamp type vegetation near an area of open water (Fig. 6.13).

Figure 6.13. Idealised transect of the dune field during full stadial conditions. The environment shows increased open water in the dune swales amongst a grass-shrubland mosaic with closed canopy woodland on the dune peaks.



This environment appears to remain relatively unchanged to the end of unit deposition ca. 21.3ka BP (Suggate & Almond, 2005) when the presence of *Phycosecis limbata* in zone

E2b indicates sand beginning to encroach into the site prior to the end of silt deposition (Fig. 6.2). This is presumably due to the re-activation of the dunefield at this time and is consistent with the stratigraphy.

The transition from E1 to E2a corresponds to the transition from pollen zones H1 to H2a which is marked by an increase in the proportion of grass pollen and a decrease in the proportion of *Halocarpus* and *Phyllocladus* (Fig. 6.10). Moar and Suggate (1979) recognised that the pollen record of acme zone H2a had similarities to pakihi bog vegetation and acknowledged that regional vegetation was a mosaic of different sub-alpine and lowland herbaceous vegetation characteristic of wet areas. The dominance of grass pollen prompted them to conclude that the Westport area was dominated by grassland with pollen from woody plants (Fig. 6.10, Fig. 6.11) derived through long distance dispersal from pockets of arboreal vegetation restricted to sheltered locations (Moar & Suggate, 1979). While such an interpretation is supported by some other pollen diagrams from the West Coast (e.g. Howard Valley (Campbell, 1986), Grahams Terrace (Mew et al., 1986)) these sites are in inland valleys near the limits of glacial ice where cold air drainage and increased frostiness would restrict the presence of forest vegetation (Smith, 1996). The WLR sites are well beyond the glacial extent, are disconnected from glacial drainages, and would not be subject to such extreme conditions. Temperature reconstructions for the LGM using pollen (e.g. Mildenhall, 1994), glacial equilibrium line altitude (ELA) estimates (e.g. Porter, 1975), Sea Surface Temperatures (e.g. Barrows and Juggins, 2005) and the beetle-based temperature reconstructions from this study all indicate the temperature reductions during New Zealand at this time were of no more than 4-5ºC and this is not enough to have excluded forest from the Westport area (McGlone, 1985; McGlone et al., 1993). To explain the discrepancy between the temperature estimates and the pollen record Moar (1980) and Moar and Suggate (1996) proposed strong winds as the reason for the apparent exclusion of trees from the Westport region. This is unlikely as the area was some distance inland and, unlike the Cook Strait region, does not act as a funnel for winds.

The apparent conflict between the pollen and beetle records can again be resolved. The change in the environment to include more open vegetation (Fig. 6.4, Fig. 6.11) and an increase in the amount of open water would have resulted in an effective increase in the size of the pollen collection area (Jacobson & Bradshaw, 1981). Grasses are known to produce abundant amounts of pollen while many New Zealand shrubland/woodland taxa are poor pollen producers due to their reliance on insect and bird pollinators (Macphail & McQueen, 1983). The contrast between the pollen and beetle reconstructions may thus simply represent a combination of an enlarged pollen collection area and low pollen producing taxa (including arboreal taxa) being overwhelmed by abundant input from increased areas of grassland and local wetland taxa such as *Myriophyllum* and Cyperaceae. Alternatively, the reduction in arboreal pollen may be the result of the lower temperatures experienced by the trees at this time. Hicks (2006) points out that when trees are exposed to summer temperatures below a certain threshold they do not produce pollen in the next year even though they are present in the landscape. She hypothesises that if this situation were to continue for several years then this would result in a time of extremely low tree pollen in pollen diagrams that does not reflect an actual change in the vegetation at the site (Hicks, 2006). This hypothesis again has a problem as cold tolerant trees which currently occupy montane regions are routinely subjected to the mild levels of summer cooling suggested from the quantitative estimates of cooling at this site (see Fig. 6.7a-c, Fig. 6.9b). Furthermore the WLR pollen diagram indicates a period of ca. 13,000 years without trees. This is well beyond the life span of most trees and it is unlikely that, even if summer temperatures were consistently low enough to inhibit pollen production, trees would forgo reproducing. It is therefore possible that the long term lack of pollen in the WLR pollen diagram reflects not only a short-term response to lowered summer temperatures but also a change in the reproductive strategy of trees in the region from sexual reproduction to dominantly vegetative means. Vegetative reproduction is already known in the New Zealand flora occurring in the swamp podocarps *Monoao colensoi* (silver pine) (Molloy, 1995) and *Phyllocladus alpinus* (mountain celery pine) (Molloy, 1995; Dawson & Lucas, 2000). *P. alpinus* in particular is one of the dominant sources of arboreal pollen in acme zone H1 but all but disappears in acme zones H2a and H2b (Fig. 6.10) (Moar & Suggate, 1979) even though it is frost tolerant (Sakai & Wardle, 1978) and known to inhabit montane areas (Macphail & McQueen, 1983). Vegetative reproduction has been demonstrated as a viable long-term reproductive strategy by a population of Huon Pine (*Lagarostrobos franklinii*) in Tasmania which shows evidence of 90% genetic similarity between different plants for a period of up to 11,000 years (Shapcott, 1997).

Shifts away from sexual and towards vegetative reproduction in modern vegetation have been observed to be triggered by an increased frequency of damage to leaves and flowers.

For example, a study of Brazilian savanna taxa shows increased vegetative reproduction amongst the studied plants in response to more frequent damage by fire (Hoffmann, 1998). An increased incidence of leaf and flower damage resulting from frost and/or wind during the last glacial may have resulted in a shift towards vegetative reproduction as offspring produced through clonal means tend to be larger than those produced through sexual reproduction (Abrahmanson, 1980; Hoffmann, 1998) and are therefore more likely to be able to survive harsh environmental conditions. Grass pollen appears at the same time that pollen from woody taxa all but vanishes from the pollen record (Moar & Suggate, 1979) (Fig. 6.10, zone H2a) and the presence of beetles associated with subalpine grassland at this time (zone B2, Table 6.1) indicates that the grass pollen is from subalpine species. These high-altitude grasses may be better suited to survive the colder conditions of the last glaciation than lowland tree taxa and thus continued produce significant amounts of pollen rather than switching to vegetative reproduction. Alternatively, the life cycle of grasses is shorter than that of most trees and if the grasses did alter their reproductive strategy, relying on vegetative reproduction before a final burst of sexual reproduction at the end of their life cycle, they would still have been producing pollen on a more frequent basis than the longer lived trees and thus dominating the pollen record.

One limitation on this hypothesis, and that of Hicks (2006), is that frost hardy trees such as *Phyllocladus alpinus* (Sakai & Wardle, 1978), which should have coped with the ca. 5°C cooling observed in the beetle based winter temperature reconstructions (Fig. 6.9a) and in other estimates of glacial cooling in New Zealand (Porter, 1975; Barrows &

Juggins, 2005), also disappear from the pollen record. This indicates that frost is unlikely to be soley responsible for a transition to vegetative reproduction and other triggering mechanisms must be investigated.

While the mosaic environment proposed here contrasts with the more inland pollen records from the Howard Valley (Campbell, 1986) and Grahams Terrace (Mew et al., 1986) it does agree, at least in part, with other records from New Zealand. Fossil bird faunas in particular concur with the beetle record. Last glacial maximum (LGM) age cave deposits from northwestern and eastern South Island, New Zealand include the fossilised remains of both small forest birds and large-bodied browsing moa characteristic of open forest-shrublands (e.g. *Megalapteryx didinus* and *Pachyornis elephantopus*) (Worthy & Holdaway, 1993; Worthy & Holdaway, 1994; Worthy & Holdaway, 1996) indicating that a palaeoenvironment comprising a mosaic of woodland, shrubs and grasses survived in these regions through the LGM (Worthy & Holdaway, 1993; Worthy & Holdaway, 1994; Worthy & Holdaway, 1996). Further evidence of the survival of woody taxa in areas thought, based on pollen records, to be deforested during glacial periods can be seen in phytolith records from loess units associated with this time period (e.g. Almond et al., 2001; Carter, 2002). As this finding disagrees with the current pollen-based palaeoenvironmental paradigm their presence was explained as representing either isolated pockets of trees (e.g. Carter, 2002) or down-profile movement of phytoliths from Holocene forests through bioturbation (e.g. Almond et al., 2001) rather than the presence of signicant amounts of woody vegetation during glacial periods. Some pollen records can also be interpreted to provide some support for the beetle record. Low amounts of tree pollen occur in the pollen record from Okarito Bog in South Westland (Vandergoes et al., 2005) although as the proportion of tree pollen is below the “cutoff” for pollen of a local origin it is considered the result of long distance dispersal and the site is interpreted as indicating a mosaic of montane-subalpine shrubs in conjunction with increased grasses throughout the period of this study. Pollen records from Wellington (Pillans et al., 1993; Mildenhall, 1994) and Wairarapa (McLea, 1990) in the southern North Island also indicate a vegetation mosaic of montane-subalpine shrubs in conjunction with increased grasses and while tree pollen is again present it was once more affiliated with long distance dispersal.

While the mosaic environment proposed here can be, at least partially, reconciled with other New Zealand environmental reconstructions for the same time period, the vegetation mosaic found in the Westport region at the glacial maximum does not appear to be similar to any modern day New Zealand flora. This is not a situation peculiar to New Zealand. Pollen studies from Chile (Heusser et al., 1999) indicate that a no-modern-analogue sub-Antarctic parkland comprising *Nothofagus* and grasses (Gramineae) occupied outwash surfaces of the Southern Lake District – Isla Grande de Chiloé, South America, at the same interstadial/stadial transition examined in this chapter. Evidence from Papua New Guinea (Hope, 1989) indicates that subalpine vegetation consisting of a shrub-grassland mosaic occurred in a zone between lowland/montane forest and alpine grassland during the last glacial maximum. This shrub-grassland mosaic was rapidly replaced during the Holocene by a structurally different, but floristically similar, forest environment (Hope, 1989). It is possible that the rapid reforestation of the Westport region following the end of the Last Glaciation was similar to that observed in Papua New Guinea consisting primarily of a change in the structure, rather than composition, of the vegetation.

While forest vegetation is indicated by the beetle fauna in this study the exact composition of the vegetation is unknown. Regardless of the composition of the woody vegetation the presence of a closed canopy woodland flora means that conditions cannot have been as harsh as previously implied in the Westport region which is in keeping with both the existing temperature reconstructions for the time period of this study (e.g. Mildenhall, 1994; Barrows and Juggins, 2005) and the palaeoclimatic reconstruction produced from the beetle fossils.

6.4.3 Palaeoclimate discussion

Outlying taxa

Two taxa, *Tormus nitidulus* Broun and *Pyncnomerus latitans* Sharp are treated as outliers in this study and are not included in the reconstructions shown in Figs. 6.6a-c, 6.7a-c or 6.8a-c. The reasons for excluding these taxa have already been discussed in Chapter 4 and are not repeated here.

Split climate envelopes

Some samples within the final palaeoclimatic reconstructions (Figs. 6.6a-c, 6.7a-c & 6.8a-c) contain multiple possible climate reconstructions for the same set of data (e.g. samples H3, H7 and H11 in Fig. 6.6a-b; samples H3, H6, H7 and H11 in Fig. 6.7a-b;

samples H9 and H11 in Fig. 6.8b-c). While these “split climate envelopes” could result from taxa with poorly delimited climate ranges the MLE envelopes are consistent with the known habitats of the beetles causing the splits. Sample H3 (Fig. 6.6a, Fig. 6.7a) is an example. Most of the taxa in this sample are associated with forest environments (Table 6.1) but *Aleochara hammondi* Klimaszewski is a tussock grassland type and is now confined to alpine settings (Klimaszewski & Crosby, 1997).

While the present day vegetation of the West Coast comprises a sequence of floristic zones from shrubby forest at the coast, through lowland podocarp-beech forest on the coastal terraces, montane beech forest on the mountain slopes and subalpine grassland above the tree line (McEwen, 1987; Wardle, 1991), this was not the case during the period covered by this record. The palaeoenvironmental reconstruction for this site illustrates that the vegetation of the Westport region during the time period covered in this study comprised a mosaic of closed-canopy lowland forest mixed with shrubs and alpine grassland. This mosaic environment, comprising flora from a number of modern environments, would enable beetle taxa from different habitat types (e.g. forest and tussock grassland) to co-exist in the same general area so long as other factors (such as climate) were not limiting. This intermingling of taxa that in a modern day setting appear climatically segregated emphasises the need to understand the ecology of beetles when attempting to interpret estimates of glacial period palaeoclimate from fossil beetle assemblages.

Beetles and climatic limitations

Beetles are poikilothermic and low temperatures can have a multitude of effects. These include slowing of metabolism (Gillot, 1991), an inability to gain enough heat energy from the environment to complete development (Hodkinson, 2005), cell dehydration (due to the removal of water through freezing) (Franks et al., 1990) and the lethal crystallisation of water in insect tissues (Sinclair et al., 2003a). Beetles are therefore actively limited by cold temperatures and the low-end estimate of the MLE minimum winter temperature reconstructions may represent hard climatic limits below which a beetle taxon is less likely to survive. This suggests that it is a reliable estimate of the lower limit of minimum winter temperatures. On the other hand, the upper limit of the winter temperature reconstruction is based on ecological preferences as there is no physiological reason why warmer than average winter minima will limit the survival of taxa (so long as the temperature remains below the taxon's upper thermal limit).

While the upper limit of the winter temperature reconstructions is unlikely to be physiologically limiting it does indicate an ecological preference and still provides useful data. As variation in the upper limit of a winter temperature reconstruction relates to the presence or absence of beetles with preferences for cooler conditions changes in the upper limit reflects variation in the temperature. For example, if taxa that prefer cold conditions disappear from a record then the upper limit of the reconstructed climate range will increase implying an amelioration of winter temperatures.

Like the beetle-based winter temperature reconstructions, the upper boundary of precipitation estimates are unlikely to be limiting as it is water stress, caused by loss of moisture from the beetle to the environment, that is the physio-chemical limitation on beetle survival (Edney, 1977; Hadley, 1994). The only time a high level of precipitation is likely to be limiting is when it is high enough to result in flooding and drowning of beetles. As this is not a function of total rainfall, but rather individual rainfall events and the hydrology of the site, high-end estimates of precipitation are unlikely to be ecologically limiting. It is therefore the minimum estimate of the upper (pink) envelope (Fig. 6.8b-c) that acts as the robust limitation on precipitation reconstructions. The exceptions to this are reconstructed envelopes based around high alpine taxa which occur above the treeline (e.g. *Aleochara hammondi* and *Adrastia nelsoni*). Limiting factors in high alpine areas include a variety of factors including high UV radiation, low minimum temperatures and moisture stress relating to drought (Hodkinson, 2005). While sporadic droughts may indeed be limiting for these taxa we consider it unlikely that annual rainfall in excess of 4,000mm is required for *A. hammondi* to survive. It is more likely that winter minimum temperature is the limiting factor for these high-altitude taxa and consequently the upper estimates for samples constrained by alpine taxa alone (samples H11, H7, H6, H3 and H2) have been ignored. The elimination of *A. hammondi* from the precipitation reconstructions damps down a pattern which is visible with or without this taxon. As the upper estimated limit of the precipitation reconstructions reflects the *ecological preference* of the taxa in the assemblage variation in the upper limits is still representative of variation in the amount of precipitation.

While beetles do appear to distribute themselves in relation to mean summer temperature (Chapter 3) it is unlikely to be a direct *physiological* control on their distribution as temperatures do not become physiologically limiting on Southern Hemisphere insects until above 40°C (Addo-Bediako et al., 2000). Additionally, the New Zealand beetle fauna tend to lack the specialised adaptations (e.g. diapause) evolved in Northern Hemisphere beetles in response to very cold Pleisotcene climates (Dumbleton, 1967). The high-altitude (cold-adapted) taxa may, therefore, have broader climatic ranges than low-altitude taxa as their upper thermal tolerance has probably remained more similar to that of the low-altitude taxa than their lower limits as observed in dung beetles from Southern Africa (Gaston & Chown, 1999). If this is the case they are likely to be capable of surviving in warmer areas then their mean summer temperature range would indicate. The summer temperature envelopes (Fig. 6.7a-c) are therefore interpreted as an ecological *preference* only and consequently both upper and lower limits are “soft”. Nevertheless there is no reason to disbelieve the summer temperature estimates as they match the observational data and have been shown to have a statistically significant role in beetle distribution (see Chapter 3). The lack of hard limitations in summer temperature reconstructions does mean that it is impossible to determine which envelope is more accurate in samples with split climate envelopes We therefore take the maximum possible range, from the lower limit of the colder (blue) envelope to the upper limit of the warmer (pink) envelope, as the estimated range of mean summer temperature from the sample (Fig. 6.7a-c).

Discussion of patterns and comparison to other records

The palaeoclimate record illustrated in Fig. 6.9 can be summarised as a series of three zones. The first zone (Zone C1) comprises the period from the beginning of the record (ca. 37ka BP) where both temperature and the precipitation reconstructions straddle the modern means (Fig. 6.9). Zone C1 is terminated by a significant drop in winter temperatures and precipitation at ca. 34ka BP (Fig. 6.9). This event coincides with an apparently slight cooling in summer temperatures. This colder, drier period is designated Zone C2 and continues until ca. 28ka BP when it is terminated by the onset of Zone C3. This zone comprises a period of variability in both MMWT and MAP from ca. 28ka BP to the end of the record at ca. 21ka BP. The variability in winter temperatures and precipitation is not as apparent in the summer temperature record although the MST record shows a broadening of the climate envelope at ca. 24ka BP and cooling at ca. 22ka BP. Zone C3 is divided into two sub-zones (C3a and C3b) as the part of the record between ca. 22-21ka BP shows higher frequency climatic oscillations than the earlier part of Zone C3. The reason why this part of the record is classified as a sub-zone of Zone C3 rather than a zone by itself is because oscillations are probably the product of the higher sampling resolution in this part of the record.

Zone C1 (ca. 37 – 34ka BP)

While summer temperatures and mean annual precipitation during Zone C1 appear similar to the present, winter temperatures appear to be reduced by an average of ca. 2-3ºC (Fig. 6.9). While other quantitative estimates of temperature for OIS 3 in New Zealand are rare, this reduction is comparable to OIS 3 estimates of cooling from a pollen study from the Tongariro region of the central North Island (ca. 3ºC cooling) (McGlone & Topping, 1983) and to the ca. 2ºC cooling indicated by sea-surface temperature (SST) estimates (Fig. 6.14) (based on the Mg/Ca ratio in forams) obtained from core MD97-

2120 on the Chatham Rise, east of New Zealand (Pahnke et al., 2003). Pollen based estimates of summer temperature from Taiquemó in the Southern Chilean lake district (Isla Grande de Chiloe) also indicate temperature depression of ca. 3-4ºC (Heusser et al., 1999) (Fig. 6.15). This is similar to the estimate of winter cooling from this record although it contrasts with the beetle based estimates of weak summer cooling (Fig. 6.9).

Zone C2 (ca. 34 – 28.5 ka BP)

The transition from Zone C1 to Zone C2 at ca. 34-33ka BP is marked by apparent reductions in both of the temperature and the precipitation reconstructions. While the upper limit of the summer temperature reconstruction falls near to the modern mean (Fig. 6.9), implying summer cooling of ca. 1°C, the MST reconstruction continues to straddle the present day and no conclusive interpretation of summer cooling is possible. Winter temperatures show a more substantial reduction with a change from ca. 3°C below present during Zone C1 to 5-6°C below modern levels (Fig. 6.9). This magnitude of cooling is similar to estimates of maximum glacial cooling made from other regional proxies including Equilibrium Line Altitudes from glaciers (e.g. Willet, 1950; Porter,

Figure 6.14. Comparison of **A.** variation in Mean Minimum Winter Temperatures from present using beetle fossils (this study); **B.** Percentage of tree & shrub pollen in the Okarito Bog pollen record, South Westland, New Zealand (Vandergoes et al., 2005); **C.** Variation in the δ^{13}C isotope record (smoothed spline) from northwest Nelson, New Zealand. (Hellstrom et al., 1998); **D.** Foram Mg/Ca ratio based sea surface temperature estimates from the Chatham Rise east of New Zealand (Pahnke et al., 2003) and **E.** the EPICA Dome C Deuterium Curve (Röthlisberger et al., 2004) The solid red lines in **A.** and **D.** represent the present day mean variable at the site. Dashed red circles indicate the zones recognised in the beetle record and the correlated match in the other proxy records. Individual zones are designated C1 for Zone C1, C2 for Zone C2 etc. The dashed purple circles represent the sub-zone C3a peaks and the green dashed circle the sub-zone C3b peak. The time scale of this figure is in thousands of calendar years BP.

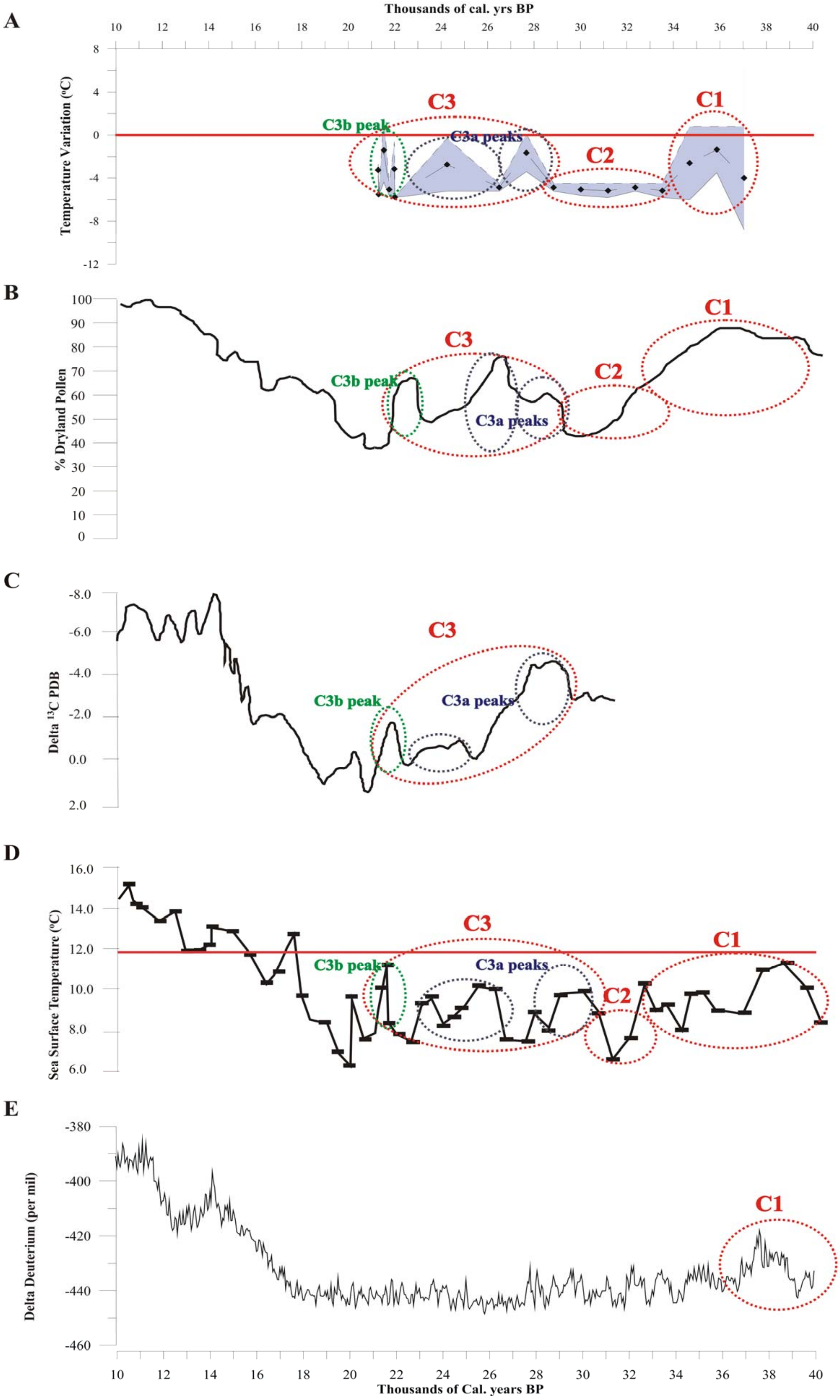
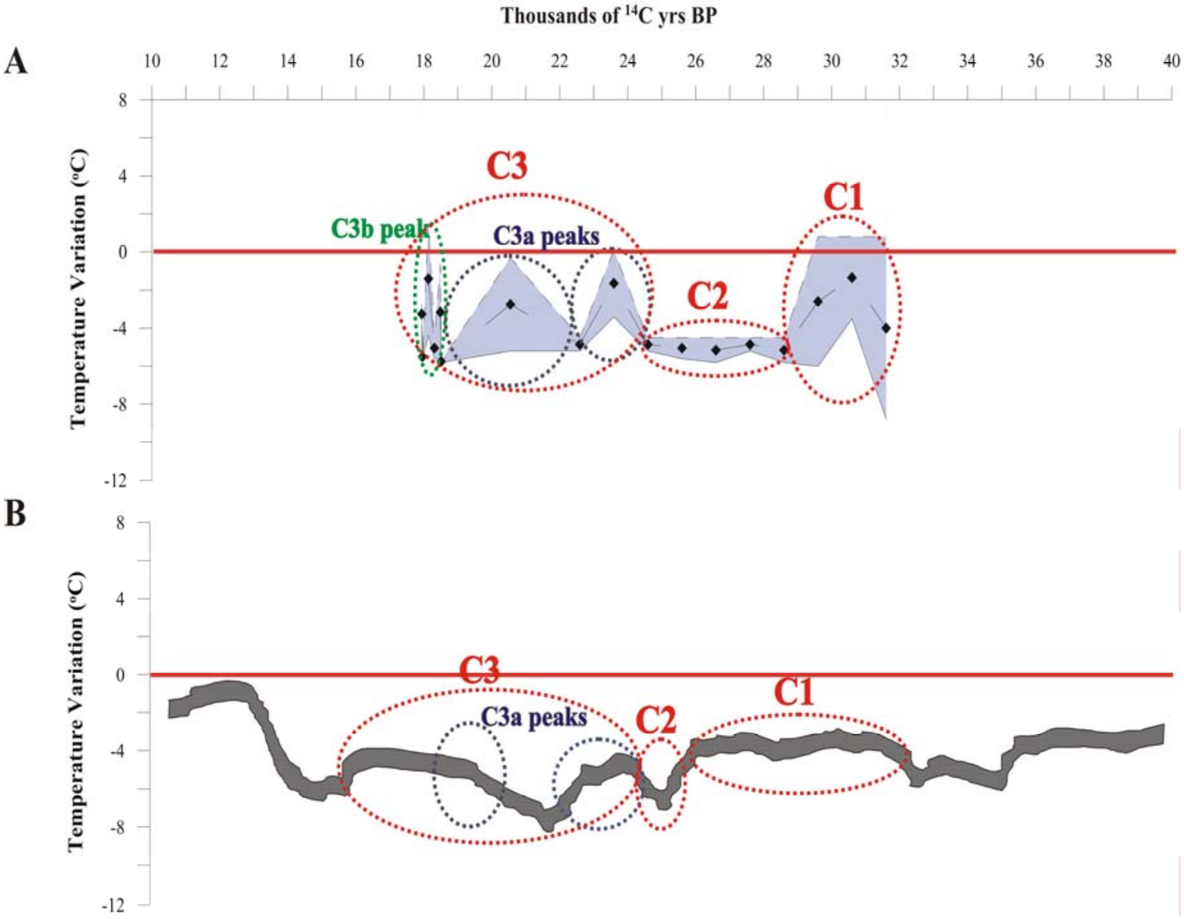


Figure 6.15. Comparison of **A.** variation in Mean Minimum Winter Temperatures from present using beetle fossils (this study) and **B.** variation in Mean Summer Temperature from present using *Nothofagus* - Gramineae ratios, Taiquemó, Chile (Heusser et al., 1999). The solid red lines represent the present day mean variable at the site. Dashed red circles indicate the zones recognised in the beetle record and the correlated match in the other proxy records. Individual zones are designated C1 for Zone C1, C2 for Zone C2 etc. The dashed purple circles represent the sub-zone C3a peaks and the green dashed circle the sub-zone C3b peak. The time scale of this figure is in thousands of conventional ^{14}C years BP.



1975), sea-surface temperatures (e.g. Barrows & Juggins, 2005) and pollen studies (e.g. Mildenhall, 1994). Mean annual precipitation also shows a reduction of ca. 40% from present levels during this zone (Fig. 6.9). Assuming that the relative humidity of the air masses remains constant through time the temperature depression of ca. 5°C winter cooling would reduce the vapour holding capacity of the air masses by ca. 30% during the winter (e.g. Sturman & Tapper 1996). Averaging of the mid-points of the range of summer and winter temperature variation obtains an average decrease in mean annual temperatures of ca. 3°C and an expected reduction of ca. 18% in mean annual precipitation. This is substantially less than the observed 40% reduction in precipitation levels and indicates a real decline in precipitation occurred with the climate becoming significantly drier as well as seasonally colder between ca. 34 and ca. 28ka BP. This confirms previous qualitative inferences of glacial age drying from other proxy records (e.g. McGlone & Topping, 1983; Carter, 2002). The timing of the onset of this zone (34-33 ka BP) is poorly constrained but there is rough coincidence with the timing of this and cooling events observed in other Southern Hemisphere proxy records. Sea-surface temperature estimates obtained from the Chatham Rise core MD97-2120 correspond to this record demonstrating a decrease in SST of approximately 6°C from present at ca. 33-32 ka BP (Fig. 6.14) (Pahnke et al., 2003). A similarly timed decrease in SSTs is observed in the alkenone-based SST estimates from the core obtained from ODP Site 1233 off the west coast of Chile (Lamy et al., 2004).

The palaeoenvironmental reconstructions from this site (see above and Moar & Suggate, 1979) indicate a change in vegetation (from E1/H1 to E2a/H2a, Fig. 6.11) to include more grasses at transition from Zone C1 to Zone C2. This matches the approximate timing of a peak in grass pollen recorded from a core obtained from Okarito Bog in South Westland, New Zealand (Fig. 6.14) (Vandergoes et al., 2005). The age of the grass peak in the Okarito Bog record is constrained only by the position in the core of the Kawakawa tephra (26.5ka BP) and correlation to a regional glacial advance (Vandergoes et al., 2005).

The regional glacial advance, designated $la_1/M5_1$ (Suggate & Almond, 2005), is itself poorly constrained to between 34 and 28ka BP by ^{14}C ages obtained from sedimentary units associated with glacial landforms such as outwash gravels and tills, and those containing pollen records indicative of glacial conditions (Suggate & Almond, 2005). This age range corresponds with the entire period of decreased winter temperatures and reduced precipitation observed in Zone C2 (Fig. 6.9). While this record is poorly constrained a better dated Chilean record (Heusser et al., 1999) also indicates an event around this time (Fig. 6.15).

Heusser et al. (1999) observed an increase in the proportion of grasses and shrubs in pollen records from Taiquemó (Southern Chilean lake district, Isla Grande de Chiloe) around 30ka BP (Fig. 6.15). While this may be a separate event to the cooling observed in this record, Heusser et al. (1999) used the variation in the ratio of *Nothofagus* beech and Gramineae (grass) pollen to estimate mean summer temperature showing a decrease to ca. 6°C below modern levels (Fig. 6.15). This is comparable to the degree of winter cooling demonstrated by the beetles at the onset of Zone C2 (Fig. 6.15) although it contrasts with the scale of the summer cooling (Fig. 6.9). Geomorphic evidence from Chilean glaciers also supports the onset of colder conditions around this time with Denton et al. (1999) using dates from glacial outwash to demonstrate a glacial advance ca. 32 ka BP (29,400 ^{14}C years BP (Denton et al., 1999)).

Comparison to the deuterium record from the EPICA Dome C Antarctic ice core record (Fig. 6.14) indicates a decline in the Δ deuterium (per millilitre) at ca. 37-36 ka BP (Röthlisberger et al., 2004). This apparent cooling precedes the onset of Zone C2 and the other mid-latitude records from New Zealand and Chile which indicate the onset of cooling at or after 34ka BP. There are two options to explain this discrepancy. The first option is that the ^{14}C ages used to date the New Zealand and Chilean records disagree with the age model applied to the Antarctic ice cores and that this decrease in Δ deuterium is actually the same event. Alternatively the Antarctic record may be a global signal while the New Zealand and Chilean records represent a southern mid-latitudes signal.

Taken in unison these records provide clear evidence that a major cooling event occurred across the southern mid-latitudes between 34-28ka BP. This precedes the generally accepted onset of glacial conditions at the beginning of OIS 2 (24.1 ka BP (Martinson et al., 1987) by ca. 10,000 years.

Zone C3 (ca. 28.5 – 21.3 ka BP)

Zone C3 comprises a period of variability in both the MMWT and MAP records. Two main peaks are recognised in the MMWT record at ca. 28 and 24ka BP and there are further episodes of raised MMWT at ca. 21.5ka BP (Fig. 6.9). When considered *en masse* there is clear evidence for at least episodically warmer winters and higher precipitation than during the preceding zone.

The ca. 28ka BP warming peak is derived from a single sample with MMWT rising to ca. 2ºC below modern MMWT before dropping back to ca. 5ºC below present at ca. 26ka BP (Fig. 6.9). This peak in MMWT is not apparent in the MST reconstruction but is accompanied by an increase in MAP which rises to between 1,710 mm yr^{-1} and 2,479 mm yr^{-1} (-22% to +13% of the present day level (2,190 mm yr^{-1})) (Fig. 6.9). Allowing for the reduced vapour holding capacity of the atmosphere with lowered temperatures the average MAP estimate (ca. 2,095mm yr^{-1}) is indistinguishable from modern values. Like MMWT the precipitation record also indicates a drop back to the level observed in Zone C2 (ca. 40% below present) at ca. 26ka BP (Fig. 6.9).

This event has poor age control, being constrained only by the basal date from this outcrop (ca. 37ka BP) and the presence of the Kawakawa tephra (at ca. 26.5ka BP) above, however, an event at roughly co-eval times is evident in other records. Speleothem records of $\delta^{18}O$ and $\delta^{13}C$ from Nelson, New Zealand, for example, show clear evidence of a short-lived change between ca. 30-27ka BP (Fig. 6.14) (Hellstrom et al., 1998). Hellstrom et al. (1998) interpret negative excursions in $\delta^{18}O$ as representative of warming and negative excursions in $\delta^{13}C$ as indicating increased vegetation cover, suggesting an amelioration of the climate during this time. A sea-surface temperature record from core MD97-2120 from the Chatham Rise east of New Zealand (Pahnke et al., 2003) (Fig. 6.14) also appears to indicate warming at around 30-28ka BP, although the record is noisy. The South Westland pollen record of Vandergoes et al. (2005), while poorly dated, indicates a sharp increase in the proportion of shrub pollen between ca. 30-28ka BP which may be indicative of warming (Fig. 6.14).

Pollen records from the lake district of Chile (Heusser et al., 1999) also display a warming event corresponding with this peak (Fig. 6.15) with summer temperatures increasing from ca. 6°C to ca. 4°C below present. Sea-surface temperatures from ODP Site 1233 west of Chile (Lamy et al., 2004) are also indicative of a warming event at ca. 30-28ka BP and together these Chilean records raise the possibility that this is a Southern Hemisphere wide event.

The second peak in the MMWT record occurs at ca. 24ka BP (Fig. 6.9). The upper limit of the MMWT record approaches modern levels however average warming increases from ca. 5ºC to ca. 3ºC below present levels (i.e. a warming in MMWT of ca. 2ºC). The MST climate envelope broadens at this time but shows no overall warming trend (Fig. 6.9). This broadening of the MST climate envelope may be an artefact of the split climate distributions resulting from the occurrence of the alpine taxon *Adrastia nelsoni* Franz in the sample relating to this period (Sample H7, Fig. 6.7b). In all probability the warmer split is correct as the appearance of *A. nelsoni* is probably controlled by the survival of tussock grassland at the site (see the palaeoenvironmental reconstruction above) rather than directly by temperature. The MST temperature reconstruction subsequently drops back to 3°C below modern levels at ca. 22ka BP. This is consistent with the timing of the decrease observed in the MMWT record.

The upper limit of the precipitation reconstruction also increases at ca. 24ka BP reaching well above modern levels although the lower limit remains static (Fig. 6.9). Unlike the MMWT and MST reconstructions MAP continues to increase after ca. 24ka BP peaking at ca. 22ka BP when MMWT and MAP are at their minimum. Accounting for changes in the vapour holding capacity of the atmosphere the increased level of precipitation at ca. 22ka BP is indistinguishable from the present day but is substantially higher than in the 34-28ka BP period.

The timing of the peak at ca. 24ka BP is better constrained that that at ca. 28ka BP, due to the presence of the Kawakawa tephra (26.5ka BP) underneath and a calibrated ^{14}C age of ca. 22ka BP above, but it is again represented by a single sample. Examination of the speleothem records from Nelson, New Zealand, again support the presence of a peak around this time with a negative excursion in both $\delta^{18}O$ and $\delta^{13}C$ isotope values between ca. 26-23 ka BP (Fig. 6.14) (Hellstrom et al., 1998). Sea-surface temperature records from core MD97-2120 from the Chatham Rise, east of New Zealand (Fig. 6.14) (Pahnke et al., 2003) also shows warming around this time with a double peak in SST between 26-23ka BP. The magnitude of this warming event is similar to that observed in the winter temperatures record from this study. The ca. 24ka BP peak may also be visible in the Okarito Bog record from South Westland where it can be roughly correlated with a short lived increase in shrub pollen ca. 26ka BP (Fig. 6.14) (Vandergoes et al., 2005). Correlations can also be drawn to pollen records from Chile (Heusser et al., 1999) where estimates of summer temperature show warming corresponding with the timing of this event (Fig. 6.15). Note, however, that the timing of this event also coincides with a period of glacial advance on the West Coast of the South Island between 24-22ka BP (Suggate & Almond, 2005) indicating that glaciers can advance during times of slight cooling and high precipitation.

Sub-zone C3b (ca. 22 - 21ka BP)

The third 'peak' in the MMWT occurs in sub-zone C3b at ca. 21ka BP and indicates a MMWT similar to today (Fig. 6.9). This peak is present in both the MST and MAP records also (Fig. 6.9). Evidence of warming around 21ka BP is present in other proxy records. The speleothem record of Hellstrom et al. (Hellstrom et al., 1998) shows a sudden negative movement in δ^{18}O and δ^{13}C isotope values at ca. 22ka BP and the SST records of Pahnke et al. (2003) also shows a short lived increase to near modern temperatures ca. 22-21ka BP (Fig. 6.14). The pollen record from Okarito Bog (Vandergoes et al., 2005) also shows a short-lived increase in the proportion of shrub pollen at this time (Fig. 6.14). While all these records are supportive of the overall warming trend indicated by the beetles in this part of the record none of them show the centennial scale variation observed in sub-zone C3b.

The centennial scaled fluctuations of sub-zone C3b are most clearly evident in the mean daily minimum winter temperature reconstruction between ca. 22-21ka BP but also occur to a less extent in the summer temperature and precipitation reconstructions (Fig. 6.9). The resolution of this part of the record is an order of magnitude higher (ca. 140 years per sample) than the rest of the record (≥ 1,000 years per sample) and the increased variability is probably a function of the higher resolution. However some workers (e.g.

McDermott et al., 2001) have identified centennial scale variability in (palaeo) climate records although modern instrumental records are too short to identify its source.

Of the possible drivers of centennial scale forcing of climate, solar cycles are widely invoked. These are a controversial topic and not fully understood (Scarfetta & West, 2005) although they are thought to operate on scales varying from decades (e.g. 11 year Schawbe cycles, 22 year Hale cycles, 88 year Gleissberg cycles (Peristykh & Damon, 2003; Braun et al., 2005)) to millennia (e.g. the ca. 2100 year Hallsatt cycle (Damon & Jirikowic, 1992)). The apparent centennial scale of the variability in this record may indicate a tie to DeCries-Suess (ca. 205-210 years) (Wagner et al., 2001; Braun et al., 2005) cycles or one of a number of other centennial scale oscillations detected in $\Delta^{14}C$ cycles from tree ring data (Damon & Sonnett, 1991) although this cannot be confirmed and no correlation is attempted.

Alternatively these fluctuations may be unrelated to climate and instead relate to autogenic or allogenic succession in the environment. The site-specific nature of fossil beetle reconstructions means that any change in the structure of the vegetation in the immediate vicinity of the deposition site would have resulted in changes in the composition of the local beetle assemblage. This includes changes such as the death of a local stand of trees and their replacement with pioneer grass species. Unless such a change is maintained by an external mechanism, normal ecological succession will result in a gradual transition back to a stable end community appropriate to the climate over a period of decades (Smith, 1996). In the early part of this record any short-term ecological changes, such as the example above, would be "averaged" out by the coarse resolution of the record (≥ 1,000 years per sample). However, the average resolution of 140 years per sample in the final part of the record is within the time range of ecological succession and thus is capable of recording auto- or allogenic changes in the environment.

While allogenic or autogenic variation in the local environment at the present day might change an *environmental* reconstruction derived from beetle fossils, for example the replacement of beetles associated with closed canopy forest with those associated with more open areas, it is unlikely to significantly change the *climatic* interpretation as all the beetles would be from environments associated with the same general altitudinal zone and thus similar climatic range (e.g. coastal forest and coastal grasses). This is because modern day vegetation is segregated into altitudinal (and latitudinal) zones such as lowland forest and subalpine grassland due, at a basic level, to a combination of temperature and precipitation (Arms & Camp, 1995; Guttman, 1999). Those beetles associated with particular altitudinal environments (e.g. *Aleochara hammondi* with subalpine grasslands) are therefore restricted from invading disturbed areas in a different zone due to this segregation of environment types. As previously mentioned this segregation of vegetation types does not appear to have occurred during the OIS 2 stadial with a mosaic vegetation of forest, shrubs and subalpine grasses occupying the region instead. The appearance of beetles associated with subalpine grasslands in a sample dominated by forest taxa (e.g sample H6, Fig. 6.6a, 6.7a & 6.8a) may not therefore be indicative of cooling or increased precipitation but rather the opportunistic invasion of subalpine grasses into the area immediately around the deposition site following a disturbance event (e.g. uprooting of a tree). The disappearance of those subalpine grassland beetles in the next sample (e.g. H5, Fig. 6.6a, 6.7a & 6.8a) may relate to ecological succession replacing pioneering grass species with trees and shrubs.

The paucity of high resolution records covering this period means that no conclusions can be made about these apparent centennial or shorter scale oscillations. Further work using high resolution proxies, focusing on this time period, is required to confirm which, if either, of these hypotheses is correct.

Reliability of comparisons

While this beetle record has been compared to a number of other proxies and drawn linkages to apparent events in those records it is necessary to comment on the reliability of these comparisons. Many studies (e.g Vandergoes et al., 2005; Denton et al., 1999) draw connections between their records and ice core and SST records and the same has been done with this record. However the inherent noise in the SST and ice core records means that the correlations made are tentative at best. Furthermore both of the SST records cited (Pahnke et al., 2003; Lamy et al., 2004) are from east of New Zealand and therefore down-system of any variations in the local climate experienced by the beetles. A more useful comparison could be drawn to a SST record from the Tasman Sea but while estimates of SST are available from the Last Glacial Maximum (e.g. Barrows & Juggins, 2005) no such records have been published for the earlier period (the OIS 3/2 transition) covered by this record.

The speleothem record of Hellstrom et al. (1998) appears to show a correlation to the series of warming peaks observed in zone C3. Speleothem records are acknowledged to be difficult to interpret, however (McDermott, 2004; Williams et al., 2005), and there is debate about whether negative excursions in the same $\delta^{18}O$ records should be interpreted as representing warming (e.g. Hellstrom et al. 1998) or cooling (e.g. Williams et al. 2005)! These correlations must therefore be treated with care.

This leaves the pollen and glacial records to corroborate the zones recognised in this study. While these records do confirm the presence of the zones indicated in this study neither is particularly robust at estimating the relative roles of temperature and precipitation. New Zealand vegetation in particular is known to be relatively insensitive to temperature (Norton et al., 1986) and most local pollen records (e.g. Vandergoes et al., 2005) are qualitative in nature. Geomorphologically based glacial records cannot distinguish glacial advances resulting from variation in temperature from advances related to changes in precipitation and the relative roles of precipitation (e.g. Rother & Shulmeister 2006) and temperature (e.g. Anderson & Mackintosh 2006) in glacial advances in New Zealand is contentious.

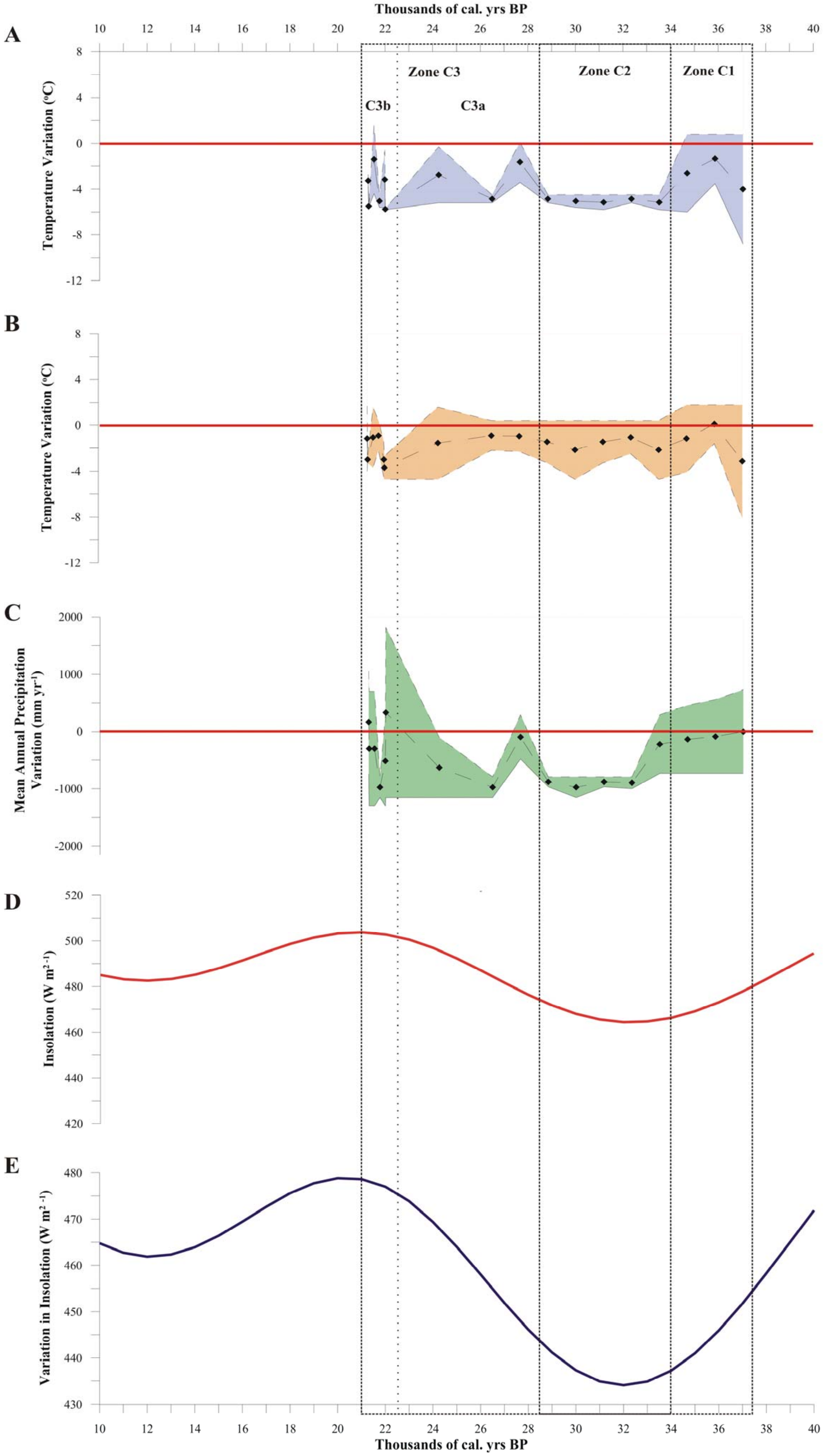
6.4.4 Types of glacial event

The statistical work presented in Chapter 3 suggests that beetles respond to variation in both temperature and precipitation. This is the first record covering the onset of glacial maximum conditions in New Zealand that provides estimates of both temperature and precipitation and it suggests two different types of glacial event.

The first type of event, exemplified by Zone C2 (Fig. 6.9), comprises cold and dry conditions and corresponds to the period of regional glacial advance termed $la_1/M5_1$ between 34 ka BP and 28 ka BP (Suggate & Almond, 2005). This coincidence of cold temperatures and glacial advance is consistent with the hypothesis of Anderson & Mackintosh (2006) who cite reduced temperature as the primary forcing mechanism behind glacial advance. In contrast the second type of event, exemplified by the middle part of Zone C3 around ca. 24 ka BP, comprises a period of milder temperatures and increasing precipitation (Fig. 6.9) and corresponds with the period of glacial advance ($la_2/M5_2$) at 24-22 ka BP (Suggate & Almond, 2005). The slightly warmer and much wetter conditions indicated by this part of Zone C3 are compatible with the hypothesis put forward by Rother & Shulmeister (2006) that glacial advance can be driven by high levels of precipitation with only slight decreases in temperature. In short, both glacial forcing models can be supported by these data and multiple forcing mechanisms should at least be considered.

The cooling and drying indicated in Zone C2 corresponds with minima in the Southern Hemisphere summer insolation budget (Fig. 6.16) and supports the hypothesis put forward by Vandergoes et al. (2005) that this minima in insolation was responsible for the onset of glacial cooling in advance of the traditionally accepted onset of glacial conditions at the OIS 2 boundary (24.1 ka BP (Martinson et al., 1987)). An alternative hypothesis is that the reduction in temperatures and the resulting glacial advance is actually the result of decreased atmospheric westerly circulation allowing the settlement

Figure 6.16. Comparison of the reconstructed climate estimates versus variation in insolation. Reconstructions are **A**. Mean Minimum Winter Temperature; **B**. Mean Summer Temperature and **C**. Mean Annual Precipitation. The red horizontal lines in the climate variable reconstructions represent the present day mean of the variable at the site. The insolation curves are from the data provided in Berger (Berger, 1992) and include **D.** Summer Insolation at 60ºS and **E.** interseasonal variation in insolation at 60ºS. The age scale is in thousands of calendar years BP. Also indicated are the three climate zones (C1, C2 etc.) discussed in section 6.5.4.



of cold air masses over the region. A reduction in the strength of the mid-latitude westerlies is implied by the greater than expected decrease in mean annual precipitation in Zone C2 and may have been caused by the minima in interseasonal variation in Southern Hemisphere insolation at this time (Fig. 6.16) (Shulmeister et al., 2004). It is impossible to distinguish between these hypothesises from this record and they may interact.

In contrast to Zone C2, which indicates reduced westerlies, the warmer and wetter phases of Zone C3 (Fig. 6.16) imply periods of enhanced westerly atmospheric circulation as increased westerly air flow also brings an increase in precipitation onto New Zealand. Additional support for enhanced westerlies during the last glaciation is relatively common and can be found in dust records (e.g. Alloway et al., 1992; Newnham et al., 1999) and records of enhanced oceanic up-welling east of New Zealand (e.g. Fenner et al., 1992; Weaver et al., 1998). While the settling of cold air over the region would be impeded by increased westerlies the increased atmospheric circulation would result in increased cloudiness and this may explain the warmer, but still slightly depressed, temperatures during this zone. As increased precipitation from increased westerly air flow has been observed, on a decadal scale, to drive expansion of the mountain glaciers of the West Coast, South Island, New Zealand (Tyson et al., 1997; Hooker & Fitzharris, 1999; Lamont et al., 1999) it is possible that a long period of enhanced westerlies could have caused the substantial increase in glacial extent observed between 24-22ka BP. While any conclusion regarding the origins of this enhancement in westerly atmospheric circulation is speculative, two main hypotheses present themselves. Shulmeister et al.

(2004) argued that enhanced westerlies may be the result of increased seasonality in Southern Hemisphere insolation levels which are nearing their peak at this time (Fig. 6.16). Alternatively Antarctic sea-ice is known to be expanded at the LGM (e.g. Crosta et al. 2004; Gersonde et al. 2005) increasing the temperature (and therefore pressure) gradient between the equator and the South Pole. This would also result in strengthened westerlies (Shulmeister et al., 2004). It is again impossible to distinguish between these hypotheses without further research. The two hypotheses are not mutually exclusive and may have complemented each other.

6.4.5 Seasonality

Like the beetle based palaeoclimatic reconstructions presented in Chapter 5, which appear to comprise part of OIS 4, this record indicates a seasonal disparity in summer and winter temperatures during a period of stadial conditions. This implies that seasonally enhanced winter cooling may be associated with stadial conditions as proposed by Denton et al. (2005). While the origin of this seasonal disparity in temperature is unknown, three possible reasons are considered: 1) direct orbital forcing of insolation, 2) reduced westerly atmospheric circulation and 3) seasonal expansion of Antarctic sea-ice.

Direct orbital forcing is considered an unlikely cause for the seasonal signal observed in this reconstruction as the seasonally disparity in temperatures occurs throughout the record and corresponds with both a trough and peak in interseasonal variation in insolation levels (Fig. 6.16) (Berger, 1992). While the seasonal signal is therefore unlikely to be a direct result of variation in the insolation budget it may have an indirect effect though enhancement and weakening of westerly atmospheric circulation.

As previously stated, Shulmeister et al. (2004) hypothesised that changes in westerly atmospheric circulation are caused by interseasonal variation in the insolation budget. Periods of increased interseasonal variation are associated with periods of strengthened westerly circulation while periods of reduced inerseasonal variation is associated with weakened westerlies. As the seasonal difference in insolation levels is at its minimum ca. 34ka BP westerly atmospheric circulation should be reduced under this hypothesis (Shulmeister et al., 2004). The substantial decrease in precipitation observed at this time (Fig. 6.16) supports this hypothesis as it is significantly in excess of the expected decrease in the water holding capacity of the atmosphere due to reduced temperatures. If westerly circulation was reduced at this time it would have promoted the settling of cold air over the West Coast of the South Island increasing the incidence of frost (as originally suggested by Moar & Suggate (1979)) and creating the pattern of seasonally enhanced winter cooling observed in the first half of this record. The later part of the record appears to indicate strengthened westerlies, however. Strengthened westerlies would result in increased cloud cover and lower temperatures but this might occur year round. An additional explanation is needed to explain the continued seasonality.

Enhanced seasonal cooling may also, as previously discussed in Chapter 5, be due to the effects of increased winter sea-ice in the Southern Ocean (Gildor & Tziperman, 2003). Increased amounts of Antarctic sea-ice are known to occur in all three of the last stadial periods (OIS 6, OIS 4 and OIS 2) (Crosta et al., 2004) and Gersonde et al. (2005) indicate an increase in the amount of Antarctic winter sea-ice of 100% over present day levels between 23-19ka BP. There is a lack of published sea-ice data for the time period of this study but it is likely that some increased seasonal sea-ice preceded the last glacial maximum. This would have resulted in reduced modification of cold polar air masses by warmer ocean water during winter as polar air masses would travel further north over the enlarged Antarctic sea ice sheet prior to moving over the ocean and onto New Zealand. The scope of this effect is an order of magnitude larger than the direct effects of insolation as seen in modern changes in the energy flux over the Greenland Sea (Deser et al., 2000). In years where sea-ice does not cover this region air masses are warmed by more than 250 W m^{-2} (Deser et al., 2000). Because increase in seasonal sea-ice is mainly a winter phenomenon, the lack of air mass modification would be seasonal and the characteristics of summer air masses would be more similar to present day conditions. In fact, expanded seasonal sea-ice would cause localised SST increases during summer as the sea-ice insulates the ocean from atmospheric cooling.

It is important to note that these effects would interact and some combination of these phenomena is probably responsible for the seasonal signal observed in this record.

6.5 Conclusions

This is the first long-term high resolution continuous beetle record from the Southern Hemisphere, and one of the first in the Southern Hemisphere, using 18 samples and covering a ca. 16,000 year period over the OIS 3/OIS 2 transition and the onset of Last

Glacial Maximum condtions. This record provides a unique insight into the last glaciation presenting palaeoenvironmental, palaeotemperature and palaeoprecipitation records and enables deeper insight into glacial environments and mechanisms of climate forcing.

6.5.1 Palaeoenvironment

The apparent restriction of forest, and later shrub, vegetation from the Westport region during glacial times (Moar & Suggate, 1979; Moar & Suggate, 1996) has always been problematic from a palaeoecological point of view. In particular, the temperature depression during the last glacial period does not appear to have been extreme enough to have excluded forest taxa from the region (McGlone, 1985). The beetle record presented here indicates that some form of forest did survive in the Westport region even though it is not reflected in the pollen record. While it is possible that this is the result of grass pollen overwhelming the arboreal pollen signal this does not explain the lack of pollen from wind pollinated trees. An alternative explanation is that the lack of arboreal pollen is the result of a change in the reproductive strategy of the trees to vegetative reproduction in order to minimise energy costs in a stressful environment. This change in strategy may have been widespread in New Zealand as this study joins an increasing number of studies using a variety of proxies including fossil birds (e.g. Worthy & Holdaway 1993; Worthy & Holdaway 1994; Worthy & Holdaway 1996), phytoliths (e.g. Almond et al. 2001; Shulmeister et al. 2001; Carter 2002) and beetles (e.g. Marra & Leschen 2004; Marra et al. 2006) which demonstrate that woody vegetation persisted through glacial times in regions of New Zealand thought to be deforested. In most cases special pleading has been used by the authors so that the records can be reconciled to the pollen based glacial vegetation paradigm but it increasingly appears that forest vegetation was more widespread in New Zealand than the pollen based records indicate.

6.5.2 Palaeoclimate

Three major zones are recognised in the beetle based palaeoclimatic record from this chapter. These zones can be replicated in other proxy records such as speleothems, SSTs and pollen records indicating that the occurance and approximate timing of the events is robust. Furthermore the magnitude of the temperature changes observed, at least in the winter temperature reconstruction, are comparable to other quantative estimates of glacial temperature change (e.g. Porter, 1975; Heusser et al., 1999; Barrows & Juggins, 2005).

There is also clear evidence from this record for a transition to glacial conditions ca. 34ka BP. This agrees with a number of other recent Southern Hemisphere studies (e.g. Denton et al., 1999; Vandergoes et al., 2005) which indicate that glacial cooling preceeded the accepted onset of glacial conditions at the beginning of OIS 2 at ca. 24ka BP (Martinson et al., 1987). The seasonally enhanced winter cooling observed in this record also supports the association of stadial conditions and seasonality as proposed by Denton et al. (2005).

This record has shed light on the recent debate regarding the mechanisms forcing glacial advance. The onset of stadial conditions at ca. 34ka BP is marked by a substantial decrease in winter temperatures and precipitation and correlates with the period of West Coast glacial advance between 34-28ka BP ($la_1/M5_1$) (Suggate & Almond, 2005). This agrees with the hypothesis of temperature forced glacial advance put forward by Anderson and Mackintosh (2006) and may be linked to Southern Hemisphere insolation minima (Vandergoes et al., 2005) or reduced westerlies (Shulmeister et al., 2004) allowing the settlement of cold air on New Zealand. The 24-22ka BP West Coast glacial advance (la$_2$/M5$_2$) (Suggate & Almond, 2005) correlates with a period of somewhat warmer temperatures and enhanced precipitation supporting the hypothesis of precipitation driven glaciation (e.g. Rother & Shulmeister, 2006). This may result from increased westerly atmospheric circulation due to maxima in interseaonal variation in insolation levels and/or increased Antarctic sea ice (Shulmeister et al., 2004; Rother & Shulmeister, 2006). This record indicates that both temperature (Anderson & Mackintosh, 2006) and precipitation (Rother & Shulmeister, 2006) driven hypotheses of glacial advance may be correct at different times and multiple forcing mechanisms for glacial advance must be considered.

Chapter 7

Discussion

This thesis has presented a series of fossil beetle studies from the Westport region of the West Coast, South Island, New Zealand. The combined record covers the last glacial cycle and includes one of the most intensive beetle studies ever undertaken in the Southern Hemisphere, comprising 18 samples from a 90cm thick unit and providing a continuous 16,000 years record across the OIS 3/OIS 2 transition. This chapter discusses the major findings of this thesis and relates them to the current understanding of New Zealand's climate and environment over the last glacial cycle. It also extends the implications of this thesis into a wider context.

7.1 Advances in understanding glacial age palaeoecology and wider implications

One of the primary objectives of this thesis was to produce a palaeoenvironmental record for the Westport region over the last glacial cycle. This record is summarised in Table 7.1 and the main palaeoecological contributions from this work are discussed below. These contributions include:

1) The first palaeoenvronmental reconstruction from the Westport region for OIS 4 (Chapter 5) indicating the presence of a lowland *Nothofagus* beech refugium in the northwest South Island of New Zealand during stadial conditions.

Table 7.1 Revised palaeoenvironmental history of the West Coast, South Island New Zealand with qualitative climate inferences. The revised Westport palaeoenvironmental history is provided in red. The rest of the table is based on the summary of Moar & Suggate (1996) with South Westland information from Almond (1996), Almond et al. (2001), Moar & McKellar (2001) and Vandergoes et al. (2005). New Zealand nomenclature of the events is given along with the associated Oxygen Isotope Stage. Approximate ages for the beginning of the events are from Martinson et al. (Martinson et al., 1987).

Stratigraphic Nomenclature	OIS	Age (ka BP)	Qualitative Climate Inferences	South Westland	North Westland	Westport (Original)	Westport (This Study)
Aranui Interglaciation	1	12.1	Warm	Podocarp forest	*Dacrydium cupressinum* forest OR *Weinmannia*/*Metrosideros* (hardwood) forest OR Shrubland	*Dacrydium cupressinum* forest	Forest with fern under-story
Late Otira Glaciation	2	24.1	Cold	Shrubland/Grassland	Grassland OR Grassland/Shrubland	Grassland	Mosaic of closed canopy forest, shrubs and grassland
Mid Otira Glaciation	3	59.0	Cool	Shrubland	Open *Nothofagus menzesii* forest	*Halocarpus*/*Phyllocladus* shrubland	Coastal-lowland forest mixed with bog trees & shrubs
Early Otira Glaciation	4	79.3	Cold	Grassland OR Shrubland	Grassland	No information	Mixed *Nothofagus* forest (inland areas)

2) The presence of a forest, shrubland, grassland mosaic in the Westport region during the later part of OIS 3 and the glacial maximum conditions of OIS 2 in direct contrast to reconstructions of grassland from the pollen record from the same site (Chapter 6).
3) The proposal of vegetative reproduction as a mechanism to reconcile pollen and beetle based reconstructions.

7.1.1 Glacial age *Nothofagus* beech refugium in the northwest South Island

While trees are thought to have been largely absent from lowland South Island during stadial periods arboreal pollen is routinely found in low amounts in pollen diagrams covering the last glaciation (McGlone, 1988; McGlone et al., 1993). The presence of these low levels of arboreal pollen is thought to be the result of long distance dispersal and combined with the rapid reforestation of lowland New Zealand within a few hundred years of regional deglaciation this has lead to the hypothesis that isolated pockets of trees survived in sheltered locations (McGlone, 1988; McGlone et al., 1993). With no direct evidence of where these refugia occurred, workers have suggested that they were restricted to sheltered locations within hilly regions (McGlone, 1988; McGlone et al., 1993) and off the modern coast of the northwest South Island (McKinnon et al., 1997).

Chapter 5 presents the first site specific evidence for a Fuscaspora beech (*Nothofagus fusca* pollen type) refugium from the northwest South Island of New Zealand during a stadial period (OIS 4) (Table 7.1). While the pollen morphology from this site identifies the vegetation as *Nothofagus fusca*-type beech it is unable to determine whether the refugium was comprised of lowland or montane species. This is because four of the five New Zealand beeches are indistinguishable from their pollen and fall within the *Nothofagus fusca*-type group. This includes the montane mountain beech (*N. solandri* var. *cliffortiodies*) and the lowland red (*Nothofagus fusca*), hard (*Nothofagus truncata*) and black (*Nothofagus solandri* var. *solandri*) beeches (Macphail & McQueen, 1983). Only *Nothofagus menziesii* (silver beech) is not part of this group (Macphail & McQueen, 1983). The problem of being unable to differentiate between plant species with different ecologies but similar pollen is relatively common in the New Zealand flora (Macphail & McQueen, 1983) occurring both in other genera as well as amongst the higher taxonomic groups such as the grasses (Gramineae) where it is virtually impossible to distinguish between those grasses found in coastal regions, at the edge of wetlands or at the edge of regenerating bush (e.g. *Poa anceps*, *Chionochloa beddiei* (Wardle, 1991; Edgar & Conner, 2000), and those more commonly associated with subalpine grasslands (e.g. *Chionochloa pallens, Chionochloa rigida* (Macphail & McQueen, 1983; Wardle, 1991; Edgar & Conner, 2000)). In order to improve palaeoenvironmental reconstructions additional information about the plant community is required.

The wide variety of ecological niches occupied by beetle taxa (Booth et al., 1990; Kuschel, 1990; Hutcheson & Kimberley, 1999) means that they often have specific associations with particular types of environment. The predatory rove beetle *Aleochara hammondi* Klimaszewski, for example, is only found in subalpine tussock grasslands (Klimaszewski & Crosby, 1997). The presence of this taxon in a fossil beetle assemblage is therefore a strong indicator that at least some of the grasses present are associated with the subalpine environment. In addition some beetle taxa provide information on the *structure* of their environment. This enables a more detailed reconstruction of the palaeoecology at a site. This is exemplified by the beetle record presented in Chapter 5. While most of the taxa from the samples analysed in Chapter 5 are associated with forest environments some, such as the species of the *Pycnomerus* genus and the Curculionidae weevils, are associated with dead wood and thick layers of leaf litter. As litter density is generally much lower in montane forests comprised of mountain (*N. solandri* var. *cliffortiodies*) than in lowland Fuscaspora beech forests (i.e. red beech (*N. fusca*), hard beech (*N. truncata*) or black beech (*N. solandri* var. *solandri*)) (Wardle, 1984) the presence of beetles associated with thick litter layers suggests that the refugium at this site most likely comprised lowland beech taxa. This conclusion is further supported by the pollen record from the site which shows a district lack of the ground flora of grasses typically associated with the more open, montane forests of mountain beech (*N. solandri* var. *cliffortiodies*).

The survival of a lowland beech forest at this location during OIS 4 raises serious questions about the assumption that high concentrations of arboral pollen represent interglacial floras (e.g. Blue Spur Road (Moar & Suggate, 1973; Moar, 1984), Sunday Creek (Dickson, 1972), Martin's Quarry, Omanu Creek and Waimea Creek (Moar & Suggate, 1979)) as it demonstrates that something approximating an interglacial flora could persist at low elevations along the West Coast during what appears to be a period of stadial-scale cooling (ca. 5°C in winter) (Chapter 5).

7.1.2 Glacial age vegetation mosaics in the northwest South Island

Like the beetle fossil record presented from Keoghan's Road (Chapter 5) the 16,000 year beetle fossil record of the OIS 3/OIS 2 transition presented from Wilson's Lead Road (Chapter 6) indicates the presence of closed canopy forest vegetation through a time at which the landscape of the West Coast region is thought to have been largely deforested (Moar & Suggate, 1979; 1996) or covered in shrub-grassland (McGlone, 1988; McGlone et al., 1993; Vandergoes et al., 2005) (Table 7.1). Unlike the Keoghan's Road record, however, the pollen record *from the same site* as the beetle record is a stark contrast (Table 7.1). The pollen record indicates a landscape of shrubland during the OIS 3 interstadial and a swampy, subalpine grassland during the OIS 2 stadial (Moar & Suggate, 1979). The beetles indicate coastal-lowland forest, including the warm-temperate New Zealand palm (*Rhopalostylis sapida*), during the OIS 3 instadial and a mixture of closed canopy forest, shrubs such as *Hebe*, and subalpine grasses during the OIS 2 stadial.

Reconciliation of these records has produced new insights on the vegetation of the Westport region during glacial periods. The interstadial (OIS 3) environment appears to share a similar structure, if not floristic composition, to the vegetation observed in modern South Westland dune fields (Dickinson & Mark, 1994) with coastal-lowland forest dominant on the dune peaks and shrubs and bog vegetation dominant in the dune swales. The vegetation of the OIS 2 stadial has no modern analogue in the New Zealand flora and comprises a mosaic of closed canopy forest, shrubland and grassland. This appears similar in structure to forest-grassland mosaics observed during the LGM in Chile (Heusser et al., 1999) and Papua New Guinea (Hope, 1989).

Unlike the purely pollen-based grassland reconstruction for the Westport region during OIS 2 this new reconstruction is compatible with quantitative estimates of New Zealand's glacial climate which suggest a maximum cooling of ca. 5°C (e.g. Porter, 1975; Barrows & Juggins, 2005; Chapter 6). This degree of cooling is not enough to have excluded trees from the Westport region and palynologists have therefore cited increased windiness (Moar & Suggate, 1996) or frostiness (Moar & Suggate, 1979) or both (McGlone, 1988) as the mechanism behind the lack of trees indicated by the pollen record (Moar & Suggate, 1979). The beetle records remove the necessity of invoking these mechanisms as they indicate that trees survived in this region even though they are not reflected in the pollen record!

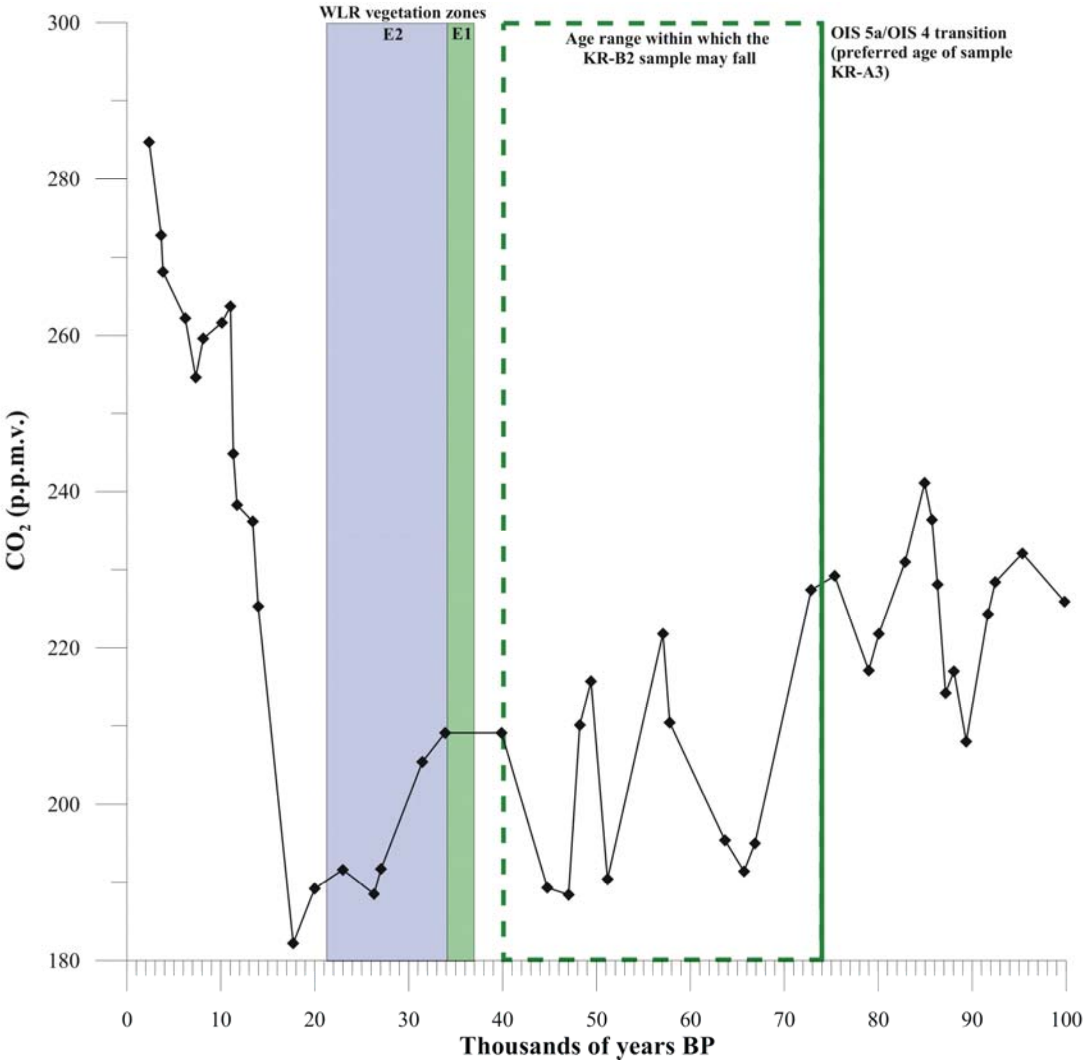
The persistence of trees in the Westport during periods of stadial cooling (Chapters 5 and 6) joins an increasing number of studies from around New Zealand which indicate that trees survived in areas thought to be deforested during glacial periods. As previously discussed, these studies, which have used a variety of proxies including beetles (e.g. Marra & Leschen, 2004), bird fossils (e.g. Worthy & Holdaway, 1993; Worthy & Holdaway, 1994), and phytoliths (e.g. Carter, 2002), have traditionally been explained away as isolated pockets of trees and this was the approach taken to explain the apparent beech refugium presented in Chapter 5. However, the increasing number of studies that indicate trees in areas apparently devoid of arboreal vegetation raises the question of whether New Zealand's trees are actually retreating into refugia, as proposed under the current paradigm, or whether they persisted within mosaics of vegetation like that reconstructed for OIS 2 in the Westport region of New Zealand (Chaper 6), the Chilean Lake District (Heusser et al., 1999) or Papua New Guinea (Hope, 1989).

The traditional pollen-based paradigm of New Zealand's glacial vegetation appears to have been based upon the Northern Hemisphere derived concept of glacial refugia. This concept makes the assumption that tree taxa retreated out of cold regions, thought to be inimical to their survival, into more favourable locations. In Europe these refugia have typically been considered to have been in southerly areas such as Italy and the Balkans (e.g. Bennett et al., 1991) but it now appears that this may be subject to debate (e.g. Whitehouse, 2006). As in New Zealand there is a growing body of evidence from plant macrofossils (e.g. Kullman, 2002), macrofossil charcoal (e.g. Willis & van Andel, 2004), DNA evidence of migration patterns (e.g. Sinclair et al., 1999), and the remains of Pleistocene mammals (e.g. Gautier et al. *in* Stewart & Lister, 2001), which all suggest that trees survived in northern and central parts of Europe during the Last Glacial Maximum. If this debate over the Northern Hemisphere glacial refugia is resolved in favour of mosaic environments, then they may have been a widespread phenomemon during stadials. This has important implications on the current understandings of glacial era floras worldwide as glacial vegetation may have a different structure to that observed in the modern flora.

7.1.3 Reasons for the lack of arboreal pollen in glacial age pollen diagrams

Three possible reasons for the lack of arboreal pollen during stadial periods are presented in Chapter 6. The first two, the overwhelming of low level arboreal pollen production by prolific production of grass pollen, and a reduction in arboreal pollen production due to lowered temperatures, are both possible contributors to the apparent lack of tree pollen but neither is a completely satisfactory explanation. The other suggestion mooted in Chapter 6 was that the arboreal vegetation may have undergone a shift away from sexual reproduction and towards vegetation reproduction with frost damage as a potential trigger to stimulate this change. While this would explain the lack of pollen, frost damage alone does not appear adequate to completely explain the change in reproductive strategy as frost tolerant trees, such as *Phyllocladus alpinus*, also appear to shift to this mode of reproduction. A further possible trigger is CO_2. Atmospheric CO_2 levels were substantially lower during OIS 2 (Fig. 7.1 (Petit et al., 1999)) and it is possible that this may have helped trigger the shift to vegetative reproduction. New Zealand's indigenous flora comprises entirely C_3 plants (plants reliant upon the Calvin Cycle to reduce CO_2 to organic compounds (Arms & Camp, 1995; Guttman, 1999)) and reduced CO_2 levels would limit the amount of CO_2 available at a C_3 plant's chloroplasts. This causes an increase in photorespiration (Farquhar & Sharkey, 1982; Ward & Strain, 1997) and a decrease in photosynthesis, reproduction and growth (Ward & Strain, 1997). The increased stress brought on by the reduced CO_2 levels may therefore have resulted in a shift away from energy and resource expensive sexual reproduction (Bloom et al., 1985) amongst the longer lived arboreal taxa. They could afford to wait for more favourable conditions before reproducing sexually or they may simply resort to sexual reproduction near the end of their life cycle. While grasses may also shift to vegetative reproduction

Figure 7.1 Atmospheric CO_2 record for the last 100ka BP from the Vostok ice core, Antarctica (Petit et al., 1999). Illustrated on the figure are the Wilson's Lead Road vegetation zones E1 (green shaded box) and E2 (blue shaded box) that relate to OIS 3 interstadial and OIS 2 stadial conditions respectively. The age range within which the Keoghan's Road samples fall is indicated by the green dashed box. The preferred age of sample KR-A3 from Keoghan's Road is marked with a solid green line.



due to the reduced CO_2 levels their relatively short life span (compared to trees) means that if they resort to sexual reproduction at the end of their life cycle they will still be producing pollen more frequently then the longer lived trees and therefore dominating pollen diagrams.

7.1.4 Pollen production during OIS 4 but not OIS 2?

A problem with the hypothesis of vegetative reproduction by arboreal vegetation during stadials is the pollen record from Keoghan's Road (Chapter 5). This record appears to relate to the OIS 4 stadial and indicates that a group of *Nothofagus fusca*-type trees were producing substantial amounts of pollen in the Westport region during a period with a similar degree of cooling to that observed during OIS 2. The question arises why were these beech trees producing pollen during OIS 4 and not producing pollen during OIS 2? Two possible explanations may explain this discrepancy.

The first is that the record relates to the transition from the interglacial conditions of OIS 5a to the stadial conditions of OIS 4 at ca. 74ka BP. This hypothesis is consistent with the palaeotemperature reconstructions from the site which show temperatures of near modern levels in the older KR-A3 sample. These temperatures decrease to stadial levels in the younger KR-B2 sample. If the KR-A3 sample relates to the transition from OIS 5a to OIS 4 the production of large amounts of *Nothofagus fusca*-type pollen in this sample may simply be the result of the forest vegetation having not yet shifted its mode of reproduction. This may be due to the atmospheric CO_2 level which is significantly higher at the OIS 5a/OIS 4 transition ca. 74ka BP then during the OIS 2 part of the Wilson's Lead Road palaeoenvironmental record when arboreal pollen all but vanishes (Zone E2, Fig. 7.1). Alternatively the sample may be from within OIS 4 and the continued presence of *Nothofagus fusca*-type pollen may be due to an abrupt shift to a period low CO_2 (Fig. 7.1) and the trees not having had time to change their reproductive strategy in response. The level of *Nothofagus fusca*-type pollen remain high in the KR-B2 sample however the indeterminate age of this sample (somewhere between ca. 74-40ka BP) means that it cannot be conclusively linked to any part of the atmospheric CO_2 record. It is possible however that the sample is associated with one of the peaks within this age range which may explain the high levels of *Nothofagus fusca*-type pollen in this sample.

The second explanation is that *Nothofagus* beeches continue to produce pollen during stadial periods (unlike the podocarps and broadleafs that appear to have dominated the Wilson's Lead Road site during OIS 2) but are restricted to inland terraces (such as at Keoghan's Road) and within the foot hills of the Paparoa ranges. Given that the prevalent winds in the Westport region is (south) westerly (Hessell, 1982) most *Nothofagus* pollen would be blown inland, away from the Wilson's Lead Road site. This would restrict the amount of pollen arriving at the Wilson's Lead Road site and may result in the low (≤10%) amount of *Nothofagus fusca*-type pollen observed in the pollen record from this site during OIS 2 (Moar & Suggate, 1979).

It is also possible that both these hypotheses may apply to varying extents. *Nothofagus* beech trees may have been both restricted to the inland terraces and foothills of the Westport region during OIS 2 and producing reduced amounts of pollen due to the low atmospheric CO_2 levels. The limited amount of pollen produced would then have been blown further inland by the dominantly (south) westerly winds.

The poor age control on the Keoghan's Road site makes a conclusive determination of why *Nothofagus fusca*-type pollen is in such voluminous amounts at this site during what appear to be stadial conditions impossible.

7.2. Constraints on beetle distributions in New Zealand

Previous quantitative beetle based reconstructions of palaeoclimate in New Zealand have produced estimates of mean summer temperature and mean minimum winter temperature. (e.g. Marra et al., 2004; 2006). It has been acknowledged, however, that the variables controlling beetle distribution in New Zealand are not fully understood, although winter temperatures were determined to be important (Marra et al., 2004). In order to increase confidence in fossil beetle based reconstructions beetle distribution data were analysed using principle components analysis. Two factors became apparent:

1) While mean daily minimum winter temperatures and mean summer temperatures are both significant controls on beetle distribution, it is mean daily minimum winter temperature is the major controlling variable. This contrasts to the Northern Hemisphere where maxiumum summer temperatures appear to be the most important controlling variable (Atkinson et al., 1987).
2) Precipitation also plays a significant role in controlling the distribution of New Zealand beetles and beetle fossils can be used as proxies for palaeoprecipitation. A similar, if more tentative, conclusion was also drawn by Marra et al. (2004).

7.2.1 Winter versus summer temperatures

While any palaeoclimatic reconstruction made from beetle fossils is optimistic due to the nature of the available collection data (presence/absence), and the complicating effects of microclimate and other environmental factors on beetle distribution (Bray et al., 2006; see Chapter 1), it appears from the statistical analysis in Chapter 3, that mean minimum daily winter temperature (MMWT) and mean summer temperature (MST) have independent effects on beetle distribution. This enables the identification of seasonal differences in the degree of winter and summer cooling. One caveat on this is that seasonal differences must be treated carefully as it is MMWT, rather than MST, that is the dominant controlling variable (Chapter 3). This is a distinct contrast between New Zealand and Northern Hemisphere studies where maximum summer temperature is the dominant variable controlling beetle distribution (Atkinson et al., 1986; 1987).

The reason MMWT, rather than MST, is the dominant controlling variable relates to the fact that New Zealand beetles are active year round (e.g. Moeed & Meads, 1992a; 1992b), and that the range of MMWT they occupy is far closer to the lower thermal tolerance of Southern Hemisphere insects (between ca. 0°C and -40°C (Addo-Bediako et al., 2000)), than the occupied range of MST is to their upper thermal tolerance (ca. 40°C and 60°C (Addo-Bediako et al., 2000)). This indicates that the *lower* limit of a MMWT reconstruction is a hard limit below which individuals will die due to the crystallisation of ice in their tissues (Sinclair et al., 2003a), disruption of their biochemical systems, and cellular dehydration (Sinclair et al., 2003b). In contrast, the reconstructed ranges for MST are generally well below the upper thermal tolerance of the beetles (Addo-Bediako et al., 2000) and probably reflect the summer temperature *preference* of the taxon (Deal, 1941) rather than a hard limitation. Beetle distributions are unlikely to vary based on physiological limits but distributions may break ecological preferences when other factors, such as suitable microclimates or habitats, are available. For example, as tussock grasslands move into lower elevation sites, beetles that are associated with them may experience higher summer temperatures than they would at higher elevations. They are unlikely to drop out of the fauna, however, as their MST ranges are probably ecological preferences rather than physiological limiting, and the invasion of tussock grassland will have provided suitable habitats at the lower elevations. This means that any interpretation of palaeotemperature from beetle remains should give more weight to the minimum daily winter temperature reconstruction, as its lower limit is more likely to represent a taxon's physiological tolerance, than the mean summer temperature reconstruction, where both upper and lower limits reflect the taxon's *preference*.

While they probably reflect the preference of the beetles, MST reconstructions do appear to accurately reflect mean summer temperatures at a site. Beetle fossil based Holocene MST estimates from the Awatere Valley in Marlborough, northeast South Island, straddle the modern day MST at the site (Marra et al., 2004) indicating, as expected, no variation from the present. Furthermore beetle based reconstructions of Last Glacial Maximum mean summer temperatures are comparable to those of other proxies which reconstruct estimates of MST. For example, a Last Glacial Maximum beetle study from Lyndon Stream in Canterbury, South Island, indicates an average MST depression of ca. 1.2°C cooler than present (Marra et al., 2006). An independent study using Chironomids (nonbiting midges) from the same site and time period indicates mean summer cooling averaging ca. 1°C cooler than present (Woodward & Shulmeister, 2007). This level of MST depression is also similar to that estimated from the OIS 3/OIS 2 beetle record presented in Chapter 6. These records indicate that while MST reconstructions are probably based on the preferences of the taxa, rather than hard climatic limits, they are still robust and while they must therefore be considered carefully they still provide valuable information on summer temperatures.

7.2.2 Precipitation

In addition to being robust estimators of temperature, Chapter 3 indicates that mean annual precipitation (MAP) also acts to constrain the distribution of beetles in New Zealand. This thesis is not the first attempt to use fossil beetles as proxies for palaeoprecipitation as Elias (1997) has previously produced MCR estimates of Mean Annual Precipitation for desert regions in North America. This study is, however, the first attempt to extend the usage of beetles as proxies for palaeoprecipitation into New Zealand, and appears to be the first study to do so outside of an arid region.

One factor to keep in mind, however, is that it is unlikely that MAP acts *directly* on beetles. Rather it is the loss of water from the beetle to the environment that is physiological factor limiting their survival (Edney, 1977; Hadley, 1994) and thus their distribution. The rate of water loss to the environment is controlled via the relative humidity of the microclimate within which the beetle lives rather than the overall precipitation level. Nevertheless, as the relative humidity affecting the beetles is derived, at least in part, from rainfall fossil beetles can work as *indirect* proxies for palaeoprecipitation. It must be noted, however, that only the lower limit of a precipitation reconstruction is likely to be physiologically limiting as water loss to the environment is only a problem in low humidity environments. High levels of precipitation are only likely to be life threatening in individual rainfall events when drowning is a possibility! This means that the upper limit of mean annual precipitation estimates must be treated as a *preference* rather than a hard physiological boundary.

Furthermore, while this thesis has produced estimates of MAP from fossil beetles it is more likely that summer rainfall, rather than mean annual rainfall, is a better precipitation variable for constraining beetle distributions. The reason for this is that the rate of water loss from insects is a function of the ratio of their volume to surface area, the humidity of the environment, and the temperature (Edney, 1977; Hadley, 1994). As moisture loss increases with higher temperatures, relative humidity (and indirectly precipitation) becomes increasing limiting (Hadley, 1994; Green & Pitman, 2003). As higher temperatures are more likely to occur during the summer months a measure of summer precipitation is probably a better representation of the true relationship between beetles and precipitation.

7.2.3 Alternative to ecological *preferences* as a limtation

While this this thesis indicates that the upper limits of MMWT and MAP reconstructions, and both the upper *and* lower limits of MST reconstructions, represent preferential limits rather than physiological limits, there is another explanation.

It is possible that the *preferential* limitations may actually represent one (or more) environmental variables which act, in conjuction with the tested environmental variables, to *indirectly* limit a taxon's distribution. For example it is recognised that some beetles, such as the New Zealand broad nosed weevils (Curculionidae: Brachycerinae: Entimini) that live within the soil in their larval form (May, 1993), may be limited by edaphic factors such as soil texture and moisture (Yazdani & Agarwal, 1997). The upper *preferential* limit of the precipitation range inhabited by these beetle taxa may therefore relate to the amount of precipitation required to form a particular soil type (Taylor & Fox, 1956) which the beetle taxon is not adapted to inhabit. In this case the limiting factor on the beetle distribution is not the precipitation level directly but the resulting soil type.

These environmental variables may also help to explain the unknown factors which are responsible for explaining 68% of the distribution of the beetle taxa examined in Chapter 3.

The presence of these unknown factors emphasises the importance of understanding the ecology of the beetle taxa within a fossil assemblage as the apparent climatic ranges occupied by those taxa may actually reflect the interaction of the different environmental variables.

7.3 Advances in understanding glacial age palaeoclimates and wider implications

Another objective of this thesis was to produce the first quantitative palaeoclimatic record for the Westport region over the last glacial cycle. Three major contributions to understanding of New Zealand, and Southern Hemisphere, palaeoclimate are apparent:

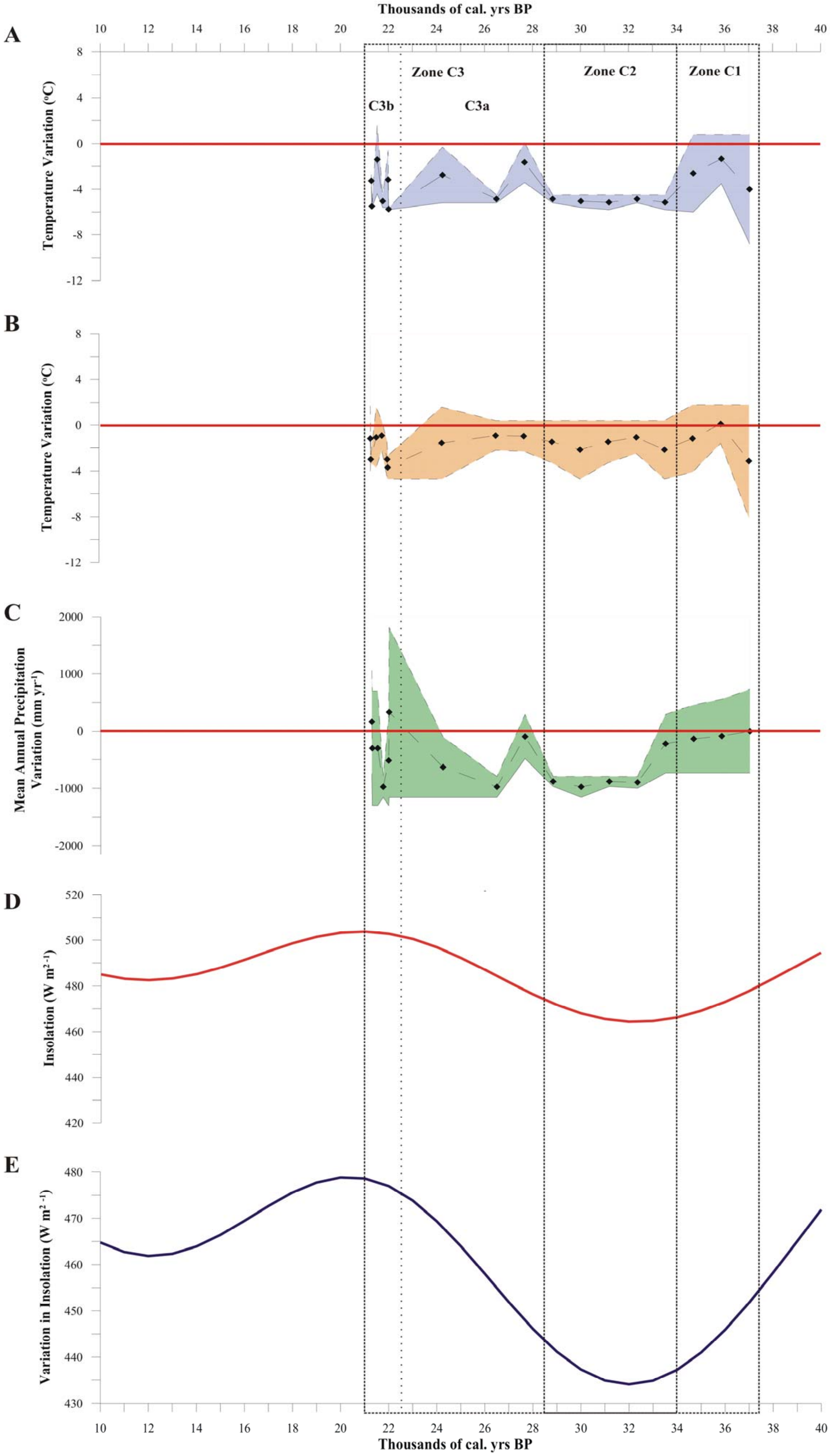
1) The onset of the last period of stadial scale cooling on the West Coast, South Island appears to occur at ca. 34ka BP. This is prior to the accepted onset of the OIS 2 stadial at ca. 24ka BP (Martinson et al., 1987), but consistent with other New Zealand studies.
2) Climate conditions during periods of inferred glacial advances were quite variable and beetle data may indicate multiple mechanisms for climate forcing and glacial advance.
3) Reduced stadial temperatures are primarily due to seasonally enhanced winter cooling.

7.3.1 The timing of Southern Hemisphere glacial cooling

The age control on the early part of the palaeoclimate record from Chapter 6 is poor but indicates stadial scale cooling between ca. 34-28ka BP (Zone 2, Fig. 7.2). This fits well with the current model of West Coast, South Island glacial advance which infers an initial period of glacial advance between ca. 34-28ka BP (la_1/$M5_1$ (Suggate & Almond, 2005)).

This age range of this period of glacial advance is itself poorly constrained with the onset of glacial conditions at ca. 34ka BP derived from correlations to quartz peaks in terrestrial (e.g. Alloway et al., 1992) and marine (e.g. Nelson et al., 1993) records (Suggate & Almond, 2005). The timing of the end of this initial phase of glacial advance

Figure 7.2. Reproduction of Figure 6.14 showing a comparison of the reconstructed climate estimates versus variation in insolation. Reconstructions are **A**. Mean Minimum Winter Temperature; **B**. Mean Summer Temperature and **C**. Mean Annual Precipitation. The red horizontal lines in the climate variable reconstructions represent the present day mean of the variable at the site. The insolation curves are from the data provided in Berger (Berger, 1992) and include **D.** Summer Insolation at 60ºS and **E. I**interseasonal variation in insolation at 60ºS. The age scale is in thousands of calendar years BP. Also indicated are the three climate zones discussed in Chapter 6.



at ca. 28ka BP is derived from radiocarbon ages from buried soils between glacial till and glacial outwash gravels (Denton et al., 1999), from lake deposits resulting from damming by glacial outwash (Suggate, 1965; Denton et al., 1999), and from pollen records indicating stadial conditions prior to the deposition of the Kawakawa tephra (ca. 26.5ka BP) (e.g. Moar & Suggate, 1996).

The onset of this period of cooling joins an increasing number of Southern Hemisphere studies that indicate the onset of stadial scale cooling somewhere between ca. 34 and 30ka BP (e.g. Denton et al., 1999; Heusser et al., 1999; Pahnke et al., 2003; Lamy et al., 2004; Vandergoes et al., 2005). While the exact timing of the onset of this period of cooling is unknown the general trend appears robust. This period of Southern Hemisphere glacial cooling correlates with minima in regional summer insolation levels (Fig. 7.2) supporting the hypothesis proposed by Vandergoes et al. (2005) which suggests that this period of glacial cooling may be triggered by regional insolation minima.

A second period of glacial advance occurred on the West Coast between ca. 24-22ka BP (in Zone C3, Fig. 7.2) ($la_2/M5_2$ (Suggate & Almond, 2005)). The age control on the timing of this period of advance appears better than that of the $la_1/M5_1$ event but is still not derived from direct dating of the geomorphic evidence but rather from radiocarbon ages obtained from associated deposits with pollen records indicating stadial condtions (e.g. Suggate & Moar, 1970; Moar, 1980; Hormes et al., 2003).

This period of glacial advance has generally been considered to relate to another period of colder temperatures and Vandergoes et al. (2005) again cite insolation forcing as the mechanism. As Southern Hemisphere insolation is increasing at this time, however, Vandergoes et al. (2005) suggest that in order to maintain glacial conditions the Northern Hemisphere insolation signal, which is at a minima at this time, is transmitted south overriding the local Southern Hemisphere insolation signal. An alternative hypothesis, which removes the requirement of overriding the local insolation signal, is that the $la_2/M5_2$ glacial advance at ca. 24-22ka BP is related to the increased inter-seasonal variation observed in Southern Hemisphere insolation at this time (Fig. 7.2) (Shulmeister et al., 2004).

7.3.2 Multiple mechanisms for Southern Hemisphere mid-latitude glacial advance & linkages to regional patterns of insolation

Debate has recently been raised about the physical mechanisms driving glacial advance in the Southern Alps of New Zealand. This debate has been driven by two main hypotheses. The first is that glacial advance is driven primarily by decreases in temperature with precipitation a secondary factor (Anderson & Mackintosh, 2006). The second hypothesis suggests that glacial advance can be driven by precipitation with only minor cooling required (Rother & Shulmeister, 2006). The ability of fossil beetles to be used as proxies for both temperature and precipitation provides a means of examining periods of glacial advance in terms of both temperature and precipitation, something impossible to do from geomorphological based glacial records. The beetle-based temperature and precipitation records from Wilson's Lead Road (Chapter 6) cover both the $la_1/M5_1$ and $la_2/M5_2$ glacial advances and indicate that different mechanisms may drive each event.

The la$_1$/M5$_1$ glacial advance between ca. 34-28ka BP corresponds with the decrease in both the temperature (mainly MMWT) and mean annual precipitation reconstructions. This event also correlates with minima in regional insolation levels (Zone 2, Fig. 7.2). As precipitation levels at this time are reduced, probably as a result of weakened westerly atmospheric circulation triggered by the minima in interseasonal variation in regional insolation levels (Fig. 7.2) (Shulmeister et al., 2004), this glacial advance appears to be the result of reduced temperatures as proposed by Anderson & Mackintosh (2006). This reduction in temperatures may in turn be related to the Southern Hemisphere minima in insolation levels, proposed as the forcing mechanism behind the onset of glacial cooling between ca. 34-30ka BP (Vandergoes et al., 2005), or the settlement of cold air on the region resulting from the reduction in the strength of the westerlies. Both effects may also combine to trigger this period of glacial advance. Further research is required to differentiate between these effects.

The la$_2$/M5$_2$ glacial advance at ca. 24-22ka BP appears to have occurred under different climatic conditions to those controlling the la$_1$/M5$_1$ advance. When the period of la$_2$/M5$_2$ advance is compared to the palaeotemperature and palaeoprecipitation records (Zone C3, Fig. 7.2) it can be seen to correlate with a period of temperatures above those occurring at the time of the la$_1$/M5$_1$ advance. Furthermore the la$_2$/M5$_2$ advance correlates with a period of significantly increased precipitation (Zone C3, Fig. 7.2) when compared to conditions at the time of the la$_1$/M5$_1$ advance (Zone C2, Fig. 7.2). This supports the precipitation driven method of glacial advance proposed by Rother & Shulmeister (2006). The timing of this event also corresponds to increasing regional insolation levels (Fig. 7.2) which may, at least in part, explain the apparent increase in temperature. An additional influence on the temperature may relate to increased cloudiness as indicated by the enhanced mean annual precipitation. Higher mean annual precipitation can be explained by increased westerlies. These could be related to increased interseasonal variation in the regional insolation levels and/or increased Antarctic sea ice which steepen the pressure gradient between the equator and southern mid-latitudes (Shulmeister et al., 2004).

It appears from the beetle-based palaeoclimatic records from Chapter 6 that both the hypothesis of lowered temperatures (Anderson & Mackintosh, 2006) and the hypothesis of increased precipitation (Rother & Shulmeister, 2006) as drivers glacial advance are plausible at different times within OIS 2 and late OIS 3. These multiple forcing mechanisms removes the necessity of overriding the Southern Hemisphere climate signal with a cooling signal of Northern Hemisphere origin (as suggested by Vandergoes et al. (2005)) as it indicates that Southern Hemisphere temperatures do not need to be particularly cold for glaciers to advance.

7.3.3 Seasonality

The onset of colder conditions observed at both Keoghan's Road after 74ka BP and at Wilson's Lead road after 34ka BP are marked by larger reduction in winter temperatures than in summer temperatures. This is the first record from New Zealand which indicates enhanced winter cooling under stadial conditions but mirrors work from the Northern Hemisphere which shows significantly more winter than summer cooling during stadials (e.g. Atkinson et al., 1987; Isarin et al., 1998; Denton et al., 2005).

Potential mechanisms for this asymmetrical cooling are discussed in Chapters 5 and 6 and include Milankovitch forcing (Berger, 1988; Berger, 1992), variation in westerly atmospheric circulation (Shulmeister et al., 2004) and increased levels of winter sea-ice (Gildor & Tziperman, 2003). The seasonally enhanced winter cooling appears to be more consistent with increased levels of winter sea ice around Antarctica than either of the other two hypotheses. This conclusion again agrees with Northern Hemisphere studies which suggest that enhanced winter sea ice in the North Atlantic is the most likely explanation for seasonally enhanced winter cooling (e.g. Atkinson et al., 1987; Denton et al., 2005). Together with this study it appears that seasonally enhanced winter cooling, seemingly associated with increased winter sea ice around the poles, is a major component of cooling during stadial periods.

Chapter 8

Limitations, Directions for Future Research & Final Conclusions

This chapter examines the problems that have presented themselves in the course of this thesis, describes directions for future research in the field of fossil beetles in New Zealand, and presents a final summary of the main conclusions.

8.1. General limitations with palaeoentomological research in New Zealand

During the course of producing this thesis several limitations with the use of fossil beetles as palaeoclimatic and palaeoenvironmental indicators in New Zealand have become apparent.

8.1.1 Lack of data on New Zealand beetle distributions and the inclusion of phytophagus taxa in palaeoclimatic reconstructions

The greatest limitation facing fossil beetle research in New Zealand is the lack of distributional data available for New Zealand beetle species (see Chapter 1). The only way to resolve this lack of distributional data is for systematic collection of native beetles to be undertaken across the country. Unfortunately such work will take decades and, while it will help improve the understanding of New Zealand's native beetle distribution, will never provide a truly accurate estimate of the pre-human distribution of New Zealand's native beetle fauna due to its restriction to areas of native vegetation (Kuschel, 1990; Klimaszewski & Watt, 1997). The majority of this native vegetation was cleared soon after European settlement and now occupies a mere 23% of New Zealand's land area (Klimaszewski & Watt, 1997) thus effectively restricting the native fauna to the same area. Beech forest and alpine vegetation is still largely intact and reconstructions for these vegetation types will be less problematic but lowland podocarp-broadleaf forest has been largely eliminated.

The restriction of the native beetle fauna is of particular concern for New Zealand palaeoentomologists due to their reliance on using phytophagus beetle species in reconstructions of palaeoclimatic. Northern Hemisphere studies typically rely on predators and scavengers, excluding phytophagus taxa due to their ties to preferred food plants, to produce estimates of palaeoclimate (Atkinson et al., 1986; 1987; Bray et al., 2006). This is not possible in New Zealand as fossil assemblages contain few of the predatory ground beetles (Carabidae) which often dominate Northern Hemisphere assemblages (Marra, 2003). New Zealand fossil assemblages are instead dominated by phytophagus weevils (Curculionidae) which, due to the restriction of the New Zealand beetle fauna to areas of native vegetation (Kuschel, 1990; Klimaszewski & Watt, 1997), are unlikely to occupy their full climatic range.

As previously discussed, Marra et al. (2004) attempted to correct for the lack of information regarding the distribution of New Zealand beetles by adding a statistical error using their MLE method of palaeoclimatic reconstruction. As the reason for excluding phytophagus taxa from palaeoclimatic reconstructions is due to the possibility that they may occupy a restricted distribution (due to ties to vegetation (Atkinson et al., 1986; 1987; Bray et al., 2006)), the MLE method of Marra et al. (2004) should also minimise any problems associated with the inclusion of phytophagus taxa in palaeoclimatic reconstructions. This postulation is supported by the fact that the MLE method has been shown to produce estimates of palaeoclimate (e.g. Marra et al., 2004) that agree with those of independent proxies (e.g. Woodward & Shulmeister, 2007). This means that the palaeoclimatic reconstructions used in this thesis should be robust although rare taxa needed to be carefully evaluated before inclusion.

8.1.2 The problems of rare taxa in palaeoclimatological studies

While the MLE method of Marra et al. (2004) is designed to account for the fact that it is not possible to know the entire distribution of a taxon, the presence of some outlying taxa in the palaeoclimatic reconstructions (Chapters 4-6) suggests that the MLE method of Marra et al. (2004) may produce inaccurate reconstructions where distribution data is particularly poor. This raises the question about the minimum number of data points required to calculate an accurate climate envelope using the MLE method.

Unfortunately there is no simple answer to this question. While some rare taxa appear to produce inaccurate climate envelopes, other rare taxa appear to produce robust ones. For example the Holocene assemblage presented in Chapter 4 contains *Tormus nitidulus* Broun, a species associated with moist forest environments (Hansen, 1997; Klimaszewski & Watt, 1997; NZAC label data) but known from only three collection locations (Electronic Appendix). While the environment associated with *T. nitidulus* is consistent with that indicated by the rest of the taxa in the assemblage, *T. nitidulus* produced a MMWT envelope between 3-6°C cooler than present! This is considerable colder than the temperature range indicated by the rest of the taxa in the assemblage and considering what is already known about Holocene temperatures, it is obviously too cold as the temperature should have been similar to present. The species was therefore treated as an outlier. While this may indicate that three data points are too few to calculate an accurate climate envelope using MLE, another species known from only three locations is *Aleochara hammondi* Klimaszewski (Electronic Appendix). While rarely collected the ecology of this species has been recently revised (Klimaszewski & Crosby, 1997) and it produces a climate envelope that is consistent with its alpine habitat of tussock grassland (Marra et al., 2004) indicating that, in this case, the MLE method produced an accurate estimate of the taxon's climate range.

Considering that the performance of the MLE method of Marra et. al. (2004) is apparently inconsistent with regards to rare taxa, it would, on the surface, seem prudent to exclude all rare taxa from palaeoclimatic reconstructions. Doing so, however, eliminates the majority of stenothermic taxa and produces reconstructions that mask significant amounts of climatic variability (e.g. Fig. 6.5, Chapter 6). It is therefore important that these rare taxa are included in palaeoclimatic reconstructions. It is not sensible, however, to simply accept climate reconstructions from rare taxa at face value and it is vital that any reconstruction based around rare taxa must examine the validity of the climate envelopes in relation to the ecology of the taxon for which they are produced.

8.1.3 Need to better understand New Zealand beetle ecology and physiology

The need to assess the validity of the climate envelopes used for beetle fossil based palaeoclimatic reconstructions in New Zealand indicates the importance of understanding the ecology of the beetle taxa contained within a fossil assemblage. This point is also emphasised by the findings of Chapter 3 which indicate that the limits of the climate envelope reconstructions may not be physiologically limiting but instead appear to represent an ecological *preference* (e.g. the mean summer temperature limits) which may be broken if appropriate ecological conditions present themselves. An alternative hypothesis, discussed in Chapter 7, is that these preferential limits may, in fact, be the result of indirect limitations imposed on a taxon's distribution via some other, unknown, environmental factor. These issues make understanding the ecology of New Zealand's beetle fauna vital.

Unfortunately, however, while some groups of New Zealand beetles have been taxonomically revised with comments made on their ecology (e.g. the ground beetles (Carabidae) (Larochelle & Larivière, 2001)), other groups remain poorly known but commonly occur in fossil beetle assemblages (e.g. the marsh beetles (Scirtidae) (Klimaszewski & Watt, 1997)). This makes it difficult to assess what ecological factors may be acting on many of the species in the New Zealand's beetle fauna. It is vital that a more complete understanding of the ecology of a wide range of New Zealand beetles be established in order to support future palaeoentomological research.

8.1.4 Problems identifying taxa to species level and the effect on paleoclimatic reconstructions

A problem previously mentioned in Chapter 2 was the difficulty in identifying beetle fossils to species level. This problem occcured due to a combination of poor fossil preservation, a lack of comparable specimens of some species in the NZAC, and the fact that some of the diagnostic features of the older specimens in the NZAC were obscured due to the manner in which they were mounted. While this made identification to species level impossible, it was often possible to ascribe them to a species group or a genus.

While this inability to confidently identify beetle fossils to species level may raise questions about the reliability and accuracy of the reconstructions presented in this thesis it has, in fact, improved the reliability of the results at the expense of their precision.

The poor level of collection of New Zealand's beetle taxa means that many species are represented in the NZAC by only a limited number of individuals. The larger number of modern specimens found within a species group or genus increases the available pool of data on which to base a reconstruction. This enables the production of a conservative estimate of the climate range. For example, the palaeoclimatic reconstructions presented in Fig. 5.3-5.4 in Chapter 5 include both "*Pycnomerus* sp. group B" and *Pycnomerus marginalis* Broun, a species that is included within "*Pycnomerus* sp. group B". In each of the palaeoclimatic reconstructions (Fig. 5.3-5.4), the climate range of *Pycnomerus marginalis* falls within the confines of that estimated for "*Pycnomerus* sp. group B". This indicates that, while the climate range produced by the species group is less precise than that based on *Pycnomerus marginalis*, it encompasses the climate ranges of its component species and thus produces a conservative estimate of the climatic range occupied by the species.

An increase in the collection of modern specimens will, in theory, increase the likelihood of being able to successfully identify fossil specimens to species level, and thus increase the precision of any reconstructions. In the meantime the use of species groups and genera allows a conservative approach to reconstructing palaeoclimates using beetle fossils.

8.2. Further Areas of Research

In addition to the need for an increase in the collection and study of the modern New Zealand beetle fauna, work is required in several additional areas in order to improve the ability of beetle fossils to be used as palaeoclimatic and palaeoenvironmental proxies.

8.2.1 Palaeoclimate

Model Development

While increasing the amount of collection data for the New Zealand beetle fauna will improve the palaeoclimatic reconstruction it will never be possible to fully model the distribution of New Zealand's pre-human beetle fauna. Studies of palaeoclimate in New Zealand using beetle fossils must therefore continue to rely upon techniques, such as the MLE method of Marra et al. (2004), which take into account the fact that the full distribution of the New Zealand beetle fauna is unknown.

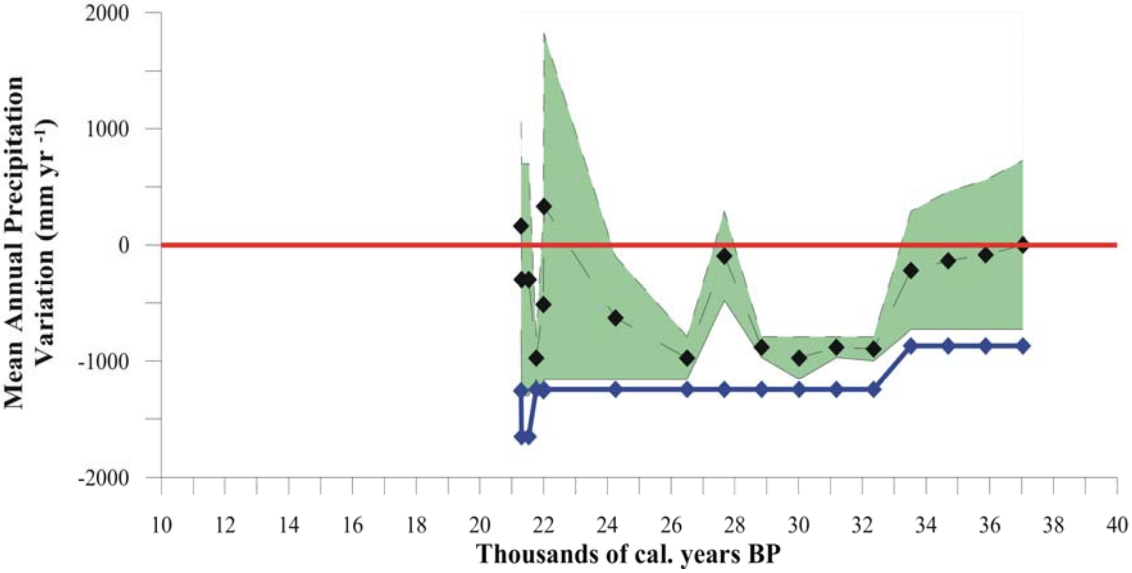
The existing model of Marra et al. (2004) does appear to produce robust error endpoints for temperature ranges (Marra et al., 2004), and also appears to provide good estimates of palaeoprecipitation (Chapter 4). Examination of the mean annual precipitation data for the beetle taxa used for the palaeoclimatic reconstructions in Chapter 6, however, indicates that the distribution of beetles in relation to mean annual precipitation typically follows a normal or log normal distribution rather than the sine curve typically used in the MLE model of Marra et al. (2004).

In light of these findings, the development of a new model is the next logical step in the refinement of beetle based palaeoclimatic reconstructions. Bray et al. (2006) have recently started work on modifying the MCR method of Atkinson et al. (1986) using ubiquitiy analysis to account for the frequency of occurrence of a species in climate space. This model is still under development but appears to offer the potential to remove much of the uncertainties associated with MCR (Bray et al., 2006).

Work on new method of producing errors for palaeoclimatic reconstructions has also begun in New Zealand in conjunction with Professor Euan Smith at Victoria University of Wellington, New Zealand. The development of this model was initially proposed in order to deal with the non-sine distribution of mean annual precipitation data, but could effectively be extrapolated to provide error estimates for any sort of climate data. Figure 8.1 illustrates some preliminary results from the Wilson's Lead Road site (Chapter 6) for Mean Annual Precipitation using this new model.

The new model makes use of the MATLAB programme (MATLAB, 2005) and unlike the current MLE model, which fits a maximum likelihood box car error to the entire known distribution of a taxon using a sine curve (Marra et al., 2004), this model examines only the last few data points in the tail of the climate distribution data for a particular taxon. It then extrapolates a maximum likelihood error term based on those points. By using this method the assumption that a species must fit a particular distribution type (e.g. unimodal) is avoided as it only examines the shape of the curve at the tail. This work was developed in conjunction with this thesis but, as it is still exploratory, it has not been formally presented here.

Figure 8.1 Comparison of the mean annual precipitation reconstruction from Wilson's Lead Road (Chapter 6) using the MLE model of Marra et al. (2004) (green boxed area) and the lower error estimates from the new model under development (blue line). The red solid line represents the modern day mean annual precipitation at the site.



Currently this model is limited to use on taxa known from five or more collection locations and only produces a minimum error estimate. In the case of the precipitation estimates from Wilson's Lead Road (Fig. 8.1) the new model predicts a slightly lower minimum MAP estimate than those produced using the sine distribution MLE model of Marra et al. (2004). The difference between the two methods is slight, however, and the general trend in the minimum estimate of precipitation is extremely similar (Fig. 8.1). This indicates that while the new model will, when completed, provide more accurate quantitative estimates of climate, the general trends observed in reconstructions undertaken with the current MLE model of Marra et al. (2004) are still likely to be robust.

Improving Palaeoprecipitation Reconstructions

Until this thesis, discussion of palaeoprecipitation in New Zealand has been largely limited to qualitative comments such as wetter or drier (e.g. McGlone & Topping, 1983). While fossil beetles have been previously used in North American deserts as proxies for palaeoprecipitation (Elias, 1997), this study has now provided a means of using fossil beetles to produce quantitative estimates of palaeoprecipitation in New Zealand. This thesis has already shown the importance of producing these estimates, indicating that precipitation may be as important as temperature in driving environmental change at different times during the last glacial cycle.

Using beetle fossils as a proxy for palaeoprecipitation in New Zealand is still in its infancy, however, and additional work needs to be undertaken. In particular it is necessary to determine which is the best precipitation variable to study using beetle fossils. The statistical analysis presented in Chapter 3 examined Mean Annual Precipitation (MAP) and the ratio of Precipitation to Evaporation (P:E), determined that MAP was the stronger controlling variable. The indirect nature of the relationship between MAP and beetle distribution, however, suggests that other moisture variables may be a better choice. Elias (1997), for example, points out that in many cases it is soil moisture that is the limiting variable on the distribution of some ground beetles. Evaporation/transpiration rates and mean *summer* precipitation may also provide a better measure of the relationship between beetle distribution and precipitation (Chapter 3). Future studies using fossil beetles as proxies for palaeoprecipitation should first attempt to determine the best moisture variable to examine in order to extrapolate an accurate estimate of precipitation.

Additional work is also required on validating the *reliability* of beetle fossils as proxies for precipitation in New Zealand. The statistical analysis (Chapter 3) is, due to the nature of the way taxa were selected, biased towards the West Coast of the South Island. Furthermore, all the reconstructions of precipitation undertaken in this thesis (Chapters 4-6) are also from West Coast, South Island sites. It is possible, therefore, that the fauna in the rest of the country will show a different relationship to precipitation than that presented in this thesis.

Validating the use of fossil beetles as proxies for palaeoprecipitation in the rest of the country will require examining the ability of modern beetle assemblages to accurately predict the known precipitation levels at a variety of sites. In particular, efforts need to be made to cover the precipitation gradient that occurs across the Southern Alps in the South Island. Comparison to other new methods of quantitatively reconstructing levels of palaeoprecipitation (e.g. isotope geochemistry of pedogenic carbon, (Alloway et al., 2007; Almond et al., In Prep)) will also assist in validating beetle fossils as proxies for palaeoprecipitation.

Further research using fossil beetles as palaeoprecipitation is also required to quantitatively compare precipitation levels on both the western and the eastern sides of New Zealand. Some early comparisons between the Wilson's Lead Road fossil beetle record (Chapter 6) from the West Coast of the South Island, and quantitative analysis of pedogenic carbon from the Ahuriri Quarry near Christchurch on the east Coast of the South Island (Almond et al., In Prep), cover the same time period and indicate that precipitation patterns may be different on the opposites sides of the Southern Alps during the last glacial. Comparative studies of palaeoprecipitation on both sides of the Southern Alps will eliminate any problems of comparing between different proxies and will help to elucidate differences in precipitation patterns during the Quaternary. Identifying these differences, or the lack thereof, are necessary in order to reconstruct regional patterns of atmospheric circulation over the last glacial period.

Exploring the causes of seasonality in stadial temperature depression

The ability to reconstruct measures of both summer and winter temperatures using beetle fossils has also highlighted an apparent seasonal difference in the degree of stadial cooling (Chapters 5 and 6). Analysis of the potential reasons for this discrepancy has indicated that this seasonal change in cooling is most consistent with the extension and contraction of sea-ice around Antarctica. Further work is required, however, in order to confirm the role of sea-ice in global climate change. In particular further research is required to establish the amount of Antarctic sea-ice present at the onset of glacial conditions as information on the extent of sea-ice outside the Last Glacial Maximum is limited (Crosta et al., 2004).

8.2.2 Palaeoenvironment

One of the most significant findings of this thesis is the disagreement between the pollen and fossil beetle records in the Westport region of the South Island (see Chapters 6 and 7). This fossil beetle record suggests that forest vegetation was able to survive *in-situ* during the last glacial maximum. This contrasts with the pollen records from the same site which suggest the complete removal of forest vegetation from the region (Moar & Suggate, 1979; 1996).

While, as previously mentioned, this sort of discrepancy has also been observed in other fossil beetle studies (e.g. Marra and Leschen, 2004), and in other non-pollen records (e.g. bird fossils (Worthy & Holdaway, 1993; 1994), phytoliths (Carter, 2002)), these generally represent spot samples in time and are not good indicators of long term environmental trends. In order to conclusively determine whether the discrepancy between pollen and beetles in Chapter 6 is in fact a country-wide trend, rather than a site specific phenomenon, will require the examination of additional sites with long pollen records using beetle fossils (and other palaeoenvironmental proxies). It would also be interesting to compare fossil beetle and pollen records from Northland (north of 37°S), where forest survived during the last glacial period (McGlone, 1988; McGlone et al., 1993), in order to determine if a discrepancy between pollen and beetle-based reconstructions is also present there.

There is also a need to try and determine what has caused the discrepancy between the pollen and beetle records. This thesis has proposed that the lack of arboreal pollen in glacial age pollen records south of 37°S may be the result of reduced pollen production by trees, perhaps due to a switch to vegetative reproduction. This hypothesised change in reproductive strategy may relate to the increased stress caused by lower temperatures and CO_2 levels during OIS 2 (Chapter 7). This hypothesis is apparently contradicted, however, by the production of pollen from what appears to be a refugium of *Nothofagus* forest during the previous stadial (OIS 4), though it is noted that the lowest CO_2 levels were not achieved until OIS 2.

While there is an existing literature regarding how vegetation may alter its reproductive behaviour in response to an increased incidence of damage (e.g. from fire (e.g. Hoffmann, 1998) or herbivory (e.g. Quesada et al., 1995), towards the latitudinal and altitudinal limits of its ecological range (e.g. Douglas, 1981; Dorken & Eckert, 2001), and in response to varied CO_2 levels (e.g. Bazzaz, 1990; Ward & Strain, 1997)), most of these studies have examined herbaceous taxa such as the annual mouseear cress (*Arabidopsis thaliana*) (Ward & Strain, 1997) or the perennial primrose monkeyflower (*Mimulus primuloides*) (Douglas, 1981). As it has previously been observed that long lived woody vegetation may exhibit a different response to a particular stimuli (e.g. defoliation), than that observed in herbaceous vegetation (Obeso, 1993), long term greenhouse studies of the effects of lowered CO_2 and temperatures on *woody* vegetation will be required in order to gauge the response of arboreal vegetation to long periods of sub-optimal temperature and lowered CO_2.

8.3 Final Conclusions

This thesis has produced a record of palaeoclimatic and palaeoenvironmental change for the Westport region of the West Coast, South Island, New Zealand over the last glacial cycle (OIS 4 to present). The core of this thesis is the longest continuous fossil beetle record from New Zealand comprising 18 samples from a single unit covering 16,000 years and including the transition from the OIS 3 interstadial to the full stadial conditions of OIS 2. While the multiple problems discussed above may suggest that the palaeoclimatic reconstructions presented in this thesis lack accuracy, this is not the case. The use of the larger distributional data sets provided by genera and species groups, combined with the MLE method of Marra et al. (2004) to produce climate envelopes which account for the fact that the distribution of a taxon is not fully known, means that the reconstructions presented in this thesis are conservative, but accurate.

Furthermore, this thesis has made significant advances in the use of fossil beetles as indicators of palaeoclimate in New Zealand. It has established the significance of mean minimum daily winter temperatures as the primary controlling climatic variable on the distribution of beetles (at least on the West Coast of New Zealand) and indicates that it is the most robust measure of temperature change available from beetle fossils in New Zealand. While estimates of mean summer temperature should be treated with care, as they probably represent an ecological preference rather than a physiological limit, they appear robust and indicate that stadial temperature depression is primarily a function of seasonally enhanced winter cooling. This is similar to observations from the Northern Hemisphere (e.g. Atkinson et al., 1987; Denton et al., 2005) and appears consistent with an increase in the amount of seasonal sea ice in the Southern Oceans during glacial times.

Fossil beetles can be also be used to produce quantitative estimates of palaeoprecipitation. This provides a means to differentiate between the relative roles of temperature and precipitation in palaeoclimatic events. This has lead to a significant revelation about the forcing mechanisms of glaciation in New Zealand. Both temperature and precipitation appear to drive periods of glacial advance at different times. This removes the need to cite the interhemispheric transmission of Northern Hemisphere cooling to promote Southern Hemisphere glacial advance at times of high Southern Hemisphere insolation as glaciers can advance during periods of moderate Southern Hemisphere cooling due to increased precipitation levels. The increased precipitation appears to be related to modification of the mid-latitude westerlies by interseasonal variation in Southern Hemisphere insolation and/or increased sea-ice although further research is required to confirm this hypothesis.

The final and perhaps most significant implication is that, at least in New Zealand, pollen records do not appear to accurately reflect stadial age vegetation. The 16,000 year beetle fossil record from this thesis indicates the continued presence of closed canopy vegetation throughout a period of stadial cooling in direct contrast to the pollen record from the same site. This joins an increasing number of non-pollen proxy studies from both New Zealand and overseas which also indicate the survival of trees in regions thought from pollen records to be deforested. This may be related to a change in the reproductive strategy of vegetation during stadial periods due to long term cooling, an increased incidence of damage due to frost or wind or due to depressed CO_2 levels. In light of these records a re-evaluation of stadial age pollen records, both in New Zealand and worldwide, needs to be undertaken.

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Appendix 1

Pilot fossil beetle sites

A list of all sites sampled in this thesis is provided. Final sites are described fully in the pertinent chapter (Chapters 4-6) but brief descriptions are provided for all sites discarded due to either insufficient numbers of fossils or poor preservation. The location of all sites sampled is indicated on Fig. 2.1 in Chapter 2. Latitude and longitude are accompanied by more precise NZMS grid references to enable the sites to be more accurate located.

1. Phelps Mine (42°44'S, 170°57'E, NZMS E2342247, N5827707). Initially sampled 08-03-2003. Re-sampled 26-05-2003.

The outcrop is situated on the at the south end, west side, of Phelp's Mine pit. The outcrop is ca. 15m a.m.s.l. The sampled section lies below extensive gravels obscured by bryophytes, ferns and grasses. The sampled layers are thought to date to ca. OIS 5a in age (ca. 91.0 – 79.3ka (Martinson et al., 1987)) (Rob Rose, pers. comm., 2003).

Depth (m)	Description	Sampled Units (and sample codes)
> 2.50	Gravels (obscured by vegetation)	
1.45 - 2.50	Sand	
1.05 - 1.45	Silt with fine sand horizons	
0.60 - 1.05	Fine sand	
0.40 - 0.60	Clayey Silt	
0.38 - 0.40	Solid wood macrofossil layer	PM1
0.21 - 0.38	Highly organic silt	PM2 (re-sampled)
0.00 - 0.21	Moderately organic silt	PM3 (re-sampled)
< 0.00	Beach sand (indeterminate depth)	

2. Brickfield Road (1) (42°43'S, 170°60'E, NZMS E2346142, N5829683). Sampled 08-03-2003.

The outcrop is a south facing road cutting in Brickfield Road ca. 76m a.m.s.l.. The outcrop is thought to rest on gravels related to OIS 6 (ca. 189.6 – 129.8ka (Moar & Suggate 1973; Martinson et al. 1987)). A pollen record exists from nearby Blur Spur Road (Moar & Suggate, 1973). Measurements were taken from the upper limit of a buried organic silt.

Depth (m)	**Description**	**Sampled Units (and sample codes)**
0.00 – 1.50	Grey loess includes modern roots	BS 1 (0.00 – 0.20m) BS 2 (0.90 – 1.20m)
< 0.00	Low organic silt including modern roots (indeterminate depth)	BS 3

3. Brickfield Road (2) (42°44’S, 171°00’E, NZMS E2346653, N5829430). Sampled 08-03-2003.

Another site from Brickfield road was also sampled. This west facing road cutting follows the stratigraphy of Brickfield Road (1) although there was a peat unit overlying the loess unit. Sample BF 1 was from this unit from 0.70 – 0.90m from the top of outcrop.

4. Sunday Creek (42°38’S, 171°07’E, NZMS E2354880, N5840420). Initially sampled 08-03-2003. Re-sampled 26-05-2003.

The Sunday Creek site is situated in the east facing bank of Sunday Creek near Chesterfield Road, Chesterton. This site was previously sampled for pollen by Dickson (1972) and the pollen diagram was redrawn by Moar & Suggate (1996). The site is currently interpreted as representing the OIS 5c interglacial period moving into the glacial of OIS 4 (ca. 110.8 – 79.3ka (Martinson et al, 1987)) (Suggate & Waight 1999).

The site is known to overlie marine sediments (Rob Rose, pers. comm., 2003) although they are not visible at the site.

Depth (m)	**Description**	**Sampled Units (and sample codes)**
1.25 – 2.25	Fluvial gravels (OIS 4?)	
1.00 – 1.25	Moderate organic silt	SC 1 (re-sampled)
0.79 – 1.00	Highly organic silt. Contains macrofossil plant remains	SC 2 (re-sampled)
0.74 – 0.79	Low organic silt	
< 0.00 – 0.74	Fluvial gravels	

5. North Beach (42°24'S, 171°13'E, NZMS E2363189, N5866271). Sampled 09-03-2003.

The outcrop is an exposed road cutting in a driveway along North Beach Road at ca. 45m a.m.s.l.. The entire outcrop sits on a marine bench which Suggate & Waight (1999) mapped as OIS 5c in age (110.8 – 99.4ka (Martinson et al. 1987)). No age control is available from the site.

Depth (m)	**Description**	**Sampled Units (and sample codes)**
> 2.00	Peat unit, mainly obscured by slump from above (gravel mixed with clay)	
1.20 – 2.00	Highly organic silt containing macroscopic wood fragments. Part of unit obscured by slump from above	NB 2
0.70 – 1.20	Organic silt (degraded peat?)	
0.50 – 0.70	Slightly organic silt containing gravel	
0.00 – 0.50	Organic clay (degraded peat?) containing macroscopic wood	NB 1
< 0.00	Greywacke & limestone overlying marine sediments (indeterminate depth) (Rob Rose pers. comm.).	

6. "The Hill" Wilson's Lead Road (41°47'S, 171°30'E, NZMS E2385410, N5935067), Initially sampled 09-03-2003. Re-sampled 14-07-2003. Final samples collected 07-04-2004.

Refer to Chapter 6 for a detailed description of this site.

7. Gibson's Beach (41°45'S, 171°29'E, NZMS E2383468, N5938671). Initially sampled 09-03-2003. Re-sampled 14-07-2003 and 20-01-2004.

This outcrop is an exposed group of units situated in a northwest-facing cliff face at Gibson's Beach, Westport. The units are situated just north of the path leading down to the beach and above ca. 10m of blue-grey sands. This sand appears to relate to the tertiary "Blue Bottom" silt- and mudstones (Moar & Suggate, 1996).

Depth (m)	**Description**	**Sampled Units (and sample codes)**
0.58 – ca. 7.00	Coarse orange sands. Tabular, cross-stratified & ripple cross laminated.	
0.57 – 0.58	Fine, cream-coloured silt. Lower contact sharp.	GB 2 (first sampled 14-07-2003)
0.42 – 0.57	Highly organic peaty-clay unit with macroscopic wood. Lower contact sharp.	GB 1 (re-sampled 14-07-2003 & 20-01-2004)
0.25 – 0.42	Cobbles mixed with sand. Cobbles dominantly granitic but also rip-up clasts. Lower contact sharp and undulating.	GB 3 (first sampled 14-07-2003)
< 0.00 – 0.25	Massive blue-grey sands. Unit mostly obscured by slumps from above.	

8. Ten Mile Creek (42°20'S, 171°16'E, NZMS E2366915, N5873475). Sampled 15-07-2003.

A sample was taken from an east facing outcrop on State Highway 6 just north of Ten Mile Creek and just south of a road sign "rest area 300m on left". Due to the potential danger of spending a long time on the side of this road a single sample was collected from an organic layer containing plant macrofossils. While the location of the site was noted so it could be returned to if the sample provided useful fossils a detailed stratigraphic record was not made.

9. Costello Hill (41°53'S, 171°30'E, NZMS E2385180, N5924030). Sampled 05-11-2003.

This site is a road cutting situated on State Highway 6 north of Charleston. The outcrop sits on a layer of granitic cobbles apparently relating to a marine incursion. The depth of the cobble layer is unknown.

Depth (m)	**Description**	**Sampled Units (and sample codes)**
2.50 – 6.50	Fluvial gravels	
0.10 – 2.50	Oxidated, interbedded sands and gravels containing fibrous organics	CH 1
0.90 – 0.10	Dark, reddy-brown silty sand with micas and fibrous organics	CH 2
0.00 – 0.90	Oxidated, interbedded sands and gravels containing fibrous organics	
< 0.00	Granitic cobbles	

10. Wilson's Lead Road (2) (41°48'S, 171°31'E, NZMS E2386920, N5933140). Sampled 05-11-2003.

A second outcrop, thought to be Holocene in age, was sampled from further southeast along Wilson's Lead Road, Westport. The outcrop was situated opposite a sign advertising the presence of "Bassett's Farm, Landcare Research Limited". The outcrop sits on what appear to be gravels of a fluvial origin however their depth is unknown as only the contact is visible.

Depth (m)	**Description**	**Sampled Units (and sample codes)**
1.67 – 2.11	Sandy, mottled top-soil with organic A- and inorganic B-horizons.	
1.36 – 1.67	Peaty, silty-sand. Reddish-brown	WLR 3

	with sharp basal contact. Contains in-situ macroscopic woody plant remains of up to 0.1m diameter. Granitic fluvial gravel laterally grades in at upper contact.	
0.98 – 1.36	Massive, silty-sand. Grey inorganic band near top of unit but otherwise brown growing darker due to increased organics up profile. Lower contact is undulating iron pan.	WLR 2
0.00 – 0.98	Massive, well sorted fine sand. Grey grading to brown with relatively straight but partially obscured lower contact.	
< 0.00	Rounded granite boulders	

11. Cape Foulwind (41°45'S, 171°28'E, NZMS E2382650, N5938870). Sampled 05-11-2003.

This southwest facing outcrop is exposed in the side of the Cape Foulwind Walkway as it begins to slope down to the beach at Cape Foulwind, Westport. The outcrop appears to rest on a wave-cut surface represented by a layer of boulders.

Depth (m)	Description	Sampled Units (and sample codes)
2.10 – ca. 3.10	Massive, poorly sorted diamicton with boulders ca. 1m x 1m x 1m. Appears to be colluvial.	
0.60 – 2.10	Fine, bedded, tabular sands & silts with mm scale laminations.	
0.50-0.60	Medium brown, finely laminated organic silt and sands.	CF 1
0.45 – 0.50	Blue-grey inorganic medium sand	
0.40 – 0.45	Dark brown, silty organic layer interbedded with blue-grey sand.	CF 2
0.00 – 0.40	Massive blue-grey medium sand. Contains mica.	
< 0.00	Pigmatic granite and greywacke boulders.	

12. South of Charleston (41°56'S, 171°26'E, NZMS E2380376, N5918164). Sampled 06-11-2003.

This site is a well defined road cutting situated approximately 3 km south of Charleston and about 100m north of an unsealed side road to the east.

Depth (m)	Description	Sampled Units (and sample codes)
> 3.70	Top soil (exact depth unknown)	
2.70 – 3.70	Fluvial gravels with sandy matrix.	
2.40 – 2.70	Brown sand	SoC 1
2.10 – 2.40	Conglomerate gravel with lens of brown sand	
0.60 – 2.10	Grey, well sorted sands with bi-directional cross bedding and gravel stringers. Appears to be of inter-tidal in origin.	
0.50 – 0.60	Boulder lag	
< 0.00 – 0.50	Marine sandstone	

13. Chesterfield Road M81/9 (42°38'S, 171°61'E, NZMS E2355180, N5840730). Sampled 06-11-2003.

This outcrop corresponds to an outcrop previously sampled for pollen by Moar & Suggate (1996) and is situated on the north side of the corner of Chesterfield and Ba Roads, Chesterton. The stratigraphy given by Moar and Suggate (1996) for the outcrop is provided below. The M81/9 outcrop rests on gravel associated with the Loopline Formation (Suggate, 1985). This formation is tied to the older part of the Last Glaciation in age (Moar & Suggate, 1996) and probably relates to the OIS 4 stadial between 91.0 – 79.3ka (Martinson et al., 1987).

Depth (m)	Description (Moar & Suggate, 1996)	Sampled Units (and sample codes)
0.50 – 0.80	Top soil	
0.00 – 0.50	Grey silt becoming increasingly organic towards base	CR81/9 A (grey silt) CR 81/9 B (organic layer at base of silt)
< 0.00	Loopline gravel	

14. Chesterfield Road M81/8 (42°38'S, 171°70'E, NZMS E2355541, N5840526). Sampled 06-11-2003.

A second outcrop from Chesterfield Road was also sampled. This outcrop is again on the north side of the road but lies ca. 500m further east in the same general region as Moar and Suggate's M81/8 outcrop (Moar & Suggate, 1996). Moar and Suggate (1996) associated the gravels underlying the M81/8 outcrop with the Waimea Glaciation (OIS 6) and the gravel underlying this outcrop should therefore be between 189.6 – 129.8ka in age (Martinson et al., 1987).

Depth (m)	**Description**	**Sampled Units (and sample codes)**
0.87 – 1.02	Dark brown silty clay. Highly organic A-horizon. Basal contact gradual over 0.02 – 0.03 m.	
0.49 – 0.87	Blue-grey sandy silt. Becomes browner with depth. Lower contact diffuse.	C81/8 A
0.39 – 0.49	Mid brown sandy silt. Becomes greyer with depth. Diffuse lower contact.	C81/8 B
0.18 – 0.39	Blue-grey sandy silt. Becomes browner with depth. Lower contact diffuse.	C81/8 C
0.02 – 0.18	Dark brown, very clayey silt containing macroscopic wood. Lightens towards base	C81/8 D
0.00 – 0.02	Pale brown, very clayey silt. Sharp contact with underlying gravels	
< 0.00	(Waimea) gravels	

15. South of Wharetea River (41°44'S, 171°44'E, NZMS E2405090, N5940340). Sampled 13-01-2004.

This site is a southwest facing outcrop in the side of a driveway mid way between the settlements of Fairdown (to the south) and Waimangaroa (to the north). The driveway is on the east side of State Highway 67.

Depth (m)	**Description**	**Sampled Units (and sample codes)**
1.80 – 1.85	Top soil	
1.55 – 1.80	Mid brown silty clay. Lightens towards base. Massive but contains macroscopic wood. Basal contact undulating.	DSWR 1
1.30 – 1.55	Dark brown, gravely sandy silt.	DSWR 2

	Massive with undulating basal contact	
1.15 – 1.30	Iron stained silty clay with undulating iron pan at basal contact	
< 0.00 – 1.15	Pale grey, massive, silty clay. Basal contact obscured	

16. Cawthron Road (41°46'S, 171°42'E, NZMS E2401300, N5937400). Initially sampled 14-01-2004. B-site sampled 07-04-2004.

This site is a southwest facing outcrop situated along a dirt road north of Cawthron Road. The outcrop is near the entrance to a quarry and is about 100m from the base of Rochfort Terrace.

Depth (m)	**Description**	**Sampled Units (and sample codes)**
0.85 – 1.00	Mid brown silty soil containing many rootlets. Graduated basal contact.	
0.60 – 0.85	Mid reddish brown sandy silt. Massive with sharp basal contact. Contains many modern rootlets.	CR 1
0.47 – 0.60	Dark brown, fine gravel with undulating but sharp basal contact.	CR 2
< 0.00 – 0.47	Orange brown silty clay. Massive. Lower contact obscured	CR 3

A second outcrop (Cawthron Road B) was also examined from this area. This outcrop was situated above a large pool of water that had formed in the quarry and faced in a southerly direction.

Depth (m)	**Description**	**Sampled Units (and sample codes)**
1.55 – 3.55	Interbedded fine gravel stringers with larger gravels at mm to cm scale.	
1.25 – 1.55	Green grey clay with *in situ* tree trunks	
1.95 – 1.25	Brown organic silty clay. Top 20-30 mm darkest with macroscopic wood	CRB 1
1.80 – 1.95	Fine gravels (sub-rounded to sub-angular) with silty sand matrix. Thickens laterally up to 0.30m	
1.60 – 1.80	Brown clay silt. Brownest material	CRB 2

	in top 20 mm. Macroscopic wood present. Thickens laterally up to 0.60 – 0.70m	
1.32 – 1.60	Alternating layers of gravel (pebbled to cobble sized) and silty sand.	
1.30 – 1.32	Organic clay layer (undulating)	CRB 3
1.02 – 1.30	Alternating layers of gravel (pebbled to cobble sized) and silty sand.	
1.00 – 1.02	Organic clay layer (flat)	
0.70 – 1.00	Alternating layers of gravel (pebbled to cobble sized) and silty sand.	
0.30 – 0.70	Organic clay layer	
0.00 – ca. 0.30	Alternating layers of gravel (pebbled to cobble sized) and silty sand.	
< 0.00	Under water	

17. Caledonian Road (41°46'S, 171°40'E, NZMS E2398510, N5397280). Sampled 14-01-2004.

This site is a southeast facing outcrop situated in a road cutting near the corner of Caledonian and Keoghans Road where Calaedonian Road becomes a gravelled, rather than sealed, road

Depth (m)	**Description**	**Sampled Units (and sample codes)**
1.30 – 1.50	Organic rich top soil with undulating, graduated lower contact	
1.05 – 1.30	Reddish brown silty clay interbedded with gravel fingers. Lower contact undulating with iron pan. Traces of iron staining also runs through horizon vertically.	Cal 1
0.76 – 1.05	Reddish brown gravely sands with occasional fingers of pure gravel. Lower contact undulating and diffuse	
0.74 – 0.76	Layer of gravel	
0.63 – 0.74	Reddish grey sandy silt with sand inter-fingered in some places. Undulating lower contact	
0.57 – 0.63	Layer of gravel	
0.20 – 0.57	Grey brown sandy silt with some inter-fingered lens of sand. Otherwise massive. Undulating	Cal 2

	basal contact	
0.12 – 0.20	Grey gravely sand with undulating lower contact.	
0.00 – 0.12	Grey brown silty clay. Massive. Lower contact with appears to be with gravel but obscured.	Cal 3

18. Waterworks Road (41°46'S, 171°39'E, NZMS E2397600, N5937300). Sampled 17-01-2004.

This east facing site is situated ca. 50m along Waterworks Road from the corner of Caledonian Road and Waterworks Road, Westport.

Depth (m)	**Description**	**Sampled Units (and sample codes)**
1.83 – 1.87	Top soil	
1.40 – 1.83	Mid brown silty clay. Massive. Basal contact undulating but sharp with slight iron pan. Unit contains macrofossil wood as well as modern rootlets	WW 1
1.20 – 1.40	Brownish grey silty clay. Massive with sharp, undulating basal contact.	WW 2
0.30 – 1.20	Grey (grading to blue grey at base) silty sand with faint cm scale laminations. Basal contact interfingers with underlying sand unit.	WW 3
0.27 – 0.30	Grey sand with sharp basal contact	
0.00 – 0.27	Blue grey silty clay. Massive with sharp basal contact marked by iron pan.	WW 4
< 0.00	Gravel unit of indeterminate thickness and lithology	

19. Keoghan's Road (41°46'S, 171°40'E, NZMS E2399000, N5936400). Initally sampled 17-01-2004. Re-sampled 06-04-2004.

Refer to Chapter 5 for a detailed description of this site.

20. 9-Mile Road (41°49'S, 171°39'E, NZMS E2397500, N5931300). Initally sampled 17-01-2004.

This east facing outcrop is set in a road cutting along 9-Mile Road, Westport. The site is located on the gravelled section of the road approximately 1 km from the road end (at the Buller River) on the eastern side of the West Creek ford.

Depth (m)	Description	Sampled Units (and sample codes)
0.95 – 1.10	Modern organic layer. Gradual lower contact	
0.39 – 0.95	Reddish brown silty clay, greys towards base. Contains some modern roots from above and isolated gravel. Lower contact sharp with iron pan.	9M 1
0.25 – 0.39	Grey sandy silt with sharp lower contact. Massive.	9M 2
< 0.00 – 0.25	Gravel layer, lower contact obscured.	

21. Alma Road (41°46'S, 171°35'E, NZMS E2391500, N5936500). Initally sampled 17-01-2004. Re-sampled 06-04-2004.

Refer to Chapter 4 for a detailed description of this site.

22. Beach Road (41°53'S, 171°28'E, NZMS E2382900, N5923800). Sampled 19-01-2004.

This site is a west facing outcrop on Beach Road ca. 4km north of Charleston where Beach Road turns off State Highway 6. The outcrop is on the switchback piece of road prior to the end of the tar seal.

Depth (m)	Description	Sampled Units (and sample codes)
1.72 – 1.98	Mid brown sandy silt. Loosely packed and containing modern rootlets. Lower contact diffuse.	
1.22 – 1.72	Mid brown sandy silt, massive. Darkens towards base. Contains modern rootlets. Lower contact undulating but diffuse.	BR 1
1.16 – 1.22	Dark brown sand. Very hard and appears iron stained. Lower contact sharp and undulating	

1.10 – 1.16	Grey sand of varying depth across face. Unit is extremely hard. Lower contact has undulating iron pan	
<0.00 – 1.10	Orange sand with irregular cm scale laminations and occasional iron staining. Lower contact obscured.	

23. Virgin Flat Road (41°50'S, 171°29'E, NZMS E2384200, N5929600). Sampled 19-01-2004.

This site is an outcrop situated approximately 1km from the Okari lagoon end of Virgin Flat Road and about 100m from the beginning of a track on the north side of the road.

Depth (m)	**Description**	**Sampled Units (and sample codes)**
1.70 – 1.80	Grey silty sand. Very friable due to modern rootlets. Lower contact diffuse.	
1.50 – 1.70	Grey silty sand. Massive with less contamination from modern roots. Lower contact undulating and sharp.	
1.35 – 1.50	Orange sandy silt. Mixed with grey sand in places. Varies in depth across outcrop. Gradual lower contact.	
0.70 – 1.35	Grey brown sandy silt. Massive and contains macroscopic wood fragments (maybe modern in origin). Lower contact sharp with iron pan.	VFR 1
<0.00 – 0.70	Orange sand, massive. Lower contact obscured.	

24. Mitchell's Gully Mine (41°54'S, 171°28'E, NZMS E2382943, N5922557). Sampled 20-01-2004.

This site is at the eastern end of the Mitchell's Gully Mine at the base of an unnamed ridge at the western edge of Browns Terrace. The site consists of a north facing outcrop on the side of a silica pit. The beds in the outcrop slope down across the face at an angle of 60° (towards the west).

Depth (m)	Description	Sampled Units (and sample codes)
1.10 – 1.25	Mid brown sandy silt. Very friable due to modern rootlets. Lower contact diffuse.	
1.07 – 1.10	Orange sand. Massive with modern rootlets. Lower contact diffuse.	
1.02 – 1.07	Gravel in orange sand matrix. Undulating diffuse lower contact. Modern rootlets.	
0.85 – 1.02	Orange silty sand. Massive with modern rootlets. Diffuse lower contact.	
0.58 – 0.85	Mid brown sandy silt. Generally massive but iron stained in places. Lower contact sharp and undulating	MGM 1
< 0.00 – 0.58	Orange sand containing occasional gravel.	

25. Candlelight (42°34’S, 171°10’E, NZMS E2359492, N5846995). Sampled 22-01-2004.

This site is a series of outcrops cut from an old gold mining sluice approximately 3km south of Camerons within the Nemona Forest plantation. The outcrops are situated off the south fork of Camerons Road approximately 1km east of the first split of the road, across a stream and a ridge ca. 100m south of the road itself. This puts the outcrops ca. 700m east of the Taramakau River. Sampling occured just after the local forest had been logged

The site was previously sampled for pollen and consists of three east facing outcrops in close proximity. The site is recorded as resting on Rutherglen Formation (early OIS 5 (Suggate, 1985; Moar & Suggate, 1996)) and is almost overtopped by Loopline formation (OIS 4 (Moar & Suggate 1973; Moar & Suggate 1996)) giving the outcrops an associated age of between 129.8 – 79.3ka (Martinson et al., 1987). The first two outcrops share similar units and are tentatively correlated to one another (indicated by numbered zones).

Candlelight Outcrop 1 (most southerly of the outcrops).

Depth (m)	**Description**	**Sampled Units (and sample codes)**	**Correlated Zones**
1.88 – > 2.00	Grey silty clay. Massive. Upper contact obscured by slip from above (out of reach). Lower contact sharp		1
1.87 – 1.88	Grey sand. Lower contact sharp.		1
1.82 – 1.87	Grey silty clay with mm scale laminations. Lower contact sharp		1
1.79 – 1.82	Interbedded layers of sand and silty clay. Layers are mm scaled. Lower contact sharp.		1
1.77 – 1.79	Grey sand with iron staining in places and iron pan at sharp basal contact.		2
1.73 – 1.77	Iron stained silty clay with iron pan at basal contact.		3
0.98 – 1.73	Grey brown sand with cm scale laminations and occasional boulders. Lens of clay occur at ca. 1.58 – 1.56m and 1.18 – 1.19m. Iron staining more pronounced towards base of unit. Lower contact sharp and undulating.		4
0.78 – 0.98	Gravels in sandy matrix (appear marine in origin). Iron pan at basal contact.		
< 0.00 – 0.78	Gravels with grey sandy matrix (appear marine in origin). Lower contact obscured.		

Candlelight Outcrop 2 (ca. 2 metres north of outcrop 1).

Depth (m)	**Description**	**Sampled Units (and sample codes)**	**Correlated Zones**
1.38 – 1.65	Light brown organic layer containing many rootlets. Very friable. Lower contact undulating but sharp.		
0.84 – 1.38	Grey silty clay. Generally massive but with lens of sand and iron staining at irregular intervals. Contains macrofossil wood but also modern rootlets. Lower contact undulating and sharp.	CL 1A	1
0.77 – 0.84	Grey sand with modern rootlets. Sharp, undulating lower contact.		1
0.51 – 0.77	Grey silty clay with mm scale laminations. Contains occasional pebbles. Lower contact sharp.	CL 1B	1
0.49 – 0.51	Grey sand with iron staining.		2

	Lower contact sharp with iron pan	
0.46 – 0.49	Iron stained silty clay. Lower contact sharp with iron pan.	3
< 0.00 – 0.46	Grey brown sand with cm scale laminations. Contains occasional boulders. Lower contact obscured	4

Candlelight Outcrop 3 (ca. 20 metres north of outcrop 2. Bottom of outcrop ca. 2m above outcrop 2).

Does not correlate with previous units.

Depth (m)	Description	Sampled Units (and sample codes)
5.10 – 5.30	Organic unit: clay? silt?. Very friable with modern rootlets. Lower contact diffuse.	
3.20 – 5.10	Pale brown silt darkening towards base. Massive. Upper half contains many modern rootlets. Lower contact diffuse.	2
2.30 – 3.20	Dark brown organic silty clay. Massive but contains woody fragments. Lower contact diffuse.	3
1.90 – 2.30	Reddish brown organic silty clay. Massive with diffuse lower contact	4
1.30 – 1.90	Dark brown silty clay. Massive but containing macroscopic wood. Lower contact sharp	5
< 0.00 – 1.30	Gravel (appears fluvial). Lower contact obscured	

26. Tasman Bay Estates (42°26'S, 171°11'E, NZMS E2360600, N5855500). Sampled 22-01-2004.

This site consists of a northwest facing outcrop cut in a ditch between two new sections in the Tasman Bay Estates above South Beach, Greymouth.

Depth (m)	Description	Sampled Units (and sample codes)
2.10 – 2.40	Modern organic layer. Very friable due to high concentration of modern rootlets. Diffuse lower contact	
1.50 – 2.10	Mid brown sandy silt. Massive but containing macroscopic wood. Undulating, diffuse basal contact.	TBE 1
1.20 – 1.50	Dark brown sandy silt. Massive but containing macroscopic wood. Lower contact sharp and undulating with iron pan.	TBE 2

< 0.00 – 1.20	Orange grey sand. Massive but iron pan from unit above partially bisects unit. Lower contact obscured

27. Blur Spur Road (42°26'S, 171°11'E, NZMS E2349000, N5830200). Sampled 23-01-2004.

This site is situated on a private gravel road off the south side of Blur Spur Road, approximately 1 km east of Blur Spur (ca. 5km east of Hokitika). This site is in the same general location as a site previously sampled for pollen (Moar & Suggate, 1973).

The primary outcrop sampled for beetles was a west facing road cutting but a second, east facing, outcrop on the opposite side of a narrow ridge (in an open pit) was also sampled. The initial stratigraphic log of this second outcrop was rough due to the outcrop being difficult to clear due to its large size and the presence of extensive gorse below the outcrop but the upper gravel unit of Outcrop 2 appears to correlate with the lower contact of Outcrop 1.

Blur Spur Road Outcrop 1 (west facing)

Depth (m)	Description	Sampled Units (and sample codes)	Correlated Zones
1.40 – 1.50	Grey brown soil. Very friable due to modern rootlets. Lower contact diffuse		
1.14 – 1.40	Grey brown silty clay. Massive with macroscopic wood. Lower contact undulating and diffuse.	BSR 1	
1.03 – 1.14	Mid brown silty clay. Massive with macroscopic wood. Lower contact undulating and diffuse.	BSR 2	
0.50 – 1.03	Pale brown silty clay. Some iron staining in places. Macroscopic wood present as well as visible modern rootlets. Lower contact diffuse and undulating.	BSR 3	
0.00 – 0.50	Grey silty clay with iron staining	BSR 4	

	in places. Massive with undulating lower contact.		
< 0.00	Obscured gravel layer		1

Blur Spur Road Outcrop 2 (east facing)

Depth (m)	**Description**	**Sampled Units (and sample codes)**	**Correlated Zones**
ca. 5.70 – 8.00	Alluvial gravel		1
1.20 – ca. 5.70	Orange silty clay	BSR 5	
1.00 – 1.20	Gravel layer		
< 0.00 – 1.00	Orange sands		

28. Scandinavian Road (42°40'S, 171°50'E, NZMS E2353400, N5836500). Sampled 23-01-2004.

This site is approximately 500m up a gravel road north from Stafford. The site was past the last house on the road and was a north facing road cutting approximately 6 metres from the brow of Scandinavian Hill.

Depth (m)	**Description**	**Sampled Units (and sample codes)**
1.95 – 2.30	Gravel layer in orange matrix. Sharp lower contact.	
1.60 – 1.95	Grey silty clay. Massive with pebbles and macroscopic wood. Lower contact sharp and undulating.	ScR 1
0.75 – 1.60	Gravel layer obscured by bryophytes. Lower contact sharp and undulating.	
0.57 – 0.75	Grey gravely sand with clay lenses at irregular intervals. Lower contact sharp and undulating.	
0.40 – 0.57	Grey silty clay. Massive with occasional pebble. Lower contact sharp and undulating.	ScR 2
0.23 – 0.40	Red grey gravely sand. Lower contact diffuse.	
0.05 – 0.23	Grey silty sand with clay lenses at irregular intervals. Lower contact diffuse.	
< 0.00 – 0.05	Gravels. Lower contact obscured	

Appendix 2

Taxonomic composition of fossil taxa used in this thesis

Table A2.1. Taxonomic break-down of all fossil taxa used in the palaeoclimatic reconstructions. Taxa were identified from modern specimens housed at the New Zealand Arthropod Collection (NZAC) in Auckland, New Zealand. Taxa use the same nomenclature used in NZAC so that collection specimens can be referred back to. Climatic data for those Taxa tied to a whole genus (e.g. *Bembidion* indet. sp.) were created from those specimens held at the NZAC and may not include all known species within the genus.

Family	**Subfamily**	**Taxon**	**Included taxa (names from NZAC label data)**
Carabidae	Psydrinae	*Bembidion* indet. sp.	*Bembidion (Ananotaphus) rotundicolle eustictum* Bates *Bembidion (Ananotaphus) rotundicolle rotundicolle* Bates
			Bembidion (Notaphus) brullei Gemminger & Harold
			Bembidion (Zeactedium) musae Broun
			Bembidion (Zemetallina) anchonoderus Bates
			Bembidion (Zemetallina) chalceipes Bates
			Bembidion (Zemetallina) hokitikense Bates
			Bembidion (Zemetallina) parviceps Bates
			Bembidion (Zemetallina) solitarium Lindroth
			Bembidion (Zemetallina) stewartense Lindroth
			Bembidion (Zemetallina) tekapoense Broun
			Bembidion (Zemetallina) urewerense Lindroth
			Bembidion (Zemetallina) wanakense Lindroth
			Bembidion (Zeperyphodes) callipeplum Bates
			Bembidion (Zeperyphus) actuarium Broun
			Bembidion (Zeplataphus) charile Bates
			Bembidion (Zeplataphus) dehiscens Broun
			Bembidion (Zeplataphus) granuliferum Lindroth
			Bembidion (Zeplataphus) maorinum levatum Lindroth
			Bembidion (Zeplataphus) maorinum maorinum Bates
			Bembidion (Zeplataphus) tairuense Bates
		Bembidion maorinum maorinum	*Bembidion (Zeplataphus) maorinum maorinum* Bates
		Bembidion tekapoense	*Bembidion (Zemetallina) tekapoense* Broun
		Bembidion wanakense	*Bembidion (Zemetallina) wanakense* Lindroth
		Oopterus indet. sp.	*Oopterus basalis* Broun
			Oopterus clivinoides Guérin-Méneville
			Oopterus laevicollis Bates
			Oopterus marrineri Broun
			Oopterus pallidipes Broun
			Oopterus patulus Broun
			Oopterus plicaticollis Blanchard
			Oopterus puncticeps Broun
			Oopterus pygmeatus Broun
			Oopterus pygmeatus/basalis Broun
			Oopterus sobrinus Broun

			Oopterus strenuus Johns
			Oopterus suavis Broun
			Oopterus sp. A
			Oopterus sp. B
			Oopterus sp. C
			Oopterus sp. D
			Oopterus sp. E
			Oopterus sp. F
			Oopterus sp. G
			Oopterus sp. H
			Oopterus sp. I
			Oopterus unidentified specimens
		Oopterus pallidipes	*Oopterus pallidipes* Broun
		Zolus indet. sp.	*Zolus femoralis* Broun
			Zolus helmsi Sharp
			Zolus ocularius Broun
			Zolus subopacus Broun
	Harpalinae	*Actenonyx bembidioides*	*Actenonyx bembidioides* White
		Dierochile flavipes	*Dierochile flavipes* Broun
		Notagonium feredayi	*Notagonium feredayi* Bates
		Notogonium indet. sp.	*Notagonium chathamense* Broun
			Notagonium feredayi Bates
			Notagonium lawsoni Bates
			Notagonium submetallicum White
		Scopodes "sp. group A"	*Scopodes edwardsii* Bates
			Scopodes pustulatus Broun
		Scopodes indet. sp.	*Scopodes basalis* Broun
			Scopodes bryophilus Broun
			Scopodes cognatus Broun
			Scopodes edwardsii Bates
			Scopodes fossulatus Blanchard
			Scopodes laevigatus Bates
			Scopodes levistriatus Broun
			Scopodes multipunctatus Bates
			Scopodes prasinus Bates
			Scopodes pustulatus Broun
			Scopodes versicolor Bates
		Zeopoeclius putus	*Zeopoecilus putus* Broun
Hydrophilidae	Hydrophilinae	*Enochrus tritus*	*Enochrus tritus* Broun
		Paracymus pygmaeus	*Paracymus pygmaeus* Macleay
	Sphaeridiinae	*Adolopus helmsi*	*Adolopus helmsi* Sharp
		Adolopus indet sp	*Adolopus altulus* Broun
			Adolopus badius Broun
			Adolopus helmsi Sharp
		Cyloma "sp group A"	*Cyloma guttatus* Sharp
			Cyloma lineatus Broun
			Cyloma stewarti Broun
		Cyloma "sp group B"	*Cyloma lineatus* Broun
			Cyloma stewarti Broun
		Cyloma indet. sp.	*Cyloma guttatus* Sharp
			Cyloma lawsonus Sharp

			Cyloma lineatus Broun
			Cyloma stewarti Broun
		Tormus nitidulus	*Tormus nitidulus* Broun
Leiodidae	Leiodinae	*Isocolon modestum*	*Isocolon modestum* Broun
	Cholevinae	*Paracatops "sp group A"*	*Paracatops lubrix* Sharp
			Paracatops triangulum Geamuel
			Paracatops sp. 3
			Paracatops lugubris Sharp
			Paracatops relatus Broun
			Paracatops sp.
		Leiodidae unnamed sp. 1	Leiodidae unnamed sp.
Scydmaenidae	Scydmaeninae	*Adrastia nelsoni*	*Adrastia nelsoni* Franz
		Scydmaenidae "sp group A"	*Adrastia angulifrous* Broun
			Adrastia augustissma Franz
			Adrastia clarkei Franz
			Adrastia edwardsi Sharp
			Adrastia greymouthi Franz
			Adrastia nelsoni Franz
			Adrastia princiceps Broun
			Scydmaenus clarkei Franz
Staphylinidae	Omallinae	*Corneolabium mandibulare*	*Corneolabium mandibulare* Steel
		Ischnoderus curtipennis	*Ischnoderus curtipennis* Broun
		Stenomalium cognatum	*Stenomalium cognatum* Broun
		Stenomalium indet. sp.	*Stenomalium* "Genus B"
			Stenomalium "Genus B" sp. A
			Stenomalium "Genus B" sp. C
			Stenomalium antipodum Broun
			Stenomalium cognatum Broun
			Stenomalium helmsi Cameron
			Stenomalium moniliferum Broun
			Stenomalium philpotti Broun
			Stenomalium sp.
			Stenomalium sp. 1
			Stenomalium spadix Broun
			Stenomalium steeli sp.n.
			Stenomalium sulcithorax Broun
	Pselaphinae	*Dalma pubescens*	*Dalma pubescens* Sharp
		Eleusomatus indet. sp.	*Eleusomatus (Euplectopsis) rotundicollis* Reitter
			Eleusomatus (Euplectus) arohaensis Broun
			Eleusomatus acuminatus Broun
			Eleusomatus allocephalus Broun
		Eupines "sp group A"	*Eupines grata* Sharp
			Eupines halli Broun
		Eupines "sp group B"	*Eupines platyarthra* Broun
			Eupines rudicornis Broun
		Eupines monstrosa	*Eupines monstrosa* Reitter
		Eupines rudicornis	*Eupines rudicornis* Broun
		Pselaphus indet. sp.	*Pselaphus* [Gen II] n. sp.
			Pselaphus citmus Broun
			Pselaphus delicatus Broun
			Pselaphus meliusculus Broun

		Pselaphus pauper Sharp
		Pselaphus sp.
	Sagola indet. sp.	*Sagola anisarthra* Broun
		Sagola bilobata Broun
		Sagola bituberata Broun
		Sagola cestanea Broun
		Sagola deformipes Broun
		Sagola duplicates Broun
		Sagola fagicola Broun
		Sagola fasciculata Broun
		Sagola fuscipalpis Broun
		Sagola genalis Broun
		Sagola histalis Broun
		Sagola indet. sp.
		Sagola insignis Broun
		Sagola laminata Broun
		Sagola maesonyx Broun
		Sagola major Broun
		Sagola minuscula Broun
		Sagola moushosie Reitter
		Sagola notibilis Broun
		Sagola pulchra Broun
		Sagola punctulatis Raffrey
		Sagola robusta Broun
		Sagola sp.
		Sagola sp. 1
		Sagola sp. 2.
		Sagola sp. 4
	Vidamus indet. sp.	*Vidamus calcaratus* Broun
		Vidamus congruus Broun
		Vidamus convexus Sharp
		Vidamus gracilipes Broun
		Vidamus modestus Broun
		Vidamus punctulatus Broun
		Vidamus trochanteralis Broun
		Vidamus validus Broun
	Zelandius indet. sp.	*Zelandius brookesi* Broun
		Zelandius clevedonensis Broun
		Zelandius coxalis Broun
		Zelandius obscurus Broun
		Zelandius raffrayi Broun
		Zelandius sandageri Broun
		Zelandius sp.
		Zelandius spinifer Broun
		Zelandius tuberalis Broun
		Zelandius usitatus Broun
Aleocharinae	*Aleochara hammondi*	*Aleochara hammondi* Klimaszewski
Scaphidiinae	*Brachynopus scutellaris*	*Brachynopus scutellaris* Redtenbacher
Osoriinae	*Paratrochus "sp group A"*	*Paratrochus arrowi* Bernhauer
		Paratrochus helmsi Fauvel
		Paratrochus monstrous Bernhauer

	Euasthetinae	*Agnosthaetus* indet. sp.	*Agnosthaetus brouni* Bernhauer
			Agnosthaetus vicimus Broun
	Paederinae	*Hyperomma* indet. sp.	*Hyperomma dispersum* Broun, specimens unsorted
			Hyperomma mandibulare Broun, specimens unsorted
			Hyperomma tenellum Broun, specimens unsorted
			Hyperomma sanguineum Broun, specimens unsorted
	Staphylininae	*Philonthus rectangulus*	*Philonthus rectangulus* Sharp
Scarabidae	Scarabinae	*Saphobius edwardsi*	*Saphobius edwardsi* Sharp
Byrrhidae	Syncalyptinae	*Curimus "sp group A"*	*Curimus* sp. 2
			Curimus sp. 3
			Curimus sp. 4
			Curimus sp. 5
			Curimus squamiger Broun
			Curimus vestitus Broun
		Curimus squamiger	*Curimus squamiger* Broun
		Curimus zeelandicus	*Curimus zeelandicus* Redtenbacher
	Byrrhinae	*Epichorius "sp group A"*	*Epichorius gemmeus* Broun
			Epichorius puncticeps Broun
			Epichorius sp. 7
			Epichorius sp. 17
			Epichorius sp. 19
			Epichorius sp. 27
			Epichorius sp. 28
		Epichorius indet. sp.	*Epichorius aemulator* Broun
			Epichorius aucklandiae Kirsch
			Epichorius bryobius Broun
			Epichorius cognatus Broun
			Epichorius coruscans Pasc.
			Epichorius foveigerus Broun
			Epichorius gemmus unattributed
			Epichorius laetus Broun
			Epichorius laevipennis Broun
			Epichorius longulus Broun
			Epichorius nigrescens Broun
			Epichorius ornatus Broun
			Epichorius picipes Broun
			Epichorius probus Broun
			Epichorius pulcherrimus Broun
			Epichorius puncticeps Broun
			Epichorius sorenseni Brookes
			Epichorius sp. 1
			Epichorius sp. 2
			Epichorius sp. 3
			Epichorius sp. 4
			Epichorius sp. 5
			Epichorius sp. 6
			Epichorius sp. 7
			Epichorius sp. 8
			Epichorius sp. 9
			Epichorius sp. 10
			Epichorius sp. 11

			Epichorius sp. 12
			Epichorius sp. 13
			Epichorius sp. 14
			Epichorius sp. 15
			Epichorius sp. 16
			Epichorius sp. 17
			Epichorius sp. 18
			Epichorius sp. 19
			Epichorius sp. 20
			Epichorius sp. 21
			Epichorius sp. 22
			Epichorius sp. 23
			Epichorius sp. 24
			Epichorius sp. 25
			Epichorius sp. 26
			Epichorius sp. 27
			Epichorius sp. 28
			Epichorius sp. 29
			Epichorius sp. 30
			Epichorius sp. 31
			Epichorius sp. 32
			Epichorius sp. 34
			Epichorius tumidellus Broun
		Epichorius sp. 3	*Epichorius* sp. 3
		Liochoria sp. 1	*Liochoria* sp. 1
Phycosecidae		*Phycosecis limbata*	*Phycosecis limbata* Fabricius
Bothrideridae	Bothriderinae	*Ascetoderes* indet. sp.	*Ascetoderes cogantus* Sharp
			Ascetoderes moestus Sharp
			Ascetoderes obsoletus Broun
			Ascetoderes paynteri Broun
Ciidae		*Orthocis undulatus*	*Orthocis undulatus* Broun
Zopheridae	Colydiinae	*Coxelus* indet. sp.	*Coxelus dubius* Sharp
			Coxelus elongatus Broun
			Coxelus graniceps Broun
			Coxelus helmsi Reitter
			Coxelus instabilis Broun
			Coxelus longulus Broun
			Coxelus oculator Broun
			Coxelus oculator Broun
			Coxelus ovicollis Broun
			Coxelus regularis Broun
			Coxelus robustus Broun
			Coxelus similis Sharp
			Coxelus sp.
			Coxelus thoracicus Broun
			Coxelus variegatus Broun
			Coxelus xanthonyx Broun
	Zopherinae	*Pycnomerus "sp group A"*	*Pycnomerus angulatus* Broun
			Pycnomerus depressiusculus White
			Pycnomerus ellipticus Broun
			Pycnomerus elongellus Broun

			Pycnomerus helmsi Sharp
			Pycnomerus longulus Sharp
			Pycnomerus mediocrus Broun
			Pycnomerus peregrinus Broun
			Pycnomerus rufficollis Broun
			Pycnomerus simplex Broun
			Pycnomerus simulans Sharp
		Pycnomerus "sp group B"	*Pycnomerus latitans* Sharp
			Pycnomerus marginalis Broun
			Pycnomerus sulcatissimus Sharp
		Pycnomerus latitans	*Pycnomerus latitans* Sharp
		Pycnomerus marginalis	*Pycnomerus marginalis* Broun
		Pycnomerus rufficollis	*Pycnomerus rufficollis* Broun
Cerambycidae	Lamiinae	*Hybolasius* "sp group A"	*Hybolasius cristatellus* Bates
			Hybolasius modestus Broun
			Hybolasius rugicollis Broun
			Hybolasius sp. 1
Chrysomelidae	Galerucinae	*Adoxia* indet sp	*Adoxia aeneus* Broun
			Adoxia asperella Broun
			Adoxia atripennis Broun
			Adoxia axyocharis Broun
			Adoxia brevicollis Broun
			Adoxia calcaratus Broun
			Adoxia cheesmani Broun
			Adoxia dilucida Broun
			Adoxia dilutipes Broun
			Adoxia fuscata Broun
			Adoxia fuscata pubicollis group
			Adoxia halli Broun
			Adoxia insolita Broun
			Adoxia iridescens Broun
			Adoxia mediocris Broun
			Adoxia monticola Broun
			Adoxia obscura Broun
			Adoxia o'connor Broun
			Adoxia oleariae Broun
			Adoxia perplexus Broun
			Adoxia princeps Broun
			Adoxia pubicollis Broun
			Adoxia puncticollis Sharp
			Adoxia pygidialis Broun
			Adoxia rugicollis Broun
			Adoxia scutellaris Broun
			Adoxia simmondsi Broun
			Adoxia sp.
			Adoxia sp. 2
			Adoxia sp. 3
			Adoxia vulgaris Broun
			Adoxia vulgaris complex Broun
	Chrysomelinae	*Caccomolpus cinctiger*	*Caccomolpus cinctiger* Broun
Curculionidae	Cossoninae	*Euophryum confine*	*Euophryum confine* Broun

Curculioninae	*Alloprocas niger*	*Alloprocas niger* Broun
	Areocryptus indet sp	*Areocryptus* unidentified specimens
	Areoscapsus indet. sp.	*Areoscapus estriatus* Broun
		Areoscapus fasciculatus Broun
		Areoscapus flavipes Broun
		Areoscapus ocularis Broun
		Areoscapus punctipennis Broun
		Areoscapus unidentified spp.
		Areoscapus subcostatus Broun
	Areoscapus estriatus	*Areoscapus estriatus* Broun
	Areoscapus subcostatus	*Areoscapus subcostatus* Broun
	Bryocatus amplus	*Bryocatus amplus* Broun
	Oreocalus latipennis	*Oreocalus latipennis* Broun
	Phemus indet. sp.	*Phemus* unidentified specimens (specimens unsorted)
	Rystheus indet. sp.	*Rystheus fulvosetosus* Marshall
		Rystheus indet. sp.
		Rystheus notabilis Broun
		Rystheus ocularis Broun
	Trindocalles indet. sp.	*Trindocalles* sp.
Entiminae	*Gromilus* indet. sp.	*Gromilus aptus* n. sp.
		Gromilus arbus n. sp.
		Gromilus arthurensis n. sp.
		Gromilus aterrimus n. sp.
		Gromilus bicarinatus Broun
		Gromilus bifoveatus Broun
		Gromilus borealis n. sp.
		Gromilus brevicornis Broun
		Gromilus caudatus Broun
		Gromilus cockaynei Broun
		Gromilus cordipennis Broun
		Gromilus digressus n. sp.
		Gromilus dorsalis Broun
		Gromilus duplex n. sp.
		Gromilus filicum n. sp.
		Gromilus furvus Broun
		Gromilus gracilipes Sharp
		Gromilus gracilipes ovipennis Broun
		Gromilus gracilipes thoraeicus Broun
		Gromilus impressus Broun
		Gromilus incomptis n. sp.
		Gromilus inflexus n. sp.
		Gromilus insularis insularis Blanchard
		Gromilus insularis robustus Brookes
		Gromilus kaikourensis n. sp.
		Gromilus laqueorum Kuschel
		Gromilus lithociodes n. sp.
		Gromilus merus Broun
		Gromilus mucronatus n. sp.
		Gromilus n. sp.
		Gromilus nestroides n. sp.
		Gromilus nitidellus Broun

	Gromilus nodiceps Broun
	Gromilus piger n. sp.
	Gromilus seclusus n. sp.
	Gromilus setosus Broun
	Gromilus simplex n. sp.
	Gromilus sp.
	Gromilus sulcicollis Broun
	Gromilus thoracicus Broun
	Gromilus variegatus Broun
Irenimus indet. sp.	*Irenimus aemulator* Broun
	Irenimus aequalis Broun
	Irenimus albosparsus Broun
	Irenimus apicalis Broun
	Irenimus areaths n. sp.
	Irenimus compressus Broun
	Irenimus costatus n. sp.
	Irenimus costifer Broun
	Irenimus duplex Broun
	Irenimus egus Broun
	Irenimus furcatus n. sp.
	Irenimus glacialis n. sp.
	Irenimus instabilis Marshall
	Irenimus limbatus Broun
	Irenimus n. sp.
	Irenimus parilis Pascoe
	Irenimus patricki Barrett
	Irenimus pensus Broun
	Irenimus posticalis Broun
	Irenimus rubidus Broun
	Irenimus similis Barret n. sp.
	Irenimus spectabilis Broun
	Irenimus stolidus Broun
	Irenimus turricola unattributed (4 specimens in NZAC)
	Irenimus vetustus n. sp.
	Irenimus vexator Broun
Nestrius “sp. group A”	*Nestrius* n. sp.
	Nestrius sp.2
	Nestrius sp. 3
	Nestrius sp. 1
	Nestrius sp. 4
	Nestrius sp. 5
	Nestrius sp. 6

Appendix 3

List of fossil taxa using in final ordination analysis (Chapter 3)

Table A3.1. List of fossil beetle taxa using in final ordination analysis (Chapter 3. Taxa are arranged taxonomically. The taxonomic composition of each taxon is given in Appendix 2.

Family	**Subfamily**	**taxon**
Carabidae	Psydrinae	*Bembidion* indet. sp.
		Oopterus indet. sp.
		Zolus indet. sp.
	Harpalinae	*Actenonyx bembidioides*
		Dierochile flavipes
		Notogonium feredayi
		Notogonium indet. sp.
		Scopodes "sp. group A"
		Scopodes indet. sp.
Hydrophilidae	Sphaeridiinae	*Adolopus helmsi*
		Adolopus indet sp
		Cyloma "sp group A"
		Cyloma "sp group B"
		Cyloma indet. sp.
Leiodidae	Leiodinae	*Isocolon modestum*
	Cholevinae	*Paracatops "sp group A"*
Scydmaenidae	Scydmaeninae	Scydmaenidae "sp group A"
Staphylinidae	Omallinae	*Stenomalium cognatum*
		Stenomalium indet. sp.
	Pselaphinae	*Eupines "sp group A"*
		Eupines "sp group B"
		Eupines rudicornis
		Pselaphus indet. sp.
		Sagola indet. sp.
		Zelandius indet. sp.
	Scaphidiinae	*Brachynopus scutellaris*
	Euasthetinae	*Agnosthaetus* indet. sp.
Scarabidae	Scarabinae	*Saphobius edwardsi*
Byrrhidae	Byrrhinae	*Epichorius "sp group A"*
		Epichorius indet. sp.
Bothrideridae	Bothriderinae	*Ascetoderes* indet. sp.
Zopheridae	Colydiinae	*Coxelus* indet. sp.
	Zopherinae	*Pycnomerus "sp group A"*
Cerambycidae	Lamiinae	*Hybolasius* "sp group A"
Chrysomelidae	Galerucinae	*Adoxia* indet sp
Curculionidae	Cossoninae	*Euophryum confine*
	Curculioninae	*Alloprocas niger*
		Areocryptus indet sp
		Areoscapsus indet. sp.
		Bryocatus amplus
		Rystheus indet. sp.

Entiminae	*Gromilus* indet. sp. *Irenimus* indet. sp. *Nestrius* “sp. group A”

Appendix 4

Pollen counts from Keoghan's Road samples (Chapter 5)

Table A4.1 Pollen counts and the environmental associations of the identified pollen taxa from sample KR-A3.

	Taxon	**# of pollen grains**	**%**	**Plant type**	**Range & Environment (Sakai & Wardle (1978); Macphail & McQueen (1983); Dawson & Lucas (2000))**
Terrestrial Pollen	*Nothofagus fusca* type	326	91.06	tree	Dominant in temperate, montane & subalpine forests. *N. solandri* var *cliffortioides* frost resistant to -13°C
	Nothofagus menziesii	3	0.84	tree	Dominant in cool temperature forests in south of South Island but normally montane to subalpine. Often forms treeline.
	Apiaceae	1	0.28	herbs	
	Ascarina lucida	1	0.28	shrub/small tree	Montane and temperate forests south of 35°S. Frost & drought intolerant
	Coprosma	7	1.96	shrub/small tree	Coastal to lower alpine zones at forest margins & in scrub & grasslands. Tolerant of poorly drained as well as exposed areas
	Dacrydium	1	0.28	shrub-tall tree	Genus occurs in temperate to montane zones
	Epacridaceae (*Leucopogon*)	1	0.28	prostrate & erect shrubs	Widespread from coastal to subalpine zones. Occurs in forest, shrublands, grassland & swamps
	Genistoma	1	0.28	tall shrub	Coastal and warm temperate forests north of 41°30'S.
	Griselinia	2	0.56	shrubs & small trees. Frequently epiphytic	Subalpine & temperate forest south of 35°S. Also occurs in subalpine scrub
	Halocarpus	2	0.56	low shrubs to small trees	Montane & subalpine zones. Also occurs in swampy areas in lowland South Island.
	Leptospermum	2	0.56	shrubs to medium trees	Subalpine to temperate zones. Common in swampy areas & those with infertaile soils. Can also occur on dunes & in open forest in drier areas
	Metrosideros	1	0.28	lianes, shrubs, small to tall trees, epiphytic juveniles	Subalpine to temperate zones. Often an important canopy species of lowland forest.
	Muehlenbeckia	2	0.56	lianes & shrubs	Subalpine to temperate zones. Common in exposed coastal regions, at forest margins, along river flats and in distrubed forest
	Phormium	1	0.28	tall tussock	Subalpine to temperate. Common in coastal scrub and in fertile swamps. Occurs at river and lake margins and in subalpine forest, scrub and grassland
	Gramineae	1	0.28	grasses	Alpine to temperate zones. Occur in grasslands and amongst other open vegetation. Also occur in boggy forests.
	Podocarpus	5	1.40	prostrate shrubs to tall trees	Montane to temperate. Some species (*P. ferrugineus*) are frost tolerant to -10°C
	Rumex	1	0.28	herb	Montane to lowland environments. Comoon on beaches, on disturbed ground and in grasslands

Total Terrestrial Pollen		358			
Aquatic Pollen & Fern Spores	Cyperaceae	23		herbs	Swamps & wetlands at all elevations
	Monolete Fern	9		ferns	Alpine to temperate. Occurs in understory of lowland and montane forests, river banks and other damp, shady habitats
	Trilete Fern	13		ferns	Everywhere except in very dry environments
Total Pollen & Spores		403			

Table A4.2 Pollen counts and the environmental associations of the identified pollen taxa from sample KR-B2.

	Taxon	**# of pollen grains**	**%**	**Plant type**	**Range & Environment (Sakai & Wardle (1978); Macphail & McQueen (1983); Dawson & Lucas (2000))**
Terrestrial Pollen	*Nothofagus fusca* type	354	93.16	tree	Dominant in temperate, montane & subalpine forests. *N. solandri* var *cliffortioides* frost resistant to -13°C
	Nothofagus menziesii	13	3.42	tree	Dominant in cool temperature forests in south of South Island but normally montane to subalpine. Often forms treeline.
	Coprosma	8	2.11	shrub/small tree	Coastal to lower alpine zones at forest margins & in scrub & grasslands. Tolerant of poorly drained as well as exposed areas
	Gentiana	1	0.26	herbs	Alpine to temperate grasslands. Also occurs in open areas in scrub & in herbfield & fell field environments
	Phyllocladus	1	0.26	shrub/small tree	Widespread genus. Occurs in temperate forest in North Island and on the northwest coast of the South Island. Also occurs in subalpine forest & Scrub (P. alpinus) down to sea level in south of South Island Frost tolerant to -18°C to -23°C.
	Prumnopitys taxifolia	1	0.26	tree	Lowland forests over most of country (excluding Stewart Island)
	Quintinia	1	0.26	small tree	Montane & temperate forest, particularly common on west coast of SI. Also occurs in montane forests of North Island.
	Solanum	1	0.26		
Total Terrestrial Pollen		380			
Aquatic Pollen & Fern Spores	Cyperaceae	22		herbs	Swamps & wetlands at all elevations
	Monolete Fern	6		ferns	Alpine to temperate. Occurs in understory of lowland and montane forests, river banks and other damp, shady habitats
	Trilete Fern	5		ferns	Everywhere except in very dry environments
Total Pollen & Spores		413			

Appendix 5

Summary table of all dates used for age control on ths sites examined in this thesis (Chapters 4-6)

Table A5.1. Radiocarbon and luminescene ages used for the sites examined in this thesis. Those ages not obtained specifically for this thesis are given alongside the reference from which they were obtained. Radiocarbon ages were calibrated using OXCAL (Bronk Ramsey, 2001) and the INTCAL 04 calibration curve. Exceptions include the Kawakawa Tephra which has a generally accepted age of 26.5ka BP and NZ 3168 which is beyond the range of INTCAL 04 and which was therefore calibrated used CALPAL (Weinger et al., 2006).

Site Name	NZMS Grid Reference	Latitude & Longitude	Unit Name/ Simplified Description	Dating Method	Age Designation	Age (^{14}C years)	Age (calander years)	Reference
Keoghans Road	E2399000 N5936400	41°46'S 171°40'E	KR-A3	Infrared Stimulated Luminescene	WLL452		36,200 ± 9,800 (2σ)	
			KR-A3	AMS ^{14}C age	NZA-20147	>40,000	-	
			KR-B2	Infrared Stimulated Luminescene	WLL451		28,400 ± 4,800 (2σ)	
			KR-B2	Gas sintillation ^{14}C age	Wk-16765	>45,000	-	
Wilsons Lead Road	E2385410 N5935067	41°47'S 171°30'E	Brown sand	^{14}C age	NZ 4409	12,200 ± 200	14,300 ± 650	Moar & Suggate, 1979
			Banded Organic silt	^{14}C age	NZ 3169	15,950 ± 350	19,250 ± 700	Moar & Suggate, 1979
			Blue sand	^{14}C age	NZ 4047	17,950 ± 200	21,300 ± 750	Moar & Suggate, 1979
			Massive Organic Silt	^{14}C age	NZ 4046	18,6500 ± 250	22,000 ± 750	Moar & Suggate, 1979
			Massive Organic Silt	Marker Tephra	Kawakawa Tephra	22,590 ± 230 (Froggatt & Lowe, 1990)	Accepted as 26,500	Suggate & Almond, 2005
			Massive Organic Silt	^{14}C age	NZ 3168	31,600 +1,700/-1,500	37,040 + 1,960/-1,720	Moar & Suggate, 1979
Alma Road	E2391500 N5936500	41°46'S 171°35'E	AR-4	Gas sintillation ^{14}C age	Wk 18280	5121 ± 45	5,790 ± 130	

Appendix 6

Papers submitted from this thesis

As of the submission of this thesis two papers have been submitted for publication. The first paper has been accepted and the other paper is currently in review. The manuscripts, and their current status, are included below.

Both of the papers included in this appendix are co-authored with Dr. James Shulmeister. In both cases Dr. Shulmeister's role was one of supervision including advice regarding interpretation of the data.

Philip. I. Burge.

A6.1 Burge & Shulmeister (In Press-a). An OIS 5a to OIS 4 environmental and climatic reconstruction from the northwest South Island, New Zealand using beetle fossils. Journal of Quaternary Science.

This manuscript was accepted for publication in the Journal of Quaternary Science on the 29th of August 2006.

An OIS 5a to OIS 4 environmental and climatic reconstruction from the northwest South Island, New Zealand, using beetle fossils.

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Short Title: An OIS 5a-OIS 4 environmental reconstruction, NW South Island, New Zealand.

ABSTRACT: A fossil beetle study is presented from the North-West coast, South Island, New Zealand. The samples were recovered from overbank deposits on a marine terrace situated 4km east of Westport, New Zealand (41°45’S, 171°36’E). The age of the site is constrained to between 74-40ka but discrepancies between luminescence and radiocarbon age results prevent more precise age control.

The older of two samples indicates a closed canopy *Nothofagus* (southern beech) forest with deep litter and dead wood on the forest floor. The younger sample yields a similar *Nothofagus* forest environment with subalpine affinities and nearby tussock grassland. For the older sample, mean summer and winter minimum temperatures were similar to modern values. Mean summer temperature was ca. 3.0ºC cooler than modern during the younger phase while mean minimum winter temperature was ca. 5.0ºC cooler than present indicating both cooling and increased seasonality. Both samples suggest a 30-40% decrease in mean annual precipitation from modern values.

Persistence of closed canopy *Nothofagus* forest during the period of 74-40ka contrasts with regional pollen studies which imply widespread shrub-land at these times. This implies that this site may have served as a glacial refugium for *Nothofagus* forest.

KEYWORDS: Fossil Beetles, palaeoclimate, seasonality, refugium, last glaciation New Zealand, beech forest

Introduction

The West Coast of South Island New Zealand is an important area for research into New Zealand climate history as the regional climate is controlled by sea surface temperatures in the Tasman Sea (Barrows & Juggins, 2005) immediately upwind of this coast. Some palaeoclimatic and palaeoecological work has been undertaken along the West Coast (e.g. Denton & Hendy, 1994; Vandergoes et al., 2005) but studies are remarkably limited given the importance of the region.

Pollen studies have provided most of the extant information on the palaeoenvironment and palaeoclimate in the northwest South Island (e.g. Dickson, 1972; Moar & Suggate, 1979; Moar & Suggate, 1996) and suggest that the region was unforested for long periods of the last glacial cycle instead being dominated by grassland or grass/shrubland during stadials (e.g. Dickson, 1972; Moar & Suggate, 1979; Moar & Suggate, 1996; Vandergoes et al., 2005) and open *Nothofagus menzesii* forest or shrubland during interstadials (e.g. Moar & Suggate, 1979; Moar & Suggate, 1996; Vandergoes et al., 2005).

Beetles are the most diverse group of organisms on the planet (Klimaszewski, 1997) filling a large range of ecological roles (Kuschel, 1990; Hutcheson & Kimberley, 1999) and, due to their ectothermic nature, they respond rapidly to environmental and climatic change. These responses appear to be via dispersal, as opposed to adaptation (Coope, 1978; Morgan & Morgan, 1980; Elias, 1991; Ashworth, 2001), as beetles have remained morphologically constant throughout the Quaternary (Ashworth, 2001). This constant morphology allows beetle fossils to be identified, often to species level, by comparison to modern specimens and their ability to rapidly disperse in response to climate change (Coope, 1978; Morgan & Morgan, 1980; Ashworth, 2001) makes them excellent palaeoclimate proxies. Fossil beetle research has expanded rapidly in New Zealand over the past few years (e.g. Marra, 2003a; Marra, 2003b, Marra & Leschen, 2004) and this study continues this development by providing both qualitative environmental and quantitative climatic reconstructions for the northwest coast of South Island during the early part of the last glaciation (ca. 74-40ka).

This paper reports on an outcrop (Keoghan's Road), located four kilometres east of Westport (41°46'S, 171°40'E) at ca. 40 metres above sea-level (Fig. 1). The outcrop is a 60 metre long exposure in the south bank of the Orowaiti River at the base of the so-called "German Terrace" (McPherson, 1978). The basal sedimentary unit of "German Terrace" is a marine gravel assigned to Oxygen Isotope Stage 5a (Nathan et al., 2002) (91-74ka). The marine sediments are capped by fluvial sediments from which the fossil beetles were recovered.

The area around Westport (Fig. 1) has a temperate oceanic climate with few frosts and is dominated by southwesterly winds (Hessell, 1982). Mean annual temperature at sea-level is 12.1°C (Hessell, 1982) with a summer (February) mean maximum of 19.8°C (mean summer temperature 16ºC) and winter (July) mean minimum of 4.3ºC (mean winter temperature 8.1ºC) (Anonymous, 1982). Mean annual precipitation is 2,150mm at Westport itself but rises inland with increasing altitude.

The native vegetation of the northwest coast of South Island New Zealand consists of a series of vegetation zones extending inland from the coast to alpine areas. Coastal areas are primarily forested in dense, shrubby broadleaf taxa such as northern rata (*Metrosideros robusta*), kiekie (*Freycinetia banksii*) and the native New Zealand palm (*Rhopalostylis sapida*) (McEwen, 1987) while manuka (*Leptospermum scoparium*), pakihi rush, umbrella fern (*Gleichenia* spp.) and mosses dominate in poorly drained areas (McPherson, 1978). Further inland, tall podocarp-beech forest of kahikatea (*Dacrycarpus dacrydioides*), rimu (*Dacrydium cupressinum*) and hard beech (*Nothofagus truncata*) dominate before grading into mixed hard beech (*N. truncata*), red beech (*Nothofagus fusca*) and silver beech (*Nothofagus menziesii*) forest on the lower slopes of the Paparua ranges (McEwen, 1987). Most of these lowland zones have been cleared for farming. *N. menzesii* becomes more dominant with rising altitude until it is replaced at the treeline (ca. 1300m) by sub-alpine herbs (e.g. *Aciphylla hookeri*, *Celmisia dallii*, and *Gentiana gracifolia* (McEwen, 1987)) and tussock grasses (*Chionochloa* spp.) (Wardle, 1991). The vegetation of the study site is now pasture but was probably a podocarp forest dominated by a mix of kaihikatea (*Dacrycarpus dacrydioides*) and rimu (*Dacrydium cupressinum*).

Extensive coastal terraces are preserved in this region due to continuing regional uplift (Suggate, 1965; Nathan et al., 2002) and each terrace has been assigned to an Oxygen Isotope Stage (OIS) based on the principle that the successively higher terraces are associated with different interglacial sea-levels (Suggate, 1990). Terrace stratigraphy is based on the sequence between Hokitika and Greymouth, some 100km south of the study area. The terraces are traceable for much of the distance along the coast and have been carefully mapped (Suggate & Waight, 1999; Nathan et al., 2002). Most terraces contain a package of marine gravels overlain by organic sediments of an apparent interglacial climate affinity (e.g. Moar & Suggate, 1979; Moar & Suggate, 1996) and capped by alluvial gravels which are derived from (in the south) or correlated (in the north) to glacial advances. Luminescence dating by Preusser et al. (2005) of terraces near Hokitika has demonstrated that the age inferences out to the last interglaciation are robust there. By extension the inferred ages of the younger (last glacial cycle) terraces near Westport are probably reliable.

Methods

Bulk samples were obtained from five units inferred to be overbank deposits (Fig. 2). Of the five samples only two contained enough fossil material to merit further examination. Sample KR-A3 was collected from a brownish-grey silty-sand unit (Fig. 2) while KR-B2 was obtained from a dark brown silty-clay unit with occasional woody remains. Unit KR-B2 is situated stratigraphically immediately above unit KR-A3 but is located in a different part of the outcrop (Fig. 2). Approximately 15 kg of material was recovered from KR-B2 and 5 kg from KR-A3. The bulk samples were boiled in water to gently break up the sediment without damaging the beetle fossils before being washed through a 297 micron sieve. The remainder was treated via the kerosene floatation method of Elias (1994) enabling the insect remains to be decanted off and mounted on palaeontological slides. Identification of beetle fossils was made by comparison to modern specimens at the New Zealand Arthropod Collection (NZAC) in Auckland, New Zealand. Modern ecological and collection data were collated for the identified beetle taxa. Collection data were used to obtain climate information from the mathematically derived climate surfaces of Leathwick et al. (1998) for the distribution of each taxon and the Maximum Likelihood Envelope (MLE) method (Marra et al., 2004) was used to produce estimates of three climatic variables; Mean Summer (February) Temperature, Mean Winter (July) Minimum Temperature and Mean Annual Rainfall.

MLE is a non-gaussian approach to reconstructing bioclimatic envelopes for taxon ranges designed for use with incomplete modern distribution data sets (Marra et al., 2004). Each taxon is assigned a known range in climate space based on its modern geographic distribution. MLE creates a box error at each end of the distribution based on the number of observations and the coherence of the data set. The less coherent the data or the fewer the number of data points, the larger the error term. The overlap of climate envelopes between taxa provides the range of climate estimates. This is compared to the modern mean values of the variables at the sample site to determine the change in climate from today.

Both units were sub-sampled for pollen and preparation followed the standard technique of Moore et al. (1991). Samples were then mounted in glycerol and identified using a ZEISS transmitted light microscope at 400x magnification using the published photographs and keys of Large and Braggins (1991), Moar (1993) and Pocknall (1981) as guides. For each sample a minimum of 300 terrestrial pollen grains were counted.

Samples for Infrared Stimulated Luminescence (IRSL) dating were obtained by driving 500 ml steel tubes into the sediment faces of each unit. These were then wrapped in aluminium foil and sealed with packing tape to preserve water content and retain cohesion. The samples were analysed at the Luminescence Dating Laboratory at the School of Earth Sciences, Victoria University of Wellington. *In-situ* wood was also obtained from the units and dried for three weeks at 60°C prior to being submitted to the University of Waikato Radiocarbon Dating Laboratory, New Zealand. Following pre-treatment only 0.17g of holocellulose was available for dating from the KR-A3 sample and it was sent for AMS dating at the Rafter Radiocarbon Laboratory in Petone, Wellington, New Zealand. 6.95g of holocellulose from the KR-B2 sample remained following pre-treatment and this was dated using the gas scintillation technique at the University of Waikato Radiocarbon Dating Laboratory.

Results

Summary stratigraphy

The clast support, discoidal shape and well sorted nature of basal gravels in section KR-B (Table 1) indicates that they are of marine origin. These gravels underlie "Grahams Terrace" and are mapped by Nathan et al. (2002) as OIS 5a (ca. 91-74ka) in age. Oxygen isotope ages follow the chronology of Martinson et al. (1987). These marine gravels are overlain by another unit of less well rounded gravels, with varied lithographic composition (Table 1), of alluvial origin. These gravels can be traced across the outcrop and are correlated to the basal unit observed in KR-A (Fig. 2). A sequence of finer sediments, some containing macroscopic wood, overlie the alluvial gravel unit and are inferred to be overbank deposits lying within an abandoned river channel (Fig. 2). A thin, intermittent layer of pebbles observed in section KR-A (Table 1) indicates a break in deposition above these deposits and divides them from a further series of sands and silts representing a new series of overbank deposits. These deposits vary in thickness along the outcrop and some pinch out entirely. Macroscopic wood is again obvious in some horizons and is often in growth position. The second group of overbank deposits are covered by a bed of gravels, again of alluvial origin, which are topped by a soil unit of varying thickness across the outcrop.

Chronology of the Keoghan's Road site

The position of IRSL and ^{14}C ages obtained for the two samples are indicated in Table 1 and their physical relationship to one another is illustrated in Figure 2. The IRSL ages are (Table 2a-b), 36.2 ± 9.8ka (2σ) for unit KR-A3 (WLL452) and 28.4 ± 4.8ka (2σ) for KR-B2 (WLL451), and place both units within OIS 3. However, while the stratigraphic relationship between the ages is correct, the IRSL ages disagree with the infinite radiocarbon ages of >40ka for KR-A3 (NZ-20147) and >45ka for KR-B2 (Waikato – 16765) which imply an older age for the sediments. A discussion of the age discrepancies is given below.

Palaeoenvironment and palaeoclimate of unit KR-A3

Palaeoenvironment – Pollen

Table 3 shows that *Nothofagus fusca* type pollen makes up more than 90% of pollen from this unit. *Podocarpus* and *Coprosma* spp. are present at 2% along with *N. menziesii* (1%). *Griselinia*, *Halocarpus*, *Muehlenbeckia*, and *Leptospermum* pollen all occur at trace levels, along with rare *Dacrydium* sp., *Genistoma*, Apiaceae, Poaceae, Epacridaceae and *Ascarina*. The tree and shrub pollen clearly indicates a closed canopy Fuscaspora beech forest with scattered silver beech (Macphail & McQueen, 1983). Podocarp pollen occurs in such low amounts that it is probably derived from elsewhere (Macphail & McQueen, 1983). Broadleafs and shrubs are typically under-represented in pollen diagrams and may indicate either long distance dispersal or rare local occurrence. Coprosmas, in particular, occur in beech forests and are well enough represented to suggest local occurrence (Macphail & McQueen, 1983). The understorey consists of a mix of mono- and trilete ferns and sedges, the relative abundance of Cyperaceae pollen (5.7%) indicates a moist environment such as would be found along a flood plain.

Palaeoenvironment – Beetles

All beetle taxa present in this sample are considered forest or forest floor species (Table 4) indicating that the site was forested at the time KR-A3 was deposited. In particular members of the genus *Nestrius* (weevils, family Curculionidae) are known for being flightless, leaf-litter inhabiting taxa (Kuschel, 1964) strongly indicating the presence of forest litter at the site. The Cryptorhynchini species, a tribe of weevils known to be endophytic on dead woody plants, (Lyal, 1993) and the presence of genus *Pycnomerus* (family Zopheridae), found predominantly in loose and rotten bark or under litter and stones in podocarp/broadleaf or *Nothofagus* forest (NZAC label information), also strongly support the interpretation that this fauna represents a forest environment. The presence of the water beetle (family Hydrophilidae) *Tormus nitidulus* Broun, a member of subfamily Sphaeridiinae, a group known for their habitation of damp, decaying matter (Booth et al., 1990) indicates that the environment was also moist.

Palaeoclimate

Collection location data, required for the construction of climate envelopes, was available for ten of the twelve taxa identified from this unit and the results of the climatic reconstructions from these taxa are presented in Figures 3a-c.

Figure 3a illustrates a mean summer temperature range of between 15.1ºC and 18.2ºC. This straddles the modern mean summer temperature at this site (16.5ºC) giving a median value of 16.65ºC suggesting no discernable change from modern conditions. The winter mean minimum temperature reconstruction (Fig.

3b) also straddles the modern mean for Keoghan's Road with a range of -0.3ºC to 4.3ºC, a mean drop of 1.1ºC from the present day mean minimum winter temperature of 3.4ºC. This variance in the difference between modern and reconstructed temperatures during summer and winter may indicate increased seasonality over the present day.

Figure 3c presents mean annual rainfall from KR-A3 and indicates that in addition to possible seasonally asymmetrical cooling at this time the environment was also drier, with mean annual precipitation (MAP) of between 1460mm and 2250mm per year. This is a reduction of 461mm to 1251mm from the current mean of 2711mm per year, or a reduction in MAP of between 17-46% from the present day.

Palaeoenvironment and palaeoclimate of unit KR-A2

Palaeoenvironment – Pollen

Table 3 illustrates the composition of the spot pollen sample taken from KR-B2. Again the pollen from this unit is greater than 90% *Nothofagus fusca* type with some *N. menziesii* (3.4%) and *Coprosma* spp. (2.1%). Other pollen types occur in extremely low amounts (<1.0%). The high proportion of *N. fusca* type pollen indicates a closed canopy beech forest with coprosmas in the understorey. *N. menziesii* is notoriously underrepresented in pollen diagrams (Macphail & McQueen, 1983) and the beech forest probably contains a significant proportion of *N. menziesii*. Fuscaspora beech forest is difficult to key to individual taxa but the beetle information (below) strongly suggests the larger, more lowland, red (*N. fusca*) or hard beech (*N. truncata*) types over mountain beech (*N. solandri* var. *cliffortioides*). The trace amounts of matai (*Prumnopitys taxifolia*) are probably wind derived (Macphail & McQueen, 1983). The ground cover remains a mix of trilete and monolete ferns and sedges. All indicate a moist environment.

Palaeoenvironment – Beetles

A total of 33 taxa from 12 families were obtained from unit KR-B2 (Table 5). Most of the taxa are known to inhabit forest litter (e.g. *Cyloma* “sp. group A”, Scydmaenidae sp., *Sagola* indet. sp., *Dalma pubescens* Sharp, *Zelandis* indet. sp., *Nestrius* indet. sp.), dead wood (e.g. *Pycnomerus* and the Cryptorynchinae weevil species) and fallen branches (e.g. *Zolus* indet. sp. 1). The presence of the hygrophilous forest-dwelling ground beetle (Carabidae) *Zeopoecilus putus* Broun (Larochelle & Larivière, 2001), the weevil *Euophryum confine* Broun (Green & Pitman, 2003) and an unidentified member of the Scirtidae (a family of beetles colloquially known as marsh beetles) (Klimaszewski & Watt, 1997), provide evidence that the site was moist and probably near a body of water. The presence of fungi at the site is confirmed by the presence of the mycophagus rove beetle (family Staphylinidae) *Brachynopus scutellaris* Redtenbacher (Löbl & Leschen, 2003) and the Ciidid *Orthocis undulates* Broun.

The >90% *N. fusca* type pollen (Table 3), the *in-situ* macrofossil wood and the dominance of forest taxa amongst the beetle fossils in both KR-A3 and KR-B2 appear to indicate a closed, tall beech forest. While it is possible that this forest was one of mountain beech (*N. solandri* var. *cliffortioides*) as proposed by Okuda et al. (2002) for Hawkes Bay at these times, the dominance of forest litter and dead wood inhabiting species (Tables 4 & 5) amongst the beetle taxa indicate a substantial ground cover of litter and fallen branches, something far more common in *N. fusca* (red beech) and *N. truncata* (hard beech) forests than in mountain beech forests. In summary, most of the beetles and ancillary evidence are consistent with a closed tall beech forest with dead wood and deep litter on the forest floor.

One taxon, *Liochoria* sp. 1, is recorded as being found exclusively on or above the tree-line amongst tussock and spear-grass species in the eastern ranges of South Island, New Zealand (NZAC label information). No other taxon present in this assemblage is restricted in their distribution to subalpine environments but the Ciidid *O. undulates* is thought to be representative of forest margin or shrubland environments.

The surroundings, at the time of deposition, are interpreted as a wet forest environment containing moist litter, decaying wood and fungi. The site is interpreted as being at, or near, the forest margin where it borders an area of tussock grassland.

Palaeoclimate

Data regarding the modern range of 23 of the 33 taxa was obtained for the reconstruction of climate envelopes. Most of those taxa excluded were those that could not be identified to a lower taxonomic group than family.

Analysis of the mean summer temperature (Fig. 4a) indicates a range of between 13.4ºC and 13.6ºC which is a reduction of approximately 3.0ºC from modern. Winter mean minimum temperature reconstruction (Fig. 4b) indicates a range of temperatures from -2.1ºC to -1.4ºC, a drop of between 4.0ºC and 5.5ºC from the present day mean minimum winter temperature of 3.4ºC.

Reconstruction of the mean annual rainfall (Fig. 5) also indicates drier conditions at this time with MAP of between 1500 and 1800mm compared to the modern value of 2711mm per year. This is a reduction in rainfall of between 30-40% annually.

Discussion

Age control

The most significant problem encountered in this study is the disagreement between the two dating techniques used. In short, the radiocarbon ages are at or beyond the range or radiocarbon (early OIS 3 or older) whereas the luminescence ages suggest a mid- to late- OIS 3 age. Both radiocarbon and luminescence dating have encountered problems in the hyper-humid environment of the West Coast of the South Island of New Zealand. Many radiocarbon ages have been discarded on the basis of contamination with younger carbon due to movement of carbon through sediments (e.g. Grant-Taylor & Rafter, 1971; Dickson 1972; Hammond et al., 1991) and luminescence ages sometimes give ages either too old or too young due to issues of zeroing and possibly weathering or the provenance of the dated material (e.g. Almond et al, 2001; Berger et al., 2001). However both techniques are known to work where samples are suitable.

In this instance, we prefer to accept the radiocarbon ages. Our logic is as follows. Firstly the samples used to obtain the ages are very good targets. Both samples are cellulose from wood taken from small tree stumps in growth position in the outcrop. There is no chance that the wood has been recycled from older deposits and the wood was in structurally good condition suggesting that contamination is a low probability. In many locations along the West Coast of New Zealand, old carbon contamination from limestone and calcareous sandstone could be an issue but at this site local lithologies are not carbon yielding (granites and phyllites). In contrast, the dose rates determined from the luminescence samples are both very high being about twice those typical of samples from the eastern side of New Zealand (e.g. Berger et al., 2002) and remarkably variable for samples that were recovered from only a few metres apart in similar lithologies. Furthermore, minor secular disequilibrium was observed (see Table 2a) and down face increase in uranium content is also evident. There is a strong suspicion that radioactive elements may be moving through the profile either vertically through soil processes or horizontally though percolation. This means that modern dose rates may not be a good indication of long term averages and substantial age variations are possible. If uranium or radium is concentrating in the organic rich layers where the beetles come from, the IRSL ages are minimum ages only. The total doses received by the samples at 126 and 226 Gy (Table 2b) are exceptionally high for samples of these young apparent ages. For example Wang et al (2006) treat samples with more than 50 Gy total doses as ‘old’ in IRSL dating terms. Our samples should be close to saturation and with these dose rates it is highly improbable that pre-OIS 5 samples would remain unsaturated. We conclude that the samples are likely to be OIS 5 or younger.

The samples are also taken from above marine gravels mapped as OIS 5a in age (Nathan et al., 2002). Although there is no direct age control on this terrace at this site the terraces are well mapped and the age assignations have been published and generally accepted as correct. In addition initial luminescence chronologies from the Westland coast south of this study support the younger part of the regional terrace chronology (out to OIS 5) (Preusser et al., 2005). On the basis of the current mapping of the marine unit as

OIS 5a, the stratigraphically younger position of the sampled sediments, and the constraints of the ^{14}C ages as being >40ka, we propose that the true age of the samples lies between ca. 74ka (end of OIS 5a) and ca. 40ka. We attempt no closer age control.

Environmental and climatic factors affecting beetles and the presence of outlying taxa

While MLE is designed to optimise outcomes where distribution data of taxa are poorly known, the technique is still limited by the available data base. Inaccurate reconstructions can be explained by numerous factors. These can range from a simple lack of distribution data to the influence of unknown factors acting to limit a taxon's range, and thus its apparent climate envelope. Unknown factors may be biotic, such as the distribution of a host plant whose modern distribution may be limited by clearance for pasture, or predation by introduced pests.

Temperature is often considered the most important abiotic factor affecting beetles (Yazdani & Agarwal, 1997) but other factors are also important. Moisture availability in particular is vital (Yazdani & Agarwal, 1997; Schowalter, 2000) and while this study measures MAP other sources of water, such as humidity and the availability of surface water, also play an important role in determining the climatic range that a species prefers (Yazdani & Agarwal, 1997). Local factors such as light, air currents and soil texture and composition (Yazdani & Agarwal, 1997; Schowalter, 2000) also affect the distribution of taxa. These additional factors can create a more restricted range than temperature and humidity tolerances imply and by limiting the distribution of taxa within their normal temperature and precipitation envelopes they may also explain the existence of outliers.

In the KR-A3 sample we treat the species *Tormus nitidulus* Broun, a water scavenging beetle (Family Hydrophilidae), as an outlier. Examination of the available distribution data for this species indicates that it is only known from four specimens and three collection localities, one from further south in Westland (42º36'S, 171º40'E), one from the Nelson region to the northeast (41º39', 172º39'E), and the last inland from the Westport region (42º04'S, 171º55'E) (NZAC label information). All the collection locations are at the base of the inland ranges of the South Island. If applied this taxon yields mean minimum winter temperatures of up to 4-5°C colder. However, this species occurs in a late Holocene lowland site from the Westport area (Burge, unpublished data) and there is no suggestion that winter temperatures in the late Holocene were ever significantly colder than at present. The Holocene evidence indicates that the taxon is, or was, far more widespread that is currently recorded and probably has a much broader climatic range than that calculated by the MLE model.

The KR-B2 reconstructions contain two outlying taxa, *Paracatops* sp. group A and *Philonthus rectangulus* Sharp. *Philonthus rectangulus* is an outlier in all three reconstructed climate variables while *Paracatops* sp. group A is only an outlier in the Mean Minimum Winter temperature reconstruction.

Philonthus rectangulus is a member of an extremely widespread genus yet this particular species is known from only five collection locations, of which only one is found outside the Auckland metropolitan area (ca. 36º56'S, 174º43'E), in the Nelson region (41º16'S, 173º01'E) of the South Island (NZAC label information). While it is possible that some factor other than temperature and humidity limits it to the area around Auckland and Nelson it is more likely that this species has a far more widespread distribution than is currently known and that the concentration in Auckland is due to the higher intensity of collection around the city.

Paracatops sp. group A is a collection of three species which, from the fossil fragment obtained, are indistinguishable from one another. Unfortunately the three species are known from only one, or in the case of *Paracatops luxbris* Sharp, two collection locations. These locations are widespread with *P. luxbris* occurring both in the far north (35º12'S, 173º27'E) and in the East Cape region (38º29'S, 178º04'E) of New Zealand. *Paracatops* sp. 3 also inhabits the East Coast region (38º276'S, 178º03'E) while the third species, *P. triangulum* Geamuel, is found in the far south of New Zealand (47º14'S, 167º24'E) (NZAC label information). This small number of collection localities and their extremely widespread distribution make any reconstruction based on these taxa suspect.

All three of these instances emphasise the need for modern distribution work to support paleoclimatic estimations. Such work will take decades to complete and in the meantime these outliers emphasise the necessity of carefully evaluating results of climatic reconstructions from beetles.

Palaeoclimate, palaeoenvironments and the presence of refugia between 74-40ka

The MLE temperature reconstructions indicate a shift in the samples from a period of similar temperature to the present (Fig. 3a-b) to a period of more severe cold (Fig. 4a-b). MAP reconstructions also indicate a transition from a somewhat drier period than present (Fig. 3c) to a period of even drier, although still wet, conditions (fig. 5). These changes are consistent with other palaeoclimate estimates for transitions to stadial conditions (e.g. McGlone & Topping, 1983, Mildenhall, 1994; Okuda et al., 2002).

Prior palaeoenvironmental information for the period between 74-40ka is extremely limited. Two pollen sites on the West Coast cover the early part of this period. The first is Okarito Bog from South Westland, approximately 200km to the south, which indicates that the early part of this period was one of transition from a podocarp-hardwood dominated flora to one dominated by montane and subalpine shrubs (Vandergoes et al., 2005). The second site, Sunday Creek (Dickson, 1972; Moar & Suggate, 1996), near Greymouth, indicates that the transition from late OIS 5 to early OIS 4 is a period of rapid change from a *Nothofagus fusca* type forest to grassland. This is similar to examples of the OIS 5a/OIS 4 transition from elsewhere in the country such as the Canterbury region of central South Island (Moar & Gage, 1973) and southern Wellington (Mildenhall, 1994; Mildenhall, 1995), Wairarapa (Harper, 1989; McGlone, 1989; Carter & Lian, 2000), central Tongariro (McGlone & Topping, 1983) and eastern Hawkes Bay (Okuda et al., 2002) regions of the North Island. In all these cases, environments dominated by *Nothofagus fusca* type forests underwent a transition to either grassland or grass/shrubland.

Sunday Creek does not cover the rest of OIS 4 and early OIS 3 but following the transition to a shrub/grassland environment records from Okarito Bog (Vandergoes et al., 2005) indicate that open vegetation continued for the entire period between 74-40ka. To the north, records from Wellington

(Mildenhall, 1994) also indicate the continuance of a shrub/grassland dominated flora through OIS 4 and OIS 3 but with stands of *N. menziesii* (silver beech) becoming more significant during the latter part of this period. OIS 3 records from south of Greymouth (e.g. Shanty Town (Moar & Suggate, 1996)) indicate that open *Nothofagus menzesii* forest was the dominant vegetation during this time in North Westland however a record from Wilson's Lead Road, 10km south of Westport (Moar & Suggate, 1979; Moar & Suggate, 1996) indicate *Halocarpus*/*Phyllocladus* shrubland was dominant in the Westport region at the same time (Moar & Suggate, 1996). In contrast to these records our site indicates the continuation of a *N. fusca* type forest though this period.

The apparent restriction of forest in the northwest South Island during glacial periods has previously been attributed to a combination of decreased precipitation and increased windiness (Moar & Suggate, 1996) or increased frostiness (Moar & Suggate, 1979). The 3-5°C reduction in temperatures indicated by the beetle fossils in KR-B2 (Fig. 4a-b) is consistent with estimates made from elsewhere in New Zealand for the period of OIS 4/OIS 3 using pollen (e.g. McGlone & Topping, 1983; Mildenhall, 1994; Okuda et al., 2002), Sea Surface Temperatures (e.g. Barrows & Juggins, 2005), Equilibrium Line Altitudes for glaciers (e.g. Porter, 1975) and beetle fossils (e.g. Marra et al., 2004), but are not enough to have excluded forest from western lowland areas (McGlone, 1985; McGlone et al., 1993). The continuous low occurrence of forest taxa in pollen diagrams (McGlone et al., 1993), and the rapid re-forestation of the region following the end of the last glacial, suggests that forest vegetation must have survived locally, even if only in small stands (McGlone et al., 1993). Wardle (1963) noted that the northwest of the South Island may have acted as a refugium for much of the present flora probably due to a wide variety of available habitats (Wardle, 1988). This low elevation site, sheltered to the east, distal to any glaciers, and set back from the coast but close enough to the sea to be relatively mild, is a perfect candidate for a refugium and we believe we have confirmed the first West Coast, South Island, stadial refugium for tall beech forest.

Moisture

Both samples suggest reduced moisture values at this site and the scale of the reduction (20-40%) is large enough that a decline is probably real. The impact of this moisture reduction is much less apparent. Both sets of samples indicate moist beech forest environments with ferns and sedges on the forest floor, thick leaf litter, and extensive amounts of dead wood. Given that the larger reduction is associated with a clearly cooler climate the more important humidity parameter is probably little affected and with the reconstructed mean annual precipitation still between 1500-1700mm, the environment was still humid. The implications of reduced rainfall at this site are potentially more significant for eastern regions of the South Island. If the reduced precipitation is due to drier air masses moving onto the West Coast then this would aid in the creation of a semi-arid (possibly even arid) environment on the Canterbury Plains during the early part of the last glaciation. In contrast if the reduction in mean annual precipitation is due to a weakening of westerly atmospheric circulation (e.g. Dodson, 1998; Shulmeister et al., 2004) this will have an inverse effect on the eastern South Island as there will be an increase in easterlies or southerlies resulting in increased rainfall along the east coast. Westerly atmospheric circulation during OIS 4 and OIS 3 is unconstrained (Shulmeister et al., 2004) and we are unable to conclude which of these two models is correct. Precipitation reconstructions from an East Coast OIS 4/OIS 3 site would help resolve this issue.

Seasonality

Denton et al. (2005) recently highlighted the importance of seasonality in understanding climate change and an important aspect of these data is that they give insight into seasonal variations. Rather than providing measures of annual temperature change the beetle data instead indicates that winter cooling in sample KR-B2 was ca. 2ºC greater than summer cooling. We consider that there are two potential reasons for this seasonal signal.

The first possibility is that the seasonal signal is the result of orbital forcing of insolation. The obliquity of the Earth to the Sun controls the ratio of summer to winter insolation. At 30ºS peak seasonal variation is about 290 W m^{-2} (Berger, 1992) while minimal seasonal variation is ca. 240 W m^{-2} (Berger, 1992). While the difference in insolation varies by only ca. 50 W m^{-2} this variation directly increases or decreases seasonal temperatures. Vandergoes et al. (2005) have invoked orbital forcing as an explanation for the onset of New Zealand glaciations and the seasonal signal apparent in our data may indicate that the younger unit is representative of stadial cooling. If this is the case it is apparent that conditions, while cooler, were not particularly harsh.

A second possible reason for the observed seasonal variation in temperature depression may be the consequence of seasonal expansion of Antarctic sea-ice. The extent of OIS 4/OIS 3 sea-ice is poorly constrained although evidence does exist to indicate a seasonal expansion during these times (Crosta et al., 2004). The effects of increased sea-ice are varied (Gersonde et al., 2005) however an important seasonal effect is that increased sea-ice would allow polar air masses to move further north from the Southern Ocean without modification by passage over warmer seas during winter. The magnitude of these modifications is extreme. A modern example is the change in energy flux over the Greenland Sea. During open water years air masses over the sea are warmed by more than 250 W m^{-2} (Deser et al., 2000). This regional effect is enormous and much larger than changes associated with insolation forcing. Because the sea-ice was seasonal the cooling would be concentrated in winter. During summer, circulation patterns would be more similar to modern conditions. Both sea-ice and insolation forcing of seasonality are possible and they are not mutually exclusive.

Conclusion

Fossil beetles are effective proxies for reconstructing local environmental conditions, and this study combines their use with spot pollen samples to provide an environmental and climatic reconstruction for the Westport region of the South Island, New Zealand. Discrepancies between the age outcomes from the luminescence and radiocarbon dating employed in this study make a conclusive age assignation impossible but the stratigraphic setting suggests an age between 74-40ka for the deposits.

This study adds to a series of beetle studies that highlight the persistence of tall forest in areas of New Zealand previously thought to be largely deforested during the last glacial cycle (e.g. Marra & Leschen, 2004). It indicates that *N. fusca* or *N. truncata* forest persisted through a time period previously thought to be characterised by the replacement of *N. fusca* type beech forest with shrub/grasslands or dominated by *N. menziesii* (silver beech) forest. The presence of beech at this site during stadials raises serious questions about attributing ages to West Coast sites based on apparent interglacial floras (e.g. Blue Spur Road (Moar & Suggate, 1973; Moar, 1984), Sunday Creek (Dickson, 1972), Martin's Quarry, Omanu Creek and Waimea Creek (Moar & Suggate, 1979)) as it demonstrates that something approximating an interglacial flora could persist at low elevations along the West Coast during *stadials* and interstadials. The results suggest that tall forest may be more extensive during glacial times than previously considered.

This study has also highlighted the potential for beetle fossils to assist in examining seasonal variation in palaeoclimate. The data implies enhanced seasonality at this site in the younger of the two units. The reasons for this seasonal shift are probably related to variation in seasonal insolation levels, sea-ice growth or some combination of these factors.

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Figure 1. Locality map showing sites and regions mentioned in the text with an inset enlargement of the Westport region showing the area around the study site.

Figure 2. Simplified stratigraphy of Keoghan's Road Site. Photograph (a) indicates the relative positions of the major units and the sections. (b) shows a summary log of profile KR-A with sample KR-A3 at 1.70-2.33m and (c) displays a summary log of profile KR-B with sample KR-B2 marked at 3.13-3.26m. A break in deposition between the different groups of fine sediment units is marked with a dashed line on the photograph.

Figure 3. Keoghan's Road (Unit KR-A3) climatic reconstructions: **3a**. Mean Summer (February) Temperature Reconstruction; **3b**. Keoghan Road (Unit KR-A3) Minimum Winter (July) Temperature Reconstruction; **3c** Keoghan Road (Unit KR-A3) Mean Annual Rainfall Reconstruction.

The black horizontal bars in these figures indicate the range of the variable within which the taxon are known to inhabit today. The lighter ends of the bars represent the error to these known ranges as calculated by the MLE model. The dark grey box indicates the reconstructed range of the variable including the MLE error while the light grey box illustrates the reconstructed range without the MLE error term. The solid vertical line represents the present day mean value of the variable at the site.

Figure 4. Keoghan's Road (Unit KR-B2) temperature reconstructions: **4a.** Mean Summer (February) Temperature Reconstruction; **4b**. Mean Minimum Winter (July) Temperature Reconstruction

The black horizontal bars in these figures indicate the range of the variable within which the taxon are known to inhabit today. The lighter ends of the bars represent the error to these known ranges as calculated by the MLE model. The dark grey box indicates the reconstructed range of the variable including the MLE error while the light grey box illustrates the reconstructed range without the MLE error term. The solid vertical line represents the present day mean value of the variable at the site.

Figure 5. Keoghan's Road (Unit KR-B2)Mean Annual Rainfall Reconstruction.

The black horizontal bars in these figures indicate the range of the variable within which the taxon are known to inhabit today. The lighter ends of the bars represent the error to these known ranges as calculated by the MLE model. The dark grey box indicates the reconstructed range of the variable including the MLE error while the light grey box illustrates the reconstructed range without the MLE error term. The solid vertical line represents the present day mean value of the variable at the site.

Figure 1

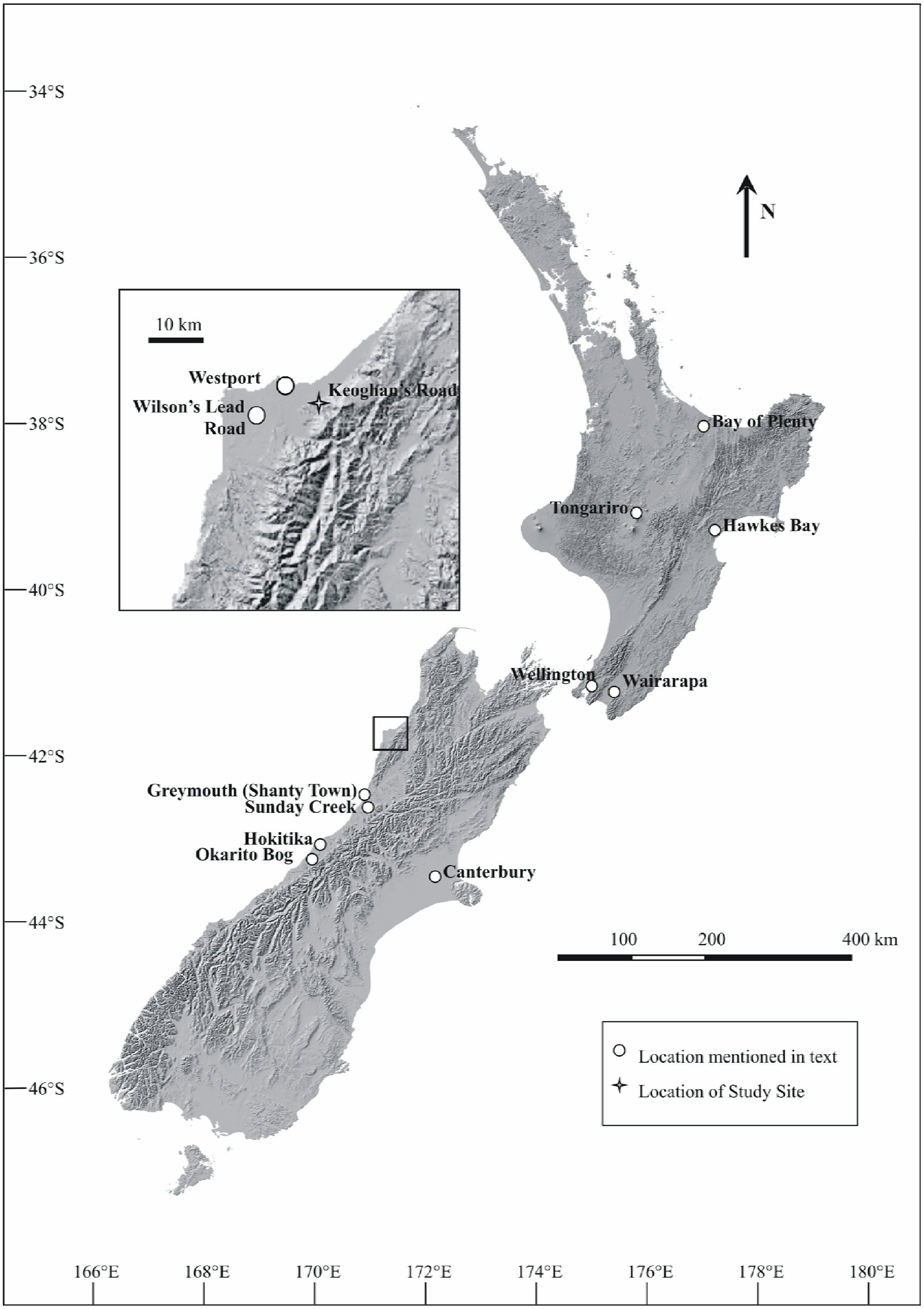
34°S
36°S
38°S
40°S
42°S
44°S
46°S
N
10 km
Westport
Keoghan's Road
Wilson's Lead Road
Bay of Plenty
Tongariro
Hawkes Bay
Wellington
Wairarapa
Greymouth (Shanty Town)
Sunday Creek
Hokitika
Okarito Bog
Canterbury
100
200
400 km
○ Location mentioned in text
✧ Location of Study Site
166°E
168°E
170°E
172°E
174°E
176°E
178°E
180°E

Figure 2

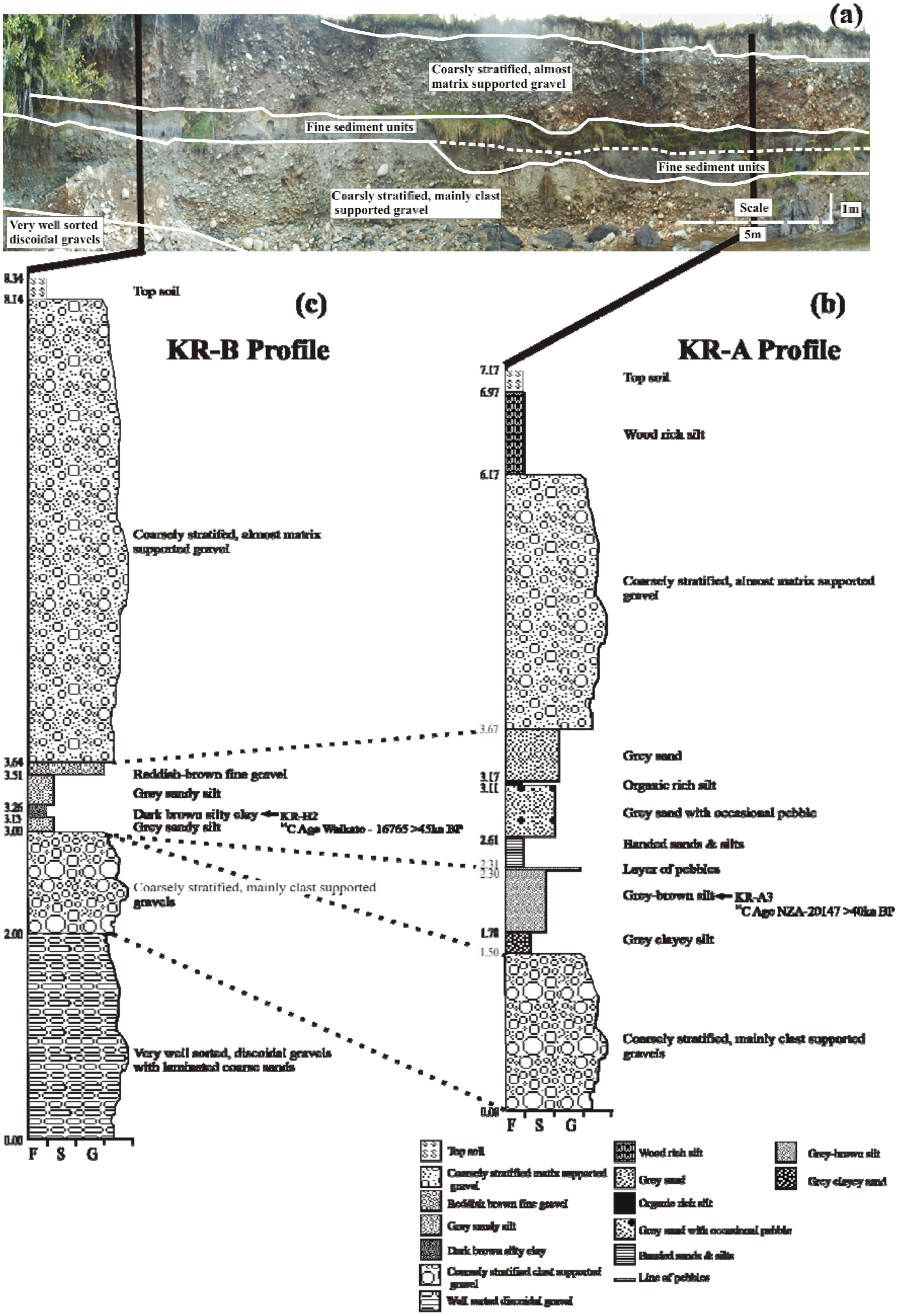
(a)
Coarsly stratified, almost matrix supported gravel
Fine sediment units
Fine sediment units
Coarsly stratified, mainly clast supported gravel
Very well sorted discoidal gravels
Scale
1m
5m
(c)
KR-B Profile
8.34
8.14
Top soil
Coarsely stratified, almost matrix supported gravel
3.64
3.51
Reddish-brown fine gravel
Grey sandy silt
3.26
3.13
Dark brown silty clay
KR-H2
^{14}C Age Waikato - 16765 >45ka BP
3.00
Grey sandy silt
Coarsely stratified, mainly clast supported gravels
2.00
Very well sorted, discoidal gravels with laminated coarse sands
0.00
F S G
(b)
KR-A Profile
7.17
Top soil
6.97
Wood rich silt
6.17
Coarsely stratified, almost matrix supported gravel
3.67
Grey sand
3.17
3.11
Organic rich silt
Grey sand with occasional pebble
2.61
Banded sands & silts
2.31
2.30
Layer of pebbles
Grey-brown silt
KR-A3
^{14}C Age NZA-20147 >40ka BP
1.78
1.50
Grey clayey silt
Coarsely stratified, mainly clast supported gravels
0.00
F S G
Top soil
Coarsely stratified matrix supported gravel
Reddish brown fine gravel
Grey sandy silt
Dark brown silty clay
Coarsely stratified clast supported gravel
Well sorted discoidal gravel
Wood rich silt
Grey sand
Organic rich silt
Grey sand with occasional pebble
Banded sands & silts
Line of pebbles
Grey-brown silt
Grey clayey sand

Figure 3

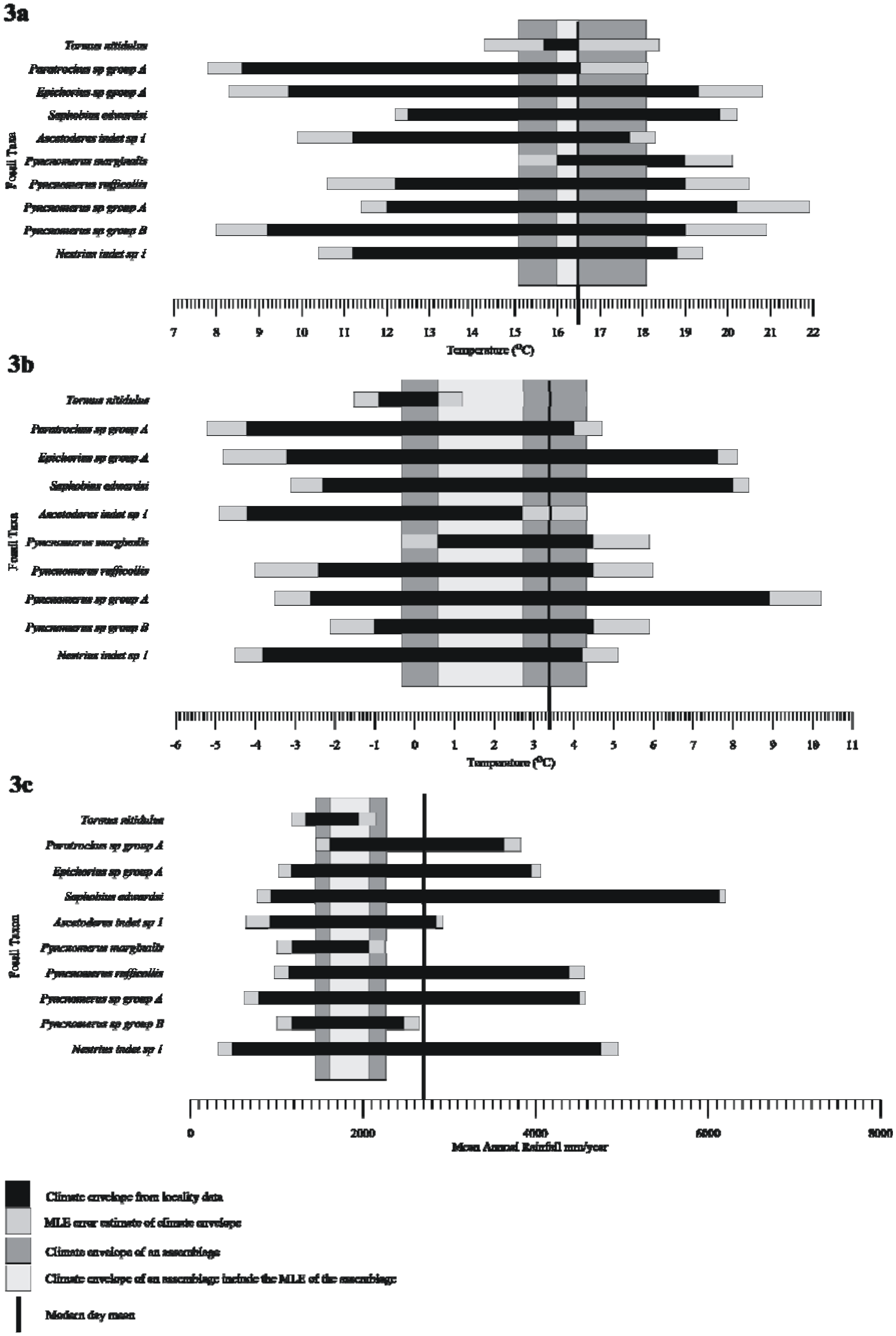
3a
Tormus nitidulus
Paratrochus sp group A
Epichorius sp group A
Saphobius edwardsi
Ascatoderus indet sp 1
Pycnomerus marginalis
Pycnomerus rufficollis
Pycnomerus sp group A
Pycnomerus sp group B
Nestrius indet sp 1
Fossil Taxa
7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22
Temperature (°C)
3b
Tormus nitidulus
Paratrochus sp group A
Epichorius sp group A
Saphobius edwardsi
Ascatoderus indet sp 1
Pycnomerus marginalis
Pycnomerus rufficollis
Pycnomerus sp group A
Pycnomerus sp group B
Nestrius indet sp 1
Fossil Taxa
-6 -5 -4 -3 -2 -1 0 1 2 3 4 5 6 7 8 9 10 11
Temperature (°C)
3c
Tormus nitidulus
Paratrochus sp group A
Epichorius sp group A
Saphobius edwardsi
Ascatoderus indet sp 1
Pycnomerus marginalis
Pycnomerus rufficollis
Pycnomerus sp group A
Pycnomerus sp group B
Nestrius indet sp 1
Fossil Taxon
0 2000 4000 6000 8000
Mean Annual Rainfall mm/year
Climate envelope from locality data
MLE error estimate of climate envelope
Climate envelope of an assemblage
Climate envelope of an assemblage include the MLE of the assemblage
Modern day mean

Figure 4

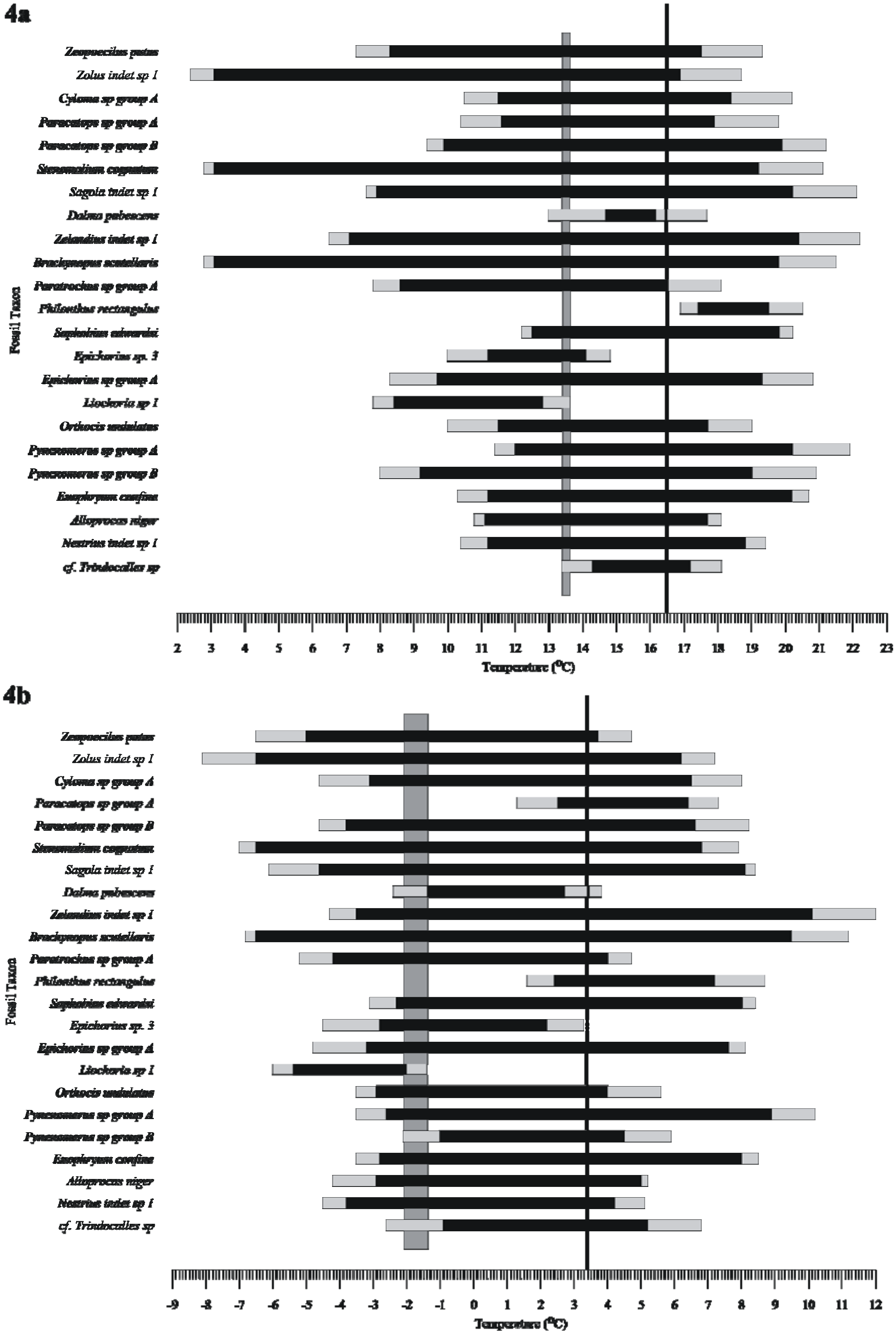
4a
Zeopoecilus putus
Zolus indet sp 1
Cyloma sp group A
Paracatops sp group A
Paracatops sp group B
Stenomalium cognatum
Sagola indet sp 1
Dalmo pubescens
Zelandius indet sp 1
Brachynopus scutellaris
Paratrochus sp group A
Philonthus rectangulus
Saphobius edwardsi
Epichorius sp. 3
Epichorius sp group A
Liochoria sp 1
Orthocis undulatus
Pycnomerus sp group A
Pycnomerus sp group B
Euophryum confine
Alloprocus niger
Nestrius indet sp 1
cf. Trindocalles sp
Fossil Taxon
2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23
Temperature (°C)
4b
Zeopoecilus putus
Zolus indet sp 1
Cyloma sp group A
Paracatops sp group A
Paracatops sp group B
Stenomalium cognatum
Sagola indet sp 1
Dalmo pubescens
Zelandius indet sp 1
Brachynopus scutellaris
Paratrochus sp group A
Philonthus rectangulus
Saphobius edwardsi
Epichorius sp. 3
Epichorius sp group A
Liochoria sp 1
Orthocis undulatus
Pycnomerus sp group A
Pycnomerus sp group B
Euophryum confine
Alloprocus niger
Nestrius indet sp 1
cf. Trindocalles sp
Fossil Taxon
-9 -8 -7 -6 -5 -4 -3 -2 -1 0 1 2 3 4 5 6 7 8 9 10 11 12
Temperature (°C)

Figure 5

-

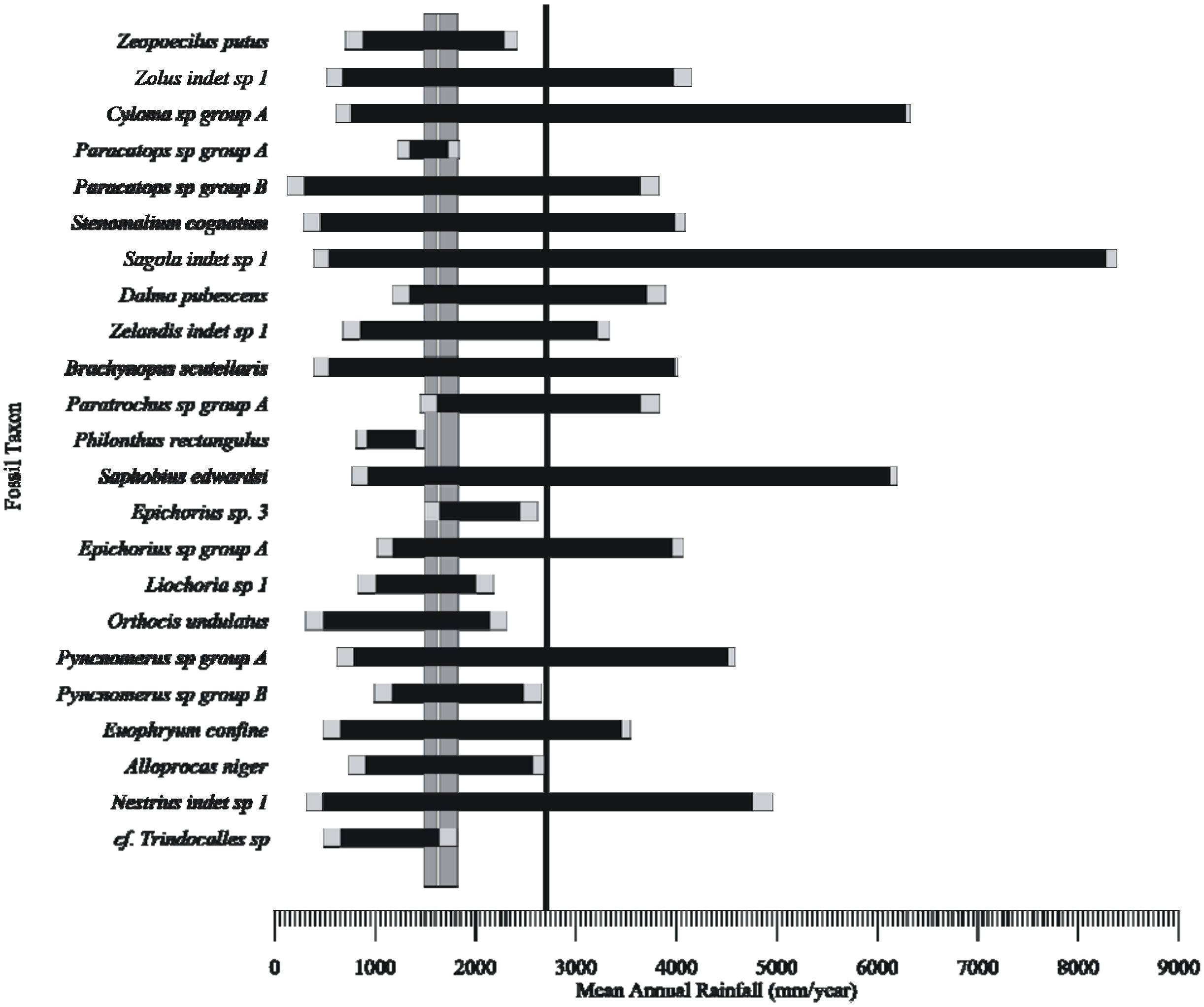
Zeopoecilus putus
Zolus indet sp 1
Cyloma sp group A
Paracatops sp group A
Paracatops sp group B
Stenomalium cognatum
Sagola indet sp 1
Dalma pubescens
Zelandis indet sp 1
Brachynopus scutellaris
Paratrochus sp group A
Philonthus rectangulus
Saphobius edwardsi
Epichorius sp. 3
Epichorius sp group A
Liochoria sp 1
Orthocis undulatus
Pyncnomerus sp group A
Pyncnomerus sp group B
Euophryum confine
Alloprocas niger
Nestrius indet sp 1
cf. Trindocalles sp
Fossil Taxon
0
1000
2000
3000
4000
5000
6000
7000
8000
9000
Mean Annual Rainfall (mm/year)

Table 1 Summary of the stratigraphy of the two sampled sections of the Keoghan's Road outcrop, West Coast, South Island, New Zealand. Location of samples and ages are marked in bold text.

Section KR-A

6.97-7.17 m	top soil
6.17-6.97 m	wood rich silt
3.67-6.17 m	coarsely stratified, weakly clast supported gravel. Clasts of up to 0.5 m diameter; dominantly granitic (80%) with low-grade serpentinite. Matrix consisting of coarse sand to granule sized particles. Lower contact sharp and undulating.
3.17-3.67 m	well sorted, coarse grey sand. Thickness of unit varies across outcrop between 0.20 and 0.50 m. Sharp basal contact.
3.11-3.17 m	organic rich silt band containing wood macrofossils in growth position. Thickness of unit varies across outcrop between 0.02-0.50 m. Sharp basal contact.
2.61-3.11 m	relatively poorly sorted brown-grey, quartz rich, coarse sand; sub-angular to sub-rounded with pebbles. Sharp undulating basal contact.
2.31-2.61 m	banded sands and silts (cm scale) with some organic lenses and macroscopic wood and leaves. Contains tree stumps in growth position.
2.30-2.31 m	break in deposition marked by intermittent line of pebbles across outcrop.
1.70-2.30 m	grey-brown silt, browning towards base. Macroscopic wood in growth position in basal 0.10 m. **Sample KR-A3. IRSL Age (WLL452) 36.2 ± 9.8 ka. ^{14}C Age (NZA-20147) >40 ka**.
1.50-1.70 m	grey clayey sand with no visible organics. Lower contact sharp and undulating.
<0.00-1.50 m	coarsely stratified, mainly clast supported, gravel. Clasts of up to 0.5m diameter; 50% granitic/50% phyllitic. Proportion of granitic clasts rises up profile from 30% at base to 70% at top. Lower contact obscured.

Section KR-B

8.14-8.34 m	top soil
3.64-8.14 m	coarsely stratified, weakly clast supported gravel. Clasts of up to 0.5 m diameter; dominantly granitic (80%) with low-grade serpentinite. Matrix consisting of coarse sand to granule sized particles. Lower contact undulating and sharp.
3.51-3.64 m	fine reddish brown gravel with sand and silt matrix. Iron pan at sharp, undulating basal contact.
3.26-3.51 m	grey sandy silt containing occasional pebbles in matrix. Unit darkens towards base. Sharp, undulating basal contact.
3.13-3.26 m	dark brown silty clay containing occasional pebbles in matrix as well as macroscopic wood. Unit lightens towards base. Lower contact undulating but sharp, unit thins towards edges. **Sample KR-A2, IRSL Age (WLL451) 28.4 ± 5.8 ka. ^{14}C Age (Waikato – 16765) >45 ka**.
3.00-3.13 m	grey sandy silt iron stained at upper and lower contacts. Sharp and undulating basal contact with iron pan.
2.00-3.00 m	coarsely stratified, mainly clast supported, gravel. Clasts of up to 0.5m diameter; 50% granitic/50% phyllitic. Proportion of granitic clasts rises up profile from 30% at base to 70% at top.
<0.00-2.00 m	very well sorted largely discoidal clasts of pebble to cobble size with very well sorted, laminated, coarse sands interbedded amongst gravels. Gravel clasts are dominantly phyllitic (70%) with granitic clasts strongly represented (30%). Sands are mica rich. Lower contact obscured.

Table 2a: Radionuclide and water contents

Sample	Unit Code	Depth below surface (m)	dD$_c$/dt (Gy/ka)[1]	Water content δ[2]	U (µg/g) from ^{234}Th,	U (µg/g)[3] from ^{226}Ra, ^{214}Pb, ^{214}Bi	U (µg/g) from ^{210}Pb	Th (µg/g)[3] from ^{208}Tl, ^{212}Pb, ^{228}Ac	K%
WLL451	KR-B2	3.5	0.1300±0.0065	1.357	**5.23±0.33**	**3.98±0.06**	**5.29±0.30**	14.91±0.17	2.15±0.05
WLL452	KR-A3	4.7	0.1121±0.0056	1.252	**6.57±0.46**	**4.70±0.07**	5.49±0.39	16.68±0.21	3.21±0.07

[1] Contribution of cosmic radiation to the total doserate, calculated as proposed by Prescott & Hutton (1994).

[2] Ratio wet sample to dry sample weight. Errors assumed 50% of (δ-1).

[3] U and Th-content is calculated from the error weighted mean of the isotope equivalent contents.

All numbers marked in bold: Minor radioactive disequilibrium (significant on 2σ-level), either between ^{234}Th and ^{226}Ra (probably due to Radium migration associated with water flow), or between ^{226}Ra and ^{210}Pb (probably due to influx of Radon).

Table 2b: Measured a-value and equivalent dose, doserate and luminescence age

Sample	a-value	D^e (Gy)	dD/dt (Gy/ka)	OSL-age (Ka)	Unit Code
*WLL451	0.069±0.005	126±3.3	4.46±0.38 (4.14±0.38)	28.4±2.9 30.6±2.9)	KR-B2
*WLL452	0.076±0.008	226±23.5	6.25±0.45 (5.90±0.45)	36.2±4.9 (38.4±4.9)	KR-A3

* These samples showed a radioactive disequilibrium (see Table 2b), and the given age was corrected accordingly. As the level of disequilibrium over time is unknown, this age is only a better estimate and cannot be seen as the true age. In brackets the uncorrected doserates and ages are given, calculated under the invalid assumption that the samples were in radioactive equilibrium (^{226}Ra contents used for calculation)

Table 4. Taxonomic list of fossil beetle taxa and their associated environments from Keoghan's Road Sample KR-A3

Taxon	Habitat/Host	Environment	Fossil Type	References/Identification Source
Hydrophilidae				
Sphaeridiinae				
Tormus cf. *nitidus*	moist leaf litter & carrion	forest floor	e	NZAC label data/NZAC
Staphylinidae				
Osoriinae				
Paratorchus "sp. group A"	primarily forest litter & humus, sometimes alpine	forest floor?	e, p	McColl, 1982; Klimaszewski et al., 1996/NZAC
Scarabidae				
Scarabaeinae				
Saphobius edwardsi	forest litter & moss	forest floorh		NZAC & LUNZ label data/NZAC
Byrrhidae				
Byrrhinae				
Epichorius "sp. group A"	moss & litter in damp areas & stream beds	nr water? forest?	p	Klimaszewski & Watt, 1997; NZAC label data/NZAC
Bothrideridae				
Bothriderinae				
Ascetoderes indet. sp.	under bark, rotting logs	forest	p	Klimaszewski & Watt, 1997; NZAC label data/NZAC
Zopheridae				
Zopherinae				
Pycnomerus marginalis	under bark, rotten logs & forest litter	forest	p	Klimaszewski & Watt, 1997; NZAC label data/NZAC
Pycnomerus rufficolis	under bark, rotten logs & forest litter	forest	p	Klimaszewski & Watt, 1997; NZAC label data/NZAC
Pycnomerus "sp. group A"	under bark, rotten logs & forest litter	forest	e	Klimaszewski & Watt, 1997; NZAC label data/NZAC
Pycnomerus "sp. group B"	under bark, rotten logs & forest litter	forest	e	Klimaszewski & Watt, 1997; NZAC label data/NZAC
Curculionidae				
Curculioninae				
Cryptorynchini				
Cryptorynchini indet spp.	forest litter & dead wood/plant material	forest	e	Lyal, 1993; May, 1993; Marra, 2003b/NZAC
"*Metacalles* genus group" sp.	forest litter & dead wood/plant material	forest	h	Lyal, 1993; May, 1993; Marra, 2003b/NZAC
Rhytirhinini				
Nestrius indet. sp.	leaf litter	forest floor	e	Kuschel, 1964; Marra, 2003b/NZAC

e = elytron, p = pronotum, h = head

Table 5. Taxonomic list of fossil beetle taxa and their associated environments from Keoghan's Road Sample KR-B2

Taxon	Habitat/Host	Environment	Fossil Type	References/Identification Source
Carabidae				
Psydrinae				
Zolus indet. sp.	fallen branches & on trees	forest	e	Larochelle & Larivière, 2001/NZAC
Harpalinae				
Zeopoecilus putus	primarily wet forest but also scrub and fellfields	forest?	e	Larochelle & Larivière, 2001/NZAC
Hydrophilidae				
Sphaeridiinae				
Tormus cf. *nitidus*	moist leaf litter & carrion	forest floor	e	NZAC label data/NZAC
Leiodidae				
Cholevinae				
Paracatops "sp. group A"	decaying organic matter, litter	forest floor?	e	Kuschel, 1990; Klimaszewski & Watt, 1997; NZAC label data/NZAC
Paracatops "sp. group B"	decaying organic matter, carrion, moss, litter	forest floor?	e	Kuschel, 1990; Klimaszewski & Watt, 1997; NZAC label data/NZAC
Scydmaenidae				
Scydmaeninae				
Scydmaenidae indet. sp.	litter, decayed wood, hollow logs, moss mats	forest floor	e	Kuschel, 1990; Klimaszewski & Watt, 1997; NZAC label data/NZAC
Staphylinidae				
Omaliinae				
Stenomalium cognatum	carrion, forest litter, under logs, vegetation nr beach	forest floor?	e	Klimaszewski & Watt, 1997; NZAC label data/NZAC
Pselaphinae				
Dalma pubescens	primarily litter & rotten wood	forest floor	e	Klimaszewski & Watt, 1997; NZAC label data/NZAC
Sagola indet. sp.	primarily litter & rotten wood	forest floor	e	Klimaszewski & Watt, 1997; NZAC label data/NZAC
Zelandius indet. sp.	litter	forest floor	e	Klimaszewski & Watt, 1997; NZAC label data/NZAC
Scaphidiinae				
Brachynopus scutellaris	underside of rotting branches/ resupinate fungi	forest	e	Löbl & Leschen, 2003; NZAC label data/NZAC
Osoriinae				
Paratorchus "sp. group A"	primarily forest litter & humus, sometimes alpine	forest floor?	p	McColl, 1982; Klimaszewski et al., 1996/NZAC
Staphylininae				
Philonthus rectangulus	forest litter, under bark, sometimes sandy intertidal	forest floor?	e	Klimaszewski et al., 1996/NZAC
Scarabidae				
Scarabaeinae				

Saphobius edwardsi	forest litter & moss	forest floor	e, h	NZAC & LUNZ label data/NZAC
Saphobius indet. sp.	primarily forest litter & moss, also on driftwood	forest floor?	e	NZAC & LUNZ label data/NZAC
Scirtidae				
Scirtidae indet spp.	vegetation near water, wet forests	nr water edge	e	Klimaszewski & Watt, 1997/NZAC
Byrrhidae				
Byrrhinae				
Epichorius “sp. group A”	moss & litter in damp areas & stream beds	nr water? forest?	h	Klimaszewski & Watt, 1997; NZAC label data/NZAC
Epichorius sp. 3	mossy logs & under *Dacrydium* bark	forest	p	NZAC label data/NZAC
Epichorius sp. 26	moss under Matagouri	forest	p	NZAC label data/NZAC
Liochoria sp. 1	tussock & speargrass above treeline	tussock grassland	p	NZAC label data/NZAC
Ciidae				
Ciinae				
Orthocis undulates	fungi, litter, shrubs and subalpine trees	forest margin/shrubland?	e	NZAC label data/NZAC
Zopheridae				
Zopherinae				
Pycnomerus “sp. group A”	under bark, rotten logs & forest litter	forest	e	Klimaszewski & Watt, 1997; NZAC label data/NZAC
Pycnomerus “sp. group B”	under bark, rotten logs & forest litter	forest	e	Klimaszewski & Watt, 1997; NZAC label data/NZAC
Chrysomelidae				
Chrysomelidae indet. sp.	low growing vegetation	forest? shrubland?	e	Klimaszewski & Watt, 1997/NZAC
Curculionidae				
Cossoninae				
Pentarthrini				
Euophryum confine	moist conditions, litter & rotten wood	moist forest	e, h	Thompson, 1989; Green & Pitman, 2003; NZAC label data/NZAC
Curculioninae				
Cryptorynchini				
Cryptorynchini indet spp.	forest litter & dead wood/plant material	forest	e, h	Lyal, 1993; May, 1993; Marra, 2003b/NZAC
“*Metacalles* genus group” sp.	forest litter & dead wood/plant material	forest	h	Lyal, 1993; May, 1993; Marra, 2003b/NZAC
cf. *Trinodicalles* indet.sp.	forest litter & dead wood/plant material, leaf mould	forest	e	Lyal, 1993; May, 1993; Marra, 2003b; NZAC label data/NZAC
Storini				
Alloprocas niger	primarily in litter & moss in *Nothofagus* forest	forest, probably *Nothofagus*	e	NZAC label data/NZAC
Rhytirhinini				
Nestrius indet. sp.	leaf litter	forest floor	e	Kuschel, 1964; Marra, 2003b/NZAC

e = elytron, p = pronotum, h = head

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Re-envisioning the structure of last glacial vegetation in New Zealand using beetle fossils

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RUNNING TITLE

Structure of the vegetation during the last glacial: A beetle's eye view.

ABSTRACT

A series of 18 fossil beetle assemblages are used to reconstruct the paleoenvironment of the north-west West Coast, New Zealand over the period of the last interstadial-stadial transition (ca. 37,000-21,300 cal yr BP). The samples were recovered from an in-filled hollow within a dune field ca. 9 km south west of Westport (41°47'S, 171°30'E). This fossil beetle reconstruction is compared to an existing palynological reconstruction from the same site.

The beetle assemblages indicate an environment of marshy shrubland interspersed with closed canopy coastal vegetation prior to glacial onset and a mosaic of closed canopy patches and open tussock grassland during full glacial conditions. These interpretations contrast with the palynologically based interpretation which indicates subalpine shrubland prior to glacial onset and widespread grassland with little woody vegetation during the period of maximum glacial cooling.

This study is consistent with other non-pollen studies in New Zealand and indicates that the palynological interpretation of the paleoenvironment of the Westport region downplays the importance of closed canopy vegetation in the area during the transition from interstadial to full glacial (stadial) conditions. It challenges the interpretation of open vegetation at low elevations during glacial periods from pollen studies.

Keywords:

Beetle fossils, glacial environment, Last Glacial Maximum, New Zealand, pollen records

INTRODUCTION

The absence of forests over much of New Zealand during the last glacial maximum (ca. 20,000 cal yr BP) is one of the long-standing conundrums in New Zealand science. Reconstructions of temperature (e.g. Willet, 1950; Barrows & Juggins, 2005) indicate that New Zealand remained warm enough to allow forest to survive over most of the North Island and in the north of the South Island (Willett, 1950) but palynological evidence appears to show that most of both major islands were vegetated with shrub- or grassland (McGlone 1988). Forest was primarily restricted to north of 37ºS (McGlone et al., 1993). Most glacial maximum pollen diagrams contain small percentages of pollen from arboreal taxa (e.g. McGlone, 1988). These have traditionally been interpreted as representing long distance dispersal of anemophilous taxa (e.g. Moar, 1972; Newnham et al., 1989; McLea, 1990) however these workers also acknowledge that some of the pollen may be locally derived.

In attempting to reconcile the pollen record with the rather moderate cooling inferred for the glacial maximum some workers (e.g. Wardle, 1988) have suggested that forest survived in refugia in the north of the South Island. This agrees with the survival of forest in the north of the South Island as previously suggested by Willett (1950) based on inferred temperature depression during glacial periods. Re-forestation of lowland New Zealand was extremely rapid, occurring within a few years hundred years of regional de-glaciation (McGlone, 1988) and while the seeds of many New Zealand forest taxa are bird-dispersed they are unlikely to have been able to spread rapidly enough from northern refugia to explain the rapid re-forestation (McGlone, 1988). This has prompted other workers (e.g. McGlone et al., 1993) to infer instead the survival of stands of sub-alpine forest in hilly regions of the North Island and in isolated pockets along the length of the South Island.

Recent evidence from phytoliths (e.g. Shulmeister et al., 2001; Carter, 2002) and beetle fossils (e.g. Marra & Leschen, 2004) indicate the survival of woody vegetation in areas of New Zealand previously thought to have been dominated by herb or grassland. These discrepancies have been explained as representing site-specific effects (e.g. Shulmeister et al., 2001) and have not been used to challenge the open landscape interpretation. New Zealand is not the only region of the world where the interpretation of the Late Pleistocene pollen record is at odds with other lines of evidence for past vegetation cover and debate has recently arisen in Europe regarding the composition of the vegetation during the last glacial period. Traditionally pollen studies indicated that central and eastern Europe was dominated by wide spread grassland with forest restricted to southern refugia near the Mediterranean (e.g. Bennett et al., 1991). More recent evidence from other proxies now indicates that conifer forest and some broadleaf taxa survived in these areas throughout the Last Glacial Maximum (LGM) (e.g. Willis et al., 2000; Willis & van Andel, 2004). This indicates that pollen records may underestimate the extent of forest vegetation in the landscape during glacial periods.

This paper reconstructs the paleoenvironment of a site near Westport, West Coast, South Island, New Zealand using beetle fossils. The insect faunal assemblages from this site cover an extended period of ca. 37,000-21,000 cal yr BP and broadly coincide with the last period of major glacial expansion during the last ice age. A palynological record from the same site has previously formed the basis of the local paleoenvironmental reconstruction for the region at this time and the results of the two methods are compared.

Fossil beetles as paleoenvironmental indicators

Beetle fossils display a remarkable degree of morphological constancy throughout the Quaternary (Ashworth, 2001) and can be identified by comparison to modern specimens. This, combined with association with macrofossils of their host plant (Coope, 1977) and ecologically compatible fossil assemblages (Coope, 1977), has lead to the conclusion that fossil beetles had the same physiological and ecological requirements as their modern descendents. Responses to Quaternary climate change were therefore probably via dispersal rather than adaptation (Coope, 1978; Morgan & Morgan, 1980) as exemplified by the migratory responses of Carabid beetles to modern climate change (Hengeveld, 1985).

The ability to identify fossil beetles by comparison to their modern descendents, their apparent ecological constancy, extreme diversity (Klimaszewski, 1997) and large range of ecological roles (Kuschel, 1990; Hutcheson & Kimberley, 1999) make them excellent proxies for identifying changes in the paleoenvironment (e.g. forest to shrub-land, shrub-land to open grassland etc.). Furthermore beetles require rapid burial to preserve as fossils and are bulky by comparison to micro-fossils so are rarely subject to long distance dispersal (Marra & Leschen, 2004). This means that, unlike palynological studies, beetle reconstructions are site specific.

Modern Physiography

The northwest coast of the South Island of New Zealand (Fig. 1) has a temperate, oceanic climate characterized by few frosts, high rainfall (mean annual precipitation of 2,150 mm) and predominantly south-westerly winds (Hessell, 1982). Mean annual temperature is 12.1 °C (Hessell, 1982) with a summer

(February) mean temperature of 16.0 °C and a winter (July) mean temperatures of 8.1 °C (Anonymous 1982).

The region is tectonically active and characterized by a series of uplifted marine terraces (McPherson, 1978; Suggate, 1989; 1992) backed to the east by the northern foothills of the Paparoa Range. The site examined in this paper is situated 9 km south west of Westport (41°47'S, 171°30'E) (Fig. 1) within a dune field that accumulated on the surface of an abandoned marine terrace. Based on the altitude of the site (ca. 35 metres above sea level) and estimated uplift rates the terrace is inferred to be last interglacial (80-125,000 yr) in age (Moar & Suggate, 1979)).

The outcrop is an exposed road cutting on the northeast side of Wilson's Lead Road (WLR) (Fig. 1). The base of the outcrop (Fig. 2) comprises a unit of coarsely stratified orange dune sands of indeterminate thickness. Weathering of these sands indicates a break in deposition between the sands and the overlying sediments (Moar & Suggate, 1979). The overlying massive organic silt unit was sampled for beetle fossils. The unit is ca. 1m thick and is the preserved remains of an in-filled hollow within the eroded remains of the dune field (Moar & Suggate, 1979). Radiocarbon dates place the beginning of silt deposition at 31,600 +1,700/-1,500 ^{14}C yr BP (NZ 3168 (Moar & Suggate, 1979)) (39,000-35,280 cal yr BP (Weninger et al., 2006)) and ending at 17,950 ± 250 ^{14}C yr BP (NZ 4047 (Moar & Suggate, 1979)) (22,050-20,550 cal yr BP (Bronk Ramsey, 2001; Reimer et al., 2004)). These dates are consistent both with the age of 18,650 ± 250 ^{14}C yr BP (NZ 4046 (Moar & Suggate, 1979)) (22,750-21,250 cal yr BP (Bronk Ramsey, 2001; Reimer et al., 2004)) from within the upper half of the unit (1.65-1.55 m) (Fig. 2) and with the position of the Kawakawa tephra (1.50-1.45 m) (Fig. 2), a volcanic ash sourced from the North Island and dated at 26,500 cal yr BP (Suggate & Almond, 2005). The organic silt unit is overlain by nearly 600 mm of finely laminated blue medium-fine sand containing visible mica. The sharp nature of the contact between this unit and the organic silt below indicates that the transition was abrupt and was probably due to erosion in the surrounding area (Moar & Suggate, 1979). This blue sand unit is in turn sharply capped by a banded, medium to coarse, brown sand unit which continues to the top of the outcrop. A 200 mm deep laminated organic silt intrudes into the brown sand unit and was dated by Moar and Suggate (1979) at 15,950 ± 350 ^{14}C years BP (NZ 3169) (19,950-18,550 cal yr BP (Bronk Ramsey, 2001; Reimer et al., 2004)) (Fig. 2).

Modern Vegetation

The native regional vegetation was cleared for pasture during the 19th and 20th centuries and information on its former composition is sparse. The local biome must therefore be extrapolated from neighboring regions. Native vegetation at the site would probably be typical of other terrace surfaces on the West Coast and consist of mixed podocarp-broadleaf-beech forest dominated by kahikatea (*Dacrycarpus dacrydioide*s), rimu (*Dacrydium cupressinum*) and hard beech (*Nothofagus truncata*) (McEwen, 1987). The proportion of these species in the forest is unknown although kahikatea tends to dominate in wet areas while rimu and hard beech dominate on older surfaces with poor soils (Wardle, 1991). Other canopy taxa likely included miro (*Prumnopitys ferruginea*), matai (*Prumnopitys taxifolia*), kaikawaka (*Libocedrus bidwillii*), kamahi (*Weinmannia racemosa*) and northern rata (*Metrosideros robusta*) with a sub-canopy of smaller trees including silver pine (*Manoao colensoi*), pigeonwood (*Hedycarya arborea*), haumakaroa (*Raukaua simplex*) and mapau (*Mysine australis*) as well as the tree ferns *Cyathea smithii* and *Dicksonia squarrosa* (Wardle, 1991). Lianas such as the ratas *Metrosideros fulgens* and *M. diffusa* and supplejack (*Ripogonum scandens*) would also have been common (Wardle, 1991). A shrub layer of *D. squarrosa*, karapapa (*Alseuosmia macrophylla*) and stinkwood (*Coprosma foetidissima*) would overshadow a fern layer dominated by *Blechnum discolor* (Wardle, 1991).

Towards the coast large canopy trees disappear and a mixture of broadleaf taxa such as northern rata (*M. robusta*), kiekie (*Freycinetia banksii*) and the New Zealand palm (*Rhopalostylis sapida*) become more dominant (McEwen, 1987). Poorly drained areas would be occupied by bog plants such as manuka (*Leptospermum scoparium*), pakihi rush (Restionaceae) and umbrella fern (*Gleichenia* spp.) (McPherson, 1978). Inland from the study site kamahi (*W. racemosa*) and hard beech (*N. truncata*) become more dominant on the lower slopes of the Paparoa Ranges although red (*Nothofagus fusca*) and silver (*Nothofagus menziesii*) beech become increasingly important with altitude (McEwen, 1987). *N. menzesii* is the dominant tree species near the tree line (ca. 1300 m) (McEwen, 1987). Above the tree line beech forest is replaced with sub-alpine herbs including *Aciphylla hookeri*, *Celmisia dallii*, *Gentiana gracifolia* and tussock grasses (*Chionochloa* spp.) (McEwen, 1987; Wardle, 1991).

METHODS

Sampling & Processing

The organic silt unit of the outcrop (Fig. 2) was sampled in 18 horizontal bands of 50 mm thickness. Each sample, designated H1 at the top of the unit to H18 at the base, was ca. 5kg. Samples were gently boiled in water to break up the sediment and disaggregated material was washed through a 297 micron sieve. The retained material was treated via the kerosene floatation method (Elias, 1994) allowing insect remains to be decanted off. Fossils were mounted on paleontology slides and identified through comparison to modern beetle specimens at the New Zealand Arthropod Collection (NZAC) in Auckland, New Zealand. Fossils were identified to species level where possible. In cases where this was impossible fossils were assigned into Recognizable Taxonomic Units (RTUs) of morphologically indistinguishable taxa (e.g. *Eupines* "sp. group A"). The term RTUs is hereafter used interchangeably with the terms "taxa" or "taxon".

Age Control

Age control on this study was based on the series of radiocarbon ages obtained by Moar & Suggate (1979) for the sampled outcrop (Fig. 2). These ages were calibrated for this study using OxCal (Bronk Ramsey, 2001) and the INTCAL04 calibration curve (Reimer et al., 2004). The exception to this was when the un-calibrated ages were beyond the range of the IntCal04 calibration curve. In these cases Calpal (Weninger et al., 2006) (http://www.calpal-online.de/) was used to obtain the calibrated ages instead.

Paleoenvironmental Reconstruction

Ecological data from the literature and entomological collections (the New Zealand Arthropod Collection (NZAC) and Lincoln University Entomology Research Museum (LUNZ)) was collated for the identified species and RTUs. These environmental data were then used to assemble a reconstruction of the past environment for each of the 18 samples based on the habitat preferences of each taxon in the assemblage. It was assumed that beetle physiology, like morphology, has remained constant throughout the Quaternary (Coope, 1977) and that the ecological requirements of modern individuals therefore reflect those of their ancestors. Each RTU was given a weighted value to provide an estimate of the openness of the environment. The weighted value was calculated from how many "habitat types" each individual RTU occurs in. Habitat types included Open Environments (e.g. grasslands, alpine herbfelds, beaches), Half-

Closed Environments (e.g. shrub-lands, forest margins), Closed Canopy Environments (e.g. forest) and Riparian/Aquatic Environments (e.g. stream edge, ponds).

RESULTS

Supplementary Table 1 contains environmental data for the 76 RTUs, from 12 Families, identified at the WLR site. Sample H18 contained only two poorly preserved fossils and as these could only be identified to the Family level sample H18 is excluded from the environmental reconstructions. The assemblages of the remaining samples indicate three assemblage zones designated as B1, B2a and B2b.

Zone B1 – Samples H17 to H15 (0.85-0.75 m) (ca. 37,000 – 34,000 cal yr BP)

Figure 3 indicates that Zone B1 is primarily dominated by a closed canopy assemblage with some taxa associated with riparian environments. An examination of the individual taxa (Supplementary Table 1) indicates that the closed canopy taxa comprise the rove beetles (Family Staphylinidae) *Brachynopus scutellaris* Redtenbacher (Klimaszewski et al., 1996; Löbl & Leschen, 2003; NZAC label data), *Vidamus* indet. sp. (Klimaszewski et al., 1996; Chandler, 2001; NZAC label data) and *Eupines* “sp. group A”, the scarab beetle (Family Scarabidae) *Saphobius edwardsi* Sharp (Emberson & Matthews, 1973; Klimaszewski & Watt, 1997; LUNZ label data; NZAC label data), the Zopheridid *Pycnomerus latitans* Sharp (Klimaszewski & Watt, 1997; LUNZ label data; NZAC label data) and a suite of indeterminate Cryptorynchini weevils (Family Curculionidae) (Lyal, 1993; May, 1993). These taxa are all associated with the forest floor where they inhabit forest litter and dead vegetation (Supplementary Table 1). The presence of the water scavenger beetle (Family Hydrophilidae) *Tormus nitidulus* Broun (Supplementary Table 1), also an inhabitant of forest, indicates that conditions were moist (Klimaszewski & Watt, 1997; Archangelsky, 2004) while a fossil elytron from the weevil *Arecocryptus* indet. sp. (Supplementary Table 1), a genus whose larvae are restricted to the native New Zealand palm (*Rhopalostylis sapida*) (May, 1993), indicates the presence of this palm at, or in close proximity to, this site. Indeterminate species of marsh beetles (Family Scirtidae), inhabitants of vegetation at the edges of streams and ponds, indicates that the site was located near a water source (Klimaszewski & Watt, 1997).

B2a – Samples H14 to H2 (0.70-0.05 m) (ca. 34,000 – 21,300 cal yr BP)

The proportion of taxa associated with riparian and aquatic environments remains relatively constant in Zone B2a which is again dominated by beetle taxa representative of a closed canopy environment (Fig. 3). The proportion of taxa associated with open environments increases (Fig. 3), however, indicating a change in the composition of the environment to a more mosaic environment of enclosed and open environments.

The closed canopy taxa include previously observed taxa such as Cryptorynchini weevils, *B. scutellaris*, and *S. edwardsi* as well as additional taxa including the Staphylinidid species *Corneolabrium mandibulare* Steel (Newton & Thayer, 1995; Klimaszewski et al., 1996), *Dalma pubescens* Sharp (Klimaszewski et al., 1996; Chandler, 2001; NZAC label data) and *Eupines rudicornis* Broun (Klimaszewski et al., 1996; Chandler, 2001; NZAC label data) (Supplementary Table 1). Terrestrial Hydrophilidae taxa (sub-family Sphaeridinae) (e.g. *T. nitidulus*, *Adolopus helmsi* Sharp) indicate that conditions under the canopy remained moist (Hansen, 1997; Klimaszewski & Watt, 1997; Marra & Leschen, 2004).

The area probably contained both streams, indicated by the presence of the Carabid beetles *Bembidion maorinum maorinum* Bates and *Bembidion tekapoense* Broun (Supplementary Table 1) (Larochelle & Larivière, 2001), and relatively still open water, indicated by the presence of the aquatic water scavenger beetles (Hydrophilidae: Hydrophilinae) *Enochrus tritus* Broun (Kuschel, 1990; Klimaszewski & Watt, 1997; Archangelsky, 2002; Archangelsky, 2004) and *Paracymus pygamaeus* Macleay (Winterbourn, 1970; Hansen, 2000; Marra & Leschen, 2004; NZAC label data). Marshy conditions are indicated by the moss beetles (Family Byrrhidae) *Curimus zeelandicus* Redtenbacher and *Curimus squamiger* Broun (Klimaszewski & Watt, 1997; Lawrence et al., 2000 onwards) and the ground beetle (Family Carabidae) *Notogonium feredayi* Bates (Larochelle & Larivière, 2001).

Notogonium feredayi is also found in tussock areas (Larochelle & Larivière, 2001) and along with the stone beetle (Family Scydmaenidae) *Adrastia nelsoni* Franz, found in alpine areas above 1,200 m (NZAC label data), and the rove beetle *Aleochara hammoni* Klimaszewski, found in tussock grasslands between 850 and 1,500 m (Klimaszewski et al., 1996; Klimaszewski & Crosby, 1997) is representative of the presence of a more open alpine grassland type environment. Open environment taxa also include the weevil genus

Irenimus, generally associated with open and forest edge environments (May, 1993; Marra, 2003; Marra & Leschen, 2004), and the weevil, *Oreocalus latipennis* Broun (Supplementary Table 1), restricted to the plant genus *Hebe* in its larval stage (May, 1993), is also indicative of open or forest-margin type vegetation as *Hebe* is typically found in open habitats and forest margins (Dawson & Lucas, 2000).

B2b – Sample H1 (0.05-0.00 m) (ca. 21,300 cal yr BP)

The final assemblage zone in Fig. 3 (B2b) is in most ways similar to the previous assemblage zone B2a (Supplementary Table 1). It is differentiated from zone B2a by the presence of the beach beetle (Family Phycosecidae) *Phycosecis limbata* Fabricius (Supplementary Table 1) which is associated with sandy environments (Klimaszewski & Watt, 1997).

DISCUSSION

Site stratigraphy & chronology

The original outcrop examined by Moar and Suggate (1979) was destroyed by road widening since it was first sampled in 1974, however Suggate and Almond (2005) determined that the modern outcrop is stratigraphically extremely similar to that sampled for the original pollen study. We are therefore confident, as in Suggate and Almond's recent re-examination of the outcrop (Suggate & Almond, 2005), in matching the results and ages from the original pollen study to those of this new reconstruction.

Environmental Reconstruction and Comparison to Pollen Record from WLR

This study recognized three different beetle assemblages designated B1, B2a and B2b. While the previous palynological study of "the Hill" (Moar & Suggate, 1979) also recognized three different zones (H1, H2a and H2b) within the same section of the outcrop the environmental reconstructions differ quite markedly from one another.

Beetle Zone B1 (ca. 37,000 – 34,000 cal yr BP)

The assemblage zone B1 correlates exactly to Pollen Zone H1 in the original pollen study of Moar and Suggate (1979). The deposition of this unit began at about 37,000 cal yr BP (Fig. 2) and is interpreted as ending at the transition between a somewhat warmer period (interstadial) into a period of full glacial conditions at ca. 34,000 cal yr BP. The beetle fossils indicate a moist closed canopy (Fig. 3, Supplementary Table 1) environment in close proximity to a water source with the beetle *Areocryptus* indet. sp. indicating the presence of nikau palm (*R. sapida*) near the site. South Island instances of *R. sapida* are found only in coastal-lowland sites north of 43º45'S (Enright & Watson, 1992) indicating that the local vegetation had coastal-lowland affinities (Dawson & Lucas, 2000).

The reconstruction of coastal closed canopy vegetation contrasts with the interpretation of the corresponding zone from Moar and Suggate (1979). That zone, H1, was correlated with other pollen diagrams from WLR (Moar & Suggate, 1979) and interpreted as representing a regional environment of wet peaty hollows and shallow ponds dominated by a *Phyllocladus* and *Halocarpus* shrub/grassland with scattered patches of *Nothofagus* in sheltered locations (Moar & Suggate, 1979). *Halocarpus* and *Phyllocladus* are generally considered to represent montane-subalpine vegetation (Macphail & McQueen, 1983; Wardle, 1991) and Moar and Suggate (1979) initially argued that, as *Nothofagus menzesii* forest survived near Hokitika (Moar & Suggate, 1973) during this time period, the Westport region must have been subjected to a regime of harsh frosts (Moar & Suggate, 1979). Moar and Suggate (1996) later revised this hypothesis arguing instead different soil development and increased windiness to explain the lack of forest in the area.

While the beetle and pollen reconstructions appear to be incongruous they can be reconciled. Examination of the pollen record from Moar and Suggate (1979) (Fig. 4) shows similarities, although not complete correspondence, to the taxonomic makeup of the lowland bogs and forest-heaths found in the Westland region near Greymouth (e.g. Mark & Smith, 1975; Wardle, 1977; Norton, 1989). This region is also known to embrace areas of coastal-lowland vegetation containing *R. sapida* (Moore & Edgar, 1970; Enright & Watson, 1992). Dickinson and Mark (1994) examined the vegetation of a Holocene dune-slack sequence near Haast in South Westland observing a pattern of herbaceous wetland taxa in poorly drained dune swales progressing through shrubland/low forest to tall mixed lowland rainforest on the dune crests (Fig. 5A). While the taxonomic composition observed at the WLR sites differs from that seen in the South Westland dune-slack sequence (Dickinson & Mark, 1994) we hypothesis that the *Halocarpus*/*Phyllocladus* shrubland indicated by the pollen (Moar & Suggate, 1979) and the closed canopy coastal vegetation indicated by the beetles could have coexisted in a similar manner.

All the WLR sites examined by Moar and Suggate (1979) occurred in “hollows in deeply eroded sands” (Moar & Suggate, 1979) and these wet, swampy areas would have been dominated by swampy herb taxa including wire brush (*Calorophus*) (Mark & Smith, 1975) which is well represented in the local pollen (Fig. 4) (Moar & Suggate, 1979). Further from the centre of these swampy areas the herbaceous vegetation would give way to woody forest-mires, similar to those seen in Westland today (Mark & Smith, 1975). These consist of a combination of *Halocarpus* and other shrubby bog taxa near the bog edge and progressively grade into a low forest of *Phyllocladus* and other low tree species (Norton, 1989). Closed canopy coastal vegetation including taxa such as *Metrosideros*, *R. sapida* and *Plagianthus* would have occupied better drained areas, such as atop dune ridges (Fig. 5A). The pollen rain into small shrub covered bogs and ponds is dominated by the pollen from the vegetation immediate surrounding the site (e.g. Jacobson & Bradshaw 1981; Macphail & McQueen 1983; Sugita, 1993) and while *R. sapida* does not occur in the pollen diagram from this site, or any of the pollen diagrams from WLR (Moar & Suggate, 1979), it is normally extremely poorly represented in pollen diagrams (Macphail & McQueen, 1983). The lack of *R. sapida* is therefore to be expected if the shrub and swamp vegetation in the immediate vicinity of the deposition zone dominates the pollen rain. Trace amounts of *Metrosideros* and *Plagianthus*-type pollen, taxa known to occur in lowland and coastal forests (MacPhail & McQueen, 1983; Allan, 1961), occur in some of the WLR pollen diagrams (e.g. Fig. 4) (Moar & Suggate, 1979) and may represent input from the local stands of coastal vegetation rather than from long distance dispersal.

Beetle Zones B2a & B2b (ca. 34,000-21,300 cal yr BP)

The transition between assemblage zone B1 and B2a is marked by an opening up of the environment (Fig. 3, Supplementary Table 1) ca. 34,000 cal yr BP with areas of open water, indicated by the occurrence of aquatic taxa such as *Paracymus pygmaeus* (Winterbourn, 1970; Hansen, 2000) and *Enochrus tritus* (Archangelsky, 2002; Archangelsky, 2004), and streams, represented by members of the *Bembidion* genus ((Larochelle & Larivière, 2001). The increase in open water is also accompanied by the spread of tussock grassland, indicated by the presence of high altitude, tussock grassland taxa such as *Aleochara hammondi*

(Klimaszewski & Crosby, 1997), and shrubby vegetation such as *Hebe*, indicated by the presence of *Oreocalus latipennis* (May, 1993). The dominant environmental signal from the beetles is, however, still one of closed canopy vegetation and the beetle assemblage is interpreted as representing a mosaic environment of woodland, tussock grassland and swamp type vegetation in an area of slow moving streams and ponds (Fig. 5B). This environment appears to remain relatively unchanged to ca. 21,300 cal yr BP when the presence of *Phycosecis limbata* in zone B2b indicates sand beginning to encroach into the site prior to the end of silt deposition (Fig. 2).

The transition from B1 to B2a corresponds to the transition from pollen zones H1 to H2a which is marked by an increase in the proportion of grass pollen and a decrease in the proportion of *Halocarpus* and *Phyllocladus* (Fig. 4). Moar and Suggate (1979) recognized that the pollen assemblage had similarities to pakihi bog vegetation in H2a and acknowledged that regional vegetation was a mosaic of different sub-alpine and lowland herbaceous vegetation characteristic of wet areas. The dominance of grass pollen prompted them to conclude that the Westport area was dominated by grassland with woody plants restricted to sheltered locations (Moar and Suggate, 1979). While such an interpretation is supported by some other pollen diagrams from the West Coast (e.g. Howard Valley (Campbell, 1986), Grahams Terrace (Mew et al., 1986)) these sites are in inland valleys near the limits of glacial ice where cold air drainage and increased frostiness would restrict the presence of forest vegetation (Smith, 1996). The WLR sites are well beyond the glacial extent, are disconnected from glacial drainages, and would not have been subject to such extreme conditions. Temperature reconstructions for the LGM using pollen (e.g. Mildenhall, 1994), glacial equilibrium line estimates (e.g. Porter, 1975) and sea surface temperatures (e.g. Barrows and Juggins, 2005) indicate the temperature reductions during New Zealand at this time were of no more than 4-5ºC and this is not enough to have excluded forest from the Westport area (McGlone, 1985; McGlone et al., 1993). Moar (1980) and Moar and Suggate (1996) again proposed strong winds as the reason for the apparent exclusion of trees from the Westport region. This is unlikely as the area was some distance inland and unlike the Cook Strait region does not act as a funnel for winds.

The apparent restriction of forest vegetation, as shown by the pollen, again contrasts with the beetle record which strongly implies the presence of closed canopy vegetation at the site. The change in the environment to include more open vegetation (Fig. 3) and the presence of streams, which are known to be important suppliers of pollen to a site, would have resulted in an effective increase in the size of the pollen collection area (Jacobson and Bradshaw, 1981). Grassland is known to be a relatively abundant producer of pollen while many New Zealand shrubland/woodland taxa are poor pollen producers due to their reliance on insect and bird pollinators (Macphail and McQueen, 1983). The contrast between the pollen and beetle reconstructions may thus simply represent a combination of an enlarged pollen collection area and low pollen producing taxa (including arboreal taxa) being overshadowed by abundant input from increased areas of grassland and local wetland taxa such as *Myriophyllum* and Cyperaceae.

The survival of a mosaic of closed canopy woodland, shrubs and grassland, while contrasting with the more inland records from the Howard Valley (Campbell, 1986) and Grahams Terrace (Mew et al., 1986), does partially agree with records from South Westland. A study from Okarito Bog (Vandergoes et al., 2005) indicates the survival of montane-subalpine shrubs in conjunction with increased grasses throughout this period. Almond et al. (2001) noted the presence of phytoliths of woody taxa in West Coast loess units associated with this time although their presence was interpreted as representing down-profile movement of phytoliths from Holocene forests through bioturbation. The persistence of woody taxa is also in agreement with records from Wellington (Pillans et al., 1993; Mildenhall, 1994) and Wairarapa (McLea, 1990) which indicate a vegetation of montane-subalpine shrubs in conjunction with increased grasses.

While similar to other New Zealand environmental reconstructions for the same time period, the vegetation mosaic found in the Westport region at the glacial maximum does not appear to be similar to any modern day New Zealand flora. This is not a situation peculiar to New Zealand. Pollen studies from Chile (Heusser et al., 1999) indicate that a no-modern-analogue sub-Antarctic parkland comprising *Nothofagus* and Poaceae occupied outwash surfaces of the Southern Lake District –Isla Grande de Chiloé, South America, at the same interstadial and stadial transition examined in this study. Evidence from New Guinea (Hope, 1989) indicates that subalpine vegetation consisting of a rich shrub-grassland mosaic occurred between lowland/montane forest and alpine grassland during the last glacial maximum. This shrub-grassland mosaic was rapidly replaced during the Holocene by a structurally different, but floristically similar, forest environment (Hope, 1989). It is possible that the rapid reforestation of the Westport region following the end of the Last Glaciation was similar to that observed in New Guinea consisting primarily of a change in the structure, rather than composition, of the vegetation.

While closed canopy vegetation is indicated by the beetle fauna in this study, the exact structure and composition of the vegetation is unknown and we cannot determine whether it was subject to increased windiness as proposed by Moar and Suggate (1996). Regardless of the structure of the woody vegetation the presence of a closed canopy woodland flora means that conditions cannot have been as harsh as previously implied in the Westport region which is in keeping with temperature reconstructions for the time period of this study (e.g. Mildenhall, 1994; Barrows and Juggins, 2005). This study is also in keeping with the recent European studies (Willis et al., 2000; Willis and van Andel, 2004) which indicate the survival of forest during glacial periods in areas that pollen records suggest are devoid of trees.

More important than any temperature inference is the observation that the current interpretation of glacial age vegetation from pollen data appears to not be robust. There are now a number of studies (e.g. Almond et al., 2001; Shulmeister et al., 2001; Carter, 2002; Marra and Leschen, 2004; Marra et al., 2006) which demonstrate that local site indicators from around New Zealand suggest woody vegetation persisting through glacial times. A variety of mechanisms have been proposed by the authors so that these differing records can be reconciled to the pollen based interpretation of glacial vegetation. Our site clearly indicates that there is at least as good a case to re-interpret the pollen information.

Conclusions

The apparent restriction of forest, and later shrub, vegetation from the Westport region during glacial times as interpreted from the pollen record has always been problematic from a paleoecological point of view. In particular the temperature depression during the last glacial does not appear to have been extreme enough to have excluded forest taxa from the region (McGlone, 1985). The beetle record presented here indicates that closed canopy woodland survived in the Westport region even though it is not reflected in the pollen record. The presence of the mosaic environment of grassland, shrubland and closed canopy woodland brings the Westport region more closely into line with reconstructions of shrub/grassland for the same time period from elsewhere in New Zealand. It also helps explain the rapid re-colonization of the area by podocarp forest at the end of the last glaciation.

Paleoecological work in New Zealand has been dominated by pollen based studies. This and other work (e.g. Marra and Leschen, 2004) indicates that the interpretation of glacial vegetation from pollen diagrams is not straightforward. Clearly the pollen diagrams accurately reflect the transmission of pollen from the host plants to the sedimentary basins but the relationship between pollen production and pollen records is not the same as during the late Holocene. A reinterpretation of glacial age floras is required.

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Fig. 1. Locality map showing sites and regions mentioned in the text. An enlargement of the study area near Westport is provided.

Fig. 2. Stratigraphy of the Wilson's Lead Road site indicating the position and description of the different units. ^{14}C ages are as previously published by Moar & Suggate (1979). Calibrated ages are from Suggate & Almond (2005).

Fig. 3. Comparison of the percentage composition of samples by habitat type. Depth measurements are the same as those illustrated in Fig. 2. Also shown is the division of the samples into the assemblage zones B1, B2a and B2b.

Fig 4. Pollen diagram from Wilson's Lead Road. The stratigraphic unit sampled for beetles is highlighted with a dashed box on the figure. Some of the plant taxa shown in the figure have undergone taxonomic revision since the original publication of this figure. Of particular relevance to this study is the change of name of the shrub taxa identified here as *Dacrydium bidwillii-biforme* to *Halocarpus bidwillii*. Figure is courtesy and copyright of the Royal Society of New Zealand (from Fig. 8, Moar & Suggate (1979)).

Fig. 5A. Idealised transect of the environment structure of the dune field at Wilson's Lead Road, Westport during interstadial conditions. The environment shifts from open water in the dune swales through mire shrubs and low trees to closed canopy coastal vegetation on the dune peaks. 5**B**. Transect of the dune field at during full glacial (stadial) conditions. The environment shows increased open water in the dune swales amongst a grass-shrubland mosaic with closed canopy woodland on the dune peaks.

Figure 1

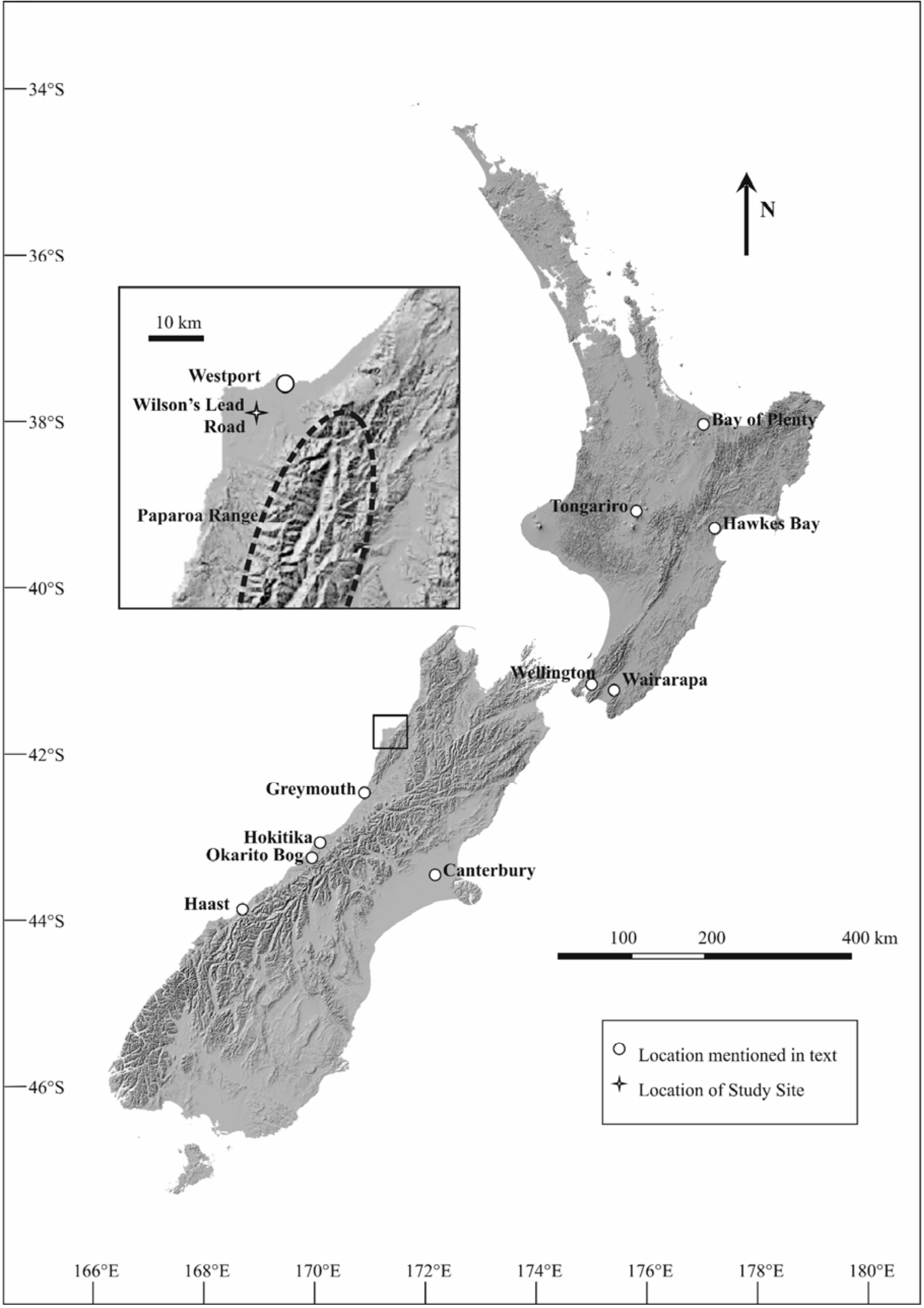

34°S
36°S
38°S
40°S
42°S
44°S
46°S
166°E
168°E
170°E
172°E
174°E
176°E
178°E
180°E
N
10 km
Westport
Wilson's Lead Road
Paparoa Range
Bay of Plenty
Tongariro
Hawkes Bay
Wellington
Wairarapa
Greymouth
Hokitika
Okarito Bog
Canterbury
Haast
100
200
400 km
○ Location mentioned in text
✦ Location of Study Site

Figure 2

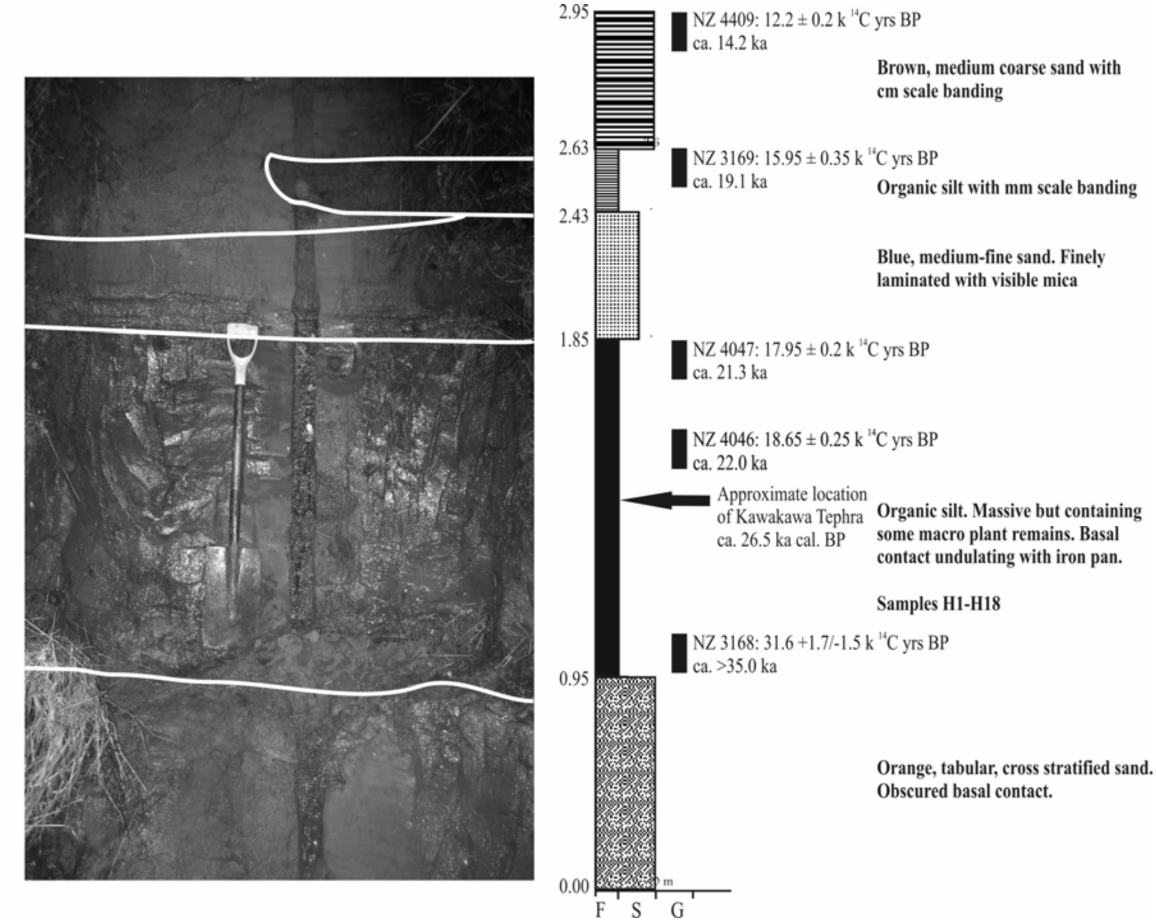
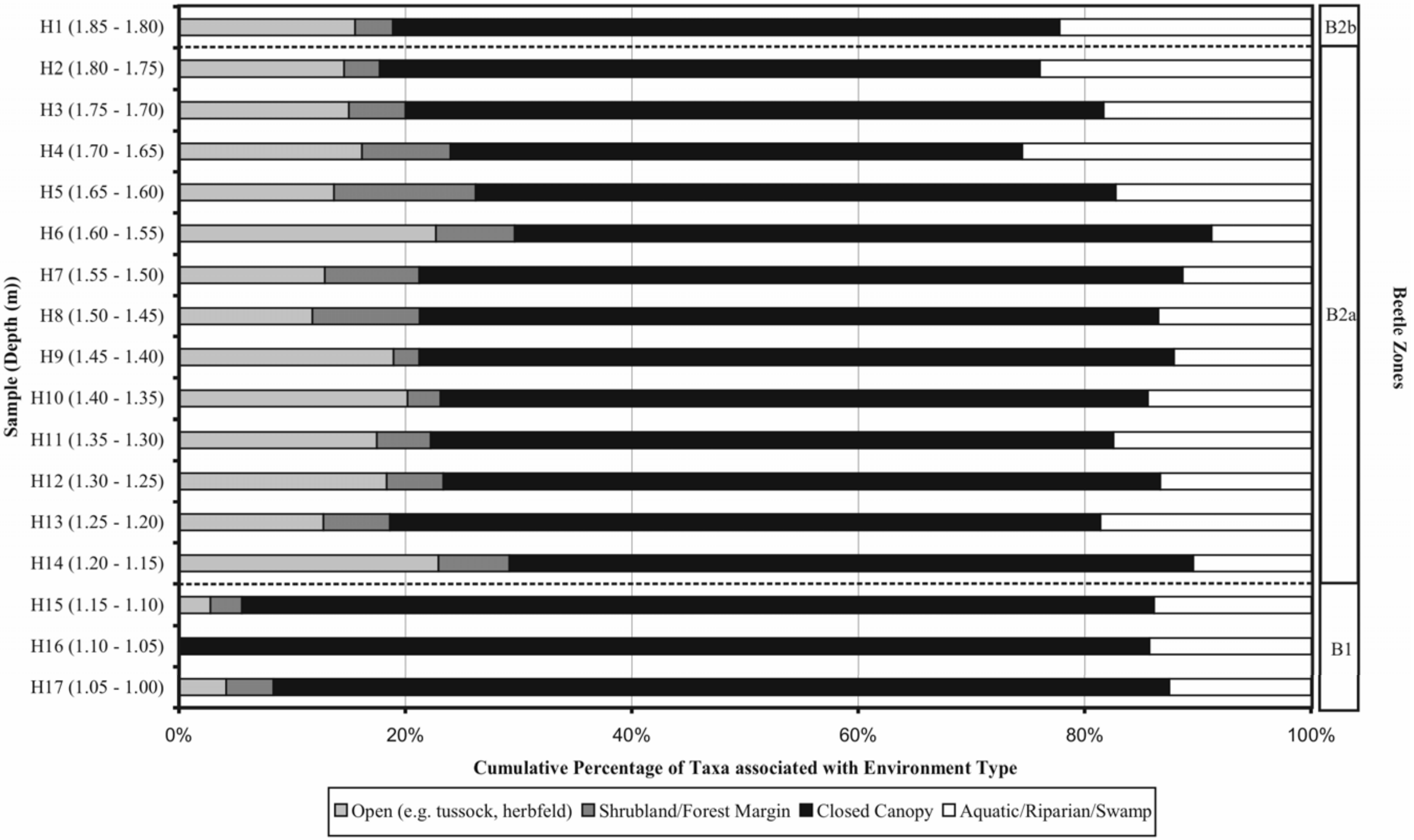

2.95
NZ 4409: 12.2 ± 0.2 k ^{14}C yrs BP
ca. 14.2 ka
Brown, medium coarse sand with cm scale banding
2.63
NZ 3169: 15.95 ± 0.35 k ^{14}C yrs BP
ca. 19.1 ka
Organic silt with mm scale banding
2.43
Blue, medium-fine sand. Finely laminated with visible mica
1.85
NZ 4047: 17.95 ± 0.2 k ^{14}C yrs BP
ca. 21.3 ka
NZ 4046: 18.65 ± 0.25 k ^{14}C yrs BP
ca. 22.0 ka
Approximate location of Kawakawa Tephra ca. 26.5 ka cal. BP
Organic silt. Massive but containing some macro plant remains. Basal contact undulating with iron pan.
Samples H1-H18
NZ 3168: 31.6 +1.7/-1.5 k ^{14}C yrs BP
ca. >35.0 ka
0.95
Orange, tabular, cross stratified sand. Obscured basal contact.
0.00
m
F
S
G

Figure 3



H1 (1.85 - 1.80)
H2 (1.80 - 1.75)
H3 (1.75 - 1.70)
H4 (1.70 - 1.65)
H5 (1.65 - 1.60)
H6 (1.60 - 1.55)
H7 (1.55 - 1.50)
H8 (1.50 - 1.45)
H9 (1.45 - 1.40)
H10 (1.40 - 1.35)
H11 (1.35 - 1.30)
H12 (1.30 - 1.25)
H13 (1.25 - 1.20)
H14 (1.20 - 1.15)
H15 (1.15 - 1.10)
H16 (1.10 - 1.05)
H17 (1.05 - 1.00)
Sample (Depth (m))
0%
20%
40%
60%
80%
100%
Cumulative Percentage of Taxa associated with Environment Type
B2b
B2a
B1
Beetle Zones
Open (e.g. tussock, herbfeld)
Shrubland/Forest Margin
Closed Canopy
Aquatic/Riparian/Swamp

Figure 4

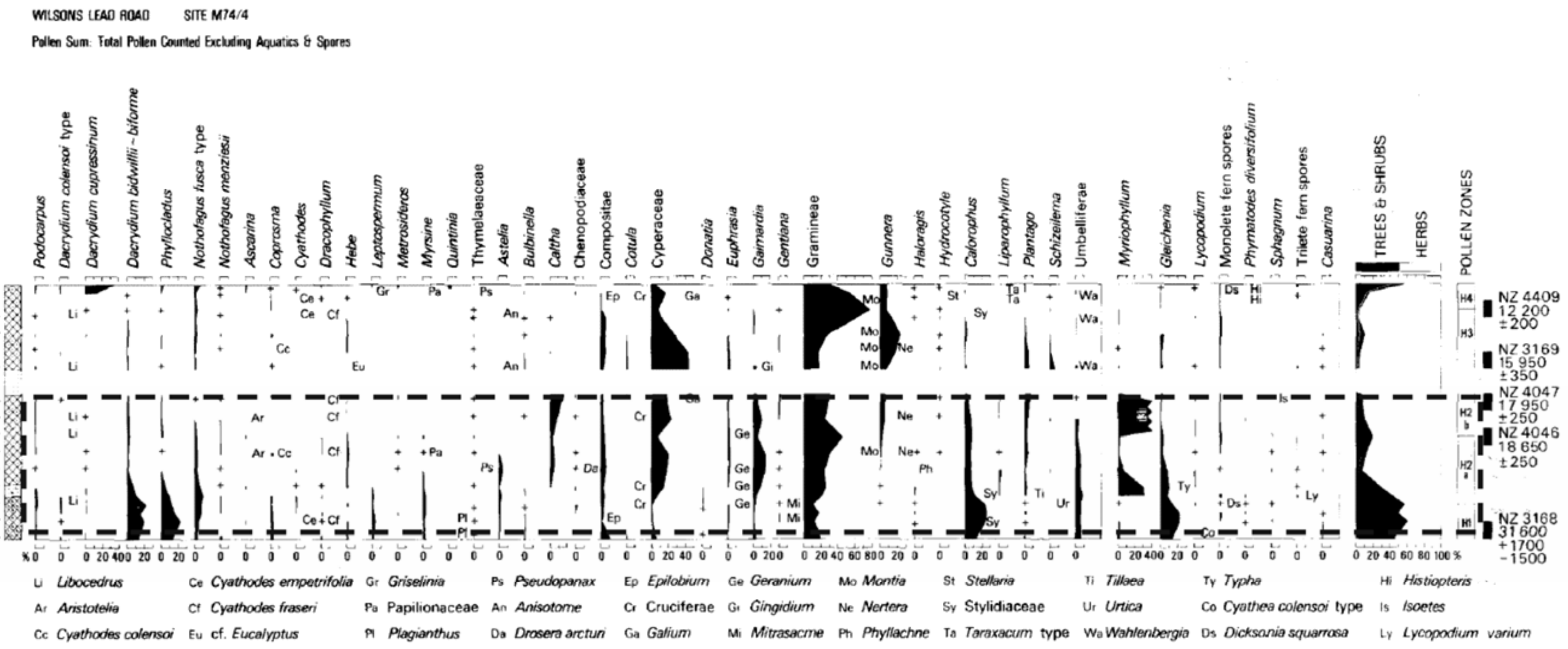
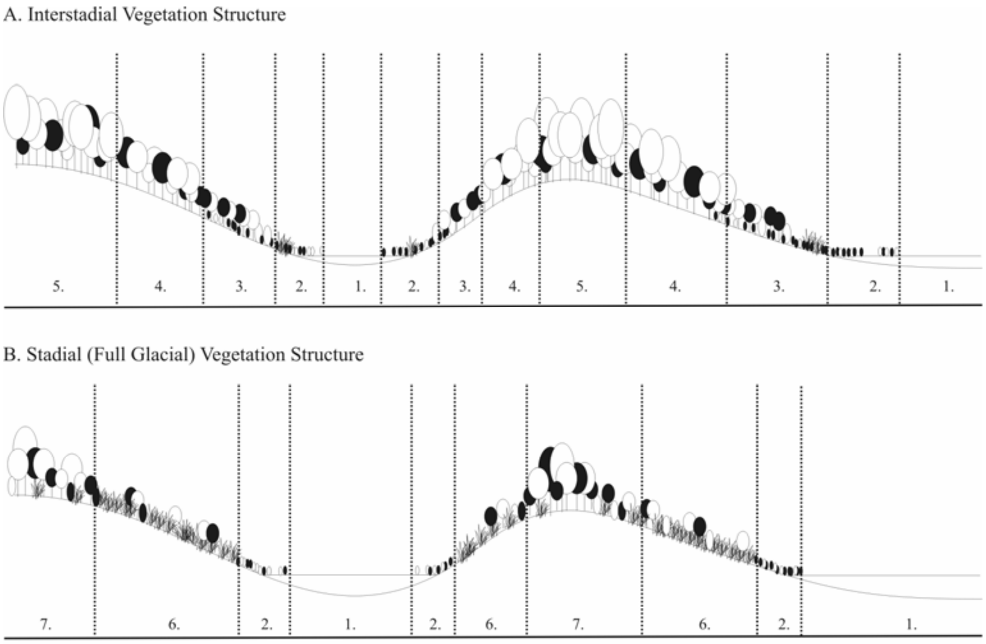

WILSONS LEAD ROAD SITE M74/4
Pollen Sum: Total Pollen Counted Excluding Aquatics & Spores
Podocarpus
Dacrydium colensoi type
Dacrydium cupressinum
Dacrydium bidwillii – biforme
Phyllocladus
Nothofagus fusca type
Nothofagus menziesii
Ascarina
Coprosma
Cyathodes
Dracophyllum
Hebe
Leptospermum
Metrosideros
Myrsine
Quintinia
Thymelaeaceae
Astelia
Bulbinella
Caltha
Chenopodiaceae
Compositae
Cotula
Cyperaceae
Donatia
Euphrasia
Gaimardia
Gentiana
Gramineae
Gunnera
Haloragis
Hydrocotyle
Calorophus
Liparophyllum
Plantago
Schizeilema
Umbelliferae
Myriophyllum
Gleichenia
Lycopodium
Monolete fern spores
Phymatodes diversifolium
Sphagnum
Trilete fern spores
Casuarina
TREES & SHRUBS
HERBS
POLLEN ZONES
cm
H4
H3
H2 b
H2 a
H1
NZ 4409 12 200 ±200
NZ 3169 15 950 ±350
NZ 4047 17 950 ±250
NZ 4046 18 650 ±250
NZ 3168 31 600 +1700 −1500
Li Libocedrus
Ar Aristotelia
Cc Cyathodes colensoi
Ce Cyathodes empetrifolia
Cf Cyathodes fraseri
Eu cf. Eucalyptus
Gr Griselinia
Pa Papilionaceae
Pl Plagianthus
Ps Pseudopanax
An Anisotome
Da Drosera arcturi
Ep Epilobium
Cr Cruciferae
Ga Galium
Ge Geranium
Gi Gingidium
Mi Mitrasacme
Mo Montia
Ne Nertera
Ph Phyllachne
St Stellaria
Sy Stylidiaceae
Ta Taraxacum type
Ti Tillaea
Ur Urtica
Wa Wahlenbergia
Ty Typha
Co Cyathea colensoi type
Ds Dicksonia squarrosa
Hi Histiopteris
Is Isoetes
Ly Lycopodium varium

Figure 5



A. Interstadial Vegetation Structure

B. Stadial (Full Glacial) Vegetation Structure

Key to Environment Types

1. Open Water
2. Mire Vegetation
3. Mire Edge Shrubs (e.g. *Halocarpus*)
4. Low Trees & Shrubs (e.g. *Phyllocladus*)
5. Closed Canopy Coastal Vegetation (e.g. *Rhopalostylis sapida*)
6. Grass/Shrub-land Mosaic
7. Closed Canopy Woodland

Supplementary Table 1. Fossils beetles retrieved from the first seventeen samples from Wilson's Lead Road and their associated environments. The 18th sample is not included as it contained no identifiable beetle remains. Environmental information was collated from [1]Linsey 1959; [2]Winterbourn 1970; [3]Emberson & Matthews 1973; [4]Lindroth 1976; [5]McColl 1982; [6]Newton 1984; [7]Barratt & Patrick 1987; [8]Thompson 1989; [9]Booth et al. 1990; [10]Kuschel 1990; [11]Chandler & Peck 1992; [12]Lyal 1993; [13]May 1993; [14]Newton & Thayer 1995; [15]Klimaszewski et al. 1996; [16]Hansen 1997; [17]Klimaszewski & Crosby 1997; [18]Klimaszewski & Watt 1997; [19]Slipinski & Lawrence 1997; [20]Hansen 2000; [21]Leschen 2000; [22]Lawrence et al. 2000 onwards; [23]Chandler 2001; [24]Larochelle & Larivière 2001; [25]Löbl & Leschen 2003; [26]Marra 2003; [27]Archangelsky 2004; [28]Marra & Leschen 2004, [29]NZAC specimen label data and [30]LUNZ specimen label data

Sample	**H1**	**H2**	**H3**	**H4**	**H5**	**H6**	**H7**	**H8**	**H9**	**H10**	**H11**	**H12**	**H13**	**H14**	**H15**	**H16**	**H17**	
Depth (m)	**1.85-1.80**	**1.80-1.75**	**1.75-1.70**	**1.70-1.65**	**1.65-1.60**	**1.60-1.55**	**1.55-1.50**	**1.50-1.45**	**1.45-1.40**	**1.40-1.35**	**1.35-1.30**	**1.30-1.25**	**1.25-1.20**	**1.20-1.15**	**1.15-1.10**	**1.10-1.05**	**1.05-1.00**	
Taxon																		**Environment**
CARABIDAE																		
Bembidion indet. sp.										*								Riparian [4, 18, 24]
Bembidion maorinum maorinum Bates											*		*					Riparian, open ground [9, 18, 24]
Bembidion tekapoense Broun											*	*						Riparian, open ground [9, 18, 24]
Bembidion wanakense Lindroth				*														Riparian, open ground [4, 18, 24]
Oopterus indet. sp.						*	*		*	*	*							Forest, open vegetation [18, 24, 29, 30]
Oopterus pallidipes Broun		*	*				*	*	*									Fell fields, forest [18, 24, 29]
Dierochile flavipes	*																	Forest [18, 24, 29]
Notagonium feredayi Bates	*	*	*	*	*			*	*									Open vegetation, swamps [18, 24, 29]
Notogonium indet. sp.									*	*	*	*	*					Hygrophilous [18, 24]
Scopodes "sp. group A"		*		*	*	*		*	*	*								Eurytopic [18, 24, 29]
Scopodes indet. sp.											*							Eurytopic [18, 24, 29]
HYDROPHILIDAE																		
Enochrus tritus Broun			*															Pond or swamp [10, 18, 27]
Paracymus pygmaeus Macleay				*				*										Slow or still water [2, 18, 20, 27, 28]
Adolopus helmsi Sharp		*	*	*	*			*	*	*	*							Moist forest [16, 18,]

																	$^{28, 29}$
Adolopus indet. sp.		*	*	*	*	*	*	*	*	*	*	*	*	*			Moist forest $^{10, 16, 18, 28, 29}$
Cyloma "sp group B"		*	*		*	*	*	*	*	*	*						Moist forest $^{16, 18, 29}$
Cyloma indet. sp.	*																Moist forest $^{16, 18, 29}$
Sphaeridiinae indet. sp.										*	*						Moist terrestrial $^{16, 18, 27, 29}$
Tormus nitidulus Broun	*	*	*	*	*	*	*	*	*	*	*	*	*			*	Moist forest $^{16, 18, 29}$
LEIODIDAE																	
Isocolon modestum Broun		*	*	*				*									Forest, swamp $^{10, 29}$
Leiodidae unnamed sp.									*	*		*		*			Forest, open grassland $^{10, 11, 21}$
SCYDMAENIDAE																	
Adrastia nelsoni Franz						*	*				*						Montane grassland, shrubland $^{6, 10, 18, 29}$
Scydmaenidae "sp group A"	*				*		*	*	*	*	*	*	*				Forest, grassland, shrubland $^{6, 10, 18, 29}$
Scydmaenidae indet. spp.										*							Forest, grassland, shrubland $^{6, 10, 18, 29}$
STAPHYLINIDAE																	
Corneolabium mandibulare Steel				*				*	*	*	*	*	*	*			Forest $^{14, 15, 18}$
Ischnoderus curtipennis Broun			*														Forest $^{10, 14, 28}$
Stenomalium cognatum Broun			*														Forest $^{14, 29}$
Stenomalium indet. sp.			*			*	*		*	*							Forest, beaches $^{14, 29}$
Dalma pubescens Sharp								*				*	*				Forest $^{18, 29}$
Eupines "sp group A"	*			*		*	*	*	*	*	*	*	*	*	*	*	Forest $^{10, 15, 18, 23, 29}$
Eupines "sp group B"		*															Forest $^{15, 18, 23, 29}$
Eupines indet. spp.					*		*	*			*						Forest $^{10, 15, 18, 23, 29}$
Eupines monstrosa Reitter									*								Forest $^{25, 23, 29}$
Eupines rudicornis Broun			*				*	*		*	*						Forest $^{15, 23, 29}$
Pselaphinae indet. spp.									*	*	*	*	*				Forest $^{18, 23}$
Pselaphus indet. sp.									*	*	*	*	*	*			Forest, grassland $^{10, 18, 23, 29}$
Sagola indet. sp.						*		*			*						Euytopic $^{10, 18, 23, 29}$

Vidamus indet. sp.								*		*	*	*			*		*	Forest [9, 15, 18, 23, 29]
Zelandius indet. sp.							*	*		*	*							Forest [10, 15, 18, 23, 29]
Aleocharinae indet. sp.										*								Eurytopic [15, 18]
Aleochara hammondi Klimaszewski		*	*			*												Montane tussock grassland [15, 17]
Brachynopus scutellaris Redtenbacher	*	*	*	*	*	*	*	*	*	*	*	*	*				*	Forest [15, 25]
Paratrochus "sp group A"														*	*	*	*	Eurytopic [5, 6, 9, 15, 18]
Agnosthaetus indet. sp.										*	*							Forest, grassland [15, 18, 29]
Hyperomma indet. sp.							*	*	*	*			*					Forest, waters edge [10, 15, 18, 29]
Philonthus indet. sp.	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*		*	Eurytopic [15]
Staphylinidae indet. spp.									*	*	*		*					Eurytopic [15]
SCARABIDAE																		
Saphobius edwardsi Sharp						*	*	*	*	*		*			*			Forest [3, 9, 18, 29, 30]
Saphobius indet. sp.							*		*									Forest [3, 9, 18, 29, 30]
SCIRTIDAE																		
Scirtidae indet. spp.	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	Vegetation nr water, forest [18]
BYRRHIDAE																		
Curimus "sp group A"	*																	Swamp [18, 22, 29]
Curimus squamiger Broun		*																Swamp [18, 22, 29]
Curimus zeelandicus Redtenbacher							*											Near swampy ponds [18, 22, 29]
Epichorius "sp group A"				*		*	*	*	*	*	*	*	*					Eurytopic [7, 18, 29]
Epichorius indet. sp.	*	*		*	*		*	*	*	*	*	*	*	*	*	*		Eurytopic [7, 18, 29]
Epichorius sp. 26							*											Insufficent habitat information [29]
PHYCOSECIDAE																		
Phycosecis limbata Fabricius	*																	Beach, dune field [18, 29]
ZOPHERIDAE																		
Coxelus indet. sp.							*											Forest, shrubland, open vegetation [10, 18, 19, 29]
Pycnomerus "sp group B"															*			Forest, dead wood [18, 29, 30]
Pycnomerus latitans Sharp															*			Forest, dead wood [18, 29, 30]
CERAMBYCIDAE																		

Hybolasius "sp group A"								*										Eurytopic [1, 9, 28, 29]
CHRYSOMELIDAE																		
Adoxia indet. sp.	*	*		*														Swamp, forest, shrubs [9, 10, 18, 29]
Chrysomelidae indet. sp. 1	*	*	*	*	*	*	*	*	*	*	*	*						Low vegetation [9, 18]
Chrysomelidae indet. sp. 2		*		*			*				*							Low vegetation [9, 18]
Caccomolpus cinctiger Broun				*														Eurytopic [9, 18, 29]
CURCULIONIDAE																		
Areocryptus indet. sp.																*		Specific to *Rhopalostylis sapida* = coastal forest [13, 29]
Cryptorynchini indet. spp.	*	*			*	*	*	*	*	*	*	*	*	*	*	*	*	Forest [12, 13, 26]
Areoscapsus indet. sp.										*								Unknown (probably forest) [29]
Areoscapus estriatus Broun	*																	Forest [29]
Areoscapus subcostatus Broun							*	*										Forest [29]
Bryocatus amplus Broun										*								Moss, sea-level to 1400m [13, 29]
Oreocalus latipennis Broun					*													Specific to *Hebe* = open vegetation or forest margin [13, 18]
Phemus indet. sp.				*		*	*	*	*		*	*	*					Forest [29]
Gromilus indet. sp.						*	*	*	*	*	*	*		*				Forest, grassland [10, 13, 18, 29]
Irenimus indet. sp.			*	*	*		*	*				*	*	*				Forest edge, grassland [13, 18, 26, 28]