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Early Holocene plant remains from the Cromwell Gorge, Central Otago, New Zealand

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Abstract: Central Otago is one of the driest parts of New Zealand, and much of the natural vegetation of the region was lost to fires following human settlement in the 13th Century AD. Plant macrofossil and pollen records have provided detailed insights into the vegetation communities that existed in Central Otago's lowlands at the time of human settlement, but relatively little is known about the regional vegetation patterns prior to ~3000 years ago. Here, we present analyses of pollen and plant macrofossil assemblages from a buried cave deposit in the Cromwell Gorge which dates to the early Holocene (~11 700–8300 years ago), a time when the climate was significantly warmer than during the late Holocene. The results show that at this time the local vegetation community consisted of low open scrubland or woodland, very similar to that found there during the late Holocene. Rare tall forest tree pollen was probably derived from distant sources in Southland or coastal Otago, where forest was spreading at this time. The absence of evidence for tree species that were regionally dominant during the late Holocene (*Phyllocladus alpinus*, *Kunzea serotina* and *Podocarpus hallii*), and the abundance of low-growing shrubs, indicates that during the early Holocene the interior valleys of Central Otago may have experienced a climate substantially drier than present.

Keywords: climate, palaeovegetation, pollen, Quaternary, seeds, vegetation history

Introduction

Within the rainshadow of the Southern Alps and >80 km distant from the nearest coast, Central Otago is home to some of New Zealand's driest ecosystems. Steep altitudinal precipitation gradients mean that while higher altitude sites in the region can receive >2000 mm of rainfall per year the adjacent lowlands receive <600 mm (Tait et al. 2001). Soon after the initial Polynesian settlement in the 13th century, almost all of the woody vegetation of Central Otago and adjacent drylands was lost as a result of human-lit fires (McGlone 2001; McWethy et al. 2010). The rapidity and completeness of this transition (McWethy et al. 2014) was doubtlessly enabled by the semi-arid climate and the lack of fire tolerance among most elements of the New Zealand woody flora (Perry et al. 2014). Present vegetation within the Central Otago lowlands consists mainly of exotic-dominated plant communities or native plant communities dominated by fire-tolerant species such as sweet briar (*Rosa rubiginosa*), matagouri (*Discaria toumatou*) and *Coprosma* spp. (Wood 2007; Wood & Walker 2008; Walker et al. 2009).

Over the past two decades significant progress has been made towards understanding the composition and structure of Central Otago's lost vegetation communities (e.g. McGlone et al. 1995, 1997; McGlone & Moar 1998; Wardle 2001; Walker et al. 2003; Wood & Walker 2008). The majority of Quaternary palaeovegetation records in the region date to the late Holocene (~ last 3000 years), and have revealed that during this time the lowland basin floors and gorges held short-statured woodland and shrubland dominated by canopy taxa such as the small tree *Plagianthus regius*, and shrubby species of *Coprosma, Myrsine* and *Olearia* (Wood & Walker 2008). The lack of tall forest in the lowland basin floors and gorges during this period reflects the mid-late Holocene dry climate within the region (McGlone et al. 1995; McGlone & Moar 1998; Wood 2007).

By contrast, very little is known about Central Otago vegetation communities of the early Holocene (~11 700–8300 BP), a time when the climate was significantly warmer than during the late Holocene (McGlone et al. 2004). This represents a particularly important gap in understanding New Zealand's vegetation history. While the reafforestation of southern New Zealand following the last glacial period had largely concluded by 12 000–10500 BP (McGlone et al. 2004; Turney et al. 2017), there are indications that forest or tall scrub may not have returned to the basins of Central Otago and adjacent regions until much later (9000–8000 cal BP) or in some areas not at all (McGlone et al. 1995, 1997; McGlone & Moar 1998; Wood & Walker 2008). However, there are several complications with interpreting the few early Holocene vegetation records that exist for the Central Otago region. Most are from shallow peat deposits, which are prone to contamination with young carbon and therefore can be difficult to accurately radiocarbon date. Moreover, most are based on pollen and spore spectra alone, which in a region with such abrupt environmental gradients raises the possibility for dominance by wind-borne pollen from nearby, but ecologically distinct, source areas.

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Here, we describe an early Holocene site from the Central Otago lowlands that was discovered in the mid-1980s. The site contained well-preserved plant microfossils and, most importantly, macrofossils, which are less prone to long-distance dispersal than pollen and therefore can provide a robust snapshot of the local vegetation community. These palaeovegetation analyses, which were performed in the late 1980s (but not previously published), provide key insights into the poorly understood vegetation and climate history of the Central Otago region during this time period.

Materials and methods

Gibraltar Rock deposit

A file of correspondence to MSM held by Manaaki Whenua Landcare Research, Lincoln, details the discovery and analyses of material from the Gibraltar Rock deposit, and forms the basis of the description presented here. The site was discovered during road construction in the vicinity of Gibraltar Rock, 4.3 km downstream of Dead Mans Point bridge across the Clutha River (World Geodetic System 1984: 45° 4′ 24.722″ S, 169° 14′ 31.665″ E, ~240 m above sea level), in mid-October 1985. The site was a small cave or crevice with an entrance measuring 1 m high and 2.5 m wide, and was buried beneath 13–14 m of chaotic landslide debris. Although some of the remains preserved in the site were lost to fossickers, rabbits and the weather, approximately 30 kg of bulk sediment containing plant and animal remains was excavated from the site by J. Bryant (site engineer), N. Ritchie and R. McGovern-Wilson. Following reports of the site in newspapers in March 1987 (Otago Daily Times 1987; Southland Times 1987) MSM contacted J. Bryant requesting a sample of the sediment for pollen and plant macrofossil analysis, and approximately 1.5 kg of the sediment was sent to specialists at the DSIR Botany Division, Lincoln, for detailed examination. The sediment consists for the most part of finely fragmented woody plant material and silt. No charcoal (either microscopic or macroscopic) was encountered. The results of these analyses are presented in this paper, and the sediment is archived at Manaaki Whenua–Landcare Research, Lincoln. The authors are prepared to make it available for further analyses to other researchers. The rest of the material was originally held at the Anthropology Department at Otago University, but attempts by MSM in 2003 to locate the faunal remains and the remainder of the sediment there were unsuccessful. The current repository of the material is unknown. The buried cave was destroyed by roadworks following the excavation of material from the site.

Radiocarbon dating

In late 1985 or early 1986 a sample of bulk plant remains from the buried cave deposit was submitted to the Institute of Nuclear Sciences at the New Zealand Department of Scientific and Industrial Research, Lower Hutt, for conventional radiocarbon dating. In 2010, two thin unidentified twigs (<6 mm diameter) from the same deposit were submitted to Waikato Radiocarbon Laboratory for accelerator mass spectrometry radiocarbon dating. These short-lived samples were selected to reduce the chance of the dates being influenced by inbuilt age. Radiocarbon dates were calibrated using the SHCal13 (Hogg et al. 2013) curve via OxCal v.4.2 (Bronk Ramsey 2009).

Pollen and plant macrofossil analyses

Pollen and spores were extracted from a well-mixed sub-sample of the fine sediment fraction using the standard palynological processing technique of dilute KOH, hydrofluoric acid, acetolysis and mounting on a microscope slide (Moore et al. 1991). In October 1987 a count of 369 pollen grains and spores was made by MSM and the slides were also scanned for additional taxa not detected during the count.

In August and September 1987, seeds were sorted from a 1 kg sample of the sediment and identified by Mary Wilson via comparison with specimens in the Allan Herbarium, Lincoln. Identifications were checked by Margaret Simpson who at the time was engaged in research for a seed atlas of the New Zealand flora (Webb & Simpson 2001) and she also microscopically examined a small subsample of fine sediment for small seeds.

Fragments of wood and bryophytes were isolated from the bulk sediment sample. Wood fragments were identified by Rajni Patel via microscopic analysis of hand sections and comparison with the wood reference collection at the Allan Herbarium. Bryophytes were identified by Allan Fife.

Results

Radiocarbon dating

The radiocarbon analysis performed in 1986 returned a date of 8650 ± 105 ^{14}C BP (9308–10 152 calibrated BP) (Table 1), indicating that the material in the site was of early Holocene age. The two subsequent AMS dates that we obtained support this conclusion, returning ages of 8137 ± 32 ^{14}C BP (8789–9233 calibrated BP) and 8779 ± 35 ^{14}C BP (9559–9888 calibrated BP). There are no records of stratigraphy for the Gibraltar Rock deposit; however, the non-overlapping 95% confidence ranges for the AMS dates indicate that material in the site may have accumulated over several hundred years.

Pollen and plant macrofossil analyses

The pollen assemblage derived from the buried cave deposit was dominated by the shrubs *Myrsine* (47.1%) and *Coprosma* (14.7%), the liane *Muehlenbeckia* (15.0%) and kowhai (*Sophora*) (8.7%) (Table 2). Tall forest tree taxa were relatively diverse but represented only a very minor part of the assemblage. For example, pollen of rimu (*Dacrydium cupressinum*), kahikatea (*Dacrycarpus dacrydiodes*), matai (*Prumnopitys taxifolia*), miro (*P. ferruginea*), tōtara (*Podocarpus* spp.) and beeches (*Fuscospora* and *Lophozonia*) were all recorded, but together comprised just 3.8% of the total pollen sum (Table 2).

Vascular plant macrofossils (seeds and wood fragments) from the sample were also dominated by shrubs and lianes (Table 2). Seeds of *Corokia cotoneaster*, *Pseudopanax ferox* (Fig. 1), *Muehlenbeckia australis* (Fig. 1) and *Sophora prostata* are sufficiently distinctive that we can be confident that these species were present. *Myrsine divaricata* seeds are indistinguishable from *M. argentea*, but as this latter small tree is confined to Mt Burnett in Northwest Nelson, it is highly unlikely to have been the source. Seeds of *Muehlenbeckia complexa*, *M. axillaris* and *M. ephredroides* are difficult to distinguish and although all of these could have grown at the site, *M. complexa* seems the most likely given the setting. *Coprosma obconica* seeds are highly distinctive (Webb & Simpson 2001) and this find is the only reliably identified

Table 1. Radiocarbon dated plant remains from the buried cave deposit at Gibraltar Rock, Central Otago, New Zealand.

Lab number/s	Material	Conventional radiocarbon age	Error	d13C	Calibrated age (BP) (95.4% confidence range)
R11198 & NZ-7004	Bulk sample	8646	137	-24.6	9308 – 10 152
Wk28338	Small twig	8137	32	-26.0	8789 – 9233
Wk28339	Small twig	8779	35	-28.9	9559 – 9888

Table 2. Vascular plant identifications from the buried cave deposit at Gibraltar Rock, Central Otago, New Zealand. +, noted but not quantified. Pollen sum includes all terrestrial plants excluding pteridophytes and lower plants.

	Taxa	**% pollen sum**	**Seeds (no.)**	**Wood**
Trees and shrubs	*Dacrydium cupressinum*	+	–	–
	Dacrycarpus dacrydiodes	+	–	–
	Fuscospora	0.3	–	–
	Lophozonia menziesii	0.3	–	–
	Prumnopitys ferruginea	0.5	–	–
	P. taxifolia	1.9	–	–
	Podocarpus	0.8	+	–
	Malvaceae	–	–	+
	Hoheria	0.3	–	–
	Plagianthus	0.3	–	+
	Phyllocladus	0.8	–	–
	Pseudopanax	+	–	–
	P. ferox	–	75	–
	Sophora	8.7	–	–
	S. prostrata	–	1	–
	Asteraceae	3.7	–	+
	Myrsine	47.1	–	+
	M. divaricata	–	>310	–
	Corokia cotoneaster	0.5	>80	–
	Coprosma	14.7	At least 6 spp.	+
	C. obconica	–	+	–
	C. c.f. *rhamnoides*	–	+	–
	Hebe	0.3	–	–
Lianes and epiphytes	*Muehlenbeckia*	15.0	–	–
	M. australis	–	>307	–
	M. complexa type	–	8	–
	Rubus	0.5	1	–
	Clematis	0.3	5	+
	Tupeia antarctica	0.3	–	–
Herbs	Brassicaceae	+	–	–
	Geranium	+	–	–
	Urtica	–	+	–
	Scleranthus	1.6	–	–
	Einadia	–	2	–
	Poaceae	1.9	–	–
Pteridiophytes	*Lycopodium fastigiatum*	0.3	–	–
	Monolete fern spores	0.3	–	–

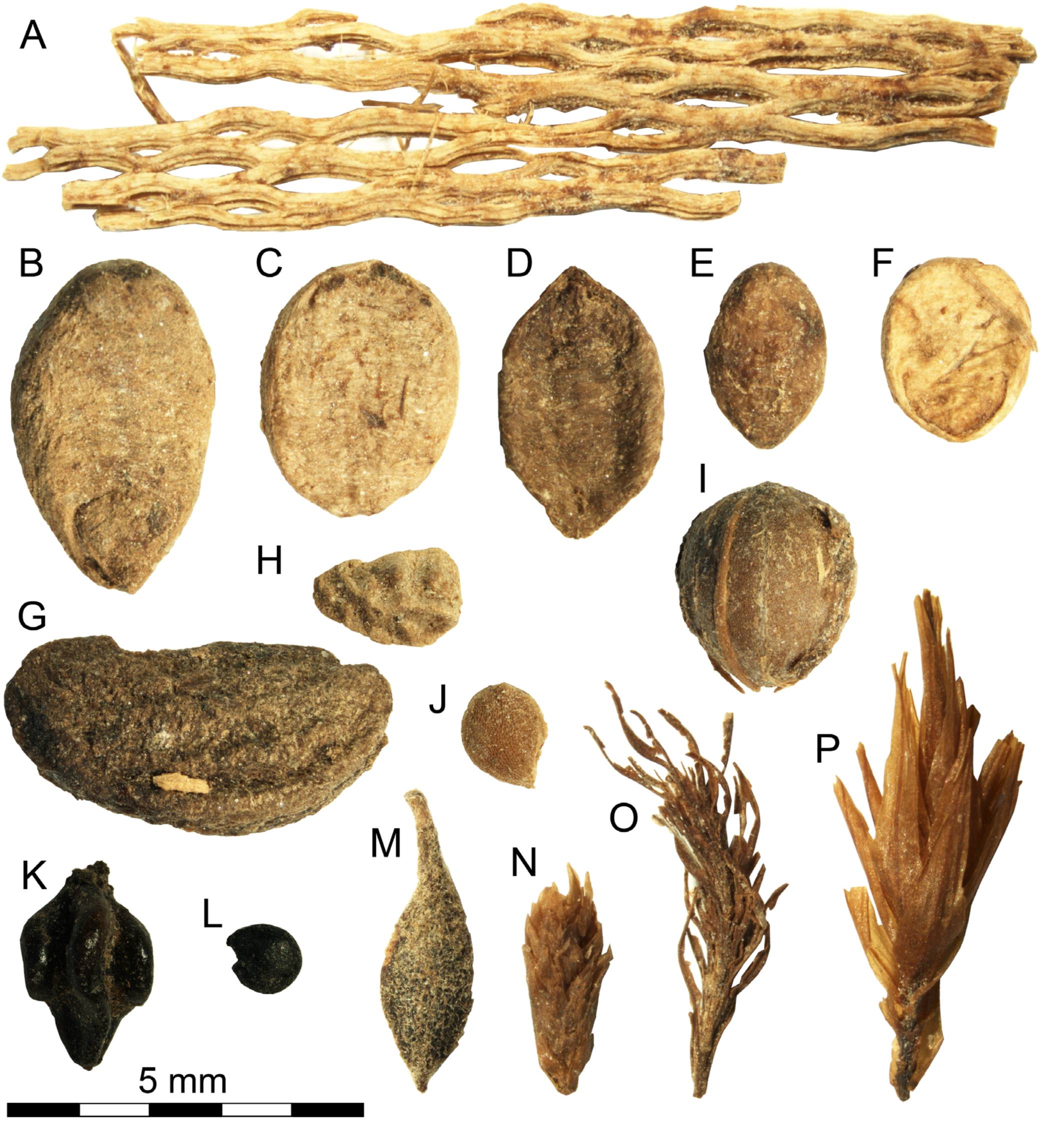

Figure 1. Early Holocene plant macrofossil remains from the Gibraltar Rock deposit, Cromwell Gorge. A, *Plagianthus* bark tissue fragment; B–F, unidentified *Coprosma* seed morphotypes; G, *Pseudopanax ferox* seed; H, *Rubus* seed; I, *Myrsine divaricata* seed; J, *Urtica* seed; K, *Muehlenbeckia* australis seed; L, *Einadia* seed; M, *Clematis* seed; N–P, fragments of mosses. Scale bar is 5 mm.

Coprosma present here. Seeds of small leaved *Coprosma* are generally distinguishable from large leaved species, and at least five unidentified *Coprosma* morphotypes (Fig. 1) most likely came from low statured species of divaricating or prostrate shrubs. *Podocarpus* seed was recorded but the species cannot be reliably distinguished. Fragments of the liverwort *Porella elegantula* and several moss species were also identified from the sample, including *Brachythecium salebrosum*, *Camptochaete arbuscula*, *Dicranoloma robustum*, *Hypnum cupressiforme*, *Lembophyllum divulsum*, *Leptodon smithii*, *Neckera* cf. *laevigata* and *Syntrichia* (*Tortula*) *serrata*.

Discussion

Early Holocene vegetation at Gibraltar Rock

Moa nested in dry cave sites throughout the Central Otago lowlands (Wood 2008) and some of the fine leaf and twig material was possibly gathered as nesting material. Moa eggshell fragments and down feathers were present in the deposit, and some of the woody material from the deposit was noted by Wood (2008) as being characteristic of twigs clipped by moa beaks. Other plant macrofossils may have fallen or been blown into the deposit. Irrespective of the mode of transport into the site, the macrofossils can only have been derived from vegetation that grew within a few tens of metres of the cave entrance. While pollen can be derived from a much wider source area, three of the four dominant pollen types identified in the Gibraltar deposit (*Muehlenbeckia*, *Myrsine* and *Sophora*) are from low-growing shrubs or small trees with poorly dispersed pollen (Moar et al. 2011), and therefore are also likely to reflect vegetation within a few tens of metres of the site. Therefore, the paleovegetation assemblage reconstructed from the buried cave deposit is almost entirely local, and provides a reliable insight into the vegetation community that grew at that site during the early Holocene.

The pollen and macrofossil assemblages are dominated by shrubby plants and climbers (*Clematis* sp., *Coprosma* spp., *Corokia cotoneaster*, *Muehlenbeckia* spp., *Myrsine divaricata*, *Pseudopanax ferox* and *Rubus* sp.) (Table 2).

Plagianthus regius is represented by some twigs and sparse pollen grains, and with a maximum height of 15 m is the tallest plant represented in the local assemblage. None of the other plants are of particularly tall stature; *Pseudopanax ferox* and *Myrsine divaricata* may reach ca. 5–8 m in height, while *Coprosma obconica* and *Corokia cotoneaster*) are in the 2–3 m range. Seeds of *Coprosma obconica* were also identified in late Holocene sites from the Central Otago lowlands, but it is now absent from inland Otago (Wood & Walker 2008). The cause of this local extirpation is uncertain as the timing of the loss is not well constrained. However, its occurrence in the late Holocene (Wood & Walker 2008) suggests that anthropogenic fires, rather than climate change, may be the most likely cause. A few herbaceous taxa (*Scleranthus*, *Geranium*, Brassicaceae and *Lycopodium fastigiatum*) and a small amount of grass pollen indicate the presence of some open ground habitat. The grass percentage is very low relative to modern pollen from shrublands (McGlone 1982; Horrocks & Ogden 1994; McGlone & Moar 1998) and we can conclude that close to the cave entrance the shrub cover must have been near complete, and that there were probably no extensive areas of grassland nearby. The mosses recorded from this site occur in a wide range of habitats, growing on bark, logs, rocks or the ground, and range from forest to grassland habitats.

A number of conifer taxa and beeches (*Fuscospora* and *Lophozonia*) are recorded in the pollen assemblage, but at such low percentages that their presence in the local area is highly unlikely. Conifer-dominant vegetation had already established in coastal Otago and Southland by the early Holocene (e.g. McIntyre & McKellar 1970; McGlone & Bathgate 1983; Turney et al. 2017; Fig. 2) and it is likely that most of the conifer and beech pollen came from these distant forests.

Overall, the assemblage reflects a local vegetation community consisting of shrubland or low woodland. The assemblage as a whole is very similar to those found in late Holocene palaeovegetation deposits in the Central Otago lowlands (Wood & Walker 2008), and in the open shrubby habitats of the eastern South Island today.

The possible absence of *Kunzea serotina* and *Leptospermum scoparium* from the Gibraltar deposit is significant. Both species

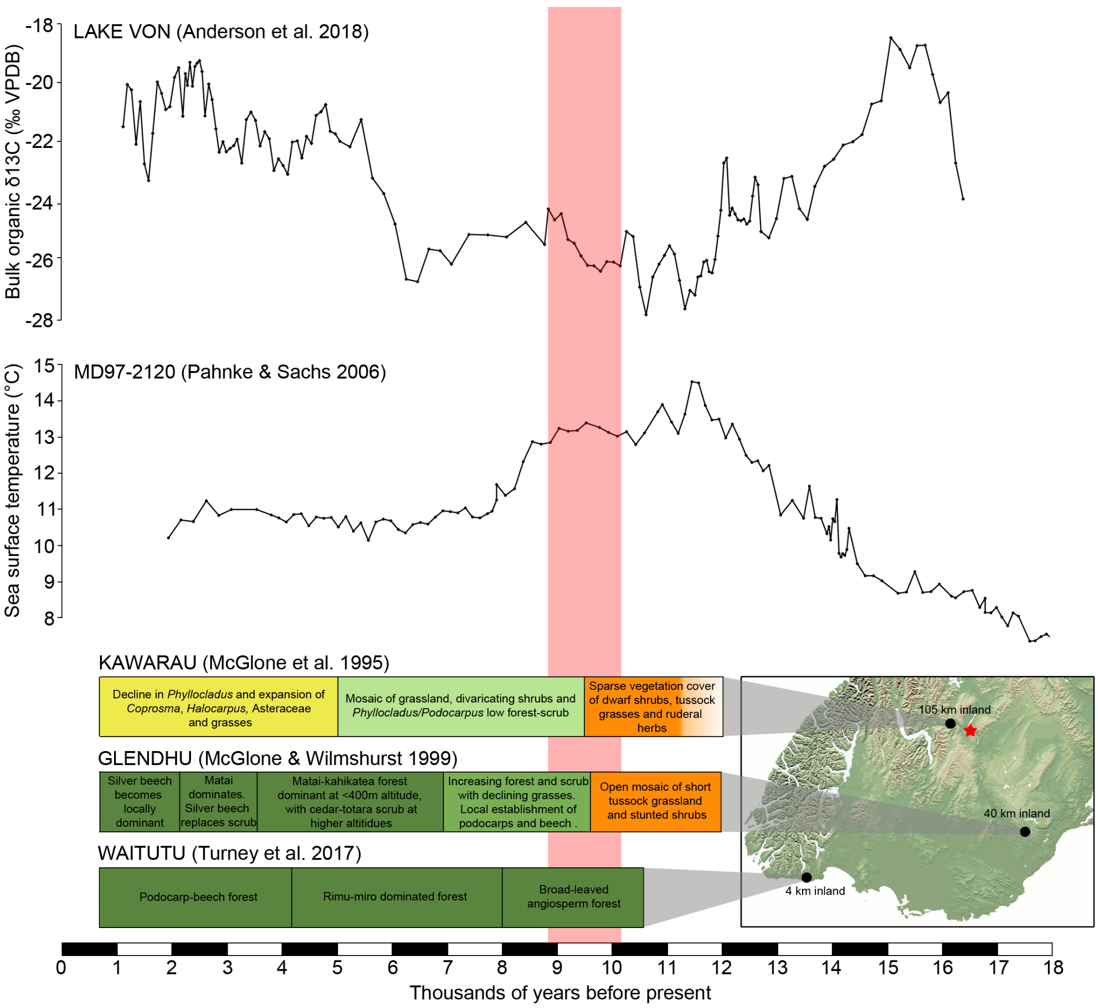

Figure 2. Post-glacial climate proxies and Holocene vegetation records from southern New Zealand. The Lake Von record (Anderson et al. 2018) represents bulk organic ^{13}C measured down a sediment core and is a proxy for distance to shore (lake depth), with more enriched values reflecting increased lake depth. The Ocean Drilling Project core MD97-2120 record is alkenone-derived sea surface temperatures off the southeastern South Island (Pahnke & Sachs 2006). Vegetation communities derived from pollen records are shown for three localities (Kawarau, Glendhu Bog and Waitutu) along a gradient of distance from the nearest coast. These records are truncated at the time of human settlement (~750 years ago). The vertical bar represents the limits of 95% confidence ranges of calibrated radiocarbon dates on plant remains from the Gibraltar Rock deposit, Central Otago (location shown by red star on map).

played an important role in the vegetation cover of Central Otago after the arrival of humans, but prior to that time were (at least in the upper Clutha catchment) usually intermixed with podocarps and therefore did not form pure stands. Moreover, charcoal of both species has only been recorded in the region after 3420 ± 80 ^{14}C BP (3413–3840 calibrated BP) (Wardle 2001). *Kunzea* and *Leptospermum* (both represented by the *Leptospermum* pollen type) are poorly represented in the pollen rain unless growing directly adjacent to the collection site. The general absence of *Leptospermum*-type pollen from Central Otago sites is not of itself good evidence for rarity of these species. However, given that both the macrofossils and pollen from the Gibraltar site are dominated by local vegetation, the absence of *Kunzea* and *Leptospermum* suggests they were not growing at this site during the early Holocene.

Relationship to other early Holocene sites within the region

The pollen spectra recorded at Gibraltar Rock is similar to that obtained from the pre-6540 ± 340 ^{14}C BP (6636–8033 calibrated BP) sediments in the Kawarau Gorge (McGlone et al. 1995), located ~16 km to the west but otherwise in the same climatic zone (Fig. 2). The most substantial points of difference between the Kawarau and Gibraltar Rock sites are: (1) the greater representation of conifer pollen at Kawarau Gorge, in particular *Prumnopitys taxifolia* (c. 15% at Kawarau vs. 2% at Gibraltar) and *Phyllocladus* (c. 8% at Kawarau vs. 0.8% at Gibraltar); and (2) the greater representation of grass pollen at Kawarau Gorge (~20% at Kawarau vs. 2% at Gibraltar). These differences can likely be attributed to the fact that the Gibraltar site represents pollen rain from beneath a scrubland canopy, while the Kawarau site was derived from wetland seeps, and thus with a more open vegetation type likely had a greater representation of long-distance transported pollen. However, by 6540 ± 340 ^{14}C BP the Kawarau record was nearly totally dominated by *Phyllocladus* pollen, and pollen from other shrubs and small trees had considerably reduced in abundance. A similar pattern is seen in a pollen record from the Ida Valley ~35 km east, where relatively high levels of *Phyllocladus* pollen suggest it was already an important component of the vegetation communities growing on the surrounding hillsides by 7070 ± 110 ^{14}C BP (7620–8045 calibrated BP) (McGlone & Moar 1998).

A late Holocene (post 2176 ± 76 14C BP: 1933–2330 calibrated BP) pollen record from Earnscleugh Cave near Alexandra (Clark et al. 1996) has perhaps the closest match to Gilbraltar Rock, as it has the same dominants (*Muehlenbeckia*, *Coprosma*, *Myrsine*, presence of *Sophora* and *Plagianthus*) and low levels (1–5%) of grass. However, the Earnscleugh Cave record differs markedly from Gibraltar Rock in the amount of conifer pollen, with *Prumnopitys taxifolia* and *Phyllocladus* making up to 25% of the pollen sum, and the abundance of charcoal.

The earliest record of *Phyllocladus alpinus* presence within the broader region is a charcoal fragment dated to 8490 ± 110 ^{14}C BP (9129–9661 calibrated BP) from the upper Motatapu Valley at an altitude of 600 m (~40 km northwest of Gibraltar Rock), under a wetter, cooler climate regime (Wardle 2001). Vegetation communities dominated by *Phyllocladus alpinus* persisted in these areas until the arrival of Māori in the 13th century AD, when repeated fire rapidly destroyed the conifer overstorey permitting the spread of angiosperm shrubs and grassland which dominates the area at present (McGlone 2001).

Further afield, a pollen analysis and wood fragments from a deep bore hole in central Queenstown (Pocknall et al. 1989) indicates the presence of a mixed *Lophozonia menziesii* and *Prumnopitys taxifolia–P. ferruginea–Podocarpus* forest community with abundant *Phyllocladus alpinus* woodland dated at 7800 ± 105 and 6392 ± 355 ^{14}C BP giving an age range of 6474–8976 calibrated BP.

The question of how much conifer forest was present in lower, drier valley slopes and bottoms in Central Otago, and thus close to sites such as Gilbraltar Rock during the Holocene is not settled. From the pollen evidence it is possible that stands of *Prumnopitys taxifolia*, *Podocarpus laetus* and *Phyllocladus alpinus* were present on favourable sites. However, the macrofossil record gives no support and the most probable interpretation is that the *Prumnopitys taxifolia* pollen was derived from distant forests in the humid western margin or in coastal eastern districts, while *Podocarpus* and *Phyllocladus* was derived from the local montane forests. The Gilbraltar site differs from Earnscleugh only in the much less substantial presence of conifer pollen and thus pre-dated the spread of forest in marginal districts and along the tops and upper flanks of the Central Otago ranges.

Climatic implications

Nearby Cromwell township has an annual rainfall mean of 396 mm and a warm summer averaging c. 17°C (1949–1970; New Zealand Meteorological Service) and is thus subhumid. McGlone et al. (1995) suggested that the increase of *Phyllocladus* and *Podocarpus hallii* cover in this region during the Holocene was largely the result of wetter climates (precipitation increasing by perhaps as much as a third relative to that of the late glacial) which permitted tree and tall shrub growth in areas that had previously been too dry to support it. A similar conclusion of substantially lower annual rainfall during the early Holocene was reached for coastal east Otago (McGlone & Wilmshurst 1999) and the inland Canterbury Cass Valley further north (McGlone et al. 2004). Evidence from Gibraltar Rock for the absence of the late Holocene tree dominants (*Phyllocladus alpinus*, *Kunzea serotina* and *Podocarpus hallii*) and the abundance of low-growing shrubs implies that during the early Holocene the interior valleys of Central Otago may have had annual rainfall of 300 mm or less, which would have induced a steppe climate regime of shrubland and grassland. The presence of *Pseudopanax ferox* may also be consistent with a drier climate as suggested by Shepherd and Perrie (2011). The absence of any charcoal from the deposit suggests that, despite the dry climate and abundant fuel, there was no fire. New Zealand has a globally low incidence of lightning strikes, and Central Otago sits at the centre of a region with few strikes even by New Zealand standards (Etherington & Perry 2017). The charcoal record from other Otago sites indicates that local fires did not affect the vegetation until after 9000 cal BP (Clark et al. 1996; McGlone & Moar 1998; McGlone & Wilmshurst 1999) and it is possible that the prevailing stable climate regime of the early Holocene resulted in even less lightning than in the later Holocene.

The broader pattern of climate and vegetation change in the region supports the local interpretation (Fig. 2). Glacial retreat began around 18 000 BP with the sustained warming of the Southern Ocean to the south of the South Island (Fig. 2). Annual temperatures rose to levels higher than present by 12 500 years ago and these warm conditions were maintained between about 13 000 and 9000 BP (Fig. 2), after which cooling commenced. By 12 000–11 500 tall conifer-broadleaf forest was present in coastal districts (Fig. 2), but inland shrubland-grassland continued to dominate until after 9000 years ago (Fig. 2). This striking early Holocene pattern of coastal forest versus shrubland–grassland interior cannot be attributed to cold conditions in the interior as the warmth of the surrounding ocean would make such a temperature gradient impossible. Furthermore, *Phyllocladus alpinus* – which later came to dominate hill forests in the region – is one of the most cold-tolerant trees in the flora and is highly unlikely to have been excluded by cool climates alone. Therefore, the conclusion is that most of the south-eastern interior remained too dry to support closed forest or tall shrubland until after 9000 years ago. Further evidence of aridity in the interior at this time comes from a recent study of lake sediments at Lake Von (some 60 km to the west of Gibraltar Rock), which showed high biological lake productivity alongside a decrease in lake extent (lower water levels) between 10 000 and 8000 BP (Anderson et al. 2018; Fig. 2). These lower lake levels can be attributed to the warm early Holocene temperatures and reduced precipitation, resulting from the weakened westerly wind flow. As suggested by Anderson et al. (2018) a strengthening of westerly-south-westerly wind flow after 8000 years ago brought rain-bearing fronts into the interior allowing the expansion of *Podocarpus*, *Phyllocladus*, *Halocarpus*, and *Lophozonia* on the flanks of the interior ranges.

Subfossil remains previously attributed to the Gibraltar Rock deposit

Based on the documentation associated with the discovery of the Gibraltar Rock deposit it appears that some previously described plant and animal remains might have been mistakenly attributed to the site. A sample of plant material containing lizard, parakeet (*Cyanoramphus* sp.) and kākāpō (*Strigops habroptilus*) remains was attributed to the Gibraltar Rock site by Wood (2006), based on the associated records that it had been collected near Gibraltar Point ca. 1990. However, it now seems unlikely that this sample was from the buried cave site. The date given for the discovery of the buried cave site by Wood (2006) was 1987, based on contemporaneous newspaper articles describing the site. However, it now appears that these articles coincided with the radiocarbon dating results, which were obtained 2 years after the site was actually discovered. This expands the time gap between the collection of material from the buried cave site in 1985 and the collection of the sample described by Wood (2006). Moreover, a radiocarbon date from the sample described by Wood (2006) was much younger (late Holocene) than any of the ages obtained for material from the buried cave site. Therefore, we now believe that the sample described by Wood (2006) probably originated from a different site within the vicinity of Gibraltar Rock that was discovered several years later than the buried cave deposit. Alternatively, if the sample described by Wood (2006) did come from the same buried cave deposit then it likely represents a distinct sample of material or different age and source to that described here, perhaps deposited by a bird nesting in crevices within the landslide deposit itself.

Conclusions

The Gibraltar site provides accurately dated and well attested fossil evidence that a low shrubland, accompanied by low statured drought-resistant trees but lacking conifers, prevailed in the heart of the central Otago region until at least 9500 years ago. On the basis of data from nearby sites, this vegetation community may have persisted until about 8000 BP, when increasing precipitation and falling annual temperatures resulted in the expansion of low-growing conifer forest to occupy all but the most drought-prone valley floors and gorges of the region.

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