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Holocene vegetation and climate of Stewart Island, New Zealand

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Abstract Stewart Island is the southernmost of the three main New Zealand islands, and is largely covered with *Dacrydium cupressinum*/hardwood forest. Pollen analyses from three Holocene sites and a modern pollen rain survey are presented. Stewart Island had a hardwood forest of *Weinmannia racemosa*, *Metrosideros umbellata*, and abundant tree ferns from before 9000 BP to 5500–4500 BP when *Dacrydium cupressinum* and *Prumnopitys ferruginea* rose to dominate the forest reducing the abundance of *Weinmannia racemosa* and greatly restricting *Metrosideros umbellata*. It is suggested that mild, cloudy climates during the early Holocene may have inhibited regeneration of podocarp trees, and that a change in climatic regime in the mid to late Holocene brought sunnier, less cloudy conditions. Several woody species absent from the island but present on the adjacent mainland (*Phyllocladus alpinus*, *Nothofagus* spp., *Libocedrus bidwillii*) probably never grew there, and their absence is attributed to failure to disperse and the limited time that suitable habitats have been available.

Keywords Holocene; Stewart Island; New Zealand; climate change; *Dacrydium cupressinum*; *Weinmannia racemosa*; *Metrosideros umbellata*; *Nothofagus*; pollen analysis

INTRODUCTION

Stewart Island, or Rakiura, is the southernmost and smallest of the three main islands of the New Zealand archipelago (Fig. 1). It is less than 35 km from the southern coast of the South Island, separated by the shallow (up to 36 m deep) Foveaux Strait that was dry during the glacial maximum until inundated by rapidly rising sea levels between 14 000 and 10 000 BP (Cullen 1967). Although modified by fire, logging, and introduced animals, a consequence of at least 700 years of Maori and 175 years of European settlement, the island's vegetation patterns are little altered from their pre-human state (Wilson 1987).

The biogeography of Stewart Island is of considerable interest as several tree and shrub species (notably *Nothofagus solandri* var. *cliffortioides**, *Nothofagus menziesii*, *Libocedrus bidwillii*, *Phyllocladus alpinus*, and *Halocarpus bidwillii*) are absent, despite being widespread, and in places dominant, in areas with similar climates and soils on the adjacent mainland. Cockayne (1909) suggested that *Nothofagus* and other absent genera were poorly adapted to Stewart Island conditions, and in the course of the Pleistocene were either eliminated or failed to colonise. He cited the highly restricted distribution of some Stewart Island plants (*Cordyline australis*, *Olearia ilicifolia*, and *Prumnopitys taxifolia*) as support for his view that the process of elimination was continuing. Zotov (1938), Willett (1950), Fleming (1963), Wells & Mark (1966), and Wilson (1982) all assumed that the cool conditions prevailing during the glacial maximum (c. 25 000–14 000 BP) would have been sufficient to eliminate forest from the island, and that the formation of the sea strait with the rise in sea level after that time would have prevented subsequent colonisation by poorly dispersed species such as *Nothofagus*

*Nomenclature follows Allan (1961), Moore & Edgar (1970), Brownsey et al. (1985), and recent taxonomic changes listed in Connor & Edgar (1987).

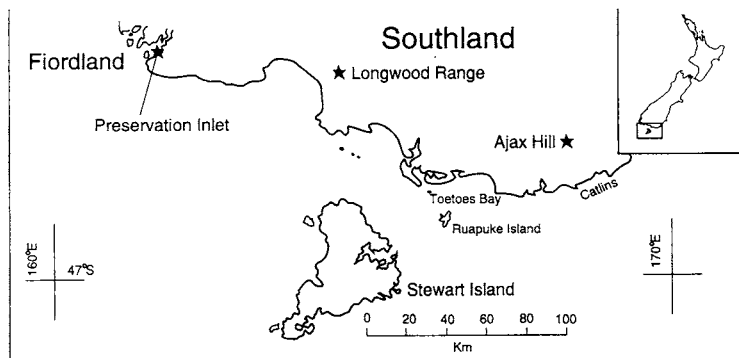
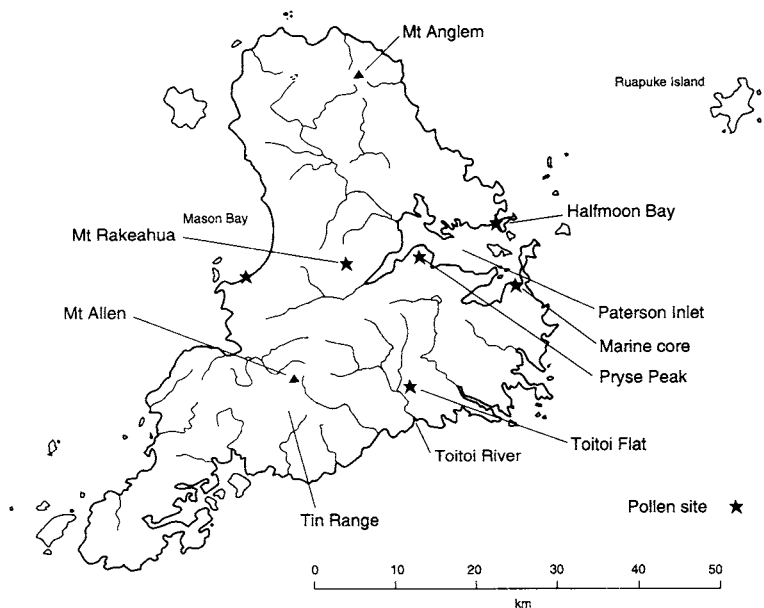


Fig. 1 Stewart Island. Inset: southern South Island.



menziesii. Wilson (1987) has argued for a more complex interpretation, pointing out that the depression of mean annual temperatures alone during the glacial maximum was not sufficient to eliminate hardy trees and shrubs. Such trees and shrubs may have persisted on the island during the glacial maximum but failed to withstand competition from trees better adapted to the mild, wet climates of the Holocene.

Two limited investigations of the vegetation history of Stewart Island have been published. Cullen (1967) presented a single pollen spectrum from a submarine peat dating to the early Holocene in Paterson Inlet. Bishop & Mildenhall (1994) analysed five samples from a thin peat layer of late-glacial to early Holocene age in sand dunes at Mason Bay. As well, Pocknall (1982) presented modern pollen rain results from two samples taken from Mt Rakeahua and Mt Anglem.

In this paper, we present a modern pollen rain survey, and pollen analytical investigations of three Holocene peats from Stewart Island. From this and previous work, we derive a vegetation and climate history of the island. Comparison of the environmental history of Stewart Island with that of nearby sites in coastal Southland and Fiordland demonstrates how its island setting and highly oceanic climate have given rise to its present unique biogeographic features.

STEWART ISLAND ENVIRONMENT, VEGETATION, AND HISTORY

The current vegetation of Stewart Island is a complex mosaic of forest, scrub, and open ground. Forest 10 m or more tall covers about 64% of the total

area. Most of this is podocarp/hardwood forest, with *Dacrydium cupressinum* (rimu) by far the most abundant podocarp emergent, and *Weinmannia racemosa* (kamahi) the dominant canopy hardwood. Hardwood forest without podocarp emergents (chiefly dominated by *Weinmannia racemosa* and *Metrosideros umbellata* (rata)) accounts for about 3.5% of the land surface. Another 25.5% is covered by short forest and scrub (woody vegetation 1–10 m tall) in which *Leptospermum*, *Dracophyllum*, *Olearia*, and small-statured podocarps are prominent. The remaining 7% is open grassland, herbfield, sedge land, fernland, shrubland, wetland, and predominately bare ground (this last < 1%); important genera are *Chionochloa*, *Empodisma*, *Gahnia*, *Carex*, *Gleichenia*, *Leptospermum*, *Dracophyllum*, *Oreobolus*, *Donatia*, and *Baumea*. The spatial variation in plant cover is related to the island's strongly oceanic, windy climate, its altitudinal range from maritime cool temperate to upper subalpine, its generally low but variable soil fertility and pH, and its wide diversity of soil drainage. Effects of historical events such as fire, milling, and landslides, which would tend to obscure the primary pattern, are both limited in extent and readily identifiable (Wilson 1987).

The present climate at sea level (records from Halfmoon Bay) is cool temperate (mean annual temperature 9.6°C; New Zealand Meteorological Service 1975–1984) and highly oceanic, being humid and windy and lacking extremes of temperature or seasonal change (mean February temperature 13.1°C; mean July temperature 6.1°C). Rainfall is evenly spread throughout the year, ranging from about 1000 mm on some coasts to perhaps 3000 mm over higher ground. Snow lies only intermittently on the tops; heavy snowfalls at sea level are very rare. Light winter ground frosts occur on the coasts, with heavier frosts inland. There is a marked contrast between the wind-exposed west- and south-facing slopes, and the sheltered east- and north-facing ones, both in erosional landform and vegetation. Differential exposure to wind-borne salt is probably a major factor in determining coastal vegetation patterns.

Soils have developed on Permian to Carboniferous intrusives of diorite, tonalite, and granite, associated in places with schist. Widespread podzolised yellow-brown earths grade into organic soils which are extensive in the lowlands south of Paterson Inlet. There are also significant areas of sand and sand-derived soils, recent alluvium, gley alluvium, and skeletal upland soils. Blanket peat is extensive in the south but very local in the north. There are substan-

tial areas of basin peat (e.g., at Toitoti Flat, Rakeahua Valley, and Deceit Peaks), but raised peat bogs appear to be restricted to small areas between the north-east corner of the Mason Bay plains and Freshwater River.

Maori have inhabited Stewart Island for at least the last 700 years and almost certainly longer (Wilson 1987). European contact began with sealing and whaling in the early 1800s and by the 1830s onwards European settlement was concentrated in the Halfmoon Bay area (Howard 1940). Timber milling began in the 1860s but was of limited extent being concentrated in the Halfmoon Bay-Paterson Inlet region. Halfmoon Bay itself was still in tall forest in the early 1870s, forest having been cleared only a couple of hundred metres back from the beach (photo in Howard 1940:176). The Halfmoon Bay township grew slowly, roading only being established after 1883. Logging ceased in 1931 and, with it, major impacts on the vegetation. Since then, the economy of the 300–400 inhabitants has been based mainly on fishing and tourism, although there are limited areas of farmland close to Halfmoon Bay township and in Mason Bay.

STUDY SITES

Toitoti

Toitoti Flat is a poorly drained depression approximately 5 km² in area in the south-east sector of the island to the east of the Tin Range. Numerous small streams drain into the depression from the surrounding low hills (100–200 m a.s.l.), and from there into the Toitoti River that flows southwards through a gorge in the low coastal hills to the sea some 4 km distant. The depression floor has a complex topography of low rises (1.5–3.0 m), basins with lakes and small tarns, and numerous channels with meandering sluggish streams. Two soils are described from the depression (Leamy 1974): Toitoti soils are sandy loams formed on the low rises, and Kini soils are loamy peats formed in swampy flood plain hollows. Our observations show that peat and peaty silts fill hollows and stream channels to depths ranging between 0.5 m and 2.0 m. The highest and driest areas within the depression have a dense 2–3 m high scrub cover mainly of *Leptospermum scoparium*. Poorly drained slopes are variously covered by a tussockland-shrubland of *Chionochloa rubra*, *Leptospermum scoparium*, *Dracophyllum longifolium*, *Hebe odora*, *Cassinia leptophylla*, *Coprosma* spp.; *Empodisma minus*-*Gleichenia*

dicarpa bog; and in areas with open water, swamp dominated by *Leptocarpus similis*, *Baumea tenax*, and *Phormium tenax*. The slopes immediately surrounding the depression are mainly in *Chionochloa rubra*-dominated tussockland and tussock-shrubland; this grades away from the depression into nearly pure stands of *Leptospermum scoparium* scrub; and the scrub gives way on the hill slopes to podocarp/hardwood forest in which small, widely spaced trees of *Dacrydium cupressinum* (with co-dominants *Prumnopitys ferruginea* and *Podocarpus hallii*) emerge above a hardwood canopy of *Weinmannia racemosa* and *Metrosideros umbellata*. The tree fern *Dicksonia squarrosa* is abundant throughout the forest, while *Cyathea smithii* is prominent in gullies along streams.

A 2.3 m core (Field core number X81/16, NZMS 260 D49/290365) was taken from beside a stream in the north-western sector of the depression, and a sample collected nearby for modern pollen analysis.

Halfmoon Bay

A core (X81/20, NZMS 260 E48/384566, c. 15 m a.s.l.) was drilled in a small, peat and silt filled valley head in the middle of the Halfmoon Bay township (also known as Oban). Vegetation of the site is a rough tussocky sedgeland of *Carex geminata* and *C. appressa*, with *Dicksonia squarrosa* and naturalised willows (*Salix* spp.) growing on the valley sides.

Baker Park swamp

Baker Park is a small scenic reserve behind Butterfield Beach, Halfmoon Bay and consists of a 200–250 m diameter patch of boggy sedge and scrub covered ground surrounded by tall forest. *Carex appressa*, *C. secta*, *Blechnum minus*, *B. penna-marina*, *Eleocharis acuta*, *Sphagnum* spp., *Juncus procerus*, *Coprosma propinqua*, and *Myrsine divaricata* dominate the boggy ground. The surrounding forest is dominated by *Dacrydium cupressinum*, with less frequent *Prumnopitys ferruginea*, emergent over *Weinmannia racemosa* and *Dicksonia squarrosa*. A surface sample (X81/15, NZMS 260 E48/388577) for modern pollen rain was taken from the centre of the boggy area.

Pryse Peak

Pryse Peak (352 m a.s.l.) is a prominent hill on the eastern side of the entrance to Southwest Arm, Paterson Inlet. Tall (3–5 m) scrub of *Leptospermum scoparium*, *Olearia colensoi*, and *Weinmannia racemosa* covers the summit. Below the summit is tall *Dacrydium cupressinum*/*Weinmannia racemosa*

podocarp/hardwood forest, with a substantial component of *Prumnopitys ferruginea* and *Metrosideros umbellata*. A surface sample for modern pollen rain (X81/18, NZMS 260 D48/296516) was taken close to the trig. station under a *Leptospermum scoparium* canopy.

Rakeahua

Mt Rakeahua (681 m a.s.l.) borders the north-eastern side of Rakeahua Inlet. *Dacrydium cupressinum*/*Weinmannia racemosa* podocarp/hardwood forest with *Prumnopitys ferruginea* and *Metrosideros umbellata* common, clothes the flanks up to an altitude of c. 300 m. *Dicksonia squarrosa* and *Cyathea smithii* are common understorey tree ferns, the latter mainly in gullies. *Leptospermum scoparium* up to 10–12 m tall is prominent on the lowland flats and with increasing altitude is dominant in forest gaps. *Dracophyllum longifolium*, *Halocarpus bififormis*, *Lepidothamnus intermedius*, *Myrsine divaricata*, and *Olearia colensoi* also become more common with increasing altitude. Above the tall forest zone is a dwarf forest of *Leptospermum scoparium*, *Olearia colensoi*, *Halocarpus bififormis*, and *Dracophyllum longifolium*, that grades into low scrub of the same species. Stunted *Weinmannia racemosa* and *Metrosideros umbellata*, and the occasional *Dacrydium cupressinum* occur within these communities. The broad summit of the Rakeahua uplands is covered with cushion bog of *Donatia novae-zelandiae*, *Carpha alpina*, *Oreobolus* spp., *Gaimardia setacea*, *Mitrasacme novae-zelandiae*, and *Dracophyllum politum*. Dwarfed *Leptospermum scoparium* scrub 10–50 cm high occurs in association with the cushion bog.

A core (X81/10, NZMS 260 D49/203491, 400 m a.s.l.) was taken from a peaty cushion bog lane 3–4 m wide within *Leptospermum scoparium* scrub close to a tarn at the southern end of Mt Rakeahua. Surface samples for modern pollen rain were taken: at the tarn site (X81/10); in cushion bog and open scrub at the junction of the Rakeahua and Southwest Arm tracks (X81/11, NZMS 260 D49/204503, 480 m a.s.l.); in a *Leptospermum scoparium*, *Olearia colensoi*, and *Dracophyllum longifolium* dominated opening in the upper *Dacrydium cupressinum*/*Weinmannia racemosa* forest (X81/13, NZMS 260 D49/222499, 200 m a.s.l.); on an open slope dominated by short (0.3–1.2 m tall) regenerating scrub of *Coprosma ciliata*, *Cyathodes juniperina*, *Leptospermum scoparium*, *Dracophyllum longifolium*, and *Gaultheria antipoda*, and surrounded by tall lowland *Dacrydium cupressinum*/*Weinmannia*

racemosa podocarp/hardwood forest (X81/14, NZMS 260 D49/229497, 80 m a.s.l.).

1. Approximate ages for other levels in the cores are interpolated from the radiocarbon dated levels by means of a cubic spline function.

METHODS

Samples from core X81/10 were collected by digging a hole in the peat and sampling from a cleaned face. The other peat cores were drilled with a 3 cm diameter Hiller borer and samples collected for pollen analysis in glass vials in the field. The larger amounts of material necessary for radiocarbon dating by the gas method were collected by repeat drilling with a large diameter (12.5 cm) head. Surface pollen samples were collected over 1–2 m², 10–12 tufts of moss or lichen being taken per sample.

Tablets with a known quantity (11 300) of exotic *Lycopodium* spores (supplied by the Department of Quaternary Geology, Lund, Sweden) were added at the first stage of preparation of the samples from cores X81/10 and X81/16 and pollen concentration per gram dry weight determined by the proportion of exotic *Lycopodium* to pollen counted. Pollen extraction followed standard palynological procedures of disaggregation of samples in 10% KOH, digestion in 40% HF, oxidation with a chlorine bleach, and acetolysis (Faegri & Iversen 1964). Pollen percentages are based on a pollen sum of all dryland plants including tree ferns and ground ferns but excluding plants confined to or characteristic of mires and open water. In most instances, a sum of 250 or more was used for percentage calculations. Relative charcoal content was assessed using the point method of Clark (1982) and is expressed as a charcoal index (total charcoal hits by an 11 point grid per field view as a percentage of the pollen sum).

Material for radiocarbon dating was air-dried and submitted either to the Waikato University Radiocarbon Laboratory, Hamilton or the Rafter Radiocarbon Laboratory of the Institute of Geology and Nuclear Sciences, Wellington. Details of all radiocarbon dates reported in this study are given in Table

RESULTS

Modern pollen rain

Results for the modern pollen study are given in Fig. 2. The uppermost sample from the Toitōi Flat core (X81/16) is also included. As with other New Zealand pollen rain studies, the proportion of a given pollen taxon in the surface samples does not bear a linear relationship to its representation in the vegetation. The main podocarp trees on the island, *Dacrydium cupressinum* and *Prumnopitys ferruginea*, are well represented in the samples. *Podocarpus hallii*, despite being abundant in many vegetation types, forms a relatively minor proportion of the pollen rain, barely exceeding 5% even on the slopes of Mt Rakeahua, where it is a prominent part of the forest canopy. The smaller podocarp trees, *Halocarpus biformis* and *Lepidothamus intermedius*, are even less well represented, averaging only 1.2 and 1.5%, respectively, of the pollen rain, even though they are abundant in upper forest and scrub. The two dominant hardwood trees, *Weinmannia racemosa* and *Metrosideros umbellata*, are well represented in the pollen rain at sites where they are close to the sampling site and abundant in the local vegetation but otherwise range between a trace and 2%. *Metrosideros umbellata* pollen cannot in practice be distinguished from pollen of the climbing vine *Metrosideros diffusa* that also occurs on Stewart Island. However, *Metrosideros diffusa* forms only a very small part of the canopy where it occurs and bears many fewer flowers than *M. umbellata*, and is therefore likely to be an insignificant contributor to the pollen rain. Most small hardwood trees, scrub species, and tree ferns, follow the *Metrosideros-Weinmannia* pattern of being well represented in the

Table 1 Radiocarbon age determinations (conventional half-life).

Site	Depth (cm)	Date yrs BP	Error	$\delta^{13}\text{C}$	Material	Lab no
X81/16	15–20	429	± 55	–27.2‰	fibrous peat	NZ 8303
X81/16	110–120	3610	± 70	–28.2‰	peaty sand	Wk–1590
X81/16	190–200	8370	± 90	–27.8‰	peaty silt	Wk–1589
X81/16	230	9877	± 91	–29.21‰	peaty silt	NZA 3492
X81/20	185–200	4510	± 60	–29.0‰	peaty silt	Wk–1669
X81/20	305–335	6220	± 57	–29.4‰	peaty silt	NZ 8304

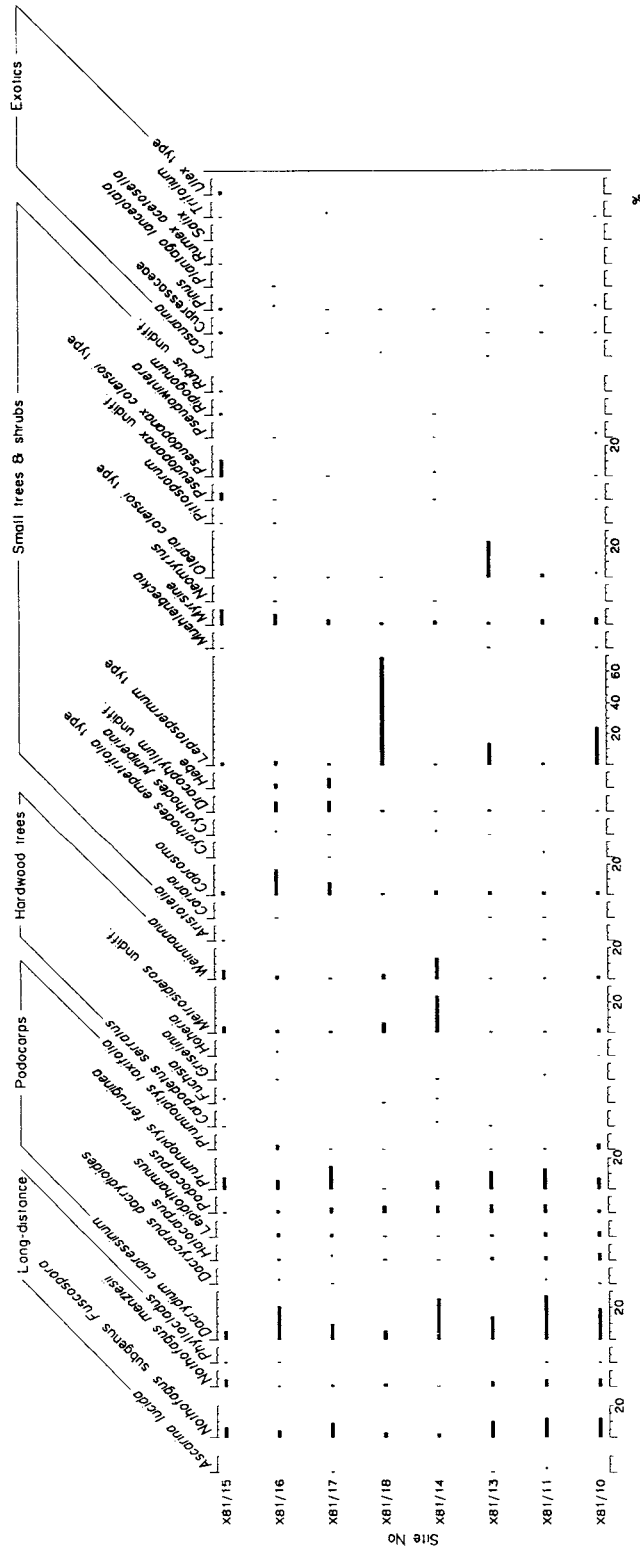




Fig. 2 Percentage pollen diagram, modern pollen rain. X81/15, Baker Park Swamp; X81/16, Toitotoi Flat drill hole; X81/17, Toitotoi Flat; X81/18, Pryse Peak; X81/14-X81/10, Mt Rakeahua altitudinal transect.

pollen rain when close to or dominating the local site but at low levels otherwise even when abundant in the general vegetation of the area. Grassland and upland cushion bog sites are easily distinguished by the high representation of grasses, sedges, Restionaceae, and certain cushion bog species such as *Mitrasacme novae-zelandiae* and *Donatia novae-zelandiae*.

A feature of the pollen rain is the high representation of certain tree and scrub species not present on the island. Subgenus *Fuscospora* (the *Nothofagus fusca* group) and *Nothofagus menziesii* are prominent in the pollen rain averaging 7.4 and 2.5%, respectively, and *Prumnopitys taxifolia* (represented by only a few trees on the island) and *Phyllocladus alpinus* (absent) are also recorded. Non-indigenous pollen rain and *P. taxifolia* accounts for an average of 11.2% (range 2.5–21%) with the highest percentages from the three upland Mt Rakeahua samples (14–21%).

Fossil sites

Toitoti Flat: X81/16

(Fig. 3)

Core stratigraphy:

Depth (cm)

below surface:

- 0–25 fibrous, slightly silty brown-grey peat;
- 25–160 slightly silty grey-brown organic mud;
- 160–192 yellow-brown peaty sand, occasional wood fragments;
- 192–200 grey-brown silty peat;
- 200–230+ yellow-brown sands and organic silts;

Pollen stratigraphy:

The pollen diagram is divided into five zones (TF-1 – TF-5) on the basis of the pollen content.

TF-1: Shrubland; 230–205 cm; c. 10 100–8800 BP. The terrestrial pollen sum is dominated by grass, scrub (*Asteraceae*, *Coprosma*, *Dracophyllum*, *Myrsine*), and tree ferns (mainly *Cyathea smithii* type, but including significant amounts of *Dicksonia squarrosa* and *D. fibrosa*). Trees make up 7–15% of the terrestrial sum. *Isoetes* is abundant in the first few samples, but diminishes to trace levels by the beginning of TF-2; *Gleichenia* and *Leptocarpus* are abundant.

TF-2: *Weinmannia-Metrosideros* forest; 205–145 cm; c. 8800–5400 BP.

Arboreal pollen and spores (mainly *Weinmannia*, *Metrosideros*, and *Cyathea smithii* type) dominates (57–64% of terrestrial sum). *Coprosma*, *Griselinia*, *Leptospermum*, and *Myrsine* are the most common shrub types,

TF-3: *Podocarp/Weinmannia-Metrosideros* forest; 145–105 cm; c. 5400–3100 BP.

The tall podocarp trees, *Dacrydium cupressinum* and *Prumnopitys ferruginea*, increase sharply but total tree and tree fern percentages remain much the same as in TF-3.

TF-4: *Dacrydium cupressinum* dominated forest; 105–55 cm; c. 3100–1400 BP.

Dacrydium cupressinum dominates the arboreal pollen spectra along with *Cyathea smithii* type tree ferns. Other components of the pollen spectra remain relatively unaltered from the previous two zones.

TF-5: Grass-charcoal; 55–0 cm; c. 1400 BP-present. All samples in this zone are distinguished from the previous by substantial quantities of microscopic charcoal. Grass and *Myrsine* levels are approximately double those of the previous zone, but otherwise it is essentially similar.

Radiocarbon dates are listed in Table 1.

Halfmoon Bay: X81/20

(Fig. 4)

Core stratigraphy:

Depth (cm)

below surface:

- 0–8 dark brown fibrous, spongy peat;
- 8–35 grey-brown fibrous peat with abundant wood;
- 35–45 transition to light brown fine sand and silt with abundant organic material;
- 45–122 grey-brown sandy silts with peaty lenses and occasional wood fragments;
- 122–140 dense wood layer;
- 140–160 sandy silt;
- 160–235 fine grey-brown sandy silt with occasional woody fragments;
- 235–265 woody layer in silt;
- 265–360 grey-brown sandy silt with occasional woody and peat layers;
- 360–390 sand;
- 390+ peaty sand.

Pollen stratigraphy:

The pollen diagram is divided into five zones (HM-1 – HM-5).

HM-1: *Weinmannia*/tree fern forest; 400–310 cm; c. 7300–6100 BP.

Weinmannia racemosa and *Cyathea smithii* type tree fern comprise up to 80% of the total pollen sum. *Metrosideros*, *Prumnopitys ferruginea*, *Griselinia*, *Myrsine*, *Rubus*, and ground ferns are present in lower but substantial amounts.

HM-2: *Weinmannia-Metrosideros*/tree fern forest; 310–210 cm; c. 6100–4700 BP.

Metrosideros increases to 25% by the top of the zone, establishing co-dominance with *Weinmannia racemosa* and *Cyathea smithii* type.

HM-3: *Dacrydium cupressinum*/*Weinmannia*/tree fern forest; 210–95 cm; c. 4700 BP–1875 AD.

Dacrydium cupressinum increases sharply to 45% of the pollen sum. *Weinmannia* and tree ferns fall to somewhat lower levels on average than those of HM-2; *Metrosideros* is unaffected until the top of the zone where it falls to register low sporadic percentages from then on; and *Prumnopitys ferruginea* increases at the beginning of the zone, and again at the top.

HM-4: Logging; 95–35 cm; 1875–1885 AD.

Dacrydium cupressinum declines by one half; there is a sharp, temporary oscillation centred on 75 cm where *Weinmannia* increases, while *Cyathea smithii* type, *Prumnopitys ferruginea*, and *Dacrydium cupressinum* decrease. *Griselinia*, *Fuchsia excorticata*, and *Carpodetus serratus* become abundant.

HM-5: Settlement expansion; 35–0 cm; c. 1885–1981 AD.

First grass and then *Blechnum* ferns increase, while *Weinmannia* and *Cyathea smithii* type decrease. Microscopic charcoal is present in large amounts, and exotic pollen types present, including *Rumex acetosella* and Cupressaceae.

Radiocarbon dates are listed in Table 1.

Rakeahua Tarn X81/10 (Fig. 5)

Core stratigraphy:

Depth (cm)

below surface:

0–3 turf of *Oreobolus pectinatus* and *Donatia novae-zelandiae*;

3–40 sandy peat, with numerous live and dead roots;

40–95 sand.

Pollen stratigraphy:

This pollen profile is unzoned because of the lack of major changes in the pollen content. It essentially is the same as the modern pollen spectra from similar sites, the extra local component being dominated by *Dacrydium cupressinum*, *Prumnopitys ferruginea*, and *Cyathea smithii* type and long distance transport of *Fuscospora*, *Prumnopitys taxifolia*, and *Nothofagus menziesii*. The local pollen component of *Donatia novae-zelandiae*, Cyperaceae, *Mitrasacme novae-zelandiae*, Centrolepidaceae, *Leptospermum*, *Myrsine*, and *Halocarpus* accurately reflects the composition of the upland bog and scrub vegetation cover.

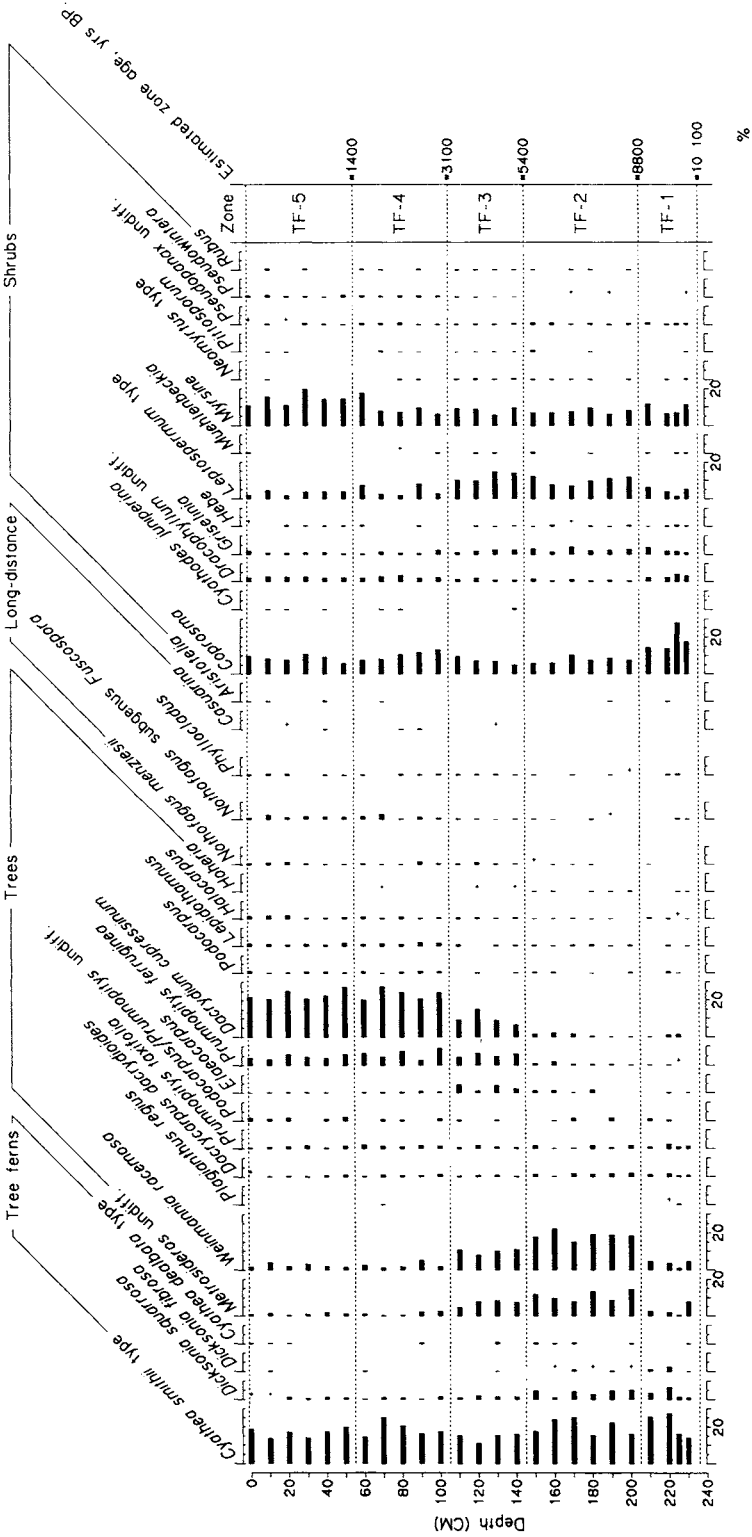
Three features of the profile are worth additional

comment. Pollen of *Phyllocladidites mawsonii* Cookson ex Couper, a presumably extinct taxon related to *Lagarostrobos franklinii*, is found in excellent condition and high numbers in the basal sample. There is a slight rise of *Pteridium esculentum* between 30 and 20 cm depth. In the upper 10 cm there is a sustained rise of *Leptospermum*.

This site is undated because of the presence of live roots throughout the profile.

VEGETATION HISTORY OF STEWART ISLAND

Widespread peat accumulation had begun on Stewart Island by c. 10 000 BP. At Mason Bay, on the western side of the island, wood from peat horizons up to 1 m thick overlying sands and gravels has been dated to 9980 ± 50 BP (NZ 7216) and 9475 ± 150 BP (NZ 6924) from the northern and southern ends of the bay, respectively (Bishop & Mildenhall 1994). A 10 cm thick peat horizon in marine sediments in 11 m of water in Paterson Inlet, on the eastern side of the island, dates to 9300 ± 80 BP (Cullen 1967). Peaty silt at the base of the Toitōi Flat core dates to 9877 ± 91 BP. The pollen spectra from these earliest peats strongly resemble one another in recording a scrub and tree fern association in which Asteraceae, *Coprosma*, *Hebe*, *Griselinia*, *Myrsine*, *Dracophyllum*, *Cyathea smithii*, and *Dicksonia fibrosa* and *D. squarrosa* were prominent. Ground ferns, including *Paesia scaberula* at Mason Bay, were abundant at all sites. Grassland cannot have been common: the highest Poaceae pollen counts (12%) are for the open Toitōi Flat site and are much less at the other three sites. All the major tree types currently on the island are recorded in these early samples. The *Podocarpus*/*Prumnopitys* group are the most abundant in the pollen rain. However, much of this pollen type could have drifted from the mainland where *Prumnopitys* and *Podocarpus* were common. *Dacrydium cupressinum* pollen occurs in most of these peats, albeit at low amounts, and this tree is likely to have been present on the island, as its pollen is equally rare on the mainland. *Metrosideros*, most likely *M. umbellata*, is present in all samples, at levels from 1–20%, and is already likely to have been a part of the developing scrub-forest mosaic. The trend of the pollen diagram from Mason Bay indicates that *Metrosideros* was present in quantity before *Weinmannia*, which agrees with the presence of *Metrosideros* and absence of *Weinmannia* from the marine Paterson Inlet site.



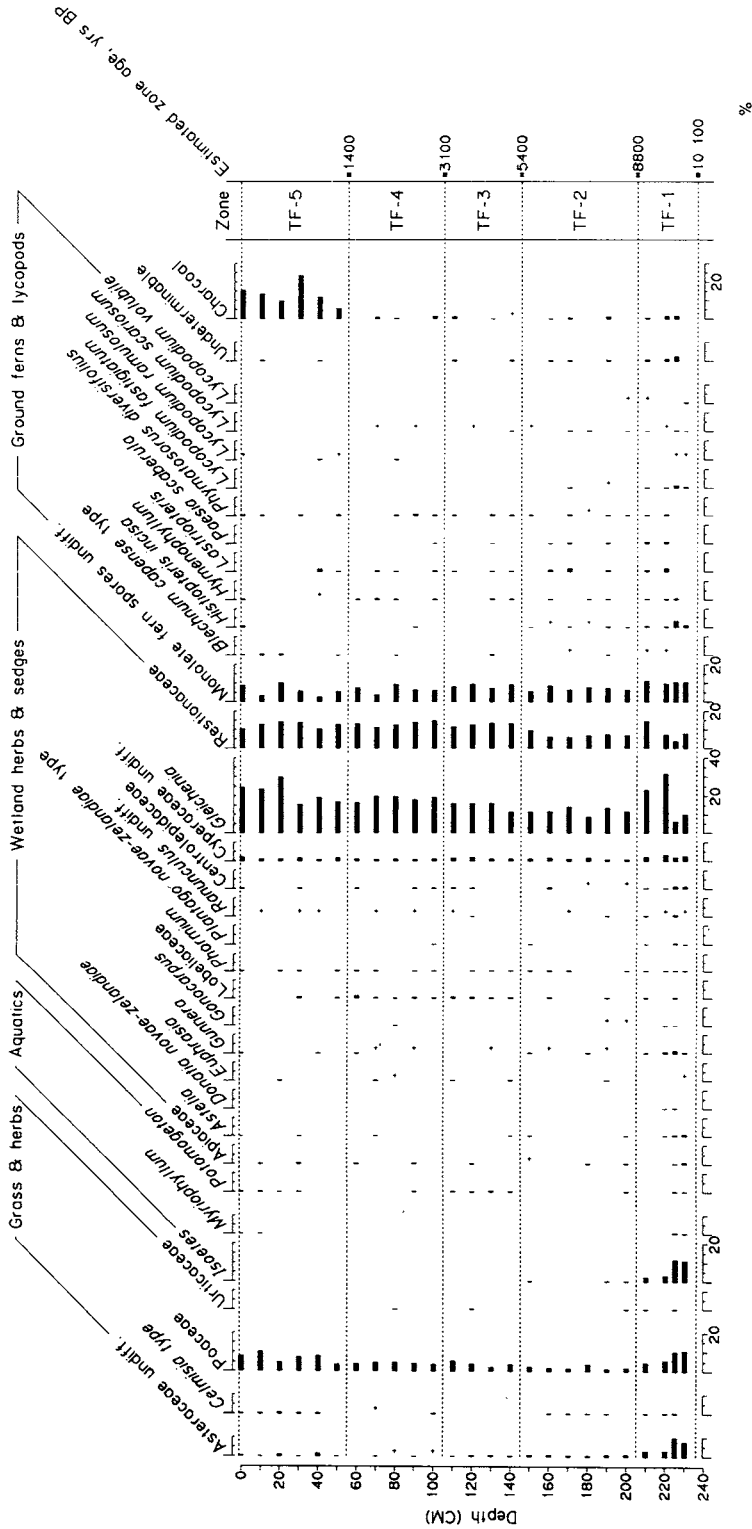
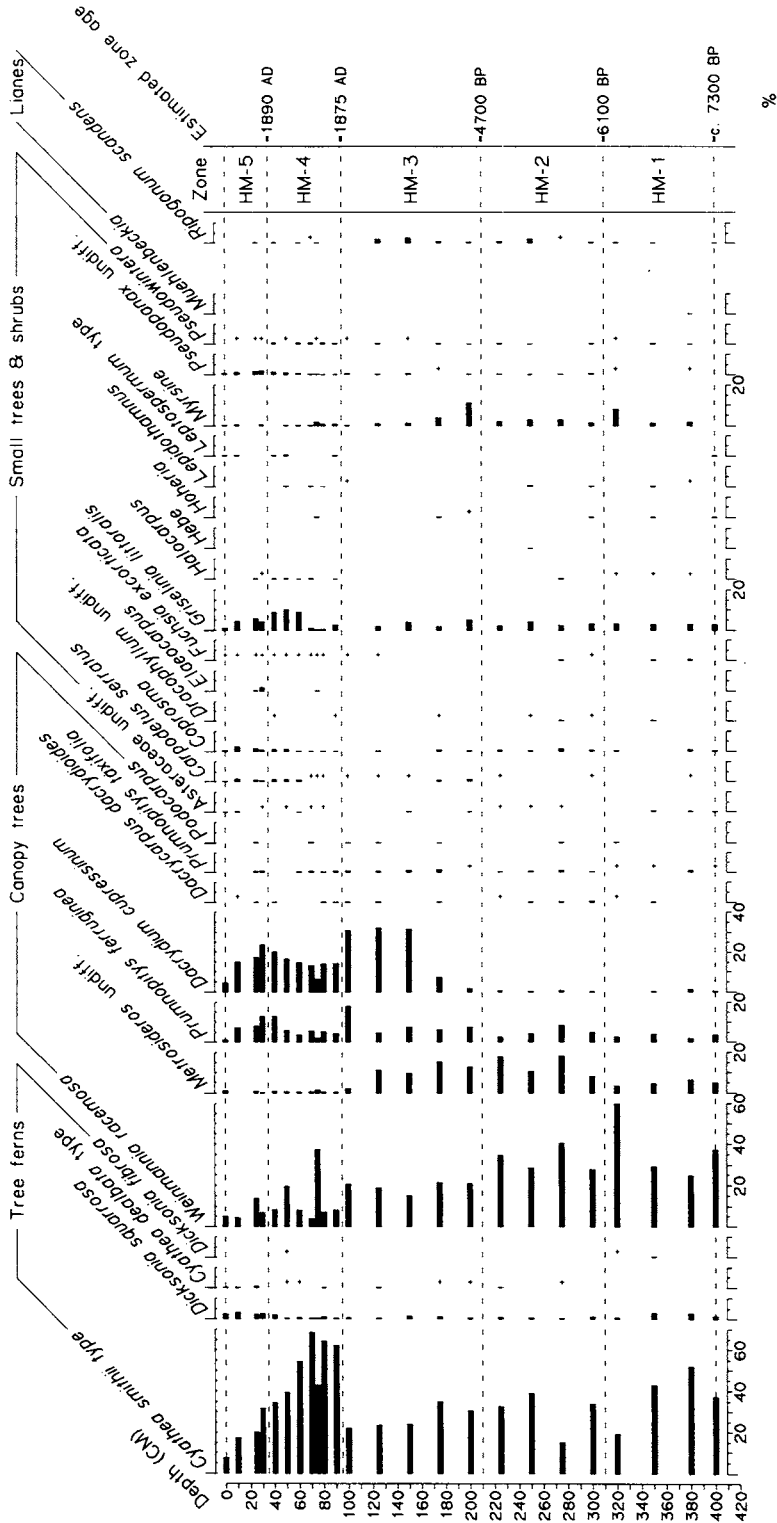


Fig. 3 Percentage pollen diagram: Toitoti Flat.



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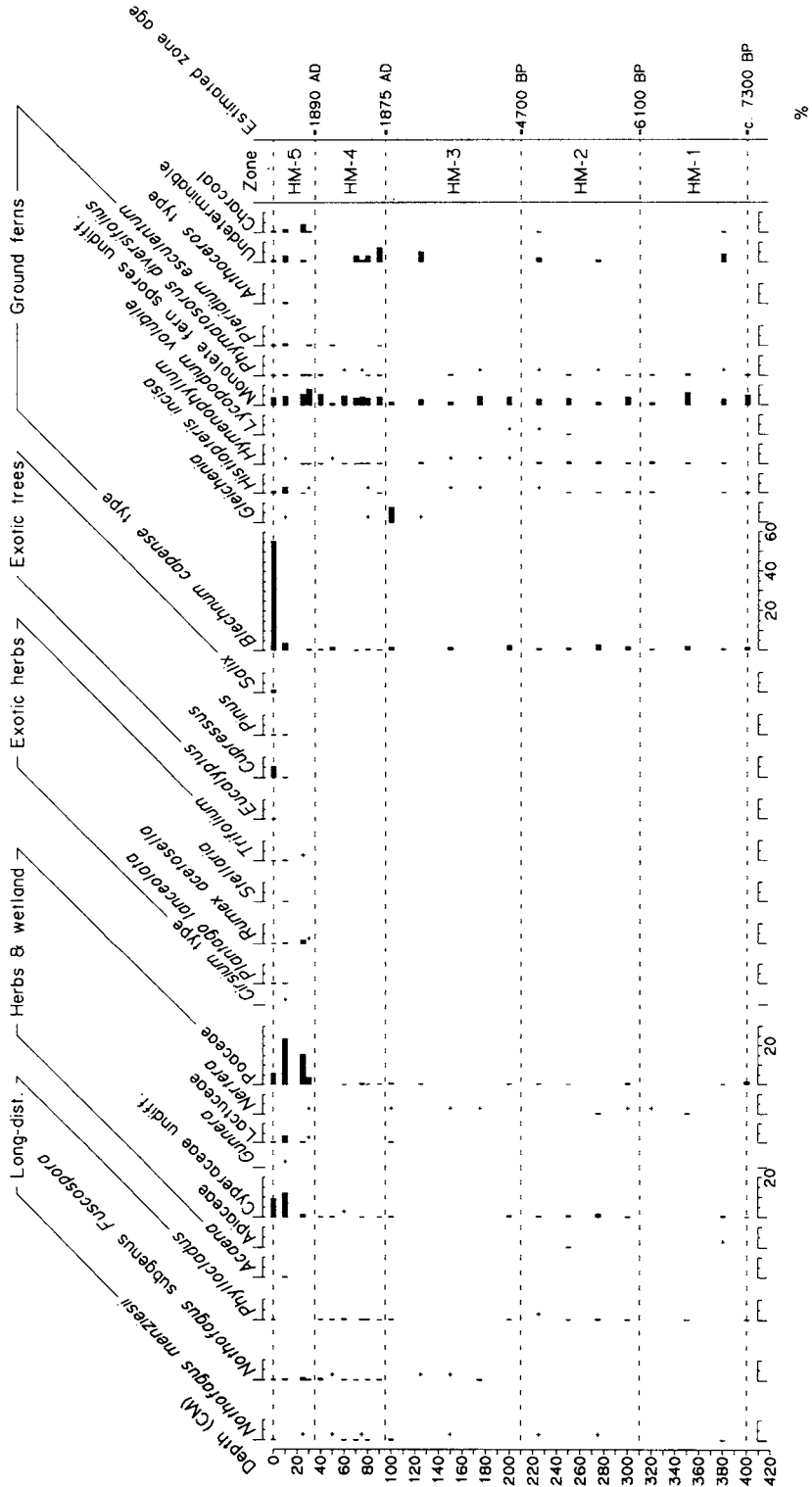


Fig. 4 Percentage pollen diagram: Halfmoon Bay.

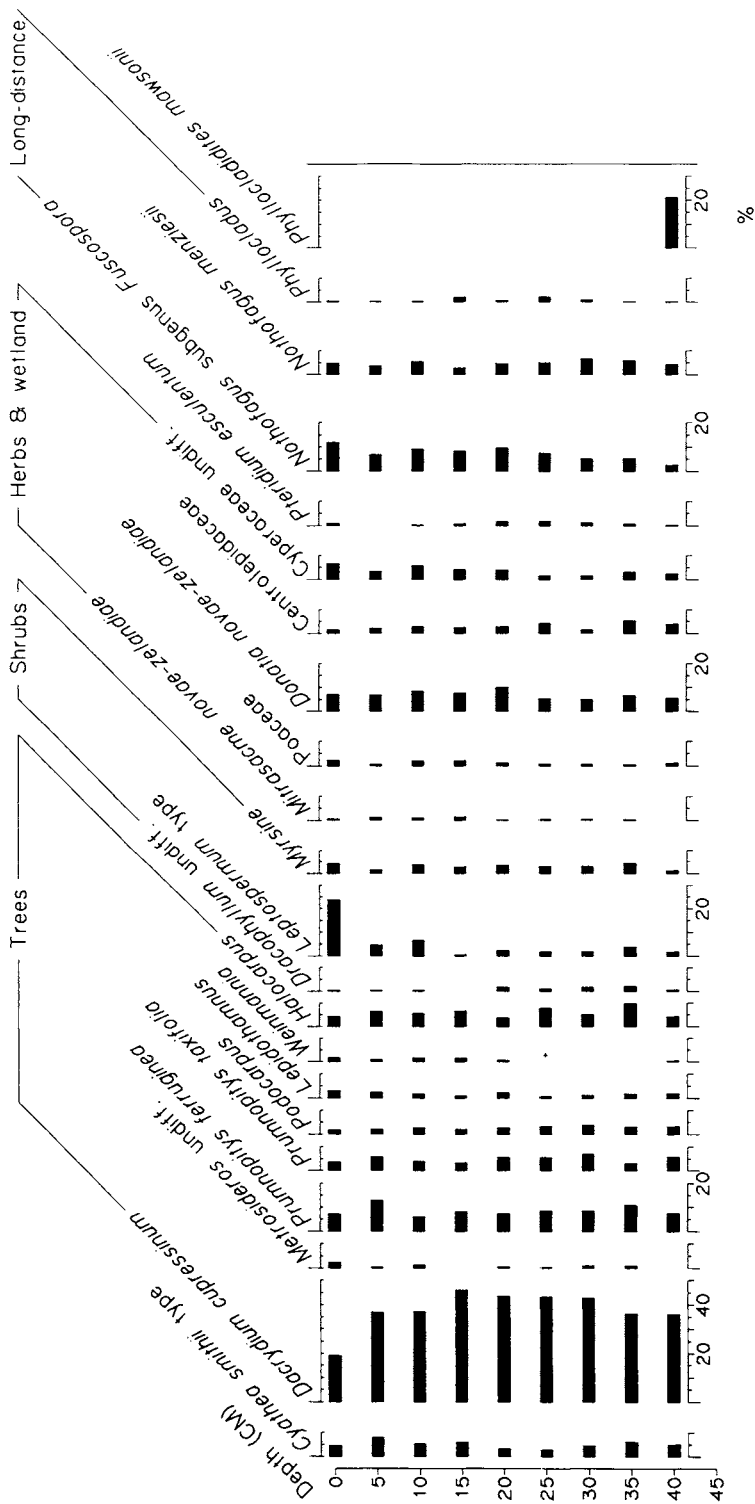


Fig. 5 Percentage pollen diagram: Rakeahua Tarn.

The combination of scrub, hardwood forest, tree ferns, and abundant ground ferns suggested by the early Holocene samples cannot be matched in the limited range of modern pollen samples. Moreover, this combination does not presently appear to exist on the island as scrub and low forest communities do not have a substantial tree fern component. Tree ferns and ground ferns may have played a more important role than later, perhaps occupying large areas as nearly pure fern communities.

Shortly after 9000 BP, *Weinmannia*, *Metrosideros*, and *Leptospermum* increased sharply to dominate the pollen influx at Toitoti Flat (zone TF-2) but, other than a decline in Poaceae and Asteraceae, there is little major change in the pollen spectra. Zone HM-1 at Halfmoon Bay has a similar pollen signature, except that *Weinmannia* and tree ferns are more abundant and *Metrosideros* is a minor component. *Prumnopitys ferruginea* makes up 4–5%, more than the 1% levels at Toitoti Flat, suggesting that it had a considerable local presence. The Halfmoon Bay site, for most of the period it was accumulating, lay either under or close to a closed forest canopy and in this early period was dominated by *Cyathea smithii* and *Weinmannia racemosa*, with *Prumnopitys ferruginea* and *Dacrydium cupressinum* probably in the local forests but not common at the site. Toitoti Flat was largely occupied by *Leptospermum*–*Coprosma*–*Myrsine* scrub and restiad wetland, but the surrounding hills were in *Weinmannia*–*Metrosideros*/tree fern low forest with *Dacrydium cupressinum* and *Prumnopitys ferruginea* both present but presumably uncommon. There is therefore considerable agreement between these two sites, despite their great differences in setting.

Beginning at c. 5500 BP at Toitoti Flat, and at 4700 BP at Halfmoon Bay, *Dacrydium cupressinum* and *Prumnopitys ferruginea* underwent a major expansion that was essentially complete by c. 3000 BP. At both sites, *Metrosideros* and *Weinmannia* declined slowly as the podocarps became more common, but tree ferns remained steady. The climax of this process occurred in zone TF-4 and the upper half of HM-3, where *Metrosideros* and *Weinmannia* become relatively scarce at Toitoti Flat, and *Weinmannia* reduced by about half at Halfmoon Bay. *Metrosideros* at Halfmoon Bay remained abundant longer than *Weinmannia*, but eventually reduced to much lower levels.

The uppermost sediments of both Toitoti Flat and Halfmoon Bay show probable effects of human intervention. At Toitoti Flat a major charcoal increase defines zone TF-1, and it is accompanied by an

increase in grass, *Myrsine*, and Asteraceae pollen, indicating creation by fire of more open habitat at the site. On the basis of extrapolated radiocarbon dates, the increased level of firing began c. 1400 BP. However, it is possible that the firing was a consequence of early Maori exploration of the island, and therefore in the range 800–600 BP. Halfmoon Bay was in dense forest at the time of European settlement in the 1830s. Logging in the early 1870s (zone HM-4) halved the influx of *Dacrydium cupressinum* pollen and increased that of *Cyathea smithii* spores, consistent with the removal of forest from Halfmoon Bay. There are two sharp peaks of *Weinmannia racemosa* which probably represent recovery of trees damaged during logging. Increases of *Dicksonia squarrosa*, *Carpodetus serratus*, *Fuchsia excorticata*, *Pseudopanax*, *Coprosma*, and *Griselinia littoralis* towards the close of zone HM-5 indicate the proliferation of a fern-rich hardwood forest and scrub cover. During the time represented by zone HM-5, the area of the present township was cleared and pasture established on its outskirts, a process that began slowly in the 1870s and accelerated after the beginning of roading works in 1883. The site gained its present cover of sedge, *Blechnum*, and *Dicksonia squarrosa* at around this time, which we have estimated as probably being in the 1890s.

The Rakeahua Tarn site falls entirely within the latest Holocene period. Radiocarbon dating is unreliable at this site because of the shallow profile and deep penetration by live roots. Being an upland site, its pollen profile cannot be directly compared with those of the two lowland sites. However, upland sites receive a substantial proportion of their pollen rain from the mainland, and comparison with well dated upland sites on the adjacent mainland, in particular Longwood Range, Southland (McGlone & Bathgate 1983) and Ajax Hill, Catlins, south-eastern Southland (M. S. McGlone, unpubl. data), can provide an accurate chronology. As the major arboreal component of the pollen profile is essentially unchanged throughout, it must be younger than c. 3000 BP, when the vegetation of Stewart Island reached a state similar to that of the present. *Fuscospora* pollen became abundant in upland mainland profiles after c. 1500 BP, and the base of the profile is therefore likely to be younger than this event. An upsurge of *Pteridium esculentum* spores is recorded both in the Ajax Hill and Longwood Range sites at close to 700 BP. Although the spore levels are correspondingly less at Rakeahua Tarn, an increase is noted at 30 cm depth. The peat therefore probably began growth between 1500 and 700 BP.

The occurrence of *Phyllocladidites mawsonii* pollen in the basal sample and its absence at higher levels is a major puzzle. Other than this Stewart Island occurrence, it was last recorded in New Zealand in the Miocene (Mildenhall 1980). *Lagarostrobos franklinii* (Huon Pine) of Tasmania is the closest extant relative to *P. mawsonii* but the pollen can be distinguished from it. It seems unlikely that the *P. mawsonii* pollen is reworked from older sediments as no Tertiary sediments have been recorded from this part of the island (Watters et al. 1968). Our tentative conclusion is that a plant producing pollen of the *P. mawsonii* type survived on Stewart Island into the late Holocene period and, if it is a low growing or dwarf shrub, it is possible that it is still present. The lack of high percentages of *Leptospermum* or other scrub types in the basal sediments (aside from the enigmatic *Phyllocladidites mawsonii*) suggests that the present boggy turf developed on a substrate free of heavy scrub cover. The tall *Leptospermum*-dominated scrub that forms the prominent windlanes is possibly a relatively recent development.

CLIMATIC AND BIOGEOGRAPHICAL CHANGE

Glaciation seems to have been slight on Stewart Island. There are two moraine-dammed cirques on the southern flank of Mt Anglem in the north of the island and less certain evidence for one on the eastern flank of Mt Allen in the south (Watters et al. 1968). The lowest undoubted cirque has a floor at c. 600 m a.s.l. Layers of angular, poorly sorted breccia that contain ventifacts occur near sea level beneath the 10 000 BP peat horizons and overlying sand dunes at Mason Bay (Bishop & Mildenhall 1994). The origin of the breccia is not clear but it is most likely to have formed by a combination of rock shattering, mass movement, and solifluction. It is difficult to come to any firm conclusions about the full glacial climate of Stewart Island from these meagre data. However, there is good evidence from lowland Southland in the form of colluvium and scree, and stripping of previous loess deposits, for a harsh, dry, windy climate (McIntosh et al. 1990). As Stewart Island was joined to Southland by a wide coastal plain (Fig. 6), it probably experienced a modified version of this climate regime, as suggested by the formation of breccia and occurrence of ventifacts at Mason Bay.

Sites on the adjacent mainland may give some

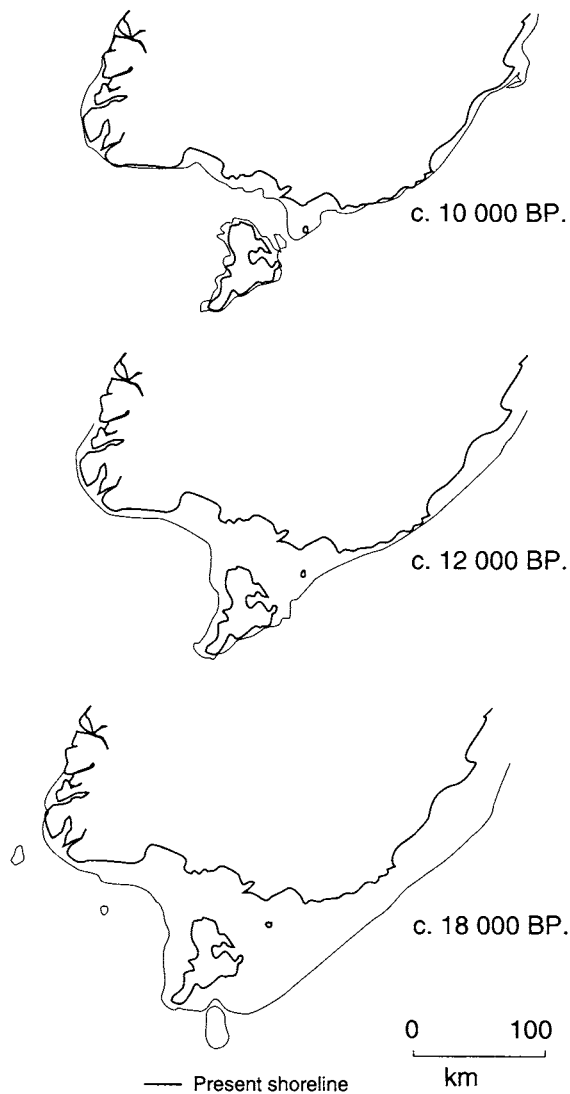


Fig. 6 Changing sea levels, southern South Island, 18 000–10 000 BP.

indication to what late-glacial conditions may have been like on Stewart Island (Fig. 7). In Southland coastal sites dating back to c. 12 000 BP (McGlone & Bathgate 1983; M. S. McGlone unpubl. data), shrubland and grassland was the earliest vegetation cover with forest taxa in low amounts. As the proportion of grassland fell, first ground ferns and then tree ferns became abundant after c. 11 000 BP. A pollen diagram from Preservation Inlet (Pickrill et al. 1992), a fiord 120 km west of Stewart Island on the Fiordland coast, reveals a substantially different vegetation history from that of Southland and one

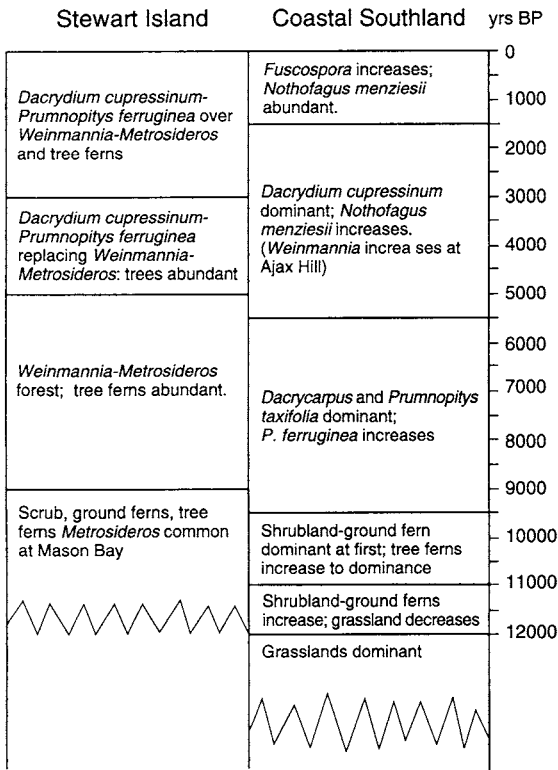


Fig. 7 Holocene vegetation history of Stewart Island and the adjacent mainland.

that may be more relevant to glacial maximum and late-glacial environments on the western side of the island. At Preservation Inlet the glacial maximum vegetation cover was mainly scrub but with abundant ground ferns. *Metrosideros*-tree fern forest had established before 14 000 BP but *Weinmannia* was not abundant until after 12 000 BP. Podocarps were rare until sometime after 9500 BP. As Fiordland formed part of the same coastline as western Stewart Island and was therefore exposed to the same weather systems, it seems likely that sheltered western sites on Stewart Island would have gained a hardwood forest cover equally early or may have had *Weinmannia racemosa* and *Metrosideros umbellata* groves throughout the glacial maximum.

Southern South Island pollen sequences show no indications of *Nothofagus* having formed a part of the early scrub and forest successions. Traces of *Nothofagus* pollen are noted in glacial and late-glacial sequences from Stewart Island, Fiordland, Longwoods, and Ajax Hill, but these could have as easily been derived from long-distance transport as

from minute local stands. The same applies to the traces of tree podocarps found in these sequences. There is, therefore, no direct support for the hypothesis that *Nothofagus*, and in particular *N. menziesii*, was present on Stewart Island and later eliminated by competition from resurgent podocarp trees as suggested by Wilson (1987). However, pollen evidence is ill-suited to establishing presence or absence: *Nothofagus menziesii* pollen is as rare in sediments of late-glacial–early Holocene age from Ajax Hill and the Longwood Range as it is in Stewart Island sediments, yet in both mainland areas this species became a dominant forest component in the late Holocene. The same analysis applies to *Phyllocladus alpinus* and *Libocedrus bidwillii*. Therefore, either *Nothofagus*, *Libocedrus*, and *Phyllocladus* were never present on Stewart Island, or they were present in small numbers at the end of the glacial maximum but were eliminated during the late-glacial or Holocene.

Movement of taxa from the South Island mainland to Stewart Island via a continuous dry land route was possible until Foveaux Strait was flooded at c. 10 000 BP (Fig. 6). Even now, a line of islands stretches from Paterson Inlet across to Toetoes Bay on the mainland and, from 9500 BP until sea level reached its current level at around 6000 BP, a chain of large islands gradually reducing in size provided narrowly separated stepping stones. For bird-dispersed taxa, the current ocean gap of 35 km is unlikely to have been a major obstacle, especially considering that the island is clearly visible from the mainland. Strong gales characterise weather patterns in the far south and wind dispersal is also likely to have been effective.

Given this lack of constraints to free movement of propagules, the marked difference between the early Holocene pollen sequences on Stewart Island and the mainland (Fig. 7) is most likely a result of differing substrate and climate. The Longwood and Ajax Hill pollen sequences record a transition lasting from c. 12 000 BP to c. 9500 BP from grassland-shrubland through a shrubland-tree fern phase to *Dacrycarpus dacrydioides*-*Prumnopitys taxifolia* dominant podocarp/hardwood forest. At about the same time that tree ferns gave way to podocarp dominant forest on the mainland, on Stewart Island *Metrosideros* and *Weinmannia* rose from being a minor constituent of the mainly scrub and tree fern vegetation to form a continuous forest cover, with only a minor podocarp tree component, that lasted until 4000–5000 BP. The coastal Southland sequences are interpreted as resulting from a

progression from a cool, cloudy, moist, late-glacial climate, that favoured ground ferns, scrub, and grassland, through a warmer (but still cooler than present) moist cloudy climate that favoured tree ferns and into a sunnier, warm, mild climate favouring tall podocarp trees (M. S. McGlone unpubl. data). *Prumnopitys taxifolia* and *Dacrycarpus dacrydioides* are presently rare on Stewart Island, being limited to scattered pockets of relatively fertile soil (Wilson 1987), and may never have been able to compete effectively given the prevailing highly infertile Stewart Island soils. This does not apply to *Dacrydium cupressinum* or *Prumnopitys ferruginea*, both of which can grow on infertile leached soils. Moreover, Stewart Island, from the evidence of the continuing abundance of tree ferns, may never have become as dry as the adjacent mainland, and a relatively cool, moist cloudy climate prevailed during the early Holocene. *Dacrydium cupressinum* and *Prumnopitys ferruginea* are favoured by moist climates, are bird-dispersed, and are therefore highly likely to have been present on the island at least by the early Holocene. The question therefore arises as to why they remained subordinate to hardwood trees for such a prolonged period. The explanation probably lies in the regeneration niche of the major tree species. Unbrowsed Stewart Island forests at present have dense ground fern and sapling understoreys, and effective regeneration of most tree species is inhibited (except in large tree fall gaps) with the exception of *Weinmannia racemosa* (and less commonly *Metrosideros umbellata*) that often begins life as an epiphyte on tree fern trunks (Veblen & Stewart 1980). Under the reduced light levels of cloudy early to mid Holocene summers, slow growing seedlings of podocarp trees would have had difficulty in regenerating on most sites. We therefore suggest that while the climate certainly was moist enough for *Dacrydium cupressinum* and *Prumnopitys ferruginea* dominance, vigorous competition from hardwood trees, tree ferns, and ground ferns under a cloudy, low radiation, mild climate may have prevented them occupying substantial areas of landscape.

McGlone & Bathgate (1983) suggested for coastal Southland that stronger, more persistently south-westerly and stormy airflow, perhaps as early as c. 7000 BP, began to cool the climate and increase rainfall, thus leading to the replacement of *Prumnopitys taxifolia*-*Dacrycarpus* dominated forests by *Dacrydium cupressinum* and *Nothofagus menziesii* forests. *Nothofagus menziesii* should be able to thrive in the upland interior of Stewart Island at present,

although it is unlikely to have been capable of doing so in the early to mid Holocene. It therefore appears that *Nothofagus menziesii* has failed to disperse to Stewart Island in the time since suitable habitats became available for it. On the other hand, increasing rainfall and cooler conditions cannot explain the rise of *Dacrydium cupressinum* as rainfall sufficient to permit growth of abundant tree ferns also suffices for *D. cupressinum* and, although it can tolerate cool temperate climates, it also thrives under warm conditions in the far north of New Zealand. Increasing solar radiation in the late Holocene, through reduced cloud and fog, particularly in summer, may have enhanced the competitive ability of *Dacrydium cupressinum* and *Prumnopitys ferruginea* versus tree ferns and hardwood trees. In the current vegetation on sheltered, sunny, north-facing slopes, *Dacrydium cupressinum* will reach the altitudinal limit of tree-sized *Metrosideros* and *Weinmannia*, but fails to do so on exposed, cool, south to south-west facing slopes. Tall *Dacrydium cupressinum*-*Prumnopitys ferruginea* forest is also increasingly uncommon towards the south of the island where persistently foggy conditions prevail, although high winds and poor drainage are as least as important.

CONCLUSIONS

The Holocene history of Stewart Island began with the replacement of tree fern and fern-rich scrub communities by *Metrosideros*-*Weinmannia*/tree fern forests at around 9000 BP. Between 5000 and 3000 BP, *Dacrydium cupressinum* and *Prumnopitys ferruginea* spread from previously restricted sites to partially supplant the hardwood forest cover and form the present dominant podocarp/hardwood forests. Stewart Island climates have been cloudy, cool, moist, and windy for the entire Holocene period. Early Holocene climates are likely to have had less solar insolation than at present, and dense fern and hardwood shrub understoreys inhibited podocarp regeneration. A gradual alteration of the climate with increased cool south-westerly airflow may have been accompanied by increased summer insolation that permitted widespread regeneration of *Dacrydium cupressinum* and *Prumnopitys ferruginea*. Boggy uplands and the prominent windlanes through sub-alpine scrub that have developed on them may, on the evidence of our single upland site, be a late Holocene development triggered by cooling climates.

Nothofagus menziesii, *N. solandri* var. *cliffortioides*, *Libocedrus bidwillii*, and *Phyllocladus alpinus* have probably not been present on the island since the glacial maximum. Even if they had persisted through this cold episode, none is likely to have been capable of expanding or perhaps persisting in the early to mid Holocene because of the prevailing dull, cloudy, moist climate. In the later Holocene, when climatic conditions began to favour them, the relatively long distance across an ocean gap to the island and the small upland and far southern area that is suitable for establishment, combined to continue to exclude them.

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