

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

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Abstract

A series of 18 fossil beetle assemblages are used to reconstruct the paleoenvironment of the northwest 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.

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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., Willett, 1950; Barrows and 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 shrubs or grassland (McGlone, 1988). Forest was primarily restricted to north of 37°S (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 anemo-

philous 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. Reforestation of lowland New Zealand was extremely rapid, occurring within a few years hundred years of regional deglaciation (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 reforestation (McGlone, 1988). This has prompted other workers (e.g., McGlone et al., 1993) to infer instead the survival of stands of subalpine forest in hilly regions of the North Island and in isolated pockets along the length of the South Island.

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Recent evidence from phytoliths (e.g., Shulmeister et al., 2001; Carter, 2002) and beetle fossils (e.g., Marra and 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 widespread 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 and 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 led to the conclusion that fossil beetles had the same physiological and ecological requirements as their modern descendants. Responses to Quaternary climate change were therefore probably via dispersal rather than adaptation (Coope, 1978; Morgan and 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 descendants, apparent ecological constancy, extreme diversity (Klimaszewski, 1997) and large range of ecological roles (Kuschel, 1990; Hutcheson and Kimberley, 1999) makes them excellent proxies for identifying changes in the paleoenvironment (e.g., forest to shrubland, shrubland to open grassland). Furthermore, beetles require rapid burial to preserve as fossils and are bulky by comparison to microfossils so are rarely subject to long-distance dispersal (Marra and 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 2150 mm) and predominantly southwesterly 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, 1988, 1992) backed to the east by the northern foothills of the Paparoa Range. The site examined in this paper is situated 9 km southwest 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 m above sea level) and estimated uplift rates, the terrace is inferred to be last interglacial (80–125,000 yr) in age (Moar and 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 and Suggate, 1979). The overlying massive organic silt unit was sampled for beetle fossils. The unit is ca. 1 m thick and is the preserved remains of an in-filled hollow within the eroded remains of the dune field (Moar and Suggate, 1979). Radiocarbon dates place the beginning of silt deposition at 31,600+1,700/–1,500 ¹⁴C yr BP (NZ 3168; Moar and Suggate, 1979) (39,000–35,280 cal yr BP; Weninger et al., 2006) and ending at 17,950±250 ¹⁴C yr BP (NZ 4047; Moar and 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 ¹⁴C yr BP (NZ 4046; Moar and 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 and 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 and 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 ¹⁴C yr 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

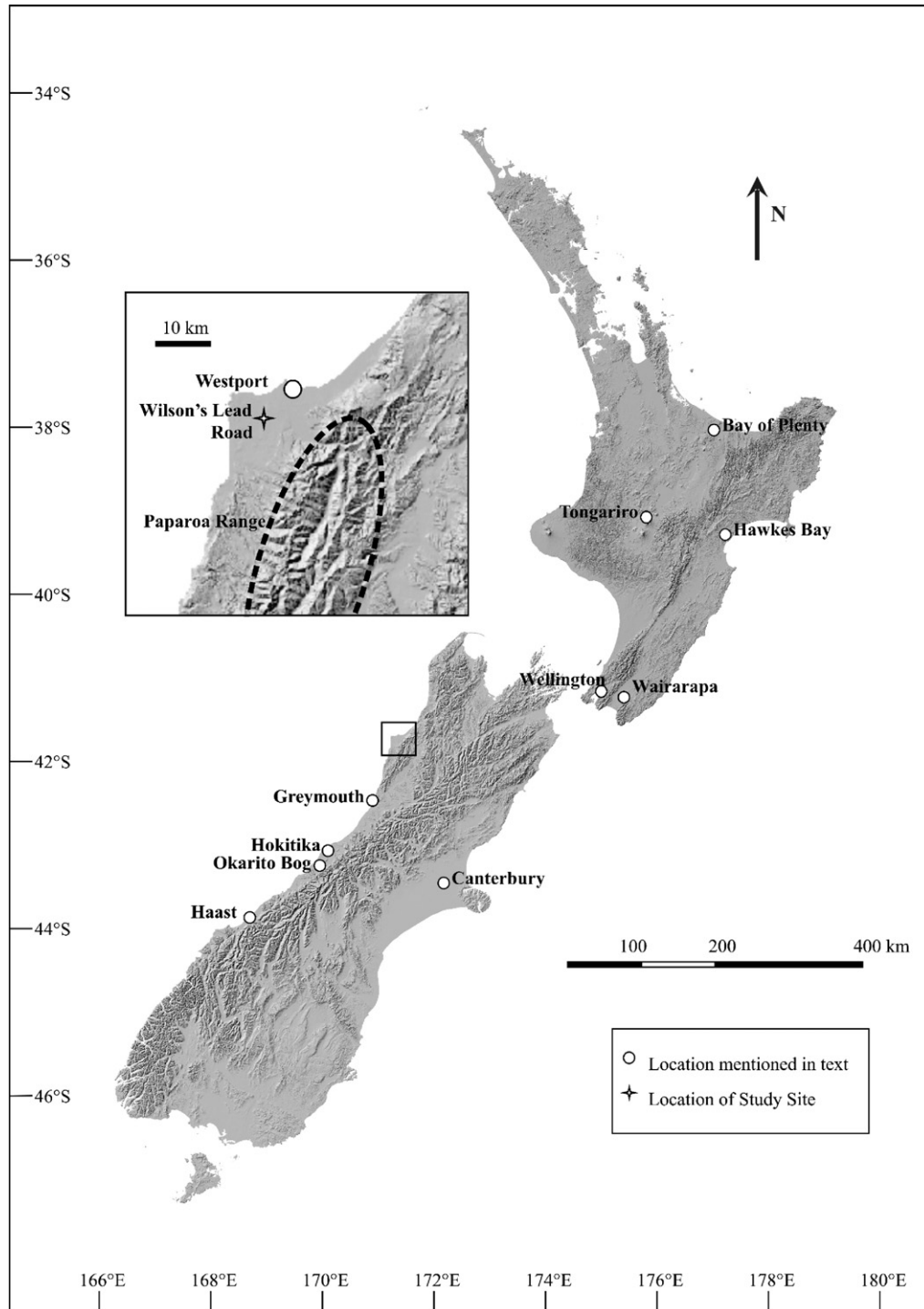


Figure 1. Locality map showing sites and regions mentioned in the text. An enlargement of the study area near Westport is provided.

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 (*Dacrydium dacrydioides*), 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 subcanopy of smaller trees including silver pine (*Manoao colensoi*), pigeonwood (*Hedycarya arborea*), haumakaroa (*Raukaua simplex*) and mapau (*Mysine australis*)

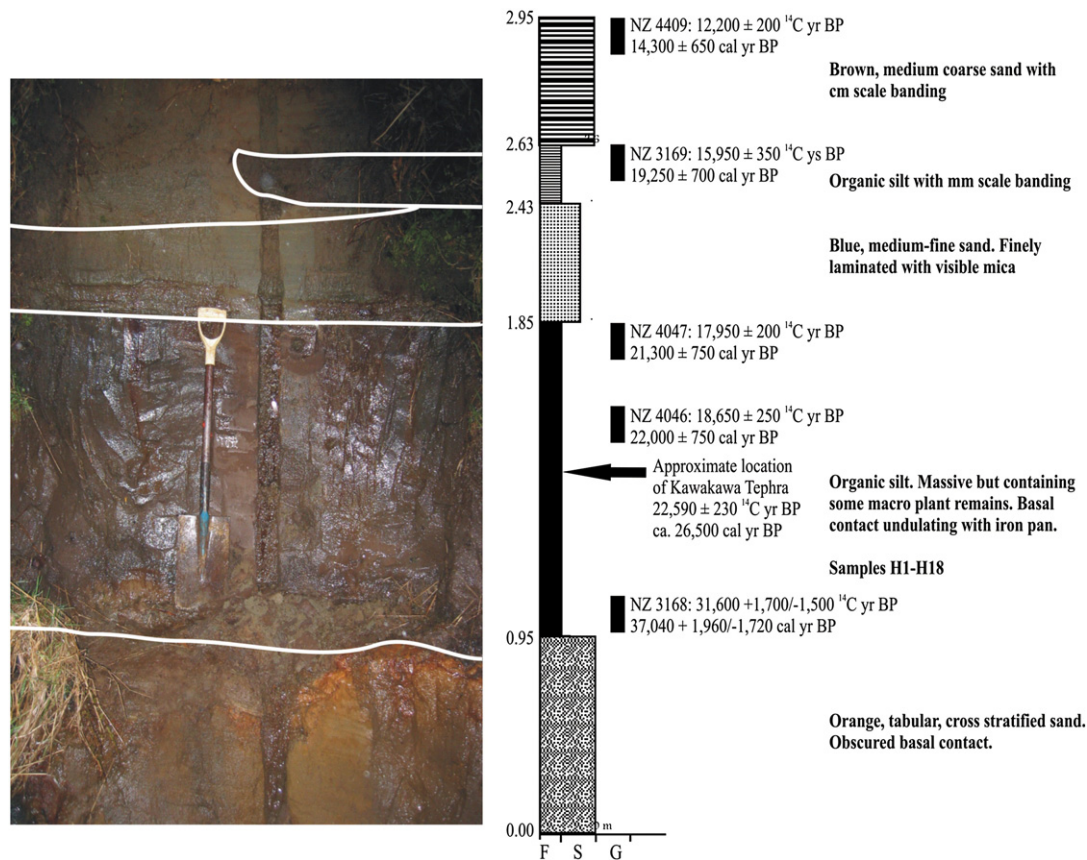


Figure 2. Stratigraphy of the Wilson's Lead Road site indicating the position and description of the different units. ^{14}C ages are as previously published by Moar and Suggate (1979). Calibrated ages are from Suggate and Almond (2005).

as well as the tree ferns *Cyathea smithii* and *Dicksonia squarrosa* (Wardle, 1991). Lianas such as the ratas *Metrosideros fulgens* and *Metrosideros 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*), pakihī 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). *Nothofagus menziesii* is the dominant tree species near the tree line (ca. 1300 m) (McEwen, 1987). Above the tree line, beech forest is replaced with subalpine herbs including *Aciphylla hookeri*, *Celmisia dallii*, *Gentiana gracifolia* and tussock grasses (*Chionochloa* spp.) (McEwen, 1987; Wardle, 1991).

Methods

Sampling and 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. 5 kg. Samples were gently boiled in water to break up the sediment and disaggregated material was washed through a 297- μm 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 and 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 uncalibrated 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)) were 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 herbfields, beaches), half-closed Environments (e.g., shrublands, 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 and 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 and Matthews, 1973; Klimaszewski and Watt, 1997; LUNZ label data; NZAC label data), the Zopheridid *Pycnomerus latitans* Sharp (Klimaszewski and Watt, 1997; LUNZ label data; NZAC label data) and a suite of indeterminate Cryptorynchini weevils (family Curculionidae) (Lyal, 1993;

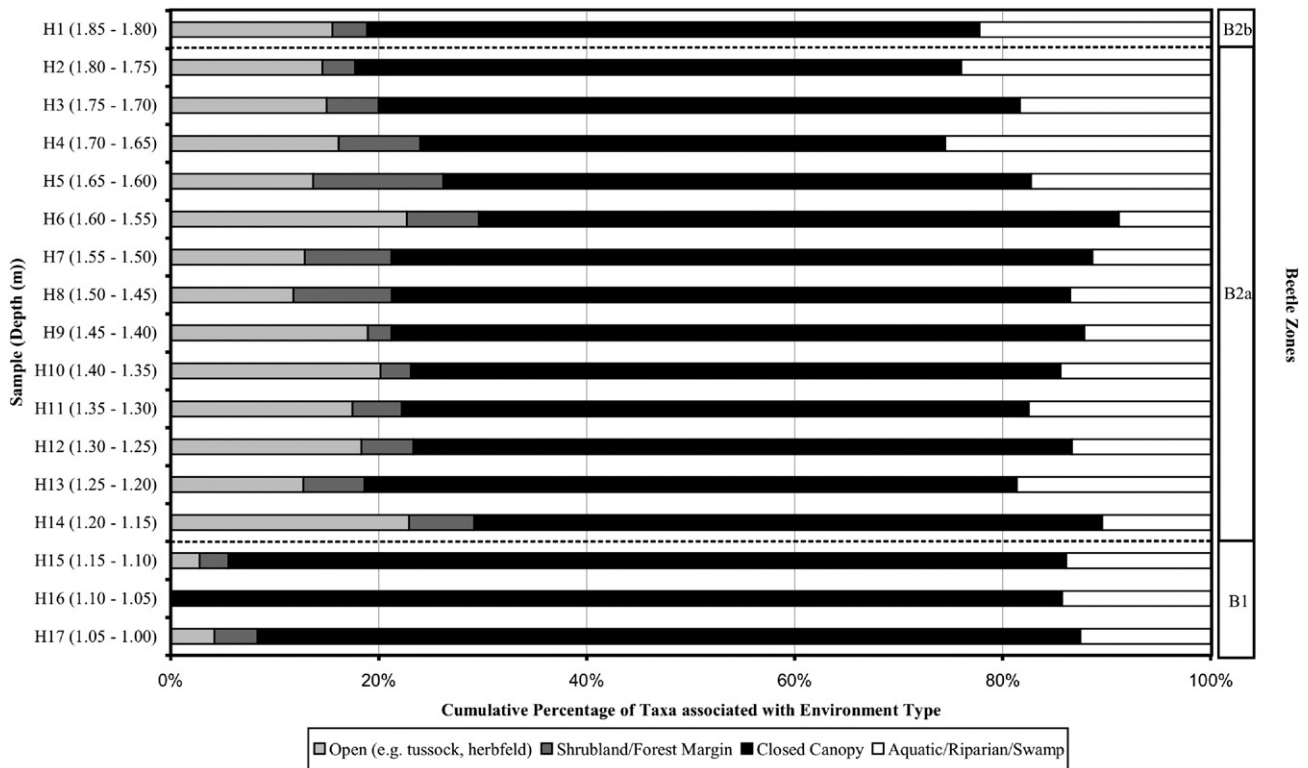


Figure 3. Comparison of the percentage composition of samples by habitat type. Depth measurements are the same as those illustrated in Figure 2. Also shown is the division of the samples into the assemblage zones B1, B2a and B2b.

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 and 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 (*R. 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 and 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 Staphylinid species *Corneolabrium mandibulare* Steel (Newton and 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 (subfamily Sphaeridinae) (e.g., *T. nitidulus*, *Adolopus helmsi* Sharp) indicate that conditions under the canopy remained moist (Hansen, 1997; Klimaszewski and Watt, 1997; Marra and 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 and 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 and Watt, 1997; Archangelsky, 2002, 2004) and *Paracymus pygamaeus* Macleay (Winterbourn, 1970; Hansen, 2000; Marra and Leschen, 2004; NZAC label data). Marshy conditions are indicated by the moss beetles (family Byrrhidae) *Curimus zeelandicus* Redtenbacher and *Curimus squamiger* Broun (Klimaszewski and Watt, 1997; Lawrence et al., 2000 onwards) and the ground beetle (family Carabidae) *Notogonium feredayi* Bates (Larochelle and Larivière, 2001).

Notogonium feredayi is also found in tussock areas (Larochelle and 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 and Crosby, 1997) are 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, 2000; Marra and Leschen, 2004), and the weevil, *Oreocalus latipennis* Broun (Supplementary Table 1), restricted to the plant genus *Hebe* in its larval stage (May, 1993), are also indicative of open or forest-margin-type vegetation as *Hebe* is typically found in open habitats and forest margins (Dawson and 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 and Watt, 1997).

Discussion

Site stratigraphy and 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 and 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 and 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 *Arecocryptus* 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 43°45'S (Enright and Watson, 1992) indicating that the local vegetation had coastal–lowland affinities (Dawson and 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 and 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 and Suggate, 1979). *Halocarpus* and *Phyllocladus* are generally considered to represent montane-subalpine vegetation (Macphail and McQueen, 1983; Wardle, 1991) and Moar and Suggate (1979) initially argued that, as *N. menziesii* forest survived near Hokitika (Moar and Suggate, 1973) during this time period, the Westport region must have been subjected to a regime of harsh frosts (Moar and Suggate, 1979). Moar and Suggate (1996) later revised this hypothesis, arguing instead for different soil development and increased windiness to explain the lack of forest in the area.

Although 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 and Smith, 1975; Wardle, 1977; Norton, 1989). This region is also known to embrace areas of coastal-lowland vegetation containing *R. sapida* (Moore and Edgar, 1970; Enright and 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 and Mark, 1994), we hypothesize that the *Halocarpus/Phyllocladus* shrubland indicated by the pollen (Moar and 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 and Suggate, 1979) and these wet, swampy areas would have been dominated by swampy herb taxa including wire brush (*Calorophus*) (Mark and Smith, 1975), which is well represented in the local pollen (Fig. 4) (Moar and Suggate, 1979). Farther 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 and 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 *Plagi-*

anthus 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 and Bradshaw, 1981; Macphail and 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 and Suggate, 1979), it is normally extremely poorly represented in pollen diagrams (Macphail and 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 *Plagi-anthus*-type pollen, taxa known to occur in lowland and coastal forests (Macphail and McQueen, 1983; Allan, 1961), occur in some of the WLR pollen diagrams (e.g., Fig. 4) (Moar and Suggate, 1979) and may represent input from the local stands of coastal vegetation rather than from long-distance dispersal.

Beetle zones B2a and 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 *E. tritus* (Archangelsky, 2002, 2004), and streams, represented by members of the *Bembidion* genus (Larochelle and 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 and 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 subalpine 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

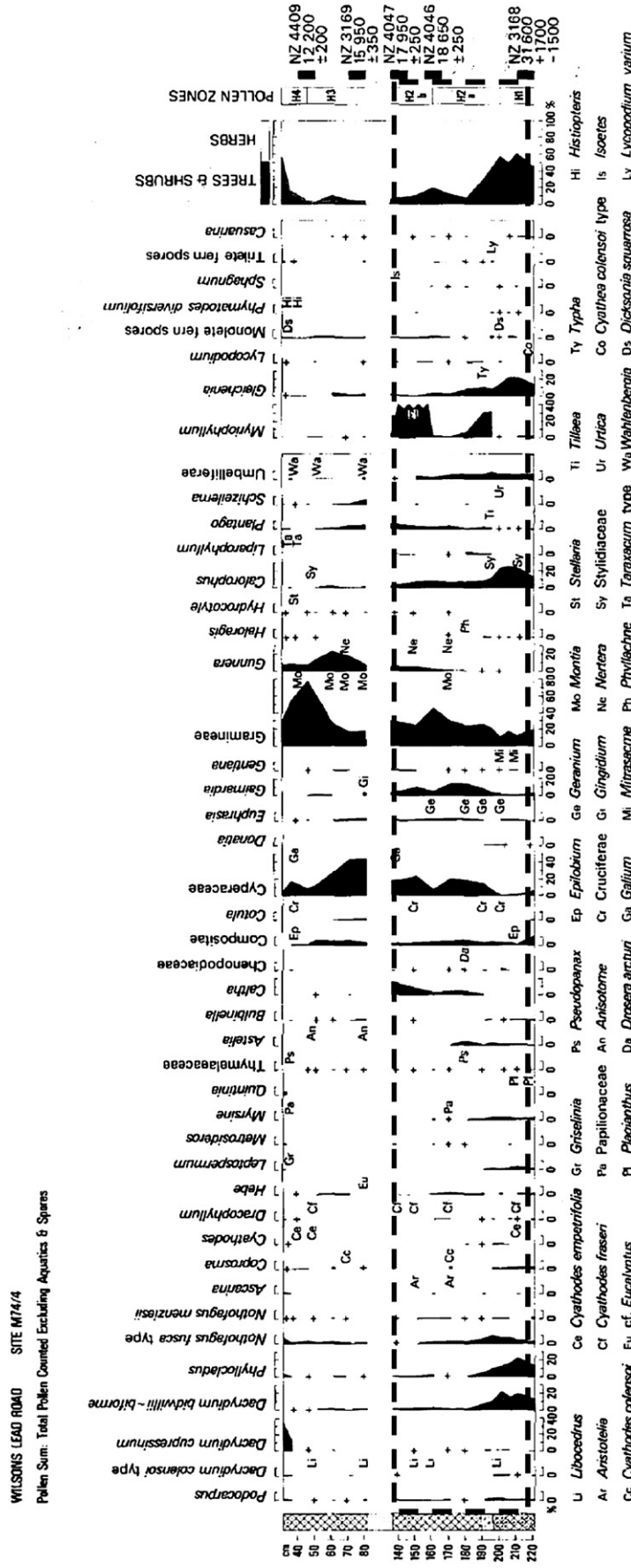
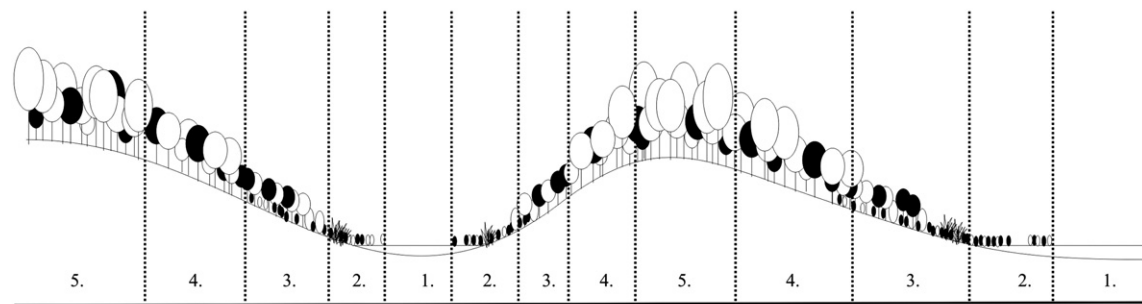
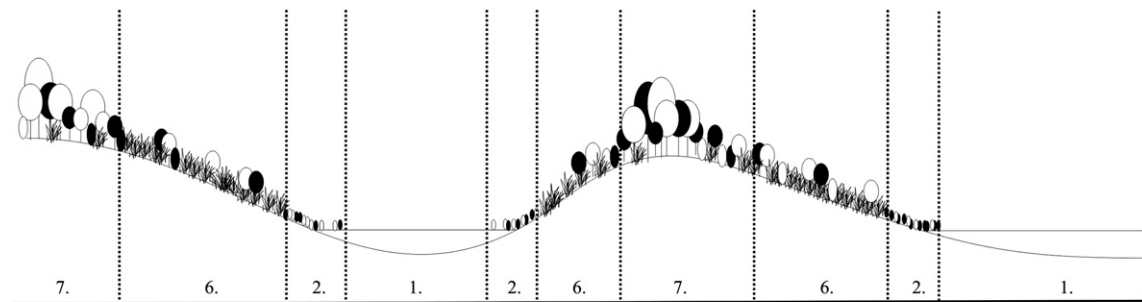


Figure 4. Pollen diagram from Wilson's Lead Road. The stratigraphic unit sampled for beetles is highlighted with a dashed box on the figure (i.e., 140–220 cm). Some of the plant taxa shown in the figure have undergone taxonomic revision since the original publication of this figure. Of particular relevance 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 of Moar and Suggate, 1979).

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

Figure 5. (A) Idealized 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. (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.

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 4–5 °C 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) that 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) indicate 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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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.yqres.2007.03.009.

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