

4.3 RESULTS

4.3.1 Vulcanism

Vulcanism (Table 2) was not part of the disturbance regime of dry eastern South Island in the late Holocene, whereas it did affect dryland North Island at its distal east coast.

Pyroclastic eruption

The Volcanic Plateau of the central North Island is primarily composed of welded or unconsolidated ignimbrite sheets derived from pyroclastic eruptions from the various Volcanic Centres, including Taupo and Okataina. Ignimbrite eruptions from the Taupo Volcanic Centre, varying widely in their magnitude, have occurred, on average, once every 1000 years over the last 26 000 years (Wilson 1993). In such eruptions, vegetation is overwhelmed and tree stems carbonised over large areas. The bare pumice surfaces that result from these high-intensity and high-severity events lead to primary successions at regional-size scales. Reforestation was complete within 450 years after the Taupo pumice eruption (Clarkson et al. 1986). Thus, the periodicity of pyroclastic eruptions did not permanently provision the Central North Island with a shifting mosaic of seral vegetation, although the depth of tephra and topography influence forest composition (Leathwick & Mitchell 1992; Wilmshurst & McGlone 1996).

TABLE 2. CLASSIFICATION OF DISTURBANCE REGIMES IN LATE HOLOCENE PRE-SETTLEMENT NEW ZEALAND.

DISTURBANCE MECHANISM	DISTURBANCE TYPE	SEVERITY	FREQUENCY (y)	SCALE	INTENSITY
Vulcanism	Pyroclastic eruption	High	c. 2000	Regional	High
	Other volcanic eruptions	Low	c. 200–400	Regional, catchment	Low
	Lahar	High	Variable	Catchment	High
Tectonic-seismic	Landslide; scree-creep	High for landslide; low for scree-creep	Varies with uplift rate	Local	High for landslide; low for scree-creep
	Snow avalanche	Low	Annual and greater	Local	High
	Glacier	High	Constant	Catchment, local	High
	Tsunami	Low	Variable	Catchment, local	High
Extreme weather events	Flooding; sedimentation	High and low	Annual and greater	Catchment, local	Low
	Snow break	Low	Variable	Catchment, local	High
	Windthrow	Low	Variable	Catchment, local	High or low
	Saltburn	Low	Variable	Catchment, local	Low
Aolian	Transgressive dunes	High	Variable	Regional	Low
Natural fire	Lightning strike	Low	High	Regional, catchment, local	High or low
Bioturbation	Seabird burrowing	Low	Constant	National	Low
Herbivory	Insects, lizards, bats, and birds	Low	Constant	National	Low

Volcanic eruption

Central North Island forests have been periodically disturbed by airfall ash and lapilli through the Holocene, with a short interval of disturbance-adapted species, often bracken (*Pteridium esculentum*), pulsing ahead of later successional species in the pollen record (Wilmshurst & McGlone 1996; Wilmshurst et al. 1997, 1999). The effects of airfall tephra will vary with radius from the volcanic cone but, in general, are high intensity but low severity. McGlone (1981) and Wilmshurst & McGlone (1996) concluded that airfall tephra less than 600 mm thick will not lead to deforestation; however, death of trees, branch-break, stripping of foliage, particularly by lapilli showers, and toxic effects of airfall ash on foliage would be expected impacts. In terms of effects on soil, airfall ash showers veneer the land with thin layers of cold, sand-sized ash that may mildly boost soil fertility and foster secondary successions around the volcano.

Evidence for fires in vegetation that have been ignited by pyroclastic or volcanic eruptions is rare in New Zealand. Druce (1966a) reported evidence of a forest fire on the western slopes of Pouakai Range, Taranaki, resulting from the Burrell eruption (c. 400 y BP). In the Bay of Plenty, McGlone (1981) showed that fires up to 150 km from the eruptive source were common over a short period following the AD 232 Taupo and Kaharoa (c. AD 1400) eruptions. Rogers (1987) and Rogers & McGlone (1989) found no evidence in peat bog charcoal or geomorphic features to indicate vegetation fires at the southeastern margin of the Taupo Pumice Ignimbrite resulting from these eruptions.

Lahars

Lahars create bouldery hummock and shallow hollow topography on volcanic ring plains, producing small-scale variability in forest composition and peat bogs in some hollows. Lahar-derived landforms litter the Mt Taranaki and Tongariro Volcanic Centre ring plains. Primary successions result from these high-intensity and high-severity events.

4.3.2 Tectonic-seismic

Landslide and scree-creep

Landslides or mass movement producing debris avalanches may be triggered by rainstorms and / or seismic disturbance. Such disturbance is of high severity and intensity, producing primary successions and is the dominant erosion process in New Zealand's wet, western mountains, which have rapid uplift rates. Fluvial erosion or storm-water scouring is less severe and probably the dominant mountain erosion process in the unglaciated greywacke mountains of Canterbury, Marlborough and the North Island (O'Loughlin & Pearce 1982). The highest sediment yields from landslides in Canterbury occur in the wet and tectonically dislocated west about the Main Divide, rather than in the drier, devegetated eastern ranges (McSaveney & Whitehouse 1989; Hicks et al. 2003a). Rates of this natural process appear to vary. Several authors have postulated discrete pulses of increased landslide, erosion and consequent sedimentation in inland and coastal catchments separated by quiescent periods. Grant (1989) deduced eight periods of increased erosion and alluvial sedimentation in

New Zealand in the last 1800 years. Atmospheric warming and increases in major rainstorms and floods were ascribed as the causal agent of the erosion phases, quite independent of human activity. In his two study areas—the eastern Ruahine Range and the Pouakai Range, central North Island—from 2.6% to > 52% of the vegetation cover was destroyed or damaged in each phase in mountain catchments. On a similar theme, McFadgen (1989) postulated three soil depositional episodes in coastal sand dune areas in the last 1800 years that are independent of human influences. In each of these three episodes, deposition was followed by a stable phase, with low deposition and soil formation. McFadgen claimed that the unstable phases were attributable to windy and dry times and stable phases to less windy and moist conditions, in contrast to Grant (1989). Jane & Green (1983) and Shaw (1983) recorded more localised cyclonic storm damage. Wells et al. (2001) determined that Westland's forest pattern has been strongly influenced by region-wide earthquakes that triggered landslides, erosion, flooding and sedimentation events. They dated three major earthquakes in the last c. 550 years whose effects on forest structure and composition varied in terms of earthquake magnitude and length of quiescent intervening period. Flooding events, perhaps triggered by the earthquake effects on upland catchments, and their effects on podocarp regeneration, extend down to Westland's coastal floodplain terraces (Duncan 1993).

Landslide frequency can be estimated using a simple probabilistic model incorporating storm rainfall magnitude and slope angle (Preston 2003). In general terms, hill-country composed of non-indurated soft rock and hard rock of the tectonically active axial mountains are the most landslide-prone landforms in the North Island (Hicks et al. 2003a; Preston 2003). However, because greywacke regolith is free draining, even the steep hill-country and mountains of Marlborough and north, west, and south Canterbury have comparatively low landslide-proneness in the frequent storm rainfall events of eastern South Island. The southernmost drylands experience few landslides because of the more subdued hill-and-block mountain relief of Otago, combined with the greater cohesion of its schist-derived soils.

Scree is the product of an erosion process producing lag surfaces of gravel. Scree surfaces can be either active or stable. Extensive active scree occurs in the greywacke and argillite terrain of Canterbury and Marlborough, with the rock supplied mainly from emergent ridges and spurs fractured by freeze-thaw. Some scree has no emergent feeder ridges or spurs above it, being sourced from underlying shattered bedrock and forming rounded hills of blanket scree. Although the surface veneer of scree gravel migrates downslope, its soil basement may be more stable. Scree is much less common in schist bedrock compared with greywacke. Stable, as opposed to active, scree is a deposit of coarse blocky talus too deep for plant roots to find a buried soil. Stable scree is common in North Otago on the flanks of ancient basaltic volcanic cones.

Marlborough and Canterbury's solifluction-prone greywacke hill-country and mountains produce abundant scree-derived sediment. Consequently, scree is the dominant erosion process of the dry, western mountains of the study area (McSaveney & Whitehouse 1989). However, because of its low intensity and severity, scree disturbance is of minor consequence for vegetation succession. The true extent of active scree may not have changed much in post-settlement times (Whitehouse et al. 1980; McSaveney & Whitehouse 1989).

Glaciers

Late Holocene glaciers are confined to the axial ranges of the South Island and to Mt Ruapehu. In the last 5000 years, a series of glacial advances and retreats followed a preceding interval of limited glacial activity in the Canterbury mountains (Burrows 1979; McGlone et al. 1993). Sequences of outwash gravels interbedded with lateral and terminal moraines form the surface topography of some western valleys and basins of Otago and Canterbury (Fitzharris et al. 1982), but their formation dates to Pleistocene cold-climate phases. Glacial disturbance can be classed as low intensity, high severity, low frequency and producing primary vegetation successions following retreat.

Tsunami

Tsunami inundation of coastal regions initiated by siesmotectonic, volcanic and landslide events is another high-intensity but low-severity disturbance mostly confined to coastal regions (Downes & Stirling 2001; Goff & McFadgen 2001). The Hikurangi Trench section of boundary between New Zealand's plates renders the North Island east coast and Cook Strait regions the most vulnerable to tsunami. Since 1840, three tsunami events with waves up to 10 m high have been documented in this region, all generated by earthquake events, one off the northern Chile coast. Tsunami are high-intensity but low-severity events, setting in place secondary successions. If those affecting New Zealand are mainly generated by tectonic adjustment of the plate boundary, their only likely influence on the study area may have been in coastal Marlborough.

4.3.3 Extreme weather events

Flooding and sedimentation

Flooding and sedimentation of erosion debris forms the terraced valleys, in-filled basins and alluvial floodplains that surround New Zealand's tectonically active mountains. In cold-climate phases of the Pleistocene, sediment supply was much greater than in today's warm phase, and the primary structure of fluvial landforms originated in glacial and peri-glacial phases. In the late Holocene, flooding and sedimentation mainly affect the riparian terraces of the alluvial floodplains. Consequently, mountain down-waste has been principally transported as river bedload. The braided gravel-bed of the Waimakariri River at Crossbank near Christchurch has been conservatively estimated to transport 109 000 m³ per annum of gravel in channel cross-section (Hicks et al. 2003b). However, overall, the suspended sediment yield of dryland rivers and streams is comparatively low compared with that of tectonically active and wet western regions (Hicks et al. 2003a).

Floods and erosion debris flush watercourses of steep hill-country and mountainlands in periods of peak flow (Trustrum et al. 1999), leading to relatively open or secondary forest and shrubland vegetation on riparian margins. These floods are often caused by storm rainfall events, including cumulonimbus cloudbursts, which are prominent in rain-shadow areas of eastern New Zealand (Brenstrum 2001).

Flooding-derived silt not only bolsters floodplain fertility, but may also be critical for the maintenance of the plants of prostrate herbfields along stream and river banks and bordering ephemeral wetlands. Periodic additions of

mineral soil and nutrients may be needed to support succeeding generations of daughter clones that establish within colonies of prostrate herbs. Wet / dry and frosty hollows occur in the ox-bows, cut-off meanders and active channels behind levees on floodplains, whose hydrology and soil properties appear to be driven principally by the disturbances of flooding and winter water lie. Only on low-lying, primary terraces bordering rivers would flooding and sedimentation have been of such severity, intensity and frequency to generate primary successions or maintain a shifting mosaic of secondary vegetation (Walker, Lee et al. 2003b). Beyond that riparian zone, only the most severe siltation events would promote secondary vegetation succession.

Snow break, hailstorms and windthrow

Causes of physical damage to forests from snow can be divided into avalanche, snow-creep and snow break (Burrows 1977; Conway 1977; Norton & Ogden 1983). Snow avalanche is restricted to steep, high-altitude, western mountain catchments, where it may maintain secondary vegetation. Its severity is less in shrubland (because shrubs shed the snow somewhat) than in forest. Tree trunks aligned downhill are likely to be the result of snow-creep. Severity and intensity of snow break in forests is a function of the snow load and stem size of the trees in the forest and has been recorded down to altitudes of 300 m. (Druce 1966b). Snow break is a low-impact and localised disturbance and, in modifying canopy intactness, it also influences understorey dynamics.

In extreme circumstances, severe hailstorms may lead to tree death (Shaw 1987) and, because of frequent formation of cumulonimbus cloud in this rain-shadow region, sporadic damage to tree foliage probably occurs.

Windthrown forests from cyclonic windstorms are found in steep mountainous terrain, mainly on leeward slopes affected by turbulence. Whole trees may be uprooted and overturned, exposing the root-plate, or trunks snapped mid-stem. Patches of thrown and broken trees in mountains at a scale normally less than 1-5 ha are widely interpreted as being caused by windthrow disturbance (Wardle 1984).

Because snow break and windthrow disturb forests mainly in western mountain districts in the lee of topographic barriers to the prevailing westerly weather, their influence is minor on the dry, eastern environment. Canopy closure and understorey plant dynamics are influenced by this mostly local and low-impact disturbance. Even if these disturbances were significant in pre-settlement times, because few forests now survive in eastern rain-shadow regions, their influence has been nullified.

Saltburn

Coastal storms transport salt-laden spindrift onshore and sometimes far inland. When the salt is delivered in crystalline rather than solution form it can puncture leaf cuticles, cause cells to desiccate and lead to defoliation (Allen et al. 2002). Salt probably caused the dieback of the eastern coast and nearshore island forests of Stewart Island (Rakiura) in the 1970s (Veblen & Stewart 1980). The effect may extend well inland and is generally of low intensity and severity. Saltburn is probably of minor consequence in eastern New Zealand because of the prevailing westerly weather and the low velocity of onshore northeast and southeast airstreams.

4.3.4 Aolian

The environments of sand and gravel beaches and coastal dunes are highly disturbed by wind and salt. Hilton et al. (2000) estimated that these environments covered 129 000 ha of New Zealand in the 1950s but are now reduced to about 39 000 ha. Most mobile sand is trapped in foredunes, but lobes of sand are occasionally transported inland through blowouts in parabolic systems, and these sand deposits inundate reardune vegetation (Hesp 2000). Where sea level is rising on coasts with high alongshore and onshore sediment supply, and on eroding coasts, there may be phases of mobile or transgressive dunes migrating well inland on a large scale. Such events were common 7000–10 000 years ago (Hesp 2000). On prograding coasts, foredune plains are formed as sequences of longitudinal sand ridges and intervening hollows that lie parallel with the coast. Good examples of these foredune plains may be seen immediately north of Christchurch, and in South Westland. Inland (rather than coastal) dunes are local in extent and sourced from wind-erodible beds of fine sediment. The Bannockburn–Cromwell sand plain in the upper Clutha Valley is a notable example, and was formed by wind-transported sediments from glacial moraine debris in a dry environment during the last glaciation (McKinlay 1997).

Along the South Island's drier east coast, prevailing westerly winds and coastal cliffs limit the extent of transgressive coastal dunes to narrow coastal platforms around promontories (such as at Cape Campbell), around the deltas of the major braided rivers, along the sand plain from Amberley to Brighton north of Christchurch, along Kaitorete Spit, and in embayments of Otago Peninsula. Thus, aolian disturbance is local in extent in the dryland zone, but may be major in severity, with primary vegetation succession resulting from the discrete phases of sand movement and dune building.

4.3.5 Natural fire and seral (grass) vegetation

Natural fire, as opposed to cultural fire, may be started by spontaneous combustion, lightning discharge or incandescent volcanic ejecta. This last cause, and its relevance to North Island drylands, is discussed in 4.3.1. However, in eastern South Island, lightning discharge is the only likely natural cause of fire. Although there is substantial evidence for natural fires, it is difficult to determine how frequent and how widespread they were (Burrows 1994; McGlone & Moar 1998). For this region, we used (a) radiocarbon-dated charcoal derived from soil and peat bogs, and (b) evidence from studies of fossil pollen, to examine the incidence and frequency of pre-settlement natural fires and the extent of grasses as fire-stimulated seral vegetation.

Radiocarbon-dated charcoal

Our database of 234 charcoal radiocarbon dates (115 pre- and 119 post-settlement) for eastern South Island is based on a list produced by Les Basher up to 1992 (unpubl. data) and updated to December 2003 by further records from the University of Waikato's Radiocarbon Dating Laboratory (A. Hogg, pers. comm.) and the Institute of Geological and Nuclear Sciences' Rafter Radiocarbon Laboratory (D. Chambers, pers. comm.). The list applies to Marlborough, Canterbury, Otago and Southland—a much larger area than our eastern dryland zone. The precision with which the dates and phase limits can

be interpreted is compromised by the inbuilt age of wood at its incineration and by possible post-depositional contamination of its original carbon content.

The frequency distribution of dates, which may be biased toward younger dates (Ogden et al. 1998), suggests four phases of fire frequency (Fig. 4):

1. The few dates from > 10 000 y BP are a result of very little forest being present in the early Holocene landscape, particularly on the exposed and cold topography of the southern South Island, which was very erosion prone (McGlone 1988; McGlone et al. 1995).
2. From 10 000 y BP to 2500 y BP, sporadic dates show few and irregular fires. There is no convincing evidence of changes in fire frequency—small peaks are often interspersed with several centuries of no dates.
3. An increased number of dates from 2500 y BP to c. 1300 y BP appears to corroborate suggestions, on the basis of pollen data, that an increase in fire frequency occurred (Leslie & McGlone 1973; McGlone et al. 1995). This may have accompanied an expansion of subalpine bogs driven by increased seasonality and colder and wetter winters (McGlone 1988, p. 595; Rogers & McGlone 1989). However, the inbuilt age of wood at incineration (trees around 1000 years old might have been burned following the arrival of humans) may conceivably account for the apparent increase in charcoal and log dates.
4. The post-settlement period (from 1100 y BP) is marked by a big increase in fire frequency, with charcoal dates peaking at 700–500 BP (Ogden et al. 1998).

The limits of each period are not precise because radiocarbon ages are affected by inbuilt age and post-depositional carbon contamination of the charcoal. Substantial variability within each phase also compromises the delimiting of each period. Such factors also inhibit defining sub-sets within the post-

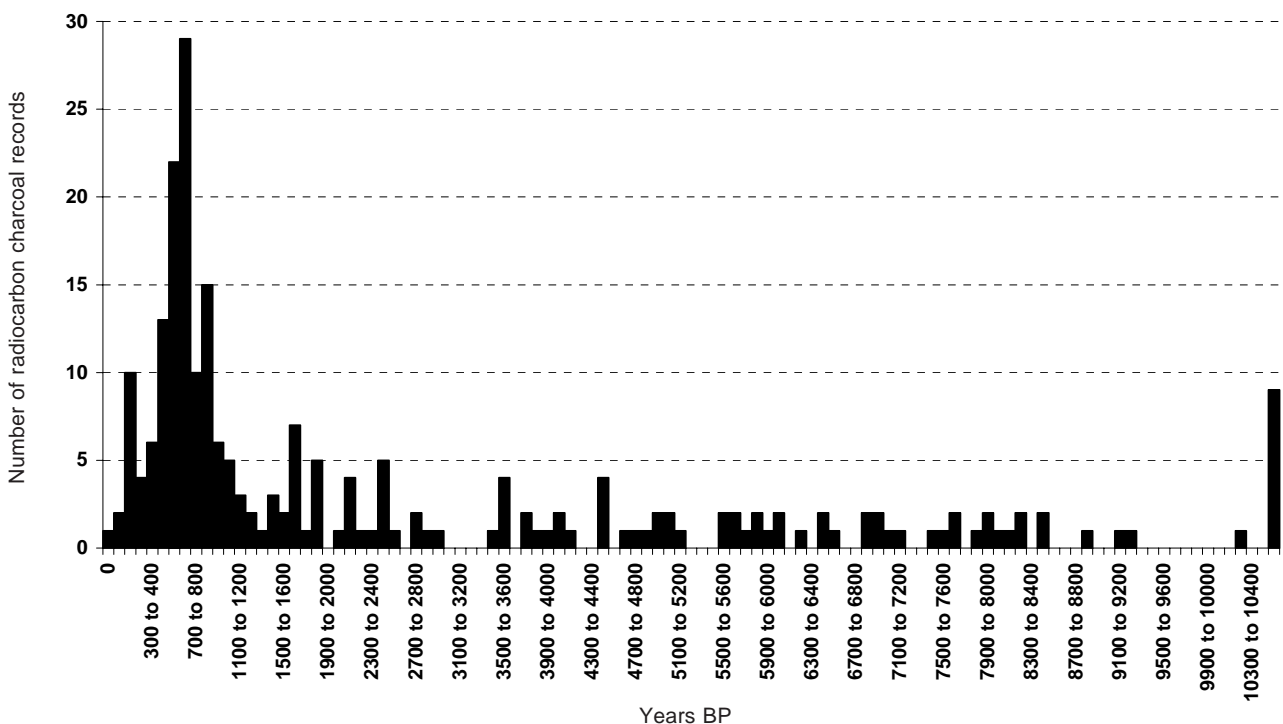


Figure 4. Frequency distribution of radiocarbon-dated charcoal from eastern South Island in 100-year intervals from present to 10 000 y BP (after unpublished data of Les Basher).

settlement period. A major increase in dated charcoals begins from 1000 y BP, and decreases after 500 y BP. McGlone et al. (1994) put the peak deforestation activity at 700–500 y BP. Although lightning-ignited fires are and were probably rare in New Zealand (S.M. Timmins in Ogden et al. 1998), we expect that Polynesian settlers would have created, unintentionally or intentionally, frequent ignition sources to burn forest, and that massive burn-offs of forest would have resulted across large areas of gently undulating topography, particularly in especially dry summers with föhn winds (El Nino Southern Oscillation (ENSO) events).

The distributions of pre- and post-settlement radiocarbon-dates are broadly similar (Fig. 5). The charcoals are spatially biased toward the hill and mountain topography of Marlborough, western Canterbury, and Central and west Otago. Both are concentrated in the uplands because:

- There is a greater chance of burial and preservation there because of post-fire slope instability.
- Correspondingly, there is a greater chance of re-exposure and discovery.
- Search effort is therefore likely to be biased toward areas of enhanced chance of discovery.

Several charcoal clusters relate partly to intensive search effort associated with regional studies of landscape history in, for instance, the Clutha River headwaters in Otago (Wardle 2001a, b), the Arrowsmith Range and Cass Basin in inland Canterbury, the environs of Christchurch city, and Molesworth Station in Marlborough. The comparative voids in Central Otago, south Canterbury and North Canterbury have received less exploratory effort. Although records in lowland Marlborough and Canterbury are sparse, we noted some striking

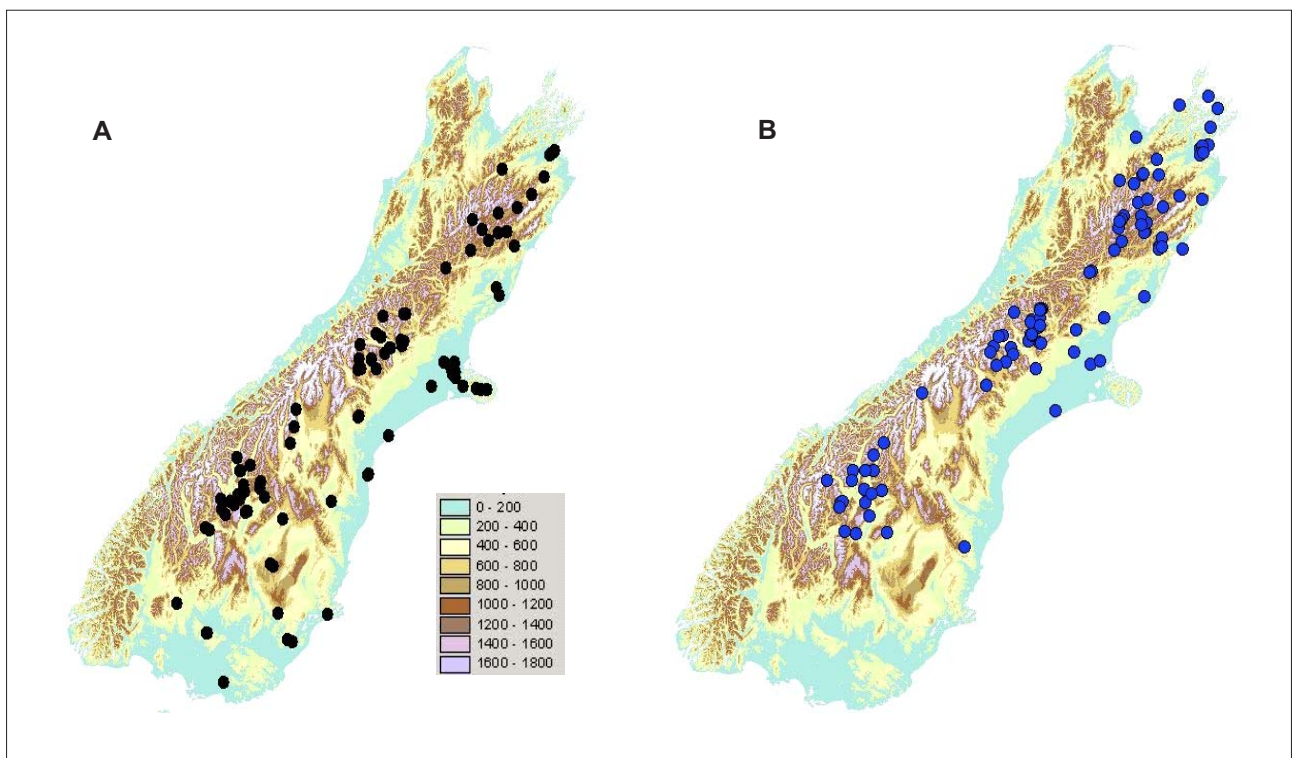


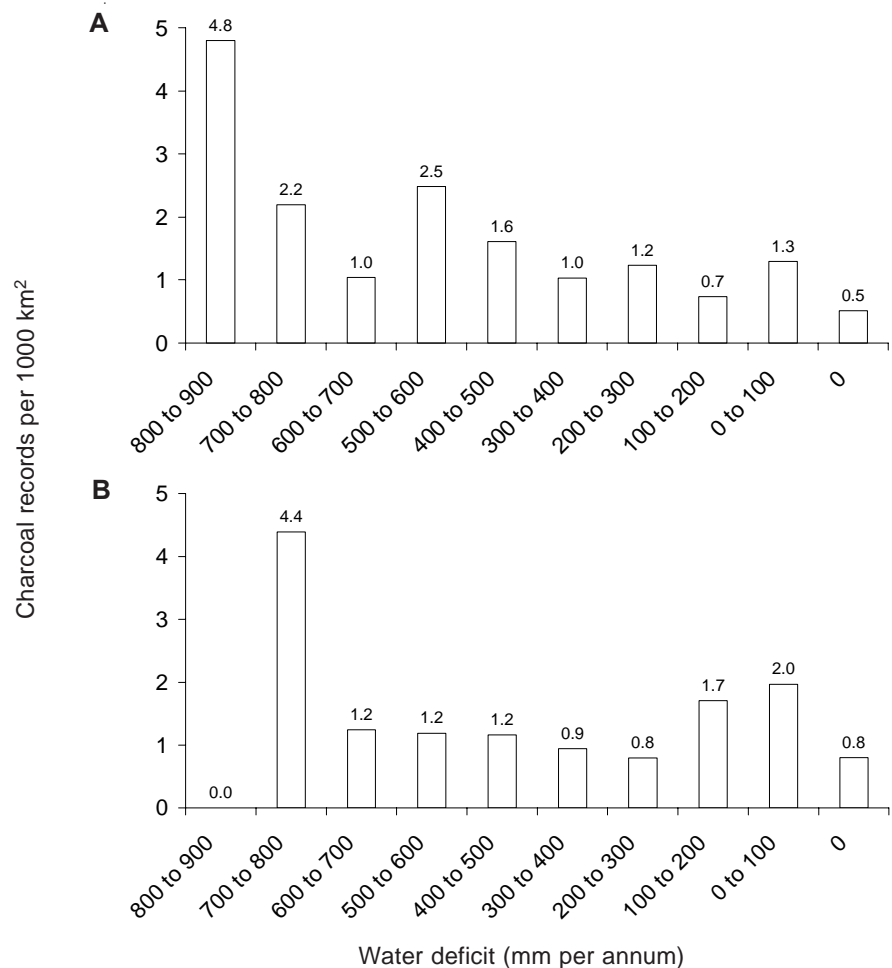
Figure 5. Distribution of radiocarbon-dated charcoal (circles) across elevation zones (m a.s.l.) of eastern South Island. A. > 1000 y BP; B. < 1000 y BP (after unpublished data of Les Basher).

differences in pattern between pre- and post-settlement dates: the Marlborough Sounds have many more post-settlement dates, perhaps reflecting few natural fires. In South Canterbury and Southland there are many more dates from the pre-settlement era than the post-settlement era. There are no post-settlement dates from Banks Peninsula—the abundant cover of forest on Banks Peninsula in early European times (Johnston 1961) suggests that, anomalously, there were few human-lit fires there.

Is there a trend in dated charcoals across a rainfall gradient or, more particularly, across water deficit zones (standardised for area) for the pre- and post-settlement periods? On an area basis, the greatest concentration of both pre- and post-settlement dates is from the driest end of the water deficit spectrum, although there are no post-settlement dates from the driest zone (Central Otago) (Fig. 6). There is also evidence for more dates in the post-settlement period at the humid end of the gradient, perhaps because these environments were less inclined to ignite and burn without human assistance.

The higher frequency of dates from the drier zone contradicts somewhat the impression of a greater density of dates in the wetter western mountains (Fig. 5). Many of the upland charcoals may be sourced from interfingering drier valleys at lower elevations that will not appear at the scale of Fig. 5.

Figure 6. Distribution of dated charcoals by water deficit zone in eastern South Island, standardised for area; in **A**, pre-settlement and **B**, post-settlement (< 1000 y BP) eras.

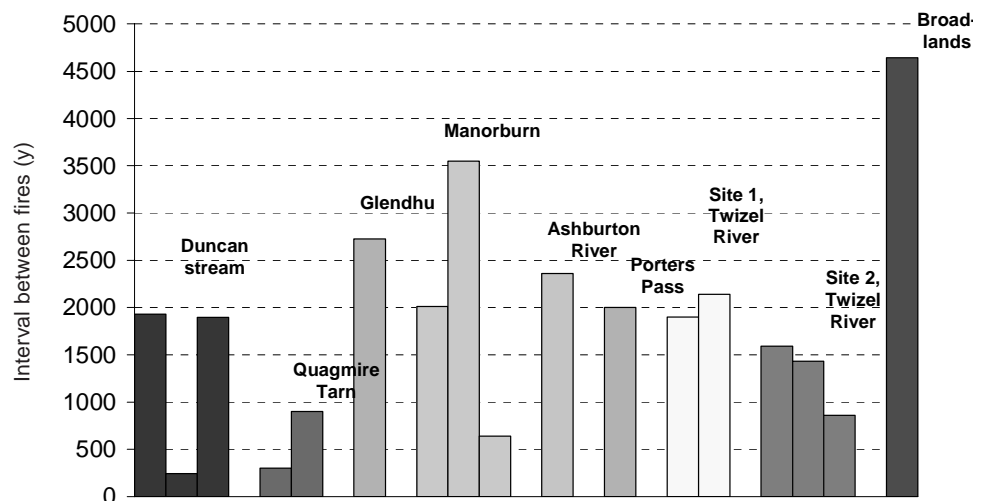


What do we know about recurrent fire intervals at any one place? In the compilation exercise undertaken for this study, we uncovered records from just nine sites where stratigraphically intact, sequentially dated charcoal lenses from soils or peat of the pre-settlement period provide a record of fire intervals. (We note our list of nine sites may not be exhaustive, and that more examples may exist that we are not yet aware of.) A wide range of intervals from 200 years to 4600 years is evident, with a cluster between 1500 years and 2000 years, which is in agreement with the conclusion of Ogden et al. (1998) (Fig. 7). The data are derived from Canterbury's greywacke mountains, which are vulnerable to post-fire erosion, from peat bogs in the Mackenzie Basin and Otago's block mountains, and the Canterbury Plains near Christchurch. These interval estimates are considered a maximum, because not all fires will produce detectible charcoal in peat cores, particularly if non-woody vegetation covers the bog.

Charcoal evidence for local fires

Charcoal spectra from peat cores provide unsophisticated but useful data for the purpose of understanding local fire histories (McGlone 2001). This is because: palynologists have not analysed charcoal consistently, not all peat bogs capture charcoal evidence of local fires and the sources of peat-bog charcoal vary widely. Topogenous or depression bogs are vulnerable to continued inwash of catchment-derived charcoal long after a local fire (McGlone et al. 1984). Charcoal in ombrogenous or blanket peats and dome peats suffers no such contamination and is generally derived *in situ*. Further, peat-bog charcoal has both microscopic and macroscopic particle sizes—the former mostly aolian (i.e. wind-blown from outside, and possibly distant, sources) in origin, the latter probably locally derived and more reliable evidence for local fires. Indeed, microscopic charcoal may be at least partly sourced from Australian fires (M. McGlone, pers. comm.). In general, charcoal spectra included in pollen diagrams consist of intermittent or more or less constant minor background amounts of microscopic particles derived from aolian dispersal. This background signature may be interspersed with lenses of abundant particles, often predominantly macroscopic, sourced from the bog surface and / or the contributory catchment. Apart from peat bogs, the incidence of mineral-soil charcoals is reported on in radiocarbon-dated charcoal.

Figure 7. Eighteen intervals of recurrent fire in the pre-settlement era as derived from nine soil profiles and peat bogs in eastern South Island (for data sources, see Appendices 2 & 3).



We report on three regions, Marlborough, Canterbury, and Otago (using 29 published pollen diagrams and associated vegetation history publications; Table 3, Appendix 2). The one diagram from Marlborough has just background levels of charcoal during the short interval covering the pre-settlement period. Unfortunately, only two of the 14 pollen diagrams from Canterbury include charcoal spectra. One from Travis Swamp north of Christchurch shows minor background levels only and no evidence of local fires in a short pre-settlement period. The other, from Duncan Stream in the upper Mackenzie Basin, has background levels of charcoal to 5000 y BP, followed by two or possibly three peaks, which are likely to correspond to local fires (see Fig. 7). This evidence suggests that natural fires were as infrequent in the Mackenzie Basin as they were on the erosion-prone soils of central Canterbury's mountains and intermontane basins (Archer 1979; Burrows & Russell 1990; Burrows et al. 1993; Burrows 1994) and the Canterbury Plains between the Waimakariri and Selwyn Rivers (Cox & Mead 1963).

TABLE 3. LOCATIONS AND REFERENCES TO POLLEN DIAGRAMS USED TO ANALYSE THE ANTHROPOGENIC RISE OF POACEAE IN EASTERN SOUTH ISLAND.

LOCATION	SITE	ALTITUDE (m a.s.l.)	REFERENCE
Inland Kaikoura Range	Winterton Bog	1480	McGlone & Basher 1995
Canterbury Plains	Timaru Downs	30	Moar 1971
	Amberley	76	Moar 1971
	Travis Swamp	5	McGlone 1995
Waimakariri River headwaters	Mt Horrible	600	Moar 1971
	Woolshed Hill	1000	Moar 1971
	Lake Hawdon	600	Moar 1971
	Kettlehole Bog	600	Lintott & Burrows 1973
Rakaia River headwaters	Lake Henrietta	600	Moar 1973
	Quagmire Tarn	740	Burrows & Russell 1990
	Windy Tarn	750	Burrows & Russell 1990
North Canterbury	Pyramid Valley	330	Moar 1970
Mackenzie Basin	Duncan Stream	900	McGlone & Moar 1998
	Ben Dhu	600	McGlone & Moar 1998
Coastal North Otago	Pleasant River	5	McGlone 2001
East Otago peneplain	Glendhu	500	McGlone & Wilmshurst 1999
	Clarks Junction	520	Leslie & McGlone 1973; McGlone 2001
Summit of Old Man Range	Potters Bog	1200	McGlone 2001
	Teviot Swamp	1020	McGlone 2001
	Swampy Hill	740	
	Campbell Creek	1200	McGlone et al. 1997
	Ruined Hut Bog 1	1410	McGlone et al. 1997
Summit of Garvie Mountains	Ruined Hut Bog 2	1410	McGlone et al. 1997
	Hyde Cirque	1550	McGlone et al. 1997
	Islands 1	1460	McGlone et al. 1995
Slopes of Pisa Range	Islands 2	1450	McGlone et al. 1995
	Kawarau Gorge	800	McGlone et al. 1995
Slopes of Old Man Range	Pomahaka Road	875	McGlone 2001
Basin floor, Central Otago	Earnsclough Cave	540	Clark et al. 1996
	Idaburn Valley	420	McGlone & Moar 1998

Ten of the 13 Otago pollen diagrams have charcoal spectra covering the pre-settlement era. Four of those 10 have peaks suggesting local fires, superimposed against minor and more or less constant background levels.

Glendhu (620 m a.s.l.) in East Otago (McGlone & Wilmshurst 1999; reproduced in McGlone 2001) has three peaks between 4000 y BP and 3700 y BP, which could relate to one or several fires over that short period because of prolonged inwash from the catchment, and one fire c. 1100 y BP. Two adjacent profiles from the Garvie Mountains (1350 m a.s.l.) each show two mid-Holocene charcoal peaks, which probably record two widespread fires. A Kawarau Gorge (800 m a.s.l.) profile shows three or possibly four charcoal peaks throughout c. 9000 years of the pre-settlement era.

The remaining six pollen diagrams from Otago and, notably, two from the driest interior basins (Earnsclough Cave and Idaburn Valley), have no charcoal evidence of local fires, being characterised by minor background quantities of charcoal without peaks. This distribution points to the humid upland peneplains and crests of mountains being more fire-prone than the dry intermontane basins. However, overall, with nine of the 13 Otago diagrams having no record of local fires, it appears that natural fires were not ubiquitous, even in this extensive rain-shadow region over substantial pre-settlement time frames.

Charcoal in relation to Poaceae and woody vegetation pollen

Next, we used pollen diagrams to search for evidence that local fire stimulated or perpetuated fire-induced seral vegetation (specifically grass, as indicated by Poaceae pollen) in the pre-settlement period. New Zealand's grass flora is typified in pollen diagrams by undifferentiated Poaceae (Gramineae), although more recent diagrams divide Poaceae into large grains (mainly *Chionochloa*) and small grains (all other grasses, including short-tussocks). We looked primarily at Poaceae and charcoal for concordance, because both spectra are characterised by low and low-variability background percentages, with infrequent peaks. However, we also commented on variations in the composition of woody species pollen associated with charcoal peaks. An assumption in the method is that time frames of sampling intervals in pollen diagrams are appropriate for detecting fire-stimulated seral vegetation in the landscape.

As reported above, the one pollen diagram from Marlborough and two of the 13 from Canterbury have charcoal spectra. Of those three, Duncan Stream, Mackenzie Basin, is the only diagram with peaks in the charcoal spectra (the other two have background levels only). At Duncan Stream, there is an increase in *Halocarpus* and a decrease in *Phyllocladus* following a major charcoal peak between 5500 y BP and 4000 y BP, and a more substantial decrease in both *Halocarpus* and *Phyllocladus* corresponding to a second large charcoal peak in the 4000–1200 y BP period. The latter is associated with a sharp peak in *Aciphylla* pollen, which decreases again as the gymnosperm scrub re-established towards c. 1200 y BP, to be finally destroyed by fires associated with human arrival. Both large- and small-grained Poaceae pollen show a shift to greater abundance from the period 5000–4000 y BP to the 4000–1200 y BP period. McGlone & Moar (1998) suggested that 'both *Halocarpus* and tussock grassland continued to increase in the scrub recovery phase after the fire.'

Of the Otago diagrams with charcoal peaks (Glendhu: McGlone & Wilmshurst 1999; McGlone 2001, Garvie Mountains and Kawarau Gorge: McGlone et al. 1995) approximately half of the irregularly spaced charcoal peaks coincide with peaks in the Poaceae curves, mainly small-grained Poaceae, with woody vegetation invariably re-establishing thereafter.

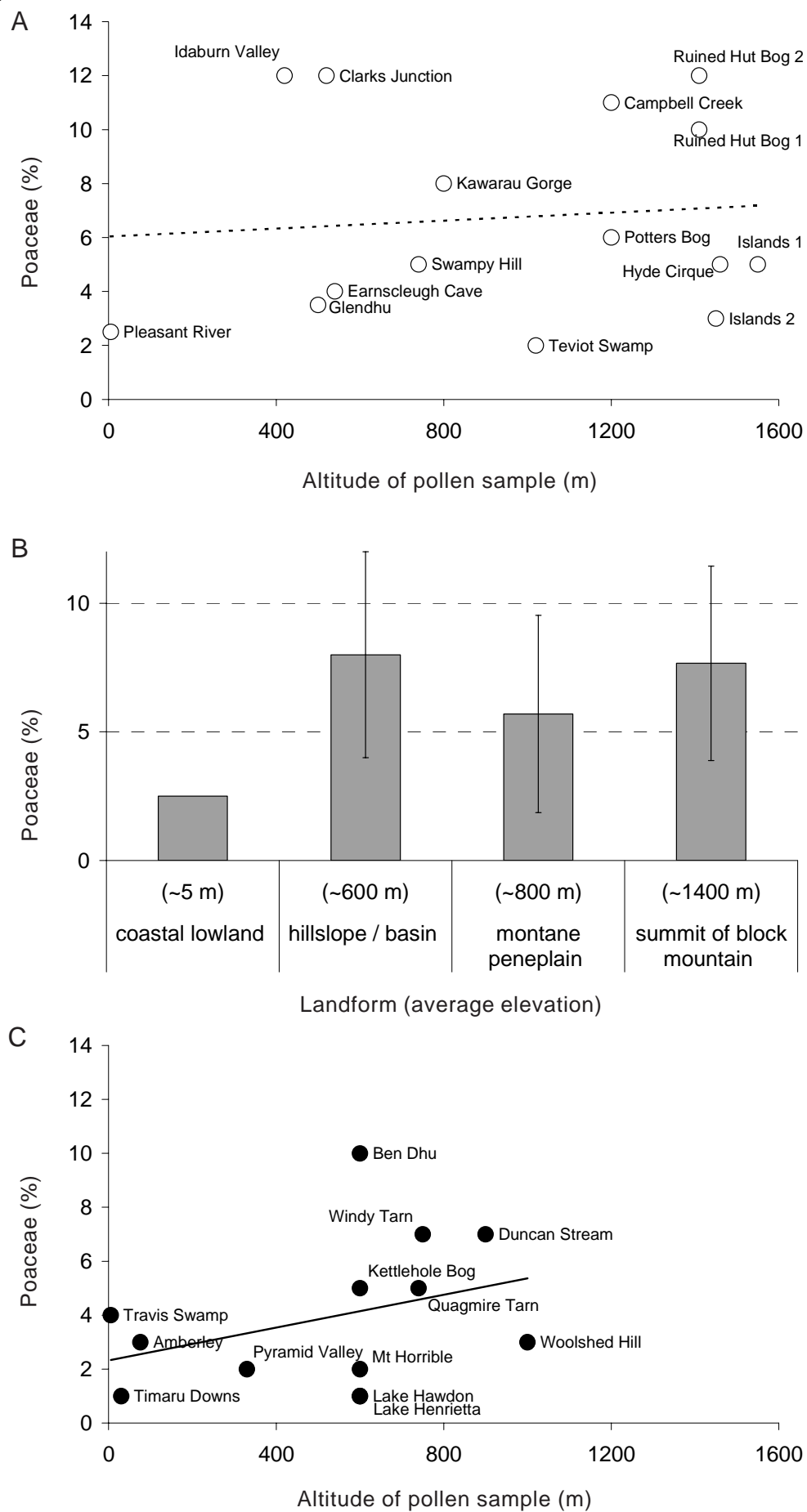
In summary, the pollen evidence shows that infrequent fire in drylands and other eastern environments prior to human settlement typically resulted in temporary suppression and subsequent re-establishment of woody vegetation, sometimes with a shift in woody composition towards more fire-tolerant grass species.

Relative pre- and post-settlement cover of grasses

Finally, to gain an impression of the quantitative increase in Poaceae from anthropogenic fire, we compared the average percentages of Poaceae pollen (in some instances both small and large grain) in the pre-settlement period with its peak percentages in the latest or uppermost post-settlement period of pollen diagrams. Our intention was to extrapolate from today's grass-dominated landscapes to provide insights into the pre-settlement cover of grasses. Cautious interpretation of the data is necessary because pollen frequencies are relative, and therefore a function of the entire contributing flora. Modern pollen-rain studies show that *Chionochloa* grasses are relatively under-represented in the pollen rain. Because small-grained Poaceae represent all other grasses, it is difficult to confidently comment on the representativeness of the respective groups, such as short tussocks and non-tussock dryland and alpine types. We suggest that short tussocks were the main contributors to small-grained Poaceae pollen rain in humid sites, but that a wider range of (non tussock-forming) grasses contributes substantially in drier environments (e.g. *Agrostis* spp., *Dichelachne* spp., *Elymus* spp., *Puccinellia* spp. and *Rytidosperma* spp.). We also note that the amounts of uppermost Poaceae pollen in pollen diagrams are probably exaggerated by that from exotic grasses.

For a treeline setting (1480 m a.s.l.), the one Marlborough pollen diagram (Winterton Bog: McGlone & Basher 1995; Table 3) showed a particularly low frequency of pre-settlement Poaceae pollen (2%). The 13 Canterbury pollen diagrams (Table 3) showed pre-settlement Poaceae at comparatively small percentages (< 5%) that increase with altitude (Fig. 8). All the Canterbury sample sites (maximum altitude 1000 m a.s.l.) are well below the regional treeline, so the positive trend with altitude probably reflects increasing proximity to alpine grass sources. Further variability may relate to a site's proximity to intermontane basin and valley sources of grasses in a potentially extensively forested region. A diagram from the Arrowsmith Range (Windy Tarn: Burrows & Russell 1990; Appendix 2) suggests temporary spread and subsequent retreat of grasses, possibly resulting from a natural fire event. At Windy Tarn, Rakaia River headwaters, Poaceae increased from 1% to 6% (Burrows & Russell 1990). At Lake Henrietta, Harper River, there was a small increase in Poaceae from 1% to 3% (Moar 1973). Overall, however, the Canterbury diagrams do not suggest a widespread and sustained expansion of grasses in the more fire-prone basins or alpine zone in the mid to Late Holocene period.

Figure 8. Relationship between percentage of pre-settlement Poaceae pollen (includes sum of small- and large-grained pollen) and altitude of the sample site in eastern South Island. **A.** Otago data. **B.** Mean percentage (with error bars) of pollen by landform class for Otago sample sites. **C.** Canterbury data. See Appendix 3 for data used to prepare this figure.



The exception is at Duncan Stream in the Mackenzie Basin where both small- and large-grained pollen increase from insignificant amounts to five times the original value and moderate amounts after 5000 BP (1% to 5% and 2% to 10%, respectively) in a period of natural fires (McGlone & Moar 1998).

The 15 Otago diagrams show comparatively small percentages of pre-settlement Poaceae pollen, although, overall, greater than those of Canterbury (Fig. 8A & 8C). Despite considerable variability across the entire dataset, variation is not great across the three broad landform and elevation classes of inland Otago—alpine summits of the block-mountains, the montane peneplains, and the hillslopes and basins (Fig. 8B). Accordingly, there is no relationship between the abundance of Poaceae pollen and elevation (Fig. 8A). In more detail, the Idaburn Valley in Central Otago has no charcoal evidence of local fire, yet Poaceae pollen gradually increased to significant amounts from 6% to 15% in pre-settlement times and *Olearia* correspondingly declined. Poaceae had a variable presence on Otago’s eastern peneplains: Clarks Junction had moderate levels of large- and small-grained Poaceae, whereas Swampy Hill, Teviot Swamp and Glendhu Bog had low percentages. There are seven diagrams from above the treeline. Of the five that differentiate *Chionochloa* pollen, four are at 1–2% and one had 3%, while the small grains are at slightly greater amounts that suggest a significant presence for short tussocks and / or other non-tussock alpine grasses. The remaining two diagrams with undifferentiated Poaceae pollen have amounts in agreement with that scenario. Accordingly, above the treeline, large grains are at amounts that lead McGlone et al. (1997) to suggest that *Chionochloa* tussocks were possibly prominent only on the summits of the ranges, in that instance, Old Man Range. Overall, Poaceae pollen frequencies are characteristically stable in the pre-settlement period of most diagrams, perhaps with rare peaks that decline again to base levels. The two exceptions, with increasing Poaceae in the late Holocene, are at Duncan Stream in the Mackenzie Basin and at Kawarau Gorge on the flanks of the Pisa Range.

TABLE 4. MEAN AND STANDARD DEVIATION OF INCREASE, IN MULTIPLES OF ORIGINAL FREQUENCY, IN POACEAE POLLEN FROM PRE- TO POST-SETTLEMENT PHASES ACROSS REGIONAL LANDFORM CLASSES IN POLLEN DIAGRAMS FROM EASTERN SOUTH ISLAND.

Some diagrams differentiate between large- (*Chionochloa*) and small-grained Poaceae pollen. *n* = number of pollen diagrams sampled.

REGION LANDFORM CLASS	DIFFERENTIATED		UNDIFFERENTIATED		COMBINED		
	<i>n</i>	LARGE- GRAINED	SMALL- GRAINED	<i>n</i>		<i>n</i>	
Marlborough							
Hillslope				1	24	1	24
Canterbury							
Hillslope				2	8.5 ± 2.1	2	8.5 ± 2.1
Interior basin or valley	1	3.5	6.0	5	13.0 ± 7.5	6	11.7 ± 7.4
Coastal lowland	1	3.0	24.0			1	13.5
Otago							
Summit of block mountain	5	7.4 ± 3.0	3.7 ± 3.2	2	12.9 ± 5.4	7	6.8 ± 5.3
Montane peneplain	2	11.0 ± 1.4	29.5 ± 12.0	1	4.2	3	15.2 ± 10.4
Hillslope				1	3.1	1	3.1
Interior basin or valley				2	6.6 ± 3.4	2	6.6 ± 3.4
Coastal lowland				1	19.0	1	19.0

There are consistently large increases in Poaceae pollen from pre- to post-settlement times (Table 4). The majority show seven-fold or greater increases. The one Marlborough diagram, which is at treeline, has a 24-fold increase in grasses. The three Canterbury landform classes show greater expansion of grasses from the highest altitude interior hill- or mountain-slopes with their relict pockets of mostly *Nothofagus* forests, down to intermontane basins, and then to the virtually totally cleared coastal lowlands. In Otago, this altitudinal trend is not apparent. Eastern montane peneplains show much greater grass expansion than landforms above or below.

In Canterbury, the limited evidence from intermontane basins and coastal lowlands is that small-grained grasses expanded more than large-grained (*Chionochloa*) grasses (Table 4). In Otago, the same theme applies on coastal lowlands, intermontane basins and montane peneplains, whereas on mountain summits large-grained grasses outstripped small-grained grasses. This accords with today's extensive *Chionochloa*-dominated alpine vegetation, although some has degraded to short tussocks and cushionfield.

Synthesis of fire disturbance evidence

Twenty-eight pollen diagrams and 234 radiocarbon-dated charcoal samples may seem a substantial database for eastern South Island. While sufficient to draw broad-scale or general conclusions on landscape history, its limitations become apparent when looking for unifying themes across the diversity of environments that occur at provincial scales. For instance, there are only two diagrams (Earnsclough Cave and Idaburn Valley) representing Otago's environmentally diverse intermontane basins and valleys (Walker, Lee et al. 2003a, 2004a); all of Marlborough is represented by a single palynological paper. Moreover, fossil pollen sites are apparently highly individual: this is highlighted by moderate variances in pollen frequencies within some provincial landform types. We can therefore draw only the most tentative conclusions from these data.

The distribution of dated charcoals suggests that natural fires may have been somewhat more frequent in drier (i.e. high moisture deficit) environments than elsewhere. However, there is also evidence for occasional widespread fires in more humid environments. For example, stratigraphically similar profiles of eroded soils with interbedded lenses of charcoal point to incidences of larger natural fires in the dry forests and scrub across parts of the Arrowsmith Range (Burrows et al. 1993), and it appears that a substantial fire swept across the Old Man Range in c. 2300 y BP (McGlone et al. 1997). However, firm interpretations of fire frequency across regional landforms is compromised by the biases outlined in Radiocarbon-dated charcoal. The scarce records from north and south Canterbury may relate to low search effort there compared with that in central Canterbury. We note that apart from variability due to climatic factors, the fire-proneness of vegetation itself also varies. For example, there is some palynological (i.e. fossil pollen) evidence that phenolic-rich conifer trees and shrubs and vegetation on peat bogs are more fire-prone than that of the surrounding forest matrix (e.g. McGlone et al. 1984; Newnham et al. 1989; Rogers & McGlone 1994). Peat bogs and alpine zones in general may have functioned as fire nodes because their phenolic-rich or sclerophyllous woody communities of *Dracophyllum* spp., *Halocarpus bidwillii*, *Phyllocladus alpinus* and *Podocarpus nivalis* have high ignitibility and combustibility. If so,

because most of our pollen evidence is sourced from peat bogs (many of these on alpine range crests) there are implications for the reliability of interpretations of pollen evidence for natural fire frequencies. In general, however, New Zealand forests and shrublands were and are not readily burnt, despite occurrences of La Nina / El Nino oscillations (ENSO) conducive to fire at intervals of < 10 years, and despite some woody vegetation being of high ignitibility and combustibility. Indeed, today's wildfires are mostly in open vegetation (Kerr & Hunter 1986) and are often contained by forest edges.

Overall, our review of the pattern or frequency distribution of dated charcoals, the return fire period at any one place, and the palynological record of Poaceae and charcoal indicates that natural fire occurred sporadically but rarely across all regions of eastern South Island before human settlement, and that these natural fires were patchy and predominantly of small scale (see also Ogden et al. 1998; McGlone 2001). McGlone (2001) concluded similarly that there was a low incidence of fire and that many areas may have experienced no fire whatsoever. This scenario, where fires were small, local and rare, 'is entirely consistent with the low but more or less regular input of predominantly small-size (< 50 µm diameter) class charcoal particles to peat and lake sites in eastern districts, and the low, persistent occurrence of grass pollen' (McGlone 2001); however, as noted, the origin of this charcoal remains unknown, and it may be partly sourced from Australian fires.

Our review suggests that grass was certainly a prominent interstitial component of intermontane basin floors, and that it was mostly insignificant on valley- or hill-slopes, and patchy on Otago's eastern peneplains. The last scenario probably derives from patches of red tussock grassland on seepages and fens across the peneplain. It contributed up to 12% of the pollen sum at Idaburn Valley, Clarks Junction and on the summit of the Old Man Range. However, we found limited evidence in our review to suggest that the interstitial presence of grass was governed by a natural regime of frequent fire.

Earlier publications (especially Ogden et al. (1998) and McGlone & Moar (1998)) have suggested that there was an increase in the frequency of fire and a consequent opening out of the vegetation accompanying a climatic shift to more droughty conditions in the late Holocene (from c. 3000 y BP). The distribution of dryland charcoal dates (Fig. 4) appears to substantiate this conclusion, but only if none of the charcoals were sourced from old trees (from c. 1000 y BP), which seems unlikely. Approximately 15% of pollen diagrams show a concomitant increase in grass pollen.

It is clear that Late Holocene fire frequencies were dwarfed by those of the early Polynesian era. A striking feature of all eastern New Zealand pollen diagrams is an abrupt decrease in woody vegetation immediately following Polynesian settlement: *Dacrydium*, *Prumnopitys*, *Podocarpus*, *Halocarpus*, *Phyllocladus*, *Myrsine*, *Coprosma* and other woody angiosperm pollens vanish abruptly and simultaneously from deposits as the frequency of fires suddenly increased. The dramatic vegetation change wrought by human-lit fires is itself compelling evidence for the rarity of pre-settlement fire disturbance, because common and widespread fire is simply incompatible with the consistent palynological evidence for largely wooded landscapes. Anything more than small, local and rare pre-settlement fire is also incompatible with the near absence in the landscape of bracken, which more or less first appears in pollen diagrams following the arrival of humans.

What was the pattern of deforestation accompanying the first widespread fires in the eastern dryland zone? Data on the areal extent of Polynesian-lit fires is limited, in eastern drylands and elsewhere in New Zealand. However, Rogers (1987, 1989) used dated charcoal and population structures of trees on burnt forest edges to reconstruct the areal extent of Polynesian fires that deforested the upper montane peneplain topography between the Kaimanawa Mountains and the Ruahine Range in the North Island. Two fires in c. 570 y BP and 430 y BP deforested 20–25-km-wide expanses of montane hill-country and peneplains that were originally covered in *Nothofagus* or *Libocedrus bidwillii*—Hall's totara (*Podocarpus hallii*) forest. Tree and shrub age structures around the fire margins pointed to deliberate, ongoing burning of the seral landscapes created by the original forest conflagrations, advantaging tussock grasses ahead of more fire-sensitive woody colonisers. Few areas marginal to the original conflagrations were reforested. One area (c. 100 ha) marginal to the unburnt, old-growth forest was the largest area reclaimed; the majority of forest margins show progressive saltatory ('jump-like') retreat or static positions with each subsequent secondary vegetation fire. Low fuel loads and humid climates have restricted the ongoing fires to the matrix secondary landscape. In total, these repeat fires have changed little the pattern of relict forest created by the original conflagrations.

All of the eastern South Island pollen diagrams that incorporate both Poaceae and charcoal data suggest that today's extensive tussock grasslands were not the product of a single deforestation fire. To the contrary, extended charcoal curves suggest that tussock grasslands emerged from a succession of fires that progressively suppressed and eliminated competing, successional woody vegetation. It is difficult to speculate on the fire frequency of this period as the charcoal-producing woody plants disappeared. However, some diagrams show charcoal production peaked around midway between Polynesian and European settlement, which may coincide with the increasing importance of seasonal foods of New Zealand's interior to Maori as the marine mammal and fish resources declined and as rock quarrying increased.

The advent of Europeans ushered in a new period of frequent burning, because surveyors and pastoralists favoured low-stature grassland ahead of woodland (Hall-Jones 1992: 50). McGlone (2001) noted that the small-size-class grass pollen increased ahead of the *Chionochloa*-type pollen where the two co-occur in the post-settlement period and were separated in palynological analysis. The non-*Chionochloa* grasses, including species of *Poa*, *Festuca*, *Rytidosperma* and *Elymus*, have a faster response to disturbance because of their high reproduction, good dispersal and fast growth rates. The centuries-long rise of *Chionochloa* pollen indicates an incremental formation of these grasslands partly at the expense of shorter grasses (Connor 1964; Connor & Macrae 1969; McGlone 2001). Pollen cores at montane elevations (e.g. Potters Bog, Pomahaka Road, Teviot Swamp; McGlone 2001: 7) show this trend as well as lower, drier sites.

4.3.6 Seabird bioturbation

Bioturbation (biotic mixing of soil profiles) by burrow-nesting petrels produces soils of homogeneous structure and enhanced aeration that are enriched with guano, bird, egg and plant-foliage remains. The importance of marine-derived

energy and nutrients in island and mainland soils is receiving much attention (e.g. Okazaki et al. 1993; Anderson & Polis 1998, 1999; Strapp et al. 1999). Markwell & Daugherty (2003) concluded that the influence of seabirds in the Marlborough Sounds is likely to be inversely proportional to the basic terrestrial productivity of the soils. Hawke et al. (1999) proposed that the cadmium:phosphorus ratio, the $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ stable isotopes of nitrogen and carbon (respectively), and the carbon:nitrogen ratio can be used to identify and map pre-European seabird breeding palaeosoils.

Predator-free offshore islands such as The Snares (Warne 2003) provide an indication of the potential impact that ground- and burrow-nesting seabirds had on soils of pre-settlement, mainland New Zealand. The Snare's titi, or sooty shearwater (*Puffinus griseus*), population is estimated at 275 000 pairs in 3 km² or approximately 1 active burrow/m². South Island colonies of Westland petrel (*Procellaria westlandica*) (< 200 m a.s.l.) and Hutton's Shearwater (*Puffinus huttoni*) (1200–1800 m a.s.l.) suggest that burrow-nesting seabirds formerly inhabited a wide range of environments on the New Zealand mainland (for small petrels see Worthy & Holdaway 1996). Nevertheless, caution is required in extrapolating from offshore island estimates of bird-disturbed soils to the mainland. This is because mainland sites probably imposed greater limitations to burrowing seabirds through, for example, the impacts of ratite and other bird locomotion (e.g. collapsing burrows in unconsolidated soils like coastal dunes), a greater diversity of predatory raptors and flightless birds such as weka (*Gallirallus australis*) and extinct adzebill (*Aptornis defossor*), and a more localised availability of friable soils for bird-burrowing. Nevertheless, given that 150 000 Hutton's shearwater now occupy a tiny fraction of their former range, it may be no exaggeration to suggest that there were hundreds of millions, if not billions, of burrow-nesting petrels on the New Zealand mainland before human colonisation (McGlone et al. 1994; Worthy & Holdaway 2002), and that nutrient enrichment probably influenced down-catchment biogeochemistry (Hawke & Holdaway 2003). The ecosystem process effects of seabirds on soil nutrients, vegetation composition, numbers of lizards and invertebrates, and predatory birds can still be quantified on some islands (Markwell 1999; Markwell & Daugherty 2002) and at the now rare mainland sites (Hawke & Holdaway 2003). However, the magnitude of pre-settlement seabird colonies on the mainland, and their effects, can now only be guessed at (Worthy & Holdaway 2002). We suggest that seabird bioturbation disturbance was largely restricted to sites with escarpments, spurs and ridges with topography suitable for bird take-off. However, such sites could have occurred locally across much of the lowland and montane land area of the eastern New Zealand dryland zone.

In summary, although locally intense, bioturbation from seabird burrowing was a low-intensity and low-severity disturbance. Intact island colonies of burrowing seabirds create patchy patterns of depletion in understoreys of forests and shrublands. However, there is no evidence that these disturbances locally eliminated woody plants, except on pathways to communal launch-sites.

In addition to the actions of burrowing seabirds, the coastal fringe was further disturbed through surface scarification by ground-nesting seabirds (shags, penguins and gulls) and marine mammal haul-out activity. The prostrate growth form of herbs of coastal turfs appears to be well adapted to this activity and may be perpetuated by surface disturbance and nutrient enrichment.

4.3.7 Herbivory

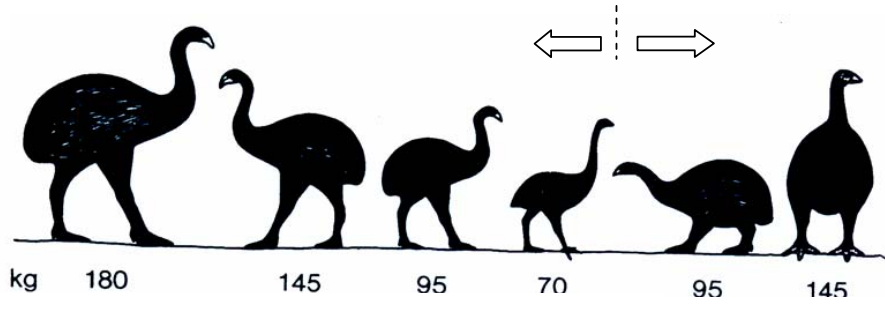
Animal sub-fossils and extant plant communities show that diverse herbivore guilds of birds, lizards, bats and large insects were present in pre-settlement New Zealand. For birds and bats, knowledge is sufficient to suggest that there were feeding guilds (e.g. Worthy & Holdaway 2002). However, pre-settlement guilds of lizards (skinks and geckos) and insects are less well understood, and both probably played important roles in pollination and seed dispersal (Whitaker 1987).

The classification of the bird and bat guilds in pre-settlement, dryland, eastern New Zealand (after Worthy & Holdaway 2002) is summarised as follows (see also Fig. 9). Chief among the terrestrial herbivorous avifauna were the giant moa (*Dinornis robustus*), the eastern moa (*Emeus crassus*), the heavy-footed moa (*Pachyornis elephantopus*), the stout-legged moa (*Euryapteryx geranoides*) and, at montane to alpine elevations, the upland moa (*Megalapteryx didinus*). Terrestrial herbivores also included: rails, such as takahe (*Porphyrio hochstetteri*), coot (*Fulica prisca*) (extinct), and Hodgens' waterhen (*Gallinula hodgenorum*) (extinct); several species of waterfowl, such as the goose (*Cnemiornis gracilis*) (extinct), Finsch's duck (*Euryanas*

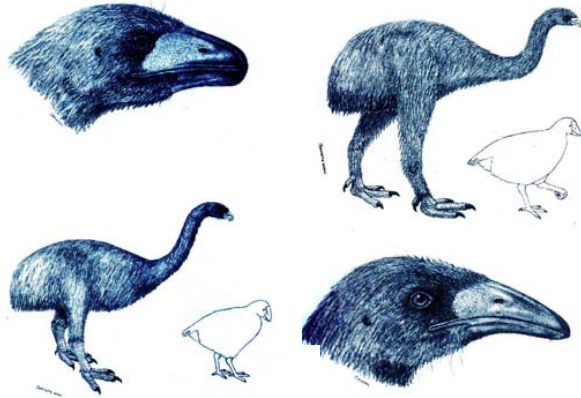
Figure 9.

- A. Body mass and profiles of examples of our forest guild of moa (left of dashed line) contrasted with examples of our eastern scrub guild (right of dashed line) (after Atkinson & Millener 1991: fig. 9). Species are, from the left: *Dinornis giganteus*, *D. novaezelandiae*, *D. struthioides* and *Emeus crassus*; those to the right are *Euryapteryx geranoides* and *Pachyornis elephantopus*. The three *Dinornis* species are an example of extreme reversed sexual size dimorphism, with taxonomic synonymy now reducing the entire genus to two species (*D. novaezelandiae*, North Island and *D. robustus*, South Island (Bunce et al. 2003)).
- B. Examples of the slender and long proportions of our forest guild of moa are left, *Anomalopteryx didiformis* and right, *Dinornis novaezelandiae* (Worthy & Holdaway 2002: figs 5.15 & 5.18). Silhouette of takahe provides scale.
- C. Examples of the squat and gravi-portal proportions of our eastern scrub guild of moa are left, *Pachyornis* (here exemplified by *P. mappini*) and right, the stout-legged moa *Euryapteryx geranoides* (Worthy & Holdaway 2002: figs 5.14 & 5.17). Silhouette of takahe provides scale. We suggest the rotund proportions probably aided penetration of thickets of shrubs and lianes in dry eastern South Island.
- D. Distribution of sites in which Haast's eagle *Harpagornis moorei* have been found (Worthy & Holdaway 2002: fig. 8.40). Sites of Pleistocene (triangles and squares) and Holocene (circles) age are shown. Apart from a small number in west Nelson, the sites are either dry inland or coastal eastern South Island. This suggests that the vegetation of the eagle's habitat was the low and partly open podocarp-hardwood and hardwood forest, scrub and small strips of riparian grassland characteristic of eastern South Island. Disturbance or edaphic stress that created a mosaic of canopy openings or short-stature vegetation provided prey-accessibility to the eagle. Alternatively, the species found the tall, multi-storeyed wet forests of the west inimical to its hunting needs. The eastern South Island moa and bird guilds in general seem to have been a richer assemblage of large herbivores, and probably in larger numbers, than the guild of wet western and northern forests of both main islands (Worthy & Holdaway 2002: 329).
- E. Fossils of Haast's eagle are commonly found in association with what is termed informally the 'eagle fauna' (Worthy & Holdaway 2002: 332) (Atkinson & Millener 1991: fig. 10). Members of this assemblage include the moa species *Pachyornis elephantopus*, *Euryapteryx geranoides*, *Emeus crassus* and *Dinornis robustus*, the goose *Cnemiornis calcitrans*, the terrestrial Finsch's duck (*Euryanas finschi*), the South Island adzebill (*Aptornis defossor*), and sometimes takahe (*Porphyrio hochstetteri*). Shown from left are: the body mass and profiles of New Zealand falcon (*Falco novaeseelandiae*); Haast's eagle (*Harpagornis moorei*) about to attack a *Euryapteryx* (moa); Australasian harrier (*Circus approximans*); Eyle's harrier (*Circus eylesi*) and South Island adzebill (*Aptornis defossor*). All weights in kg. Extinct species partly or wholly silhouetted.

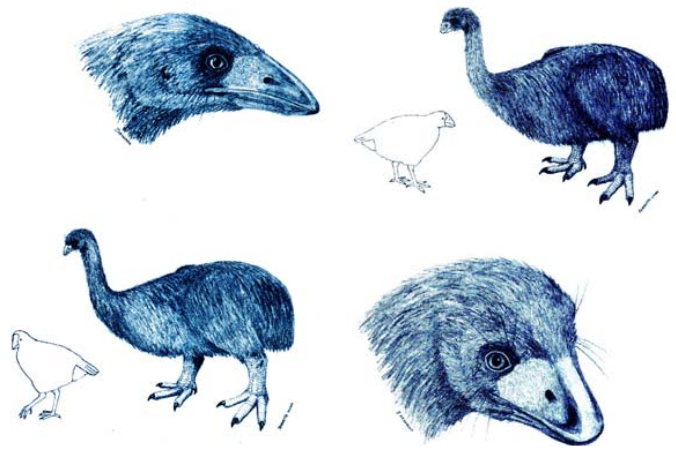
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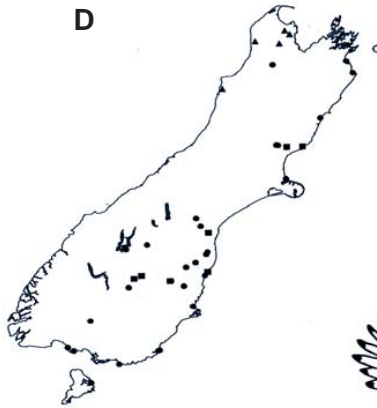
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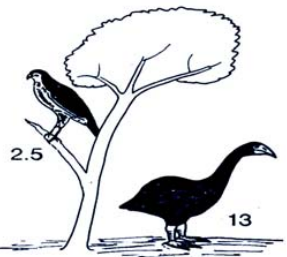
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finschi) (extinct), Paradise shelduck (*Tadorna variegata*), and swan (*Cygnus sumnerensis*) (extinct); and the kakapo parrot (*Strigops habroptilus*). Most of the waterfowl species were terrestrial, in that they spent much time away from water. The terrestrial omnivorous avifauna included the blue duck (*Hymenolaimus malacorhynchus*, which nocturnally forages among forest understoreys far from streams), quail (*Coturnix novaezealandiae*) (extinct), and weka. We also included the adzebill (extinct) in this group, because the evidence is that it was both herbivorous and carnivorous (Worthy & Holdaway 2002). The arboreal frugivore-folivore guild included wood pigeons (*Hemiphaga novaeseelandiae novaeseelandiae*), kokako (*Callaeas cinerea*) and kaka (*Nestor meridionalis meridionalis*). Parakeets (*Cyanorbampbus* spp.) were arboreal-terrestrial frugivore-folivores. Arboreal-terrestrial omnivores were kea (*Nestor notabilis*), piopio (*Turnagra capensis capensis*) and raven (*Palaeocorax moriorum*) (extinct). Two short-tailed bat species (*Mystacina robusta* and *M. tuberculata*) were the sole members of a remarkably adaptable aerial-arboreal-terrestrial insectivore-nectivore-frugivore guild. The biomass and contribution to ecosystem processes of geckos (*Hoplodactylus* spp., *Naultinus* spp.), skinks (*Oligosoma* spp., *Cyclodina* spp.) and insects, and their importance in herbivory, pollination, seed dispersal and litter decomposition, were probably considerable. Tuatara (*Sphenodon* spp.) were insectivorous and carnivorous, while frogs (*Leiopelma* spp.) were insectivorous.

The disturbance effects of the avifauna extended beyond the above species; many insectivore, nectivore and predator guilds added considerably to avifaunal diversity. For example, in addition to these species, dryland faunas previously included raptors, kiwi (*Apteryx* spp.), the owl-nightjar (*Aegotheles novaezealandiae*), waders, herons, the little bittern (*Ixobrychus novaezealandiae*), grebes (Podicipediformes), songbirds, gamebirds and seabirds, including gulls, terns, gannets, shags, penguins, petrels, prions and shearwaters (see Section 4.3.6 for bioturbation by seabirds).

Overall, the fossil record suggests that the higher-nutrient eastern ecosystems supported a richer array (and probably larger numbers) of large herbivores than did western and northern South Island forests, with their more leached and often podzolised soils (Worthy & Holdaway 2002). Likewise, it appears that herbivory was probably at relatively high levels around the coast because soils have high nutrient levels there. Even aquatic and tidal vegetation can be grazed by native birdlife (Wilson 2002). Of all habitats, wetland surrounds were impacted by the greatest range of large-bodied birds; here, a suite of moa species were typically supplemented by the goose, swan and adzebill (Holdaway & Brathwaite 1987).

Large birds probably also imposed disturbance through trampling. The static footprint pressure of moa has been estimated as one-half to one-third that of introduced ungulates in New Zealand (Duncan & Holdaway 1989). Whereas an ungulate hoof typically has a shearing edge and action, the toe edge of the ratite foot probably caused little or no cutting damage, due to a flexible, rolling action when it lifts off the ground. Nevertheless, there was probably considerable compaction pressure from ratite locomotion. Generally, on well-drained soils, ratite traffic would have caused soil compaction and minor surface disturbance, whereas wet and peat soils were clearly susceptible to churning. Some

terrestrial birds (e.g. moa, rails, wrens and kokako) probably foraged by scratching and, in combination with a plucking feeding action, scarified soil surfaces and turned over litter.

We have only partial understanding today of just how vegetation was affected by the browsing actions of the herbivorous pre-settlement bird fauna. Bond et al. (2004) proposed that a portion of the woody flora is strongly adapted to ratite browsing. They suggested specifically that ratites employ a different mode of browsing to the secateur action typically used by mammalian browsers: i.e. they clasp, then pluck or pull, either severing individual leaves, or breaking off unpredictable lengths of twigs and their attendant leaves from woody plants. This, they argue, promoted the evolution of stems with exceptionally high tensile strength, particularly in divaricating plants. But did moa pluck and pull, or did at least some species clip stems with secateur action, as their fossil gizzard contents suggest (Burrows 1980)? If clipping or slicing was the norm, how is the high tensile strength in woody plants explained? Whatever the answers, what we do know is that New Zealand's woody flora evolved to survive a persistent onslaught of browsing beaks. Therefore, it is likely that the distinctive divaricating growth form of many New Zealand shrubs and trees are at least partly an evolutionary adaptation to this. Other growth forms in dryland plants may also have evolved partly in defence against ratite browsing—the armoured stems of *Melicytus* spp.; the dead appearance of *Helichrysum dimorphum*; the impenetrable mass of thick cladodes of cushion-forming *Carmichaelia* species; the spiny tussocks of *Aciphylla* spp. and the lianoid stems of *Muehlenbeckia* spp., *Rubus* spp. and *Clematis* spp.

The array of pre-settlement herbivores would have disturbed all vegetation communities and strata in a variety of ways. Large-bodied birds were probably the chief mechanical disturbance agents in the vegetation tiers accessible to their bipedal stance. Of the lowland eastern guild of moa, the giant moa was primarily a forest dweller. In contrast, the eastern, stout-legged and heavy-footed moa were thick-set and squat, and had massive weight-for-height profiles (Worthy & Holdaway 2002). We suggest that their thick-set bodies would have aided their penetration of shrubland thickets and tangles of lianes. The relatively weak mandible, small gizzard and small stones, and broad flat bill suggest that the stout-legged moa was specialised to herbs and grasses of low fibre content within shrubland understoreys. The heavier mandible, narrow and pointed bill, and larger body mass suggest that the heavy-footed moa was a twig-eater of the dry shrublands.

We suggest that shrubland and low forest habitats would have been preferred to open areas, because these conferred some measure of protection against predation by large raptors, particularly Haast's eagle (*Harpagornis moorei*, which had a Holocene eastern New Zealand distribution; Worthy & Holdaway 2002: fig. 8.40). Moa have a particularly short set of upward-rising vertebrae, conferring a neck-forward posture that enables horizontal extension, which contrasts with the vertical reach typical of ratites that have evolved in savannah vegetation (Worthy & Holdaway 2002). We propose that this may be an adaptation for access across and through lianoid and shrub thickets and to avoid aerial predation in low stature woodland.

4.4 DISTURBANCE: SUMMARY

In terms of landscape disturbance phenomena, dry eastern South Island is relatively stable compared with the western mountains and coast, with their seismic activity and high rainfall.

Narrow eastern coastal zones about Marlborough were probably affected by occasional tsunamis, while aeolian transport of sand across sandplains affected many coastal zones (e.g. Kaitorete Spit and Amberley).

Braided rivers intermittently adjusted their positions across the floodplains, creating fresh alluvium for primary or secondary successions. Within their channels, the meandering braids provided a shifting pattern of primarily early successional islands and terraces of coarse debris. Flooding and sedimentation affected riparian zones of all rivers and streams in the uplands. Floodwaters deposited periodic veneers of mostly silty sediment that boosted fertility across these floodplains.

Snow break, snow avalanche and windthrow of trees affected mainly the western forested catchments, but their destructive influences applied at patch scales. Landsliding was concentrated in wetter western mountain catchments, although low-frequency landsliding also affected the greywacke ranges of Marlborough and South Canterbury. In contrast, Otago's schist block mountains with low uplift rates show little evidence of slumping activity. Solifluction-derived scree mainly affected greywacke bedrock, and was therefore concentrated in Marlborough and Canterbury uplands, and is rare in Otago.

There is no evidence that natural fire was anything other than extremely rare, patchy and predominantly small scale, even in New Zealand's driest environments. Although the charcoal and palynological database is limited, both suggest that grasses temporarily exploited burnt areas only to later retreat again, as successional shrubs and trees re-asserted their dominant stature. The frequency and scale of fire as a disturbance was so altered with human arrival that an entirely unprecedented imbalance in the competitive interactions between grasses and woody plants ensued.

5. Potential dryland vegetation in relation to the environment

5.1 INTRODUCTION

The development of forest and shrubland may be limited by climate or substrate factors, rather than (or in addition to) the disturbances discussed in the previous section. Understanding the influence of the environment on the pre-settlement composition of the eastern New Zealand dryland zone is essential for our understanding of the relative importance of disturbance for the biota. In this section, we review and synthesise evidence of the pre-settlement vegetation composition of the eastern New Zealand dryland zone. We focus

particularly on evidence for environmental limitations to the spread of forest and shrubland in pre-human times. For this task, we used recently published models of potential vegetation, and our field knowledge of relict vegetation in other areas for which evidence has not been collated and published.

Our present knowledge about the likely composition of pre-settlement vegetation of dry eastern New Zealand relies on evidence from vegetation remnants, charcoal in alluvial and colluvial sediments and soils, pollen and charcoal from wetlands, macrofossil remains, sub-fossil logs, soil surface forest dimples, and on modelling techniques that predict potential species distributions in relation to environmental gradients. Because many taxa are not represented, or only very conservatively represented, in fossil pollen profiles, only the coarsest-scale predictions of former dryland vegetation patterns have been possible until recently (e.g. McGlone 2001). In the last 5 years, forest reconstructions have modelled patterns of forest tree species and relict woody floras on environmental gradients (Leathwick 2001; Walker, Lee et al. 2003a, 2004b; Leathwick et al. 2004). These later studies have used regression-based modelling techniques to estimate the potential limits of different woody species, and combined these to predict potential vegetation types across the landscape. Leathwick et al. (2004) and Walker, Lee et al. (2003a, 2004b) produced national- and regional-scale reconstructions, and their predictions are at 100-m² and 1-km² grid resolution, respectively. Thus, neither study attempts to distinguish fine-scale environmental and vegetation variation (e.g. patterns determined by local topography). Indeed, this would require spatial information not yet available in national and regional digital databases. Moreover, neither study analyses the role of disturbance in any detail.

Leathwick et al. (2004) used plot-based measurements of forest trees, mainly from closed-canopied forests. Because closed-canopied forest remnants are rare in dry eastern New Zealand, few of the plots used for tree species abundances and forest classes are located within that dry environmental envelope. Moreover, many woody species that grow in drier areas (mainly small trees or shrubs of little merchantable value) were excluded from the dataset and predictions. The modelling of Leathwick et al. (2004) is therefore weakest in the thoroughly deforested environments of dryland eastern South Island, which are the focus of this study; the most extreme dryland environments are assigned to a single vegetation class, and no attempt is made to describe the vegetation types therein in any detail. The study modelled the distribution of annual extreme minimum temperature (AEMT), and used the temperature tolerances for forest species proposed by Sakai & Wardle (1978) and Wardle (1991) to set a conservative lower extreme temperature limit for tall trees of -10°C AEMT. This identified extensive areas in the inland basins east of the Southern Alps that were unlikely to support tall forest. However, the authors noted that a few tree species occasionally occur on sites with temperatures as low as -12°C AEMT. These include mountain beech (*Nothofagus solandri* var. *cliffortioides*), Hall's totara (*Podocarpus hallii*), mountain toatoa (*Phyllocladus alpinus*) and broadleaf (*Griselinia littoralis*), all of which were canopy dominants in pre-settlement forests of dry eastern New Zealand. It seems likely, therefore, that tall forest vegetation may potentially have extended well below the -10°C AEMT isotherm. Within this inland zone (i.e. < -10°C AEMT) Leathwick et al. (2003) made no attempt to distinguish or map different types of scrub and low

forest in their non-tall-forest zone. However, non-forest ecosystems such as wetlands are distinguished where very poorly drained substrates and peat occur, and dunelands were identified on recent or raw soils.

The study of Walker, Lee et al. (2003a, 2004b) focused on one particular part of the eastern New Zealand dryland zone: a 15 500-km² area of Central Otago. This study predicted the probability of occurrence across the whole region of 15 potential canopy-dominant trees and shrubs, based on the current, largely relict distributions of these woody species, using the environmental surfaces underlying LENZ (Leathwick et al. 2003). This study included many trees and shrubs that are not considered in national predictions of potential forest distribution (e.g. Leathwick 2001; Leathwick et al. 2004). Twelve zones of potential woody vegetation were defined, and the driest, coldest, frostiest 10% of the Central Otago study area (lower hillslopes, and basin and valley floors) was mapped as potential woody vegetation (mostly shrubland). Because the distributions of most woody relicts have been severely altered since human settlement, modelled potential species distributions, and the 12 potential woody vegetation zones, cannot be construed as simple reconstructions of the pre-settlement pattern (see Walker, Lee et al. 2003a: 18–19, 71–72); additional information from pollen, subfossil wood and charcoal records are needed to account for a suite of fire- and browse-sensitive species that have been entirely lost since human settlement.

In this section, we examine the results of these two different modelling exercises, and discuss their implications for our understanding of the potential vegetation of the eastern New Zealand dryland zone.

5.2 METHODS

We used available digital surfaces of environmental factors and derived estimates of forest and non-forest cover types to estimate the areas of land in our different dryland types that were potentially covered by tall forest prior to human settlement and those areas that probably supported non-forest vegetation. We calculated the land areas and percentages of our different dryland types mapped in the 24 vegetation classes of Leathwick et al. (2004). We also calculated areas of land classified as recent soils in LENZ (Leathwick et al. 2003), based on the NZLRI recent and raw soil categories, and those in which AEMT is estimated to lie below -10°C (J.R. Leathwick, unpubl. data). Finally, we calculated the percentage of each dryland type that is assigned to the 20 different forest types defined by Leathwick et al. (2004) and to each potential woody vegetation zone of Walker, Lee et al. (2003a, 2004b).

5.3 RESULTS

The classification of potential vegetation cover of Leathwick et al. (2004) suggests that 81.4% of the land area we classify as dryland may have been occupied by tall forest (Table 5), based on a conservative temperature (-10°C AEMT) limit for forest.

Wetlands and coastal dunes are estimated to have made up a small fraction of the dryland zone (1.2% and 0.2%, respectively), and the remainder (17.2%) is classified as non-forest by Leathwick et al. (2004) on the basis that it experiences cold winter temperature minima. The dryland type with the lowest predicted percentage cover of potential forest (53.4%) is the southern type G, since a high percentage of the land area experiences low AEMTs. Recent soils cover a high percentage (23.2%) of the type G landscape, and a proportion of these would have supported early- and mid-successional species. In northern dryland types (A to F), potential forest cover is estimated at > 90% by Leathwick et al. (2004), despite extensive areas of recent soils.

As might be expected, a distinct north-south gradient in potential forest types is predicted within the eastern New Zealand dryland zone (Fig. 10; Table 6). Northern rimu / tawa-kamahi forest (*Dacrydium cupressinum* / *Beilschmiedia tawa-Dacrycarpus dacrydioides*) is predicted across small areas of dryland types A, B and C only. Matai (*Prumnopitys taxifolia*)-kahikatea-totara (*Podocarpus totara*) forest is predicted further south, across 22% of the dryland zone, largely within dryland environment types C to H. Kahikatea-pukatea (*Laurelia novae-zelandiae*)-tawa forest in the north (dryland types A to D) and Hall's totara-broadleaf forest in the south (dryland types E to H) are each predicted across 11% of the dryland zone.

Some 18% of the dryland zone intersects the study area of Walker, Lee et al. (2003a, 2004b), which accounts for 35% and 57% of the land area of the southern dryland types G and H, respectively. The dryland zone intersects areas of nine of the woody vegetation zones classified for the Central Otago region (Table 7); only the three zones at highest elevations (Zones IIX, IX and X of Walker, Lee et al. 2003a, 2004b) lie outside it. Scattered relict shrubs, and the pollen, subfossil wood and charcoal records corroborate the woody potential of the most climatically extreme zones (i.e. I, II and III) (Walker, Lee et al. 2004a, b).

TABLE 5. ESTIMATED TOTAL AREA AND PERCENTAGE AREA OCCUPIED BY PRE-SETTLEMENT VEGETATION TYPES (FROM LEATHWICK ET AL. 2004) THAT PROBABLY HAD ENVIRONMENTAL LIMITATIONS TO DEVELOPMENT OF TALL FOREST.

DRYLAND TYPE	TOTAL (km ²)	PERCENTAGE AREA (LEATHWICK ET AL. 2004)				PERCENTAGE AREA (OTHER SOURCES)	
		TALL FOREST	OTHER NON-FOREST	WETLAND	DUNE	RECENT SOILS*	OTHER LOW-LAND WITH AEMT [†] BELOW -10°C
A	1430	91.9	0.3	7.3	0.5	48.0	0.0
B	8674	99.7	0.1	0.2	0.0	1.3	0.0
C	2525	92.3	0.3	5.4	2.0	39.0	0.0
D	1021	98.2	0.4	1.2	0.2	27.7	0.0
E	5313	92.2	7.8	0.0	0.0	0.2	7.6
F	11650	97.8	0.5	1.2	0.6	7.8	0.0
G	9117	53.4	44.4	2.2	0.0	23.2	21.2
H	10527	61.3	38.7	0.0	0.0	0.1	38.6
Total	50259	81.4	17.2	1.2	0.2		

* LENZ, Leathwick et al. 2003.

† annual extreme minimum temperature, J.R. Leathwick, unpublished data.

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