REVIEW

Postglacial history of New Zealand wetlands and implications for their conservation

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Abstract: Most New Zealand wetlands formed at or after the end of the last glaciation (c. 18 000 cal yrs BP). Those associated with major rivers and close to the coast tend to be young as erosive processes both destroy and initiate wetlands. However, there is a strong linear trend in initiations since 14 000 cal yrs BP, which suggests that geomorphic processes such as soil deterioration, landslides, sand dune movement and river course changes are constantly adding new, permanent wetlands. Most wetlands began as herbaceous fens but usually transitioned to shrub- or forest-covered bog–fen systems, in particular after the beginning of the Holocene (11 500 cal yrs BP). Raised bogs formed from fens during the late-glacial and early Holocene, when river down-cutting isolated them from groundwater inflow. As climates warmed through the late-glacial and early Holocene, wooded wetlands spread and over 75% of lowland peat profiles preserve wood layers. Large basins with high water inflow often contain lakes or lagoons and have maintained herbaceous swamps, whereas those with limited catchments have become almost entirely covered with forest or shrubs. Wetlands in drier districts tend to have been initiated during the mid- and late Holocene as the climate cooled and rain-bearing systems penetrated more often. Ombrogenous montane and alpine bogs may have been initiated by the same climate change. Natural fires frequently burnt some wetlands, particularly within the vast bog complexes of the Waikato Basin, but many wetlands record occasional fire episodes. By the time Māori arrived in the 13th century, about 1% of the landscape was covered with some form of wetland and most of that wetland was under woody cover. Māori firing of the landscape began the process of removing the woody cover, which induced wetter, more herbaceous systems and initiated new wetlands. Deforestation of catchments in drier districts increased water yield that may in turn have created lowland fens and lagoons. European logging, fire and draining destroyed both pristine forested wetlands and fire-transformed systems from the Māori settlement era. The loss of wetlands is now largely a crisis of continued degradation through draining, weed invasion and fire in already human-altered systems in productive landscapes. Wetland history can help assess values and inform goals for conservation of wetlands, but transformation of the lowland landscape has been so complete that an historically authentic endpoint is unrealistic for most wetlands. The major conservation emphasis should be on larger wetlands that provide a range of ecosystem services.

Keywords: climate, fire, Holocene, peat, peat growth, wetland restoration

Introduction

Before European settlement, New Zealand wetlands covered 1% of the mainland, or c. 2.5 m ha (Ausseil et al. 2008, unpubl. report). Since then, drainage of lowland and montane wetlands for development and agriculture has reduced them to roughly 10% of their previous extent. Many have survived as physically intact wetlands, if greatly altered through repeated fire since Māori settlement and spread of introduced weeds. Survival of even this much altered remnant remains precarious in many lowland areas, and wetlands are a priority ecosystem for conservation (Gerbeaux 2003). The history of wetlands gives insights into these ecosystems that can be obtained in no other way, and provides a background essential for conservation that aims to do more than simply prevent further degradation.

Although there have been a number of reviews of New Zealand plant history based largely on pollen-analysed cores from wetlands, there has been no overview of the history of the wetlands as wetlands. The primary aim of this paper is to fill this gap by reviewing the wetland history of the main islands of New Zealand. Peatlands of the southern oceanic islands have been recently discussed in detail (McGlone 2002a). New Zealand wetland history extends back to its separation from Gondwana some 80 million years ago. However, the termination of the Last Glacial Maximum at about 18 000 cal yrs BP (= calendar years before 1950 AD) provides a convenient starting point, as few extant wetlands were in existence before then. Wetland origins, development and ecological trajectories, and the influence of landscape alterations, climate change and natural fire are reviewed. The arrival of humans and the effects, both direct and indirect, of their activities on wetlands are examined. The review concludes with a discussion of how this historical dimension might be used to inform conservation and management policy.

New Zealand wetland nomenclature

Wetlands are areas with water-saturated soils or that are covered with shallow water. A typology and nomenclature for New Zealand wetlands has been proposed and key types described and illustrated in a recent monograph (Johnson & Gerbeaux 2004; see also Ward & Lambie 1998). The basic terms are *marsh*, a wetland with a largely mineral substrate, and *mire*, a peat-forming wetland. Much of the complexity surrounding the terminology of wetlands centres on peat, defined as an accumulation of deep (> 30 cm depth), primarily organic deposits (>65% dry weight) largely of incompletely decomposed organic matter (Wieder et al. 2006). Mires are variously subdivided according to the source of the water that sustains them, nutrient status, topographic setting, hydrology, structural form and vegetation cover. A bewildering set of often ambiguous terms are used to describe them (Charman 2002). Water source for a mire is the most important consideration. If the water is derived from precipitation alone, the mire is *ombrogenous*. If the water source has been in contact with the mineral soil, the mire is *minerogenic*. If the mire is minerogenic, but the water is not flowing, it is a *topogenous* mire; if the water is flowing in from the catchment, it is *soligenous*. The nutrient status of mires follows the familiar aquatic designations of *oligotrophic* (low), *mesotrophic* (moderate), and *eutrophic* (high). Two terms are commonly used to describe the origin of mires: *terrestrialisation* refers to the infilling of water bodies by organic sediments to form mires; *paludification* is the process of mires forming or extending over mineral dryland soils.

The fundamental mire types are *bog* and *fen* representing endpoints on a continuum from ombrogenous to minerogenic states. *Swamp* is a well-established term, in fact *the* term for mires in New Zealand '...preferred in New Zealand to *bog*, *fen*, *marsh*, *moss*' (Orsman 1997). However, internationally it is not synonymous with mire: in British scientific usage *swamp* is nothing more than a wet fen (Charman 2002), whereas in North America it is defined as a tree-covered wetland on hydric but not peat soils (Keddy 2000). Nevertheless, *swamp* is worth retaining as a local term provided that it can be defined in a way that is both reasonably distinctive and consistent with past usage. Here I follow Johnson & Gerbeaux (2004) and define *swamp* as a soligenous, mainly peat- or mud-forming system obtaining most of its water through surface flow with water usually present at the surface and flooding common. Lastly, *pakihi* or *gumland* are local New Zealand terms that refer to an array of wetland types united solely by their regional setting and supposed origin (Mew 1983). Sometimes they are simply saturated mineral soils and the distinction between the two terms is obscure (Williams et al. 2007). Where peat is accumulating in these systems, they are best accompanied by the relevant descriptor – as for instance, *pakihi* bogs, *gumland* fens.

Marshes often intergrade with mires. Two common marsh types in New Zealand are the ephemeral wetlands that form in winter-wet hollows but dry out or shrink dramatically over summer, and coastal or estuarine salt marshes.

All mire types intergrade and any narrow definition will fail when confronted with the messy realities of most wetlands. Bogs are often associated with fens, which occupy the transition zone or lagg at the bog edge where groundwater flow from the bog dominates the hydrology; and swamp–fen–bog complexes are also common, where bogs raised above the general water table grade into fens and are surrounded by swamps exposed to flooding and surface water flow.

Wetland vegetation

A surprisingly large (c. 470) number of New Zealand vascular plant species regularly occur or specialise in wetland environments, and many others are found from time to time on saturated soils (Johnson & Brooke 1989). Some of the more significant wetland groups and species are discussed here.

Trees and shrubs

There are seven trees, taller than 10 m, which can grow in saturated soils and tolerate extended periods of flooding: *Dacrycarpus dacrydioides*, *Dacrydium cupressinum*, *Elaeocarpus hookerianus*, *Laurelia novae-zelandiae*, *Lepidothamnus intermedius*, *Manoao colensoi*, and *Syzygium maire*. These are the dominant trees in swamp or bog forest communities. *Metrosideros umbellata* grows on poorly drained peat soils on subantarctic Auckland Island. Although widespread also on dry soils, *Cordyline australis* is a prominent component of swamp forest and scrub.

There is a large number (>30) of small trees and shrubs that exploit poorly drained soils. The most prominent of these are: *Leptospermum scoparium*, several *Dracophyllum* spp., several small-leaved *Coprosma* spp., *Epacris pauciflora*, *Myrsine divaricata*, *Neomyrtus pedunculata*, the conifer shrubs *Halocarpus bidwillii*, *H. biformis*, and *Phyllocladus alpinus*. Subshrubs or prostrate, stoloniferous shrubs are often abundant on bogs, and include several members of the Ericaceae (*Androstoma* *empetrifolia*, *Dracophyllum* spp., *Gaultheria depressa*, *Pernettya* spp., *Pentachrondra pumila*), *Coprosma* spp., and a conifer (*Lepidothamnus laxifolius*).

Sedges, rushes, Typhaceae, Hemerocallidaceae

New Zealand has a rich cyperaceous flora, the major wetland genera being: *Baumea*, *Carex*, *Carpha*, *Cyperus*, *Eleocharis*, *Gahnia*, *Oreobolus*, *Uncinia*, *Isolepis*, and *Schoenus*. Species from these genera are prominent in all major wetland communities, and often dominate fens and bogs. *Carex secta* is notable for its habit of forming large tussocks on elevated pedestals in shallow water. Juncaceae are represented by many species of *Juncus*, which are prominent as emergent reeds in shallow water; and *Luzula* as stoloniferous broad-leaved rushes in bogs. Raupō (*Typha orientalis*) is an abundant tall rush-like plant of nutrient-rich shallow water. Flax (*Phormium tenax*) is a giant tussock herb with robust, erect leaves up to 3 m long, common in swamps and damp ground. Mountain flax (*P. cookianum*) is a less robust plant more typical of poorly drained peaty soils.

Restionaceae, Centrolepidaceae and Poaceae

These three families also play an important role in New Zealand wetlands. The tall restiad *Sporodanthus* is confined to the northern North Island (*S. ferrugineus*) and Chatham Island (*S. traversii*). *S. ferrugineus* can grow to 1–5 m tall as it has a robust culm; *S. traversii* is less robust and has a height range of 0.6–2 m. *Empodisma minus* is perhaps the most important peat-forming species in the country being found throughout New Zealand except on the southern oceanic islands, from sea level to above the treeline in bogs, fens, swamps and damp ground. *Apodasmia similis* is a tall rush, emergent in salt marshes and dune hollows but also occasionally on the shores of inland lakes and freshwater marshes. *Centrolepis* and *Gaimardia* are genera of low-growing, cushion-forming Centrolepidaceae.

A range of grass species are found on peats, but the two dominants are *Cortaderia* spp., which form giant tussocks in swamps and along waterways, and *Chionochloa rubra,* which often is the main cover on bogs and damp hollows in southern districts.

Forbs

Prominent monocotyledonous forbs are species of *Potamogeton* (open water, tarns and wet hollows), *Bulbinella* (damp hollows), *Astelia* (bogs and cushion bogs) and Orchidaceae (bogs).

There are a large number of dicotyledonous forbs, especially in bogs, seepages and ephemeral wetlands. Species of *Callitriche*, *Ranunculus* and *Myriophyllum* are found in all habitats from flowing water to bogs; *Caltha* in upland turfs and seepages; *Crassula*, *Gnaphalium*, *Gonocarpus*, *Gunnera*, *Leptinella*, *Montia fontana*, *Neopaxia australasica*, *Nertera*, *Plantago*, and *Rumex neglectus* in ephemeral wetlands, lake edges, and seepages; *Drosera*, *Euphrasia* and *Gentianella* on bogs and damp soils. There is a wide range of plants that form extensive low cushions on bogs, including *Colobanthus*, *Donatia novae-zelandiae*, *Drapetes*, *Forstera tenella*, *Phyllachne colensoi*, *Stackhousia minima*, Apicaceae (most prominently *Actinotus novae-zelandiae*, *Centella uniflora*, *Lilaeopsis novae-zelandiae*, *Oreomyrrhis ramosa*, *Schizeilema*, *Hydrocotyle*), and *Abrotanella*.

Ferns, fern allies and bryophytes

All of the New Zealand *Lycopodium* spp., *Schizaea australis* and *Blechnum penna-marina* are found in bogs. *Ophioglossum coriaceum* occurs on turf and lake margins. *Blechnum minus* is abundant in swamps and on lake margins, and *Gleichenia dicarpa* forms major ground cover on bogs. *Gleichenia microphylla* occurs as a scrambler in swamps.

There are 12 *Sphagnum* species in New Zealand, but only two are of importance in wetlands. *S. cristatum* favours drier hummocks within bogs and fens; *S. falcatulum*, wet, low-lying hollows and lawns. A number of non-sphagnum mosses and liverworts are prominent, including *Campylopus kirkii* and *Drepanocladus aduncus* (aquatic).

Pollen, spore and macrofossil representation of wetland vegetation

Pollen, spores and macrofossils are well preserved in organic sediments. Vegetation on the wetland surface is usually very well represented in fossil assemblages and several studies have analysed the relationship between them (McGlone 1982; McGlone & Moar 1997; McGlone & Meurk 2000; Deng et al. 2006a).

Mosses are in general barely represented as spores, but preserve well as macrofossils in peat that is only moderately decomposed. *Sphagnum* spores are an exception in that they may be abundant, but in most cases only the leaf and stem macrofossils (which preserve very well) are common. Sedges are generally well represented both as pollen and macrofossils; pollen groups have been described (Moar & Wilmshurst 2003) although they are often not distinguished in routine analysis. Seeds of Cyperaceae are often found in sediments. Juncaceae have delicate pollen that is frequently unidentifiable or poorly preserved, and because the seeds of Juncaceae are not often encountered, they represent an important gap in our understanding of wetland history. Pollen of *Typha* (Typhaceae), Restionaceae and Centrolepidaceae is well represented and often completely dominates pollen sums. Restiads form a distinctive fibrous peat and whereas *Typha* peat is usually highly decomposed, it is easily distinguished in the field by its light colour and texture. Grasses are also well represented, although grass pollen types are generally not separated in routine analysis, and because they are wind-transported, they are often problematical with regard to possible sources. Other monocotyledonous pollen types are generally well represented in the pollen rain with the exception of Orchidaceae and *Phormium*, which despite bearing tall culms of large flowers, is rarely represented by more than a grain or two even when completely dominating a site. However, the tough *Phormium* leaves and leaf bases preserve very well and create a distinctive dark, fibrous peat. All the trees, shrubs and dicotyledonous herbs mentioned in the vegetation overview above are regularly found in pollen and spore preparations. Apicaeae, *Gunnera*, *Myriophyllum*, and *Gonocarpus* are the best represented of the herbs. With the exception of *Laurelia novae-zelandiae*, which has sparse pollen production, the trees are all well represented when on the site. All the shrubs are usually represented to some extent in the pollen rain if they occur on the bog. Pollen of *Leptospermum scoparium* and *Dracophyllum* is very poorly dispersed, and hence terrestrial stands are usually poorly indicated in the pollen rain. However, on mires, they often dominate the pollen sum as pollen and flowers are shed directly onto the surface below.

Postglacial wetland development and trajectories

Locations of the major wetlands discussed are given in Fig. 1.

Forest and shrubland mires

Forested alluvial mire systems have been described (e.g. Wardle 1974; Mark & Smith 1975; Dickinson & Mark 1994) and peat or silty peat up to several metres deep has been recorded beneath them. There is no direct historical evidence for their development but peat cores have been pollen analysed from pakihi mires close to forested terrace mires and they show there has been very little change in these forests since they became dominant 11 000 cal yrs BP (Newnham et al. 2007). Persistent rainfall, low sunshine and cool summers lead to peaty soils forming under forests in coastal south-western New Zealand (McGlone 2002a) and in mountainous regions throughout the country. Soil cores near the treeline on Mt Hauhangatahi (Tongariro) show peat growth began between 12 000 and 4500 cal yrs BP with a forest cover of montane conifers expanding and retreating in response to climate variability and volcanic impacts (Horrocks & Ogden 2000). Montane peats on Mt Taranaki appear to have been constantly forming and re-forming in response to volcanic eruptions (Lees & Neall 1993) with variable vegetation cover; on the southern Ruahine Range they began forming c. 9300 cal yrs BP and since then have occurred continuously under *Olearia colensoi* scrub (Lees 1986).

Coastal marshes and mires

The conjunction of marine and riverine influences at the coast results in constant wetland responses to sea level fluctuations (due to both ocean levels changing and tectonic subsidence and uplift), sand dune formation, progradation and shifting river courses. Sea level reached its postglacial high point c. 7500 cal yrs BP, and since then has not fluctuated more than 0.5 m (Gibb 1986). As a consequence, coastal wetlands tend to have formed relatively recently.

In a comprehensive study of Great Barrier Island coastal marshes Deng et al. (2006b) showed that when marine sedimentation dominated, estuarine marsh communities followed a relatively linear sequence from mangroves through *Juncus–Apodasmia–Baumea* associations. However, following *Baumea* dominance and build-up of peat, pathways were more diverse. Where terrigenous input was slight, the major pathway was towards increasingly oligotrophic systems via a *Gleichenia–Leptospermum* stage to a low *Leptospermum* forest. Where there has been major terrigenous input, a more eutrophic pathway is followed via *Gleichenia* to *Typha*, *Carex*, *Phormium* and *Cordyline* dominance, and eventually to a *Dacrycarpus dacrydioides* swamp forest with subdominant *Laurelia novae-zelandiae*, and *Syzygium maire*. Fire, deforestation and increased siltation and raised water levels tend to push these sequences towards eutrophic conditions dominated by rhizomatous herbaceous macrophytes and away from oligotrophic to eutrophic shrubland and forest, which otherwise may have been the inevitable outcome.

Coastal dune swale wetland sequences predictably move from an initial herbaceous fen towards a shrub or forest cover, depending on the local hydrology. A number of studies of dune swale sequences along the Bay of Plenty coastline (Campbell et al. 1973; Newnham et al. 1995b; McGlone & Jones 2004) and in the Wanganui district (Bussell 1988) demonstrate a variety of outcomes. In some cases, the dune swales formed from estuarine sediments and initially saline *Leptocarpus–Juncus* communities were followed by oligotrophic *Empodisma–Gleichenia–Leptospermum* fens and bogs. Moar (1952) showed several Wellington sequences in which freshwater sedge peat was topped by woody (*Dacrycarpus dacrydioides*) peat. More extensive mires on prograding coasts (e.g. at Kohika, Bay of Plenty) began with low forest, but as sand-impounded rivers and streams raised water tables, soligenous fens formed with rushes, sedges and restiads in wetter areas, *Leptospermum* shrubland in more oligotrophic raised areas, and eutrophic fen forests at the margins grading to dryland forest on the ridges (McGlone & Jones 2004).

Swamps and wet fens

Swamps are dynamic wetlands, usually forming when drainage is blocked by landslides, tectonic or volcanic

Figure 1. Locations of major wetland sites referred to in the text.

activity, changing river courses or coastal processes. Most current swamps have persisted as such from their initiation, often as a complex with lakes, sluggish streams and fens, although those with small catchments often transition to oligotrophic fens or bogs. Here I deal with systems that have remained swamps or wet fens usually because they have large catchments with significant streams. Thus, they often include ponds and lakes. I recognise three major settings in which they originate.

Lake to swamp

Most typically, swamps begin as lakes or lagoons and then transition to swamps. There are four common natural situations in which these wetlands initiate:

- Sand dunes migrating inland block off streams.
- A landslide, tectonic or volcanic event blocks a valley. An example is Wharau Swamp in Northland blocked by a basaltic lava flow c. 5000 years ago and which has since been a lake–wet fen (Elliot et al. 1997)
- River meanders are abandoned leaving typically broad depressions which become shallow swamps or fens (e.g. Pohehe Swamp; McLea 1990).
- Glaciers leave over-deepened valleys or moraine complexes in which ponds or lakes form followed by swamps. An example is Kettlehole Bog (inland Canterbury), a small depression left in a moraine field formed by the retreat of glaciers about 18 000 cal yrs BP. It began as a deep pond but became shallow and then transitioned to a wet fen with a *Leptospermum scoparium* margin by 11 500 cal yrs BP (McGlone et al. 2004). Many swamp sequences from inland eastern districts of the South Island show similar dynamics (Moar 1970, 1971, 1973).

Bog/fen to swamp/lake

Less commonly, an initial fen or bog is replaced by a lake–swamp complex. Lake Poukawa (central Hawke's Bay) is an example of a lake–mire system that began as *Dacrycarpus dacrydioides* fen in the mid-Holocene c. 7000 cal yrs BP, but through rising water levels, formed a lake–swamp–fen association by about 6000 cal yrs BP (McGlone 2002b; Fig. 2). Once formed, the lake fluctuated in size, probably as a consequence of prolonged periods of wetter than normal years. As long as tectonic down-warping of the basin continues and the current rainfall pattern is maintained, a lake–fen wetland will persist. A similar transition occurred at Pyramid Valley (inland Canterbury) where an initial sedge- and flax-dominated wet fen gave way to a shallow, fluctuating lake (Moar 1970).

Lake/marginal swamp/fens

Deep lakes may have marginal swamps or wet fens, often in shallow embayments or on alluvial fans. These usually are partly built from silt in-wash or lake sediment infill and maintained by the water level of the lake. A typical example is Holdens Bay at the margin of Lake Rotorua where a rising lake level deposited organic lake muds beginning 4500 cal yrs BP, and later transitioned to sedge peats forming under a shrub and tree covered fen (McGlone 1983). Where the marginal organic sediment is initially lacustrine and transitions to fen peat, no interpretive problems arise. However, fens may edge deep lake basins but be underlain by metres of fen peat. At Lady Lake in north Westland (Pocknall 1980) a narrow marginal fen is underlain by 7 m of fen peat with woody layers, which initiated c. 6500 cal yrs BP. Similar, near-vertical peat margins have been noted next to other lakes, and peat growth must have been controlled by slowly rising lake levels caused by sediment accretion at the lake outlet.

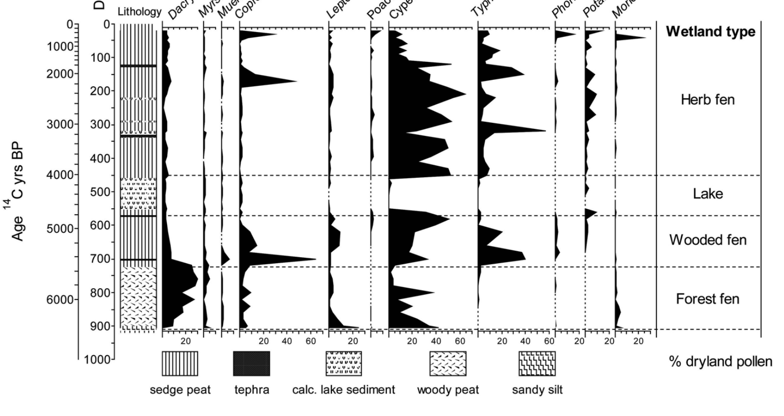

Figure 2. Percentage pollen diagram, Lake Poukawa, Hawke's Bay. Example of fen–lake complex. The lake basin at the end of the last glacial was dry. In the mid-Holocene a forested fen formed, but increasing water levels transformed it into a shrub fen, then a fluctuating lake–wet-fen system (from McGlone 2002b).

Basin and valley mires

Basin and valley mires are relatively common in the North Island and the west coast of the South Island. They generally have small catchments of low relief, sluggish or no clear drainage, and mostly lack lakes or ponds. The older examples occupy tectonic or glacial moraine-outwash depressions, ancient river courses or dune fields, whereas more recent examples are impounded by coastal dunes or beach ridges. Some are extensive, covering many hectares, but they can be as small as a few metres across. The oldest basins have had wetlands, usually oligotrophic bogs with restiad, sedgeland or woody cover – for many thousands of years, and in some cases through several glacial–interglacial cycles. Well-studied old basin mires extending back into or through the last glaciation are the Kaitaia Swamp (Elliott 1998) and Otakairangi (Newnham 1992) bogs in Northland, western Waikato (Lees et al. 1998), Rotoaira/Otamangakau peat basin, central North Island (McGlone & Topping 1977, 1983), Eltham Bog in Taranaki (McGlone & Neall 1994), and Okarito, Westland (Newnham et al. 2007). Young examples are Halfmoon Bay bog, Stewart Island (McGlone & Wilson 1996), and the Rangitaiki Plains and Maketu basin peats in the Bay of Plenty (Campbell et al. 1973).

Although now only rarely surviving with vegetation intact, many of these basins had dense forest cover during the postglacial. The best documented of these, the Eltham bog in Taranaki (Fig. 3), began in the early postglacial as an ephemeral wetland, transitioned to a shrub-covered fen, but by 11 500 cal yrs BP was covered with *Syzygium maire*, *Dacrydium cupressinum*, *Manoao colensoi* forest and had continued rapid peat accumulation (McGlone & Neall 1994). Many other basin peat deposits show signs of having had forest cover in the form of in situ stumps or abundant wood (e.g. Otakairangi, Newnham 1992; Halfmoon Bay, McGlone & Wilson 1996).

Valley-head bogs and fens

Fens and bogs are ubiquitous in high rainfall mountainous areas and support a great variety of graminoids, herbs and mosses. In the moister, higher altitude regions of the south-eastern South Island, these mires form at the heads of small valleys and are continued downstream as riparian fens and marshes (Rapson et al. 2006). The amphitheatre-shaped heads of these valleys were formed by periglacial or glacial activity over repeated glacial cycles that carved out small catchments from the jointed schist bedrock and draped them with colluvium and loess (Webb et al. 1999). Typically, valley-head peats form behind a rock or colluvial sill.

Detailed hydrological studies of a typical valley-head peatland in Otago demonstrate that most of its water is derived either from overland flow through upper soil layers during storms, or by constant ooze from loessial subsoils, colluvium and jointed bedrock (Bowden et al. 2001). During a 10-day rainless period in summer the bog lost 7 mm day^{-1} through evapotranspiration and 9.2 mm day^{-1} via base flow into the stream for a net change in water storage of −2 mm day^{-1}. The non-peat catchment therefore provided 14 mm day^{-1} as subsoil and bedrock flow (which is likely to be a minimum year-round flow) compared with the 3.7 mm day^{-1} provided annually by precipitation directly onto the bog surface. Valley-head peatlands are therefore sustained mainly by catchment-derived soil-water, and on this basis are strictly fens rather than bogs. However, parts of the peatland complex may be slightly raised and dominated by plants typical of oligotrophic conditions such as *Sphagnum*, and *Empodisma minus*, although their ombrotrophic status is probably marginal due to the occurrence of nutrients in subsoil water (Mark et al. 1995; Walker et al. 2001).

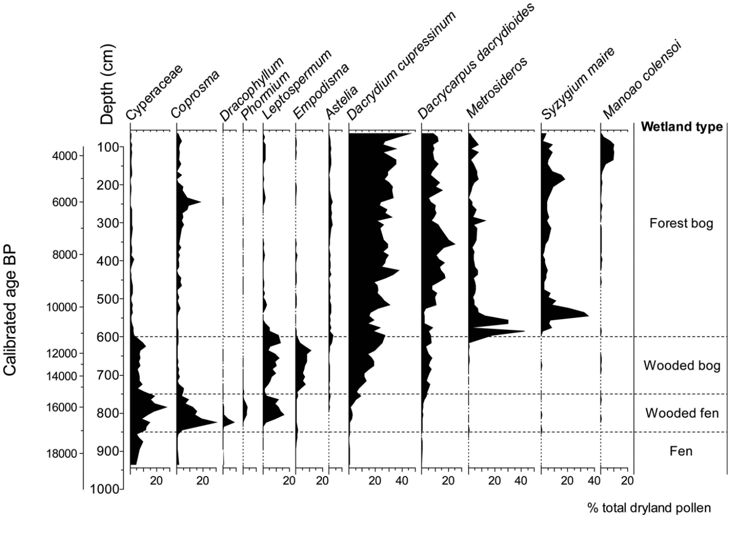

Figure 3. Percentage pollen diagram, Eltham Bog, Taranaki. Example of a wetland sequence in a lowland basin bog. It began as a wet herbaceous fen, transitioned to a wooded fen during the late-glacial, and became a forested bog in the Holocene. Upper levels destroyed due to European farming. Data from McGlone & Neall (1994).

Stratigraphic, pollen and macrofossil studies of valley-head peatlands (McGlone et al. 1995; McGlone & Wilmshurst 1999) show they began to form mainly in the early to mid-Holocene, although earlier initiation may have taken place in more coastal locations (Walker et al. 2001). They appear to have formed in response to an increase in rainfall. *Sphagnum*-dominated bogs have become common only recently, mostly after human arrival, and it is clear that most were drier and woody earlier in their history (McGlone & Wilmshurst 1999).

Montane bogs and sloping fens

Bogs and fens are relatively common in montane, high-rainfall, low-sunshine regions where a combination of persistent mist and rain and low evaporation favours high water tables and peat growth, and thus the presence of mires in situations where at lower altitudes, dryland communities would be present. Ombrogenous mires that cover an entire landscape (blanket bogs) are common in the boreal zone of the Northern Hemisphere under cool, cloudy, high humidity conditions. They are essentially absent from mainland New Zealand but are the dominant land cover on oceanic islands to the east and south of the South Island mainland (McGlone 2002a).

Montane mires in New Zealand fall into two categories: bogs that form on poorly drained sites, and sloping fens (which are also called *seepages* or *flushes*) fed by groundwater oozing from the soil and regolith. They are generally shallow, as the cool summers decrease wetland productivity. The northernmost montane bogs occur in the Coromandel Range where persistent cloud shrouds the upper slopes of Mt Moehau. They are also found on the central Volcanic Plateau (Clarkson 1984) and down the axial Kaimanawa, Kaweka and Ruahine ranges (Froggatt & Rogers 1990) and in the main mountain ranges of the South Island down to Stewart Island. In the east of the southern South Island, wide bogs and fens are found wherever flat or gently sloping country occurs at high altitude. The broad flanks of the flat-topped central Otago mountains are draped with long reaches of colluvial silts, sands and gravels, which support shallow sloping fens dominated by sedges and cushion plants (McGlone et al. 1995). Cushion bogs are a type of montane bog found usually at high altitudes in which low-growing cushion-forming dicotyledons provide the main tightly packed vegetation cover.

While not montane, similar bogs and fens, often with scrub or forest cover, occur at lower altitudes in coastal districts along the cloudy Southland, Fiordland and Stewart Island coasts (Wright & Miller 1952; Leamy 1974; Johnson 2001). The Awarua bog system at the Southland coast near Invercargill is an example of an extensive bog complex formed over a broad, poorly drained, low-angle fan (Johnson 2001). Here a regionally high water table, and a cloudy, cool, moist climate have combined to create an extensive wetland dominated by *Empodisma*, sphagnum, and *Leptospermum* and *Dracophyllum* scrub, which early palynological work suggests has been largely unchanged for much of the Holocene (Cranwell & von Post 1936).

Montane to alpine bogs and fens began forming around 13 000 cal yrs BP (Rogers & McGlone 1989; McGlone et al. 1995). However, mires continued forming throughout the Holocene (Frogatt & Rogers 1990; McGlone et al. 1997), some well after 5000 cal yrs BP (e.g. Kaiparoro, Tararua Range; Rogers & McGlone 1994). These bogs formed mostly on weathered clay-rich tephra or colluvium (Moar 1956,1961,1967; Froggatt & Rogers 1990). They first formed in depressions or on flat sites, ridge-top and sloping bogs forming later.

Montane bogs and cushion bogs show very little local vegetation change once formed: a cover of graminoids, restiads, low-growing herbs, cushion-forming herbs and subshrubs typically persists throughout (McGlone et al. 1997). Where pools form part of the complex, there may be abrupt changes to fine-grained organic muds and aquatic plants (e.g. *Sphagnum falcatulum*, *Myriophyllum* spp.) resulting from small changes in water balance (e.g. Garvie Range; McGlone et al. 1995).

Patterned wetlands

Pools occur occasionally in most large peatlands but are so frequent in some as to define a separate class of *patterned* wetlands. Patterned bogs fill gently sloping, shallow depressions where pools, often elongated across the direction of water flow, create mosaics of alternating peat ridges and water. Two areas of patterned mires (or aapa mires) have been examined in detail in New Zealand: Roaring Meg (Garvie Mountains; Mark et al. 1995; McGlone et al. 1995) and the Lammermoor Ranges (Otago; Rapson et al. 2006). In these mires *Sphagnum* is abundant close to the pools and along the streams feeding the fen edges. Elsewhere, typical moss, graminoid, restiad, herb, cushion and subshrub associations dominate.

The patterning of these mires, bogs and fens is influenced by the general topography and hydrology of slopes on which they form, but the immediate cause is faster growth of peat in the ridges and slow growth or peat decay in poorly drained flarks and pools (Mark et al. 1995; Charman 2002). Roaring Meg revealed a complex history in which sedge and cushion-dominated mire and shallow pools coexisted from about 13 000 cal yrs BP, and the present pool-ridge pattern developed only after burning following human settlement. McGlone et al. (1995) suggested that either increased precipitation and/or more inflow from a fire-modified landscape promoted the shift by increasing the duration of open water on the surface and the subsequent formation of deep pools. This scenario is consistent with proliferation of erosional peat tunnels in the underlying silt–peat interface, which now drain considerable portions of the mire and have emptied some pools (Mark et al. 1995; Dickinson et al. 2002). Accumulation of lower peat sediments cannot have occurred if pipes formed in the growing peat. Peat pipes are under-reported and little understood but carry a very significant part of the water flowing out of bogs and are common worldwide in peat-covered catchments (Holden 2005).

Raised and spring bogs

Raised bogs are peat water-table mounds fed by rainfall alone, and their oligotrophic surfaces are often elevated metres above their surroundings. Raised bogs are constrained both in their distribution and height by the annual climate water balance, which must be positive (at least in the northern cool-temperate–boreal zone; Charman 2002). In the Northern Hemisphere raised bogs are abundant in the boreal zone and in highly oceanic settings (Ireland, Scandinavia and coastal north-eastern North America have large concentrations) but are restricted to the north by cold winters and to the south by high evaporation (Glaser & Janssens 1986). They almost invariably form on flat interfluves or alluvial terraces (Heinselman 1970). Nutrient-rich, oxygenated water promotes higher rates of decay and thus flowing water generally prevents raised bog formation, although raised fens may form in the face of moderate soligenous inflow (Gignac et al. 2000). The essential elements therefore are moderate to high rainfall, a moist cool summer regime, poor drainage, and isolation from flowing water. The more positive the water balance and the greater the area for lateral extension, the taller the ombrogenous dome. The pressure of the dome forces water via internal peat and substrate pathways down and to the side. The vertical distance the water is driven into the underlying substrates is an order of magnitude greater than the height of the overlying water mound, resulting in water table mounds being disproportionately important in local hydrology (Siegel & Glaser 2006).

Domed elements are relatively common in fen–bog complexes in mainland New Zealand, but classically large raised bogs are (or were) abundant only in two areas: Southland and the Waikato–Hauraki Plains regions. Very large examples are extant (Otautau, Southland, 12.2 km^2, 10 m deep; Kopouatai, Thames, 240 km^2, up to 14 m deep). Even though Southland has cool summers and year-round rainfall, it provides marginal environments by Northern Hemisphere criteria as it has a low monthly water balance and summer water deficits (Leathwick et al. 2003). The Waikato–Hauraki region is even less suitable as it has warm and often dry summers with extended water deficits and a negative annual water balance. This extension of the raised bog wetland type beyond its typical global climatic distribution needs comment.

The main (nearly the only) peat-formers in the raised bogs of northern New Zealand are the restiads *Sporadanthus traversii* and *Empodisma minus*. Hairy root clusters are a much commented on feature of restiads. These, and the similar proteoid and dauciform root clusters, have arisen in a limited group of families as a response to nutrient-poor substrates, particularly in dry areas (Lamont 1993). These roots proliferate as dense mats in the humus and decomposing litter layers and appear to be important in phosphorus uptake (Clarkson et al. 2005). As oligotrophic bogs are extremely nutrient-poor substrates, their dominance by restiads is thus explicable.

Restiad roots are densely matted and hold a very large amount of water relative to their dry weight (Campbell 1964). This water-retaining trait of the restiad root-mat is often thought of as being functionally equivalent to the stems and leaves of *Sphagnum*, the dominant plant of most Northern Hemisphere raised bogs. However, much more important in raised bog formation is the fact that bog surfaces with dense *Empodisma minus* canopies have much lower rates of evaporation than other wetlands. Summer evapotranspiration from the Kopouatai Dome was only 34% of the open water rate, the dense canopy and associated thick root mulch preventing water loss from the peat surface, and the aridity-adapted shoots of *Empodisma* restricting transpiration (Campbell & Williamson 1997). The net effect is that the *Empodisma* canopy is unusually warm and dry creating what Campbell & Williamson termed a ‘wet desert’. *Sporadanthus ferrugineus*, a much taller and robust restiad, typically occupies the most oligotrophic central part of the raised bog; its communities also have low evaporation rates but higher than those of *Empodisma* and more typical of those of other vascular wetland plants (Thompson et al. 1999).

As well as *Empodisma*, southern raised bogs tend to have extensive cover of *Chionochloa rubra* and *Sphagnum*. On the raised bogs of the subantarctic islands where evaporation is low, both *Sporodanthus* and *Empodisma* are absent, *Sphagnum* is uncommon or absent, and a range of rushes, sedges, forbs, *Chionochloa antarctica* and *Poa* spp., none of which have any particular water-retaining feature, dominate (McGlone 2002a). Ajax Bog, in the Catlins, is a mainland example of a raised bog from a cool summer district that had little input from either *Sphagnum* or *Empodisma* until grazing and fire in European times (Fig. 4; Johnson et al. 1977). Thus, while raised bogs can form under virtually any vegetation type, there is a case to be made that without the water-retentive canopies and ground mulches of restiads, raised bogs may not have formed in the summer-dry regions of New Zealand.

All raised bogs appear to have had a shrubby component on the high dome. *Leptospermum scoparium* is perhaps the most abundant and frequently occurring shrub, but commonly encountered taxa are: *Coprosma* spp., *Dracophyllum* spp., *Epacris pauciflora, Halocarpus bidwillii* and *Phyllocladus alpinus*.

Detailed studies have been carried out on the largest extant raised bog, Kopouatai (de Lange1989; Newnham et al. 1995a; Clarkson et al. 2004), and less comprehensive studies on a Southland raised bog at Merrivale (McGlone & Bathgate 1983). Both bogs began as ponds or fens in poorly drained shallow depressions formed by abandoned

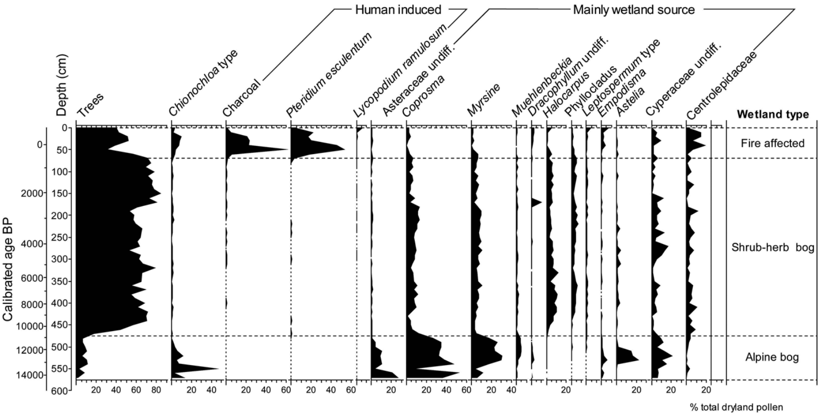

Figure 4. Percentage pollen diagram, Ajax Bog, the Catlins, Otago. An upland raised bog that transitioned from a shrub–herb alpine bog in the late-glacial to a raised bog with a persistent but thin shrub cover of *Coprosma*, *Myrsine* and *Halocarpus bidwillii* during the Holocene. Note the effect of Māori and European fire on the composition of the bog vegetation with the decline of scrub and rise of Centrolepidaceae, Cyperaceae, and *Lycopodium ramulosum*. Previously unpublished data.

floodplains or channels. In the case of Kopouatai, pollen of *Empodisma* and *Sporodanthus*, along with Cyperaceae, *Coprosma* and *Leptospermum* and macrofossils of *Baumea* etc., show an oligotrophic fen forming c. 14 000 cal yrs BP with extensive restiad-dominated oligotrophic raised bog domes present by 9500 cal yrs BP; at Merrivale, fens formed and raised bog formation commenced at about the same time. The transition from rush, sedge and flax dominated fens to restiad-dominated oligotrophic bog is rapid and almost certainly provoked by down-cutting of adjacent rivers depriving the fen of soligenous water. The area covered by a raised bog is critical to its final morphology, with large bogs developing extensive flat tops often with internal drainage and ponds. Shrub cover fluctuates over time. Kopouatai includes several wood layers in the peat, and had a major excursion of *Leptospermum* centred on 8000 cal yrs BP. In Southland, many raised bogs have marginal deposits of *Halocarpus bidwillii* wood, and at times wood layers extend across the bog. A wood and shrub pollen layer at Merrivale formed around 5600 cal yrs BP.

An unusual feature of the extensive raised bogs of the Waikato Basin is the peat lakes at their margins. These are small lakes that are impounded by walls of oligotrophic bog. They are generally older than the raised bogs themselves, having formed behind gravel or sand bars of the Waikato River at the end of the last glacial but have deepened with the growth of peat in their surrounds (McCraw 1967; Newnham et al. 1989).

Where groundwater discharges at the base of hills, raised bogs that owe little or nothing to rainfall may form even in dry regions (e.g. Treasure Downs, North Canterbury – Moar 2008; Idaburn Valley – McGlone & Moar 1998). These 'spring bogs' often contain badly deteriorated pollen and spores because the extra oxygen and nutrients encourage high levels of microbiological activity.

Natural fire in wetlands

Despite their saturated substrates, wetlands will burn after dry summer spells (Keddy 2000). The dense, often uniform canopy of many wetlands and their invariably flat or gently sloping topography means they lack natural fire breaks. Awarua Bog in Southland, an extensive shrub–*Empodisma*-covered fen, has suffered two major fires within the last 20 years that each burnt c. 1400 ha over c. 6–8 km (Townsend & Anderson 2006). Many New Zealand wetlands survive fire well, and recovery after recent fires shows that as a general rule fire will reset a wetland trajectory, but not alter it (Timmins 1992; Clarkson 1997; Johnson 2005). Mineralisation of peat creates a temporary spike in nutrients, and this, plus opening up of a dense canopy, allows new plant entrants, and appears to be the major mechanism behind short-term change (Clarkson 1997). New Zealand non-forest dominants all recover after fire. Some can resist fire because of well-insulated stems (e.g. *Cordyline australis*), because of their ability to resprout from burnt bases (e.g. *Phormium tenax*, *Coprosma* spp.) because of deep buried rhizomes (e.g. *Empodisma minus*), or by seeds either buried or dispersed to the site (e.g. *Leptospermum scoparium*).

Although fires were not generally common in prehuman New Zealand (Ogden et al. 1998), many wetlands in New Zealand, especially large raised bogs, have a history of natural fire. A long history of fire may be responsible for the maintenance of serotiny (retention of seeds in capsules beyond one year as a fire adaptation) in *Leptospermum scoparium*. Thus, Bond et al. (2004) reported that *L. scoparium* populations were serotinous in wetlands with a burnable area greater than 30 km^2. In the North Island, fires appear to have been largely generated by lightning strikes on the bogs themselves as the surrounding landscapes generally appear to have been fire-free. McGlone et al. (1984) found abundant microscopic charcoal in a southern Waikato bog at Ohinewai, Newnham et al. (1995a) showed regular fire occurred in the Kopouatai bog (Thames Valley), and macroscopic charcoal fragments were recorded by Campbell et al. (1973) from Bay of Plenty coastal fens and bogs. At Ohinewai, fire appeared to favour *Empodisma* over *Sporodanthus*. On the Kopouatai bog, fire may have repeatedly created conditions suitable for *Leptospermum scoparium* to briefly dominate through mineralisation of the surface peat (Newnham et al. 1995a). However, not all raised bogs were fire-prone and the few southern raised bogs examined have only sporadic, low levels of charcoal.

In the South Island, fire in wetlands is mainly a consequence of fire in the surrounding landscape, suggesting that lightning strikes on the bogs themselves are either less common than in the north or less effective. Glendhu bog (a 0.4-ha wetland) in coastal east Otago has had several fire episodes in which substantial forest change occurred as well as destruction of the woody cover of the bog itself (McGlone & Wilmshurst 1999). Such fires have probably had a long history in the drier south-eastern districts of New Zealand (McGlone 2001).

Fire in some settings has been responsible for the formation of the wetland itself. Kaiparoro Clearing in the northern Tararua Range has a shallow tussock-covered peat bog that may have been formed as a result of fire, as abundant charcoal is included in the basal sediments (Rogers & McGlone 1994). Peats in clearings in Waipoua Forest, Northland (Ogden et al. 2003), and peaty pakihi soils in Westland probably originated in a similar way, as basal charcoal is often present. Removal of the forest cover from a fen or bog surface has the immediate effect of reducing transpiration and interception of rainfall by foliage, and thus creates a wetter surface (Fahey & Jackson 1997). The resultant increase in water available at the surface of the soil is apparently sufficient to initiate a mire or to cause a pre-existing mire to transition to a wetter state.

Peatland trajectories

Mires are dynamic, constantly responding to changing water flow, nutrients and the consequences of their peat accumulation. Despite this complexity, it is possible to group changes faced by mires into a relatively small number of trajectories.

Lake to bog

The classic peat bog formation process depicted in many text books, of a lake in a small enclosed basin slowly becoming filled with mud, passing through a swamp phase with emergent vegetation to become a true bog, is of limited application in New Zealand. Steep-sided small depressions formed by blocks of stagnant ice left by glaciers in the Southern Alps and adjacent forelands follow this trajectory, but with sediments forming first in what may have been ephemeral wetlands, then passing through a deep water pond phase and finally transitioning abruptly to bog. On a larger scale, the glaciated western districts of the South Island resembled a vast lake district during glacier retreats in pre-Holocene times. Some of these glacially created lakes persist, many have been filled with silt, lake sediments and peat, and are now fens or bogs (e.g. Gillespie's Beach Road; Moar 1973), while some have transitioned to fjords as a result of rising sea levels (e.g. Preservation Inlet; Pickrill et al. 1992)

Herbaceous swamp/fen to wooded bog/fen

This is the nearly invariable sequence observed in closed basins or coastal systems where dunes block drainage. Initial swamp/fen systems become wooded over, and in the lowlands often support tall eutrophic forest. Well-documented examples are Eltham Basin (McGlone & Neall 1994; Fig. 3) and Great Barrier Island coastal marshes (Deng et al. 2006b).

Swamp/fen to raised oligotrophic ombrogenous bog

This is the typical sequence for raised bogs. Often the initial swamp/fen phase is very brief and it could be argued that the bog formed on something equivalent to a marsh or ephemeral wetland. The well-described Kopouatai Bog complex appears to have formed by extension over large areas of fen and marsh (Newnham et al. 1995a).

Wooded bog/fen to lake/swamp/fen

This transition is known only from drier eastern districts and is evidence for a major climatic change towards wetter regimes in the mid-Holocene (McGlone 2002b). Examples are Lake Poukawa (Fig. 2) and Pyramid Valley, which began as wooded fens and passed through to sedge and *Typha*-dominated lake/swamp systems.

Herbaceous raised bog to wooded raised bog

In Southland and Otago, many raised bogs have layers of wood including *Halocarpus* within them, but pollen analyses of these layers show that, at times, dense shrubby cover has persisted. Similar woody intervals have been noted as far south as Campbell Island (McGlone 2002a; McGlone et al. 2007).

Dryland to bog

Sequences in which forest or scrub is destroyed and a mire system forms are relatively common in high-rainfall, low-evapotranspiration areas such as the west coast of the South Island where permanently wet soils form thin peats after loss of forest.

Peatland and climate change

It is often supposed that initiation of peatlands is connected

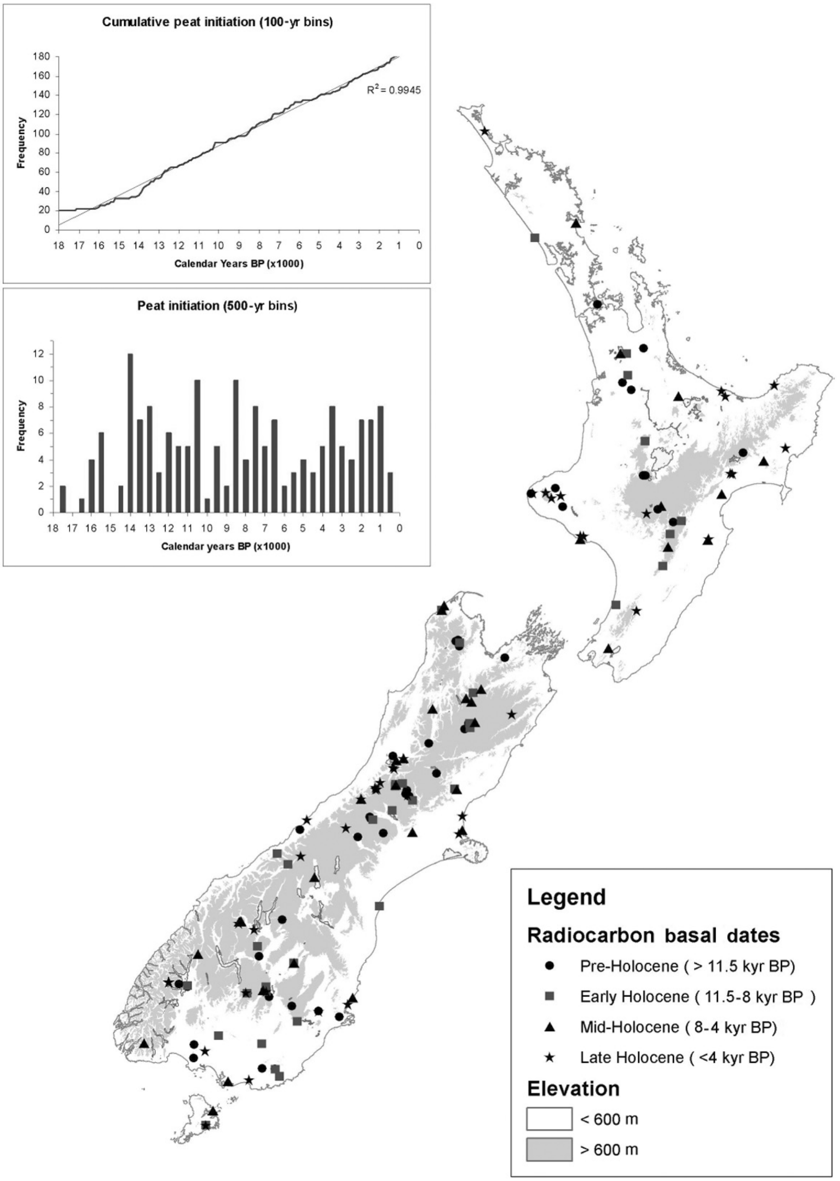

Figure 5. Basal dates (kyr = 1000 cal yrs BP) for mainland wetlands. Insets: cumulative curve for wetland initiations since the termination of the last glaciation and peat initiations (each bar centred in a bin spanning 500 years).

to changing climate regimes and that peat accumulation and structure and the vegetation cover likewise reflects climate change. A wide range of peatland indicators including morphology of the mires, decomposition of the peat itself, and the myriad range of fossil organisms and organic compounds preserved within peatland have been used to reconstruct climates over time (Charman 2002). Little work has been done on this aspect in New Zealand.

Peatland initiations and climate change

In Fig. 5 I present radiocarbon or tephra dates for the lowermost organic sediments in 190 wetlands that have persisted through to the present from 18 000 cal yrs BP (approximately the end of the last glaciation). Few initiations are recorded in the first 4000 years, presumably because harsh climatic conditions during the late-glacial continued to disturb landscapes and rainfall may have been low (McGlone 1995). However, after 14 000 cal yrs BP, there is a linear trend indicating a steady addition of new wetlands. Many of the events or processes that initiate wetlands are irreversible in the medium term, for instance blocking of valleys by changing river courses or massive landslides, rising sea levels, and deterioration of the permeability of soils. On the other hand, those processes that destroy wetlands, mainly river erosion on alluvial plains, and coastal erosion and inland movement of sand dunes consequent on sea level rise, necessarily create as many wetlands as they destroy. The steady upward trend with time suggests an increasingly larger proportion of the landscape became wetland. There is no clear spatial pattern to the initiation of wetlands, other than a tendency for high altitude and coastal sites to be young, and a lack of pre-Holocene mires forming in dry (<1000 mm yr^{-1}) eastern districts.

Wetland initiations do not significantly deviate from a linear trend from 14 000 cal yrs BP, despite significant climate change. In particular, there is no upsurge with the onset of the Holocene 11 650 cal yrs BP (Walker et al. 2008), an event characterised by a nation-wide increase in temperature (Wilmshurst et al. 2007) and an increase in rainfall in western and northern districts (McGlone et al. 1993). As a first approximation, I suggest that peatland initiations are largely due to landscape change and have been independent of climate change since the late-glacial transition between 18 000 and 14 000 cal yrs BP.

The most compelling departures from this scenario are a handful of swamp/lake complexes in the drier east coast districts and some upland peat initiations along the axial ranges of the southern North Island and in Central Otago. In dry eastern districts, swamps or lakes did not develop until after 7000 cal yrs BP when rainfall increased and wind flow probably switched flow from a predominately northwesterly to southeasterly pattern (McGlone 2002a). Montane and alpine bogs show two different patterns of initiation: deep, topogenous bogs started forming between 18 000 and 14 000 cal yrs BP; shallow, largely ombrogenous bogs between 8500 and 5000 cal yrs BP (Rogers & McGlone 1989; Froggatt & Rogers 1990; McGlone et al. 1992, 1997; Shulmeister et al. 2003). The explanation given for this dual pattern is that topogenous bogs started forming as landscapes became stable at the end of the last glaciation, whereas a pattern of dry, warm winters inhibited ombrogenous peat development until climate patterns altered in the mid-Holocene, when an increasing southerly influence brought cooler, wetter winters.

Peat accumulation and climate change

The formation of peat requires nearly total inhibition of decay through high water tables preventing oxygen reaching decay organisms. Virtually all decay occurs within the acrotelm (the upper, aerated and incompletely decomposed layers of a peatland). However, as peat accumulation is the net outcome of primary production and decay, it has no simple relationship with any major environmental variables. For instance, increasing temperature accelerates primary production on the surface but also increases biological activity and hence decay. Increasing productivity thickens the acrotelm until the increasing amount of decay leads to decreasing net accumulation, thus giving a humpbacked relationship (Belyea & Clymo 2001). High water tables will inhibit decay, but slow primary production. It is often assumed that low water tables, especially fluctuating ones, will accelerate decay. Whether this leads to slower peat growth almost certainly depends on the often positive effect of the drier surface on the vegetation: forest-covered bogs in many parts of the world have low water tables but still have fast peat growth. Gorham et al. (2003) found that dry, midcontinental North American bogs and fens had the highest rates of accumulation, a finding which suggested that productivity rather than inhibition of decay by high water tables drove their accumulation. That deep peats occur both in the warm Waikato Basin (raised bogs up to 14 m deep) and in the cool subantarctic (raised bogs up to 10 m deep) suggests there is a broad optimum for rapid peat growth.

McGlone (1990) found that low peat accumulation rates characterised early Holocene peatlands (beginning at 10 000 cal yrs BP) at a range of South Island sites and argued they were a response to low rainfall at that time; accumulation rates in the large northern Kopouatai Bog were slowest between 10 000 and 8000 cal yrs BP (Newnham et al. 1995a). A few studies have also demonstrated very slow peat growth in the centuries before human arrival in the 13th century (e.g. McGlone et al. 1997). However, without a better understanding of the various factors controlling it, peat growth cannot be used as a reliable climate proxy.

Woody growth on bogs

Wood-covered bogs, or those with woody episodes in the past, are common. Thus, at least 56 of 73 major lowland peatlands throughout New Zealand had wood recorded at some level in the profile (Davoren 1978). While patterns of woody growth on bogs are generally attributed to lower water tables because of strong present-day field correlations (Dickinson & Mark 1994), it does not necessarily follow that past changes in woody cover are due to precipitation changes. For instance, under a scenario of increased rainfall and temperature, more summer warmth would lower water tables through increased evapotranspiration, whereas increased precipitation in winter may raise water tables with little effect on woody plant survivorship, as growth is slow or halted (Crawford 2000). More woody cover may thus result from a rise in rainfall. This is almost certainly what occurred at the beginning of the Holocene (11 650 cal yrs BP), when forested peats (as evidenced by wood and pollen in profiles) began to spread, coinciding with an increase in both temperature and rainfall (McGlone &

Topping 1977; McGlone & Neall 1994; Newnham et al. 1995b). Likewise, the mid- to late Holocene spread of trees and shrubs on to raised bog and fen surfaces noted at several southern South Island sites (e.g. McGlone & Bathgate 1983; Vandergoes et al. 1997) is highly likely to have been driven by summer warmth, rather than precipitation decreases or autogenous mire changes. Increased continentality of the climate during the mid-Holocene may be the major cause (Wilmshurst et al. 2002). A regime of wet cool winters (which recharge the bog but have minimal effect on the growth of dormant mire plants) followed by dry warm summers (which encourage woody growth by providing non-saturated surfaces) might best explain this mid-Holocene feature.

Increased woody growth on raised bogs need not always have a climatic explanation: Kopouatai has prominent stick layers reflecting periods of *Leptospermum* abundance. Although these might be thought to be a consequence of periods with low summer water tables, the favoured explanation is that fire temporarily destroyed competing *Sporodanthus*, thus providing opportunities for *Leptospermum* regeneration (Newnham et al. 1995a).

Other peat proxies for climate change

Peat-preserved wetland microfossils and chemical alteration of peat profiles have been widely used to document past climate changes via inferences primarily based on their correlation with water table and temperature. Interpretation of these proxies is often controversial (Barber & Langdon 2007). Studies on southern South Island mires using testate amoebae and peat decomposition (humification) as proxies for water table depth showed that mid-Holocene water tables were high, but that increasing seasonality after about 3500 cal yrs BP resulted in drier and possibly warmer summers but cooler winters (McGlone & Wilmshurst 1999; Wilmshurst et al. 2002).

Anthropogenic change

The impact of human activity on peatlands results from: (1) burning of the mire vegetation; (2) deforestation of the surrounding landscape; (3) increased nutrient flows through introduction of livestock; and (4) drainage.

Burning of mires

Studies of fire in current mire systems radically underestimate the original transformative effects that anthropogenic fires have had. Human-lit fires have been much more frequent than natural fires. Some fire-sensitive elements (e.g. conifer shrubs) have vanished over large areas where they were once an integral part of the mire and marginal vegetation. Destruction of marginal woody vegetation has removed a seed source for many woody species that once played a role on wetland surfaces, coming and going in response to changes in water levels. Kohika swamp in the Bay of Plenty is a well-documented example of this process (McGlone & Jones 2004). Forested fens and bogs are now uncommon except on the wet, heavily forested west coast of the South Island, whereas before human settlement they were one of the chief wetland types.

Fire has also altered the relative abundance of species on mire surfaces. In southern bogs and fens, *Empodisma*, *Sphagnum*, *Lycopodium ramulosum*, *Pteridium esculentum* and *Chionochloa* tussocks have tolerated fire well, whereas the shrubby cover that grew on many bogs has been much reduced (McGlone & Wilmshurst 1999). The best-documented of these transformations comes from valley-head bogs in Otago and Southland. Typically, these bogs have dense *Sphagnum* cover (Walker et al. 2001), but in virtually every case the dense *Sphagnum* cover was initiated by fire, which reduced a previously much drier shrubby cover (McGlone & Wilmshurst 1999). Both deforestation of these catchments and the sweep of fire across the bog surface would have increased water input to the bogs, favouring *Sphagnum* dominance.

On the domes of North Island raised bogs, human fire appears to have had far less impact, presumably because natural fire was already part of the system and the bogs appear to have been naturally species-poor. However, there is abundant evidence for destruction of marginal wetlands through the elimination of forest and scrub (Cranwell 1939, 1953).

Deforestation

Removal of forest by fire during the Māori era, and then by felling and fire during European settlement, has massively altered the hydrology of many mire systems. Deforestation of a catchment is frequently accompanied by destruction of woody vegetation on the mires, so it is not possible to separate out the direct effects of fire on the mire surface, altered hydrology, and erosion. Three distinct wetland changes have resulted.

First, global studies have shown that for every 10% reduction of evergreen or coniferous forest cover in a catchment, annual water yield tends to increase by about 40 mm (Bosch & Hewlett 1982). A similar value was obtained for a New Zealand catchment by Fahey and Jackson (1997), who attributed most of the increased water yield to lower interception of rainfall by the canopy. Deforested catchments in New Zealand may therefore generate 20–25% more water flow relative to rainfall, and have increased storm peak flows and reduced low flows. Stable, sluggish streams become more active, carry more sediment and nutrients, and wetter flax, raupō and tall rush and sedge communities develop. Nutrient-rich swamps where common sedges such as *Carex secta*, rushes, flax, raupō and ferns (such as *Blechnum minus*) dominate are now the most common wetland type in New Zealand.

Second, the burning of poorly drained or peat-covered forested lowlands has induced sedge and rush fens over large areas, notably in the Waikato Basin, Bay of Plenty, Taranaki, Hawke's Bay and Southland. There are some indications that burning by Māori was much more extensive than is apparent from merely comparing the deforested versus forested landscape. Wooded wetlands in lowland Westland may have been burnt, giving rise to peat-forming pakihi bogs (Williams et al. 1990). Even high altitude bogs were burnt with marked effects on the vegetation through loss of shrub cover (McGlone et al. 1995).

Third, removal of forest and scrub from coastal dune systems induced dune movement inland, blocking drainage and forming sand ponds and fens (McGlone & Jones 2004).

The major effect of settlement by Māori and their liberal use of fire was to alter the ratio of the various wetland types in favour of dynamic rather than stable wetlands, and to favour nutrient-rich fens and lagoons over forested fens and bogs. While this transformation may not have been deliberate, it created much more productive wetland systems. As the oligotrophic, heavily wooded, lowland wetlands vanished, ducks, rails and other wetland birds became more abundant and eels and freshwater fish flourished.

Increased nutrients

Although the major increase in nutrients came via altered landscape hydrology, livestock have almost certainly had an effect. This effect is likely to have been most strongly marked around ephemeral wetlands in the drier areas of the South Island, in valley-head bogs and fens in tussock-clad uplands, and in fens, swamps and marshes in heavily stocked farmland throughout the country. Raupō and flax are found throughout the fens of montane to lowland areas of the South Island and may owe their prominence in part to this livestock-promoted switch in nutrient status.

Drainage

In most cases drainage has led to conversion of what were once mires to productive farmland and hence more or less permanently removed them from consideration as peatlands. However, partial drainage of swamps sometimes has promoted the formation of fen or bog situations in which woody vegetation – often with a strong exotic component – has asserted itself.

Conservation implications

The wetland crisis

The current state of New Zealand wetlands is often presented as a crisis in which they have been reduced to a shadow of their former extent (Hunt 2007). Remaining examples are often thought of as fragile and there is now a tendency to see every wetland as important, and its loss a part of an unfolding tragedy. Two points can be made with regard to this scenario.

First, the term *wetland* is too broad to be a practical conservation category (Johnson & Gerbeaux 2004). Wetlands are only united by their possession of a saturated substrate and, as we have seen, vary enormously on every other physical, biological and historical dimension. Statements such as the one with which I began this review, that wetlands now are reduced to 10% of their original extent, are factually correct but largely meaningless from a conservation viewpoint. The loss has been largely of wetlands within now deforested country, and mostly of poorly drained soils and fens of floodplains and coastal districts (Ausseil et al. 2008, unpubl. report). Mires surrounded by intact indigenous vegetation are usually in better ecological condition than the adjacent forest as they are not subject to the same intensive herbivore pressure. Although often portrayed as a crisis of loss of wetland area, loss of unique wetlands is much more important.

Second, as we have seen in this historical overview, wetlands are not inherently more fragile than other indigenous ecosystems. In fact, given the vigorous, often fire-adapted vegetation that now covers them, wetlands are less prone to accidental destruction than dryland systems. Although they are vulnerable to change in water supply and water quality due to drainage and runoff, permanently altering wetlands is an expensive and resource-intensive activity. Without a deliberate effort to destroy them, wetlands will persist. The contrast with the plight of many of New Zealand's native vertebrates, which will continue to decline without deliberate efforts to save them, is stark.

However, there clearly is a crisis as wetlands continue to be deliberately destroyed and the ecological condition of many of those that remain is almost certainly deteriorating.

Key issues

About 250 000 ha of wetland remain (Ausseil et al. 2008, unpubl. report). Out of the >7000 discrete wetlands identified, 74% are <10 ha in area. About half of the wetland area is contained by just 77 that are over 500 ha. Preservation of self-sustaining wetlands dominated by indigenous plants and animals is clearly the ideal. However, management and restoration of wetlands is expensive, fraught with practical difficulties, and hence aims must be clear. But there are many obstacles. For instance, many wetlands, while remaining largely indigenous, have been comprehensively transformed, leaving little sign of previous states. Thus, uncertainty exists as to what an appropriate endpoint for restoration or management might be. Given the many thousand patches of wetland in developed environments, an undifferentiated approach to them will impose a severe burden on landowners and regulatory agencies for little biodiversity gain. Close attention has to be paid to what sort of wetlands will be managed or restored and what values they offer. Leaving aside economic extractive or development values, wetlands have physical values (water storage, nutrient and carbon sequestration), biodiversity values (provision of habitats), social values (aesthetic, recreational), and historical values (repositories of natural archives).

The physical value of wetlands may be less than is often claimed. Wetlands, particularly lake–mire complexes connected to a wider hydrological system, provide base flow. However, this is largely independent of mires. Bogs are saturated, hold little surplus water, and therefore cannot moderate floods and contribute little to base flow (Holden 2005). Significant wetland water storage occurs when temporary ponds and lakes form over swamps, fens or areas of poorly drained soils. These spillover areas, having been cut off from flood water by levees and improved drainage channels, are now mainly developed. However, earth dams or reservoirs are more effective at absorbing peak water flows and facilitating later redistribution of water. Nutrient stripping by wetlands is another overemphasised benefit inasmuch as few indigenous wetlands are physically well placed to undertake this role, and those that are are negatively impacted by enhanced nutrients. Hence, the focus is on creating artificial wetlands with fast-growing nutrient-absorbing species, basically biodiversity-impoverished farm extensions (Zedler 2003). While carbon sequestration in wetlands is now increasingly talked about as a wetland service, how effective this will be is difficult to assess (Belyea & Malmer 2004). Wetlands can easily become net greenhouse gas emitters, especially through methane production (Yu et al. 2008).

The question of which sort of wetland is best in a particular situation can be difficult to answer in the face of their multiple values. Authenticity is a powerful unifying concept in conservation, and palaeodata can provide the necessary historical environmental template (McGlone 2000). For no ecosystem are these data more complete and accessible than for wetlands. An historical perspective is therefore one of the important sources of information that should contribute to planning for wetlands at all levels from national to local.

There are problems with a purist historical approach, however. In the case of dry lands, self-sustaining authentic natural communities usually maximise the biodiversity, physical, and social aspects we value. With wetlands, this is not always the case. For instance, much of the social value of wetlands derives from vistas, birds, and easy access, all of which are most easily provided by open water. Lowland wetlands in a prehuman condition often have saturated or flooded soft ground, tall, vexatious ground cover, and a dense woody overstratum that impedes movement, reduces visibility, and supports few waterfowl and fish. Moreover, there are major impediments to re-establishing authentic wetland communities.

The first, as discussed earlier, is that the settled New Zealand landscape has water and nutrient flows that are very different from those of the prehuman past. A higher volume, more flood-prone hydrology has resulted from deforested catchments. Large swathes of the landscape have been dried out through artificial drainage. The passage of water across the landscape has been canalised and controlled. All work strongly against maintenance or restoration of historical wetlands.

A second set of issues concerns the irreversibility of changes in the wetlands themselves. Drainage of the land surrounding mires and abstraction of water from aquifers can be reversed, but at considerable economic and social cost. Only limited restoration can be attempted when the adjacent water tables are low, particularly in bogs and poor fens whose peat surfaces will compact and shrink. Largely irreversible (at least over a century timescale) loss of peat and peat structure takes place when permanent lowering of the water table occurs. Peat accumulation is slow, rarely more than 2-mm vertical height increase per year and, when peat is drained and dries, it becomes waxy and water-repellent and inhospitable for plants.

Finally, wetlands, especially fens and swamps, are exceptionally open to invasion by weeds, and by woody weeds in particular.

Historical value of lowland wetlands

The fundamental questions are: How valuable is this wetland habitat? And how much is needed? An historical perspective can assist in answering them.

Lowland bogs

The irreversible consequences of draining wetlands which have built thick peat substrates that provide an oligotrophic surface environment make them an absolute priority for protection. In particular, the remaining lowland raised bogs are of unique value as spectacular landforms, superb archives of past environmental change, and as a home to a limited but ecologically intriguing biota. Fortunately, their position on interfluves and their extremely oligotrophic surfaces makes them resilient in the face of most disturbances except drainage. Most surviving raised bogs now have artificial drainage running up into the lagg – the mesotrophic moat that surrounds individual domes – and often through into the bog itself. Much of the biological interest resides in the spectacular transition from forested or wooded surrounds to fen, and finally to the ombrotrophic heart. No bog restoration project can be regarded as complete until these historical sequences are re-established.

Lowland fens, swamps and marshes

The situation is very different with regard to these now ubiquitous wetlands of the developed landscape. The economic value of the largely alluvial land that surrounds and underlies them puts many under constant threat. From an historical perspective, they have very mixed origins: some have been in existence for many thousands of years, fluctuating but essentially similar over time; some have been induced from a previously wooded, drier or more oligotrophic state; and yet others have been created recently, largely through fluvial landscape changes or artificial dams. Fire, deforestation and fertilisers have had a homogenising effect on these systems, regardless of origin, promoting the expansion of wet, often eutrophic fens and swamps at the expense of nearly every other type of wetland.

Fens and swamps are highly invasible. Clarkson et al. (2008, unpubl. report) found that exotic plants had invaded many New Zealand wetlands, but most comprehensively the more fertile open marshes and swamps. Much of the concern about weeds has centred on woody weeds, including alder (*Alnus* spp.), blackberry (*Rubus* spp.), gorse (*Ulex europeaus*), Spanish heath (*Erica lusitanica*) and, most importantly, several willows (e.g. *Salix cinerea* in the Whangamarino Wetland; Clarkson 1997). Willows have faster relative growth rates, better adaptations to flooding and sediment deposition, and better reproductive rates than most competing indigenous species and thus can dominate the wet margins of many fens and swamps (West 1994; Lee 1998).

A major consequence of the human transformation of wetlands from a drier to a wetter state is a loss of endemic biodiversity. The wetter a wetland is, and in particular the more open water or pools it has, the less endemic the biota. With regard to the vascular flora, open water and swamp/lagoon emergents are 34% endemic at the species level. In contrast, bog and bog-marginal plants are more than 65% endemic (McGlone et al. 2001). Non-endemic indigenous bird species in New Zealand are overwhelmingly of wetland habitats (70%). Widespread herbaceous plants and wetland birds almost certainly became more abundant with the opening up of the forested lowlands (Worthy & Holdaway 2002) and doubtlessly so did many fish species.

Many lowland wet fens and swamps of agricultural or urbanised landscapes (i.e. those at most risk) have been in their current state for a relatively brief period of time, and do not have highly distinctive biodiversity as individual sites. Often they simply replicate the same common cluster of species. That is not to say they are therefore unimportant; we must have such wetlands, but not necessarily any one of them in particular. The key questions are how many, how large, and how closely spaced they need to be to conserve wetland biodiversity and services across a region?

Responding to the crisis

Two activities are often undertaken or suggested as solutions to the wetland crisis: creation of new wetlands; and restoration that seeks to create more authentic wetlands out of degraded examples. While creating wetlands *de novo* is a worthwhile activity, in that social values are thereby catered for, the physical and inherent biodiversity values of such wetlands as individual sites is usually low. Even if indigenous plants are used and indigenous animals attracted, the end result is usually not a unique New Zealand community but a generic wetland with Australasian dominants of recent origin such as raupō, swamp harrier (*Circus approximans*), and pūkeko (*Porphyrio porphyrio*). If the goal is to create a more authentic wetland environment in an historical sense, the cost of doing so has to be balanced against the loss of existing ecological values, services and opportunities. Social wetland ecosystem services mainly concern birds, fish and recreation, and are mostly derived from open water, the most historically recent and changeable element in the mix.

The value equation is biased heavily against investing in small fens, swamps and marshes. If a wetland is small, has a high water table, has weeds, and receives nutrient-rich runoff, it adds very little to biodiversity of the region as a whole and does not provide much in the way of ecosystem services. Moreover, it would be expensive to ameliorate these negative attributes as they are essentially a function of the surrounding landscape. Large wetlands, especially those associated with rivers, estuaries and lakes, are quite different propositions because of what they provide over and above their inherent biodiversity status. Birds, fish and open water for recreation provide valuable ecosystem services that justify maintaining them, and their very size, wide range of habitats, and insulation from external influences provide opportunities for biodiversity enrichment via indigenous replanting schemes or drainage blocking.

Travis Swamp, Christchurch City, is a key example of a restored wetland as it exemplifies all these questions and points a way forward (see Meurk 1995, unpubl. report; Orwin 2005). It is a fen wetland of 56 ha, with significant peat areas, and preserves some biodiversity components now rare in the region. Developers opposed the establishment of the wetland reserve, which impinged on their housing estate plans, and argued that a new ahistorical wetland would be created out of what was, objectively viewed, a much degraded pasture–wetland system. In this, they were correct. Moreover, if it had not been within city boundaries, neither the funds nor the human effort would have been forthcoming; its worth is contingent on its accessibility.

Travis Swamp is formed from an old estuary of the Avon River, but was essentially a freshwater fen at the time of Māori settlement. Three past states of the freshwater fen can be identified (McGlone unpubl. data; Fig. 6): (1) Prehuman: tall sedge (*Carex* and *Baumea* dominant) in association with manuka-dominated scrub; (2) Maori: fire-induced raupō–sedge vegetation with only limited scrub; (3) Early European, and burnt raupō–sedge in which palatable species were reduced or eliminated, and in which artificial drainage encouraged growth of manuka and introduced woody weeds. Each of these states was induced by a different combination of intensity of fire,

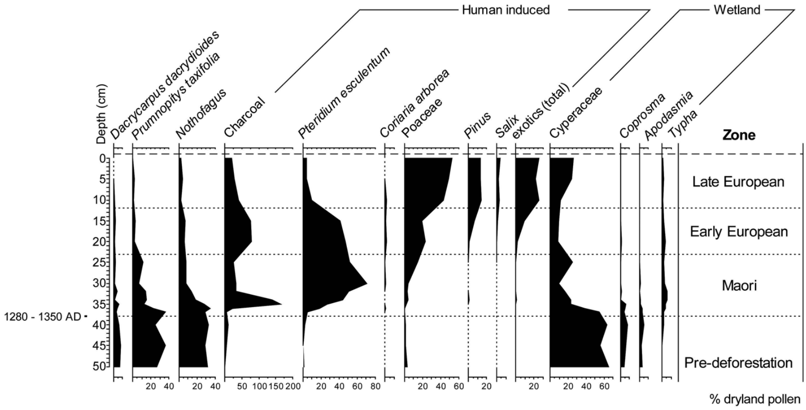

Figure 6. Percentage pollen diagram, Travis Swamp, Christchurch. Initially a wet sedge fen with some *Coprosma* and *Myrsine* scrub cover and a forest fringe. Burning by Māori and then European development turned it into a wet pasture with invasive *Leptospermum* and *Salix* (McGlone unpubl. data).

grazing and drainage. Under farm management but without fire for most of the 20th century, it degraded to mainly wet pasture with abundant rushes and aggressive willow. It resembled past wetland states only by virtue of some patches of native wetland species surviving through to the present and the presence of residual peat soils.

If the prehuman historical setting was regarded as the ideal towards which these Travis Swamp sites should be managed, the dryland margins of the swamp would have had to have been reconstituted in open indigenous forest and the surface of the mire converted to a sedge-dominated fen with a manuka overstorey. Instead, the pragmatic choice was to strengthen the amenity that most people enjoy about a wetland, i.e. water, vistas and birds. The prominent feature of the swamp now is a large artificial pond that has been excavated to provide habitat for birds, many of which (Canada geese, mallard, swan) are introduced. However, action has been taken to ensure the indigenous biota can sustain itself at the site through pest and weed control, water-table management and forest–scrub plantings, albeit in reconstructed communities not close to those historically documented. Management for plant elements now rare or vulnerable on the Canterbury Plains (e.g. mānuka, *Carex flaviformis*, *Baumea rubiginosa*, *Luzula* sp., *Corybas macranthus*, *Ranunculus glabrifolius*) ensures that it remains a crucial biodiversity node and reservoir of genetic variation.

Conclusions

Wetlands have the best documented, best understood history of any New Zealand ecosystem. As shown here, we have continuous records going back thousands of years in virtually every region of the country and covering most wetland types. However, this history has been an underutilised resource. For instance, two recent books, one a descriptive manual (*Wetland Types in New Zealand*, Johnson & Gerbeaux 2004) and the other a popular account (*Wetlands of New Zealand*, Hunt 2007), all but ignore the rich documentation explored in this paper. There are a number of reasons for this neglect. As pointed out in my Introduction, those studying wetland archives have for the most part concentrated on dryland vegetation history and climate change, and not on the study of wetlands as an end in itself. The conventions for presentation of palaeoecological results, and the unfamiliarity most ecologists have with the interpretation of palaeodata, is also an obstacle to uptake. Finally, the literature is scattered, often in specialist journals, much of it old, and until now has not been reviewed.

I have emphasised in the last section of this paper the use of historical data to inform goals for wetland conservation. Awareness of wetland history, although just one factor in wetland decision making, is vital. Even if past historical states are not regarded as suitable endpoints, the choice of other endpoints should be made with this history in mind.

Finally, now that environmental change is accelerating due to pervasive human influences, the role of wetlands as unique archives of local and regional environmental changes has never been more important (Willis et al. 2007; Froyd & Willis 2008). New techniques (such as molecular and stable isotope studies), new fossils (e.g. testate amoebae) and new statistical approaches to conventional data have transformed the quality of the information and scope of questions that can be asked. Wetlands need preservation as archives, which will, as the science of palaeoenvironmental studies advances, become ever more valuable.

Acknowledgements

I thank Rowan Buxton and James Barringer for assistance with the figures, and members of the Ecosystem Resilience OBI and in particular Janet Wilmshurst and Stephen McNeill for data and discussions on this topic. I am grateful to Anne-Gaelle Ausseil, Bev Clarkson and Colin Meurk for access to their unpublished reports. This research was funded by the Foundation for Research, Science and Technology under contract CO9X0502 (Ecosystem Resilience OBI). I am grateful to Rewi Newnham and an anonymous referee for their supportive review comments, and Mike Winterbourn, the handling editor, for his substantial input to the manuscript.

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Editorial Board member: Mike Winterbourn
Received 1 August 2008; accepted 17 December 2008