

Figure 10. Eastern New Zealand dryland environments by potential vegetation type (Leathwick et al. 2004). Insets show the Central Otago study area (Walker, Lee et al. 2003a, 2004b). A. Detail from Leathwick et al. (2004). B. Woody vegetation zones (Walker, Lee et al. 2003a).

TABLE 6. ESTIMATED PERCENTAGE AREA OF DRYLAND TYPES COVERED BY THE 11 POTENTIAL PRE-SETTLEMENT FOREST VEGETATION TYPES OF LEATHWICK ET AL. (2004) THAT OCCUR IN EASTERN NEW ZEALAND DRYLANDS.

DRYLAND TYPE	2.RIMU / TAWA-KAMAHI	3.KAHIKATEA-PUKATEA-TAWA	4.MATAI-KAHIKATEA-TOTARA	5.KAHIKATEA-MATAI / TAWA-MAHOE	6.MATAI-TOTARA KAHIKATEA-RIMU / MAHOE BROADLEAF-FUCHSIA	7.HALL'S TOTARA / BROADLEAF	11.KAHIKATEA-TOTARA	16.SILVER BEECH	18.MOUNTAIN BEECH-RED BEECH	19.MOUNTAIN BEECH	20.MATAI-TOTARA / BLACK / MOUNTAIN BEECH
A	5	87									
B	49	14		25						3	6
C	6	63	12	9							
D		57	11	16							11
E		2	11	4		9			3	26	34
F		5	67	4	5	4	4			2	5
G		3	15		4	22	2			5	
H			9		10	25		7		6	3
Total	9	11	22	6	4	11	1	2	1	6	7

TABLE 7. ESTIMATED PERCENTAGE AREA OF DRYLAND TYPES COVERED BY 9 OF THE 12 POTENTIAL WOODY VEGETATION ZONES OF WALKER ET AL. (2003A).*

DRYLAND TYPE	TOTAL km ² (% OF TYPE)	I. KANUKA-KOWHAI	II. KOWHAI-KANUKA SAVANNA	III. KOWHAI SAVANNA	IV. KANUKA-KOWHAI-HALL'S TOTARA	V. KOWHAI-HALL'S TOTARA-SNOW TOTARA	VI. KOWHAI-BEECH-LANCEWOOD	VII. BEECH-HALL'S TOTARA-SNOW TOTARA	XI. BEECH-KOWHAI-CABBAGE TREE	XII. MANUKA-MOUNTAIN TOATO-KOWHAI-BEECH
F	95 (1%)								1	
G	3195 (35%)	5	7	6	3	1	7	1	4	1
H	5958 (57%)	3	4	3	10	6	2	14	8	8
Total dryland	9248 (18%)	1	2	2	3	1	2	3	3	2

* The three vegetation zones with no area covered by the dryland types are: VIII. Snow totara-mountain toatoa; IX. Bog pine-snow totara-mountain toatoa; X. Alpine heaths.

5.4 DISCUSSION

Both studies offer persuasive evidence that woody vegetation dominated almost all environments below the treeline, and supplement conclusions based on fossil charcoal and pollen studies (e.g. Molloy et al. 1963; McGlone 2001; Wardle 2001b). Specifically, the study of Leathwick et al. (2004) shows the potential extent of several tall forest types in the dryland zone, based on a conservative estimate of the temperature tolerance of tall forest trees. The study of Walker, Lee et al. (2003a, 2004b) indicates that there are few, if any, environments in the dryland zone that would not potentially support woody vegetation. The latter study provides evidence that a variety of woody communities (shrubland as well as low forest) were potentially widespread in the environmental zone categorised as inimical to tall trees by Leathwick et al. (2004). Because Walker, Lee et al. (2003a, 2004b) targeted New Zealand's most environmentally extreme dryland environments in Central Otago, their conclusions are likely to apply to most other parts of the eastern dryland zone, where environments are less limiting to woody vegetation, but similar compilations of evidence have not yet been carried out. For example, many locations of relict shrubs and low trees are recorded in survey reports from the Protected Natural Area Programme and other field inventories across the driest, most frost-prone and coarse-textured outwash terraces and basin floors of the Mackenzie Basin.

6. Pre-settlement vegetation of dryland environments: a synthesis

6.1 INTRODUCTION

In this section, we draw together understanding from our reviews of (a) pre-settlement disturbance (Section 4) and (b) the likely community structure and composition of pre-settlement vegetation in relation to the environment (Section 5). We firstly suggest the likely place of herbaceous plants in these pre-settlement ecosystems, and secondly describe the likely pattern of vegetation in dryland South Island using seven broad types.

6.2 HERBACEOUS SPECIES IN PRE-SETTLEMENT VEGETATION

In Europe, palaeoecological evidence indicates that closed forest predominated in pre-civilised northern Europe, while forbs and grasses survived in understoreys; localised openings perpetuated by fire, large herbivores, floods

and infertile soils; and chalklands of the continental and Mediterranean zones (Svenning 2002). Human-induced open vegetation in parts of Europe is currently undergoing secondary succession toward a pre-civilisation closed-forest structure, provoking debate on the survival of the herbaceous flora, which has led to renewed efforts to understand the place of herbaceous species in pre-civilised times. Vines (2002) pictured Europe as a shifting patchwork of communities (localised grassy glades, scrub and tall woodland with grass and herb understoreys) that was principally maintained by large grazing animals. It is likely that driest eastern New Zealand was, to some extent, analogous to pre-civilised northern Europe, with avifaunal herbivory being a dominant and ubiquitous form of background disturbance. We do not suggest that the pre-settlement vegetation structure of eastern New Zealand drylands was continuous closed forest and shrubland bereft of herbaceous plants. Rather, we suggest that the rich herbaceous component of dry eastern floras (e.g. Druce 1993) points to a diverse array of pre-settlement microsites for these species. We suggest that these species occupied three major niches: shrubland and forest understories, physiographically stressed ecosystems, and frequently disturbed sites. These are discussed further in the following subsections.

6.2.1. Shrubland and forest understoreys

Understoreys of dry forests and shrublands in pre-settlement eastern New Zealand would have provided habitats for grass and forb species. It is possible that many dry shrubland and forest types were relatively simply tiered, with discontinuous understoreys due to the modifying role of large, herbivorous birds. Dryland environment examples of remaining (albeit highly modified) light-canopied hardwood tree communities contain semi-deciduous and deciduous species such as kowhai (*Sophora microphylla*), narrow-leaved lacebark (*Hoheria angustifolia*), ribbonwood (*Plagianthus regius*), wineberry (*Aristotelia serrata*) and *Olearia hectorii*, which provide relatively brightly lit understoreys. Lateral, or columnar, caged growth forms are common among the divaricate shrubs (e.g. *Coprosma*, *Myrsine*, *Pittosporum* spp.) that were prominent understorey components. We assume that this architectural adaptation defended nutrient-rich leaves borne on internal stems from bird browse (since highly fibrous stems are a physical barrier to access and yield low energetic rewards if ingested by birds) while allowing light to penetrate into the protected centre and lower parts of the shrub (Atkinson & Greenwood 1989; Archibald & Bond 2003), and hence into the understorey. Although eastern dryland forbs and grasses mostly grow in open, human-induced communities today, this does not mean they are obligate or high-light-demanding constituents of open, non-woody vegetation, and many are capable of vegetative and reproduction in semi-shaded woody understoreys (e.g. *Australopyrum calcis* var. *calcis* has been found in the shade of fragmented old-growth shrublands and forests; Molloy 1994). More recently, a perception that the threatened sedges *Carex inopinata* and *Uncinia strictissima* are obligate high-light-demanding species has been challenged by discoveries of them in semi-shaded understoreys of dry South Island hardwood forests and shrubland. In summary, we reiterate that birds probably played a significant role in maintaining relatively high-light understoreys and small glades in pre-settlement forests and woodlands. In this, their role may have been equivalent to that of the large-bodied herbivorous mammals of pre-civilised European forests and woodlands.

6.2.2 More physiographically stressed ecosystems

Presently, there appear no environmental limits, climatic or edaphic (soil-related), to the formation of closed-canopied forest over the great majority of eastern South Island's dry hill-country. Open shrublands dominate the woody relicts across most dry hill-country, but their early successional openness will eventually succeed to closed shrubland or forest as evidenced by the rare, relict stands predominantly in fire-sheltered gullies in the driest zones. For dry forest, we therefore picture bird-maintained open understoreys, with tree recruitment fostered by heteroblasty (different leaf forms between seedlings and adults) and by nurse thickets of divaricating or lianoid shrubs.

If most dry hill-country is potentially tall forest, what and where are physiographically stressed ecosystems that might favour the non-woody flora? We suggest that these were many, diverse, but local in extent. One example is localised areas of thin soils or exposed bedrock on ridges and spurs, gullies, screes and escarpments of alluvial terraces that occur throughout the hill-country, basins and valleys of eastern South Island. Their edaphic stress is from summer drought and / or nutrient impoverishment. Cliffs and their basal talus may be similarly affected, especially ledges and crevices of northern aspects. Other sites experiencing high levels of physiographic stress include those with extreme chemistry (e.g. saline patches and calcium-rich substrates) and standing or ephemeral water-bodies (wetlands). By virtue of reduced competition from woody plants, all these sites today support forb and grass floras. In combined cover, physiographically stressed ecosystems represent a small yet significant proportion of dryland, eastern South Island.

Woodland and treeland have occasionally been suggested as important vegetation units in eastern South Island in pre-settlement times. Atkinson (1985) defined treeland as vegetation in which trees form a discontinuous canopy above a lower canopy of predominantly non-woody vegetation or bare ground. The concept therefore embodies an incomplete or non-closed tree and / or shrub canopy. This could result from a density-dependent open spacing of tree stems imposed by environmental stress. In interior basins, the driest parts of the more arid, alluvial terrace, fan and glacial outwash plain ecosystem with stony pavement substrates may have shown a density-dependent, open spacing of shrubs and low trees in late successional vegetation, owing to root zone competition extending well beyond the maximum canopy dimensions of the individual shrubs. Another candidate is the stoniest soils of alluvial plains—today, non-woody species account for over 80% of the species in relict communities of open *Kunzea ericoides* woodland at Eyrewell and Bankside on the Canterbury Plains (N. Head, pers. comm.).

6.2.3 Frequently disturbed sites

Early successional communities rich in disturbance-exploiting forbs and grasses are fostered on: braided riverbeds; riparian flood zones; coastal dunes; coastal littoral zones; margins of fluctuating (ephemeral) wetlands; the fetch zone of water-bodies such as kettles, tarns and lakes; rock-fall sites on cliffs; and screes and talus. Natural fire of sufficient frequency and / or extent also promoted early successional forbs and grasses, particularly after c. 2500 y BP on Otago's montane peneplains and on drier intermontane basins.

6.3 PRE-SETTLEMENT VEGETATION TYPES

Drawing on the reconstructions of pre-settlement vegetation (Walker, Lee et al. 2003a, 2004c; Leathwick et al. 2004, section 5), our classification of dryland environments (Section 3), and our field knowledge of relict vegetation, we propose seven broad vegetation types for pre-settlement dryland South Island.

6.3.1 Dry angiosperm shrubland-low forest

We prefer the prefix 'dry' for the shrubland associations of eastern New Zealand drylands, since the commonly used epithet 'grey' applies physiognomically to a small subset of these diverse communities that occur throughout the entire rainfall gradient. Their chief components are described below.

The coldest and driest basins and valleys were beyond the limits of tall trees (Leathwick 2001) but a rich array of shrubs and low trees dominated the shrubland and treeland there (for Otago see Walker, Lee et al. 2003a). Chief among them are *Olearia lineata*, *O. odorata*, *O.* unnamed (Canterbury Plains), kanuka (*Kunzea ericoides*), *Carmichaelia* spp., small-leaved *Coprosma* spp., *Aristotelia fruticosa*, matagouri (*Discaria toumatou*), *Sophora prostrata*, *Phormium cookianum*, *Ozothamnus leptophylla*, *Melicytus* spp., *Pimelea* spp., *Corokia cotoneaster*, *Hebe cupressoides*, and lianes such as *Carmichaelia kirkii*, *Clematis* spp., *Calystegia tuguriorum*, *Convolvulus* spp., *Muehlenbeckia* spp., and *Rubus* spp. Large-grained Poaceae (*Chionochloa* type) pollens are present at very low levels in pollen cores from the dry interior (Figs 3–5; McGlone & Moar 1998; McGlone 2001). This suggests that *Chionochloa* tussocks were relatively unimportant in the driest environments, with the exception of *C. rubra*, which occupied the dampest soils. Short-tussocks and other dryland grasses (see below) were also important. The extant flora also includes a rich array of forbs, including *Raoulia* spp., *Leptinella* spp., *Lepidium* spp., *Gingidia* spp., *Einaridia* spp., *Galium* spp., *Acaena* spp., and *Stellaria* spp.

Compositional variation was likely to be high, judging by relict communities, which are themselves fire-filtered, depauperate remnants of the original mixes (Walker, Lee et al. 2003a). Several factors drove wide compositional variation: large herbivorous birds (the chief mechanical disturbance agent); edaphic (soil-related) variations in fertility and moisture; atmospheric humidity and cold-air inversion; and riverine disturbance. Natural fire also played a role (McGlone & Moar 1998).

6.3.2 Dry conifer shrubland-low forest

This is included as a further discrete shrubland-low-forest community adapted to a particular fertility subset of intermontane valleys and basins. On low-fertility, glacio-fluvial outwash terraces, various mixes of mountain toatoa and bog pine (*Halocarpus bidwillii*) shrubland or low forest dominated. Extant examples are scattered through the basins, including Enys Scientific Reserve in Castlehill Basin and Quail Burn, Ben Dhu and Gladstone Stream in the Mackenzie Basin. Pollen diagrams attest to their historical significance in intermontane basins in the driest interior (McGlone & Moar 1998; McGlone 2001). Several other dryland shrubs co-occur at low frequency.

6.3.3 Dry hardwood forest

A hardwood forest of varying composition extended beyond the moisture-deficit tolerances of *Nothofagus* forest in dryland hill-country. Because the fertility, moisture and depth of dry hill-country soils exceed the tolerances of tall podocarps, these forests were dominated by drought-tolerant hardwood trees. Hall's totara was probably the main podocarp, although scattered matai were likely. Hardwood trees of the dryland zone included in the predictions of Leathwick (2001, 2004) include pokaka (*Elaeocarpus bookerianus*), broadleaf, *Pittosporum eugenioides* and *Melicytus ramiflorus*. To these, we can add several tree species that are frequently relicts, namely narrow-leaved lacebark, lacebark (*H. populnea*), ribbonwood, kowhai, *Myrsine australis*, ti kouka (*Cordyline australis*), kanuka, kohuhu (*Pittosporum tenuifolium*), *Melicope simplex*, fierce lancewood (*Pseudopanax ferox*), *Olearia paniculata* and *O. fragrantissima*. There are many relict stands of this community, where kanuka, broadleaf, narrow-leaved lacebark and ribbonwood predominate. Relatively drought-tolerant shrubs, grasses and forbs formed diverse understoreys and dominated more-open clearings on thin-soil sites (see dry angiosperm shrub for composition).

6.3.4 Dry conifer forest

Reconstructions from subfossil pollen and logs (Beattie 1947; Molloy et al. 1963; Hall-Jones 1992; McGlone 2001) provide strong evidence for an extensive drought-tolerant upland conifer forest dominated by Hall's totara and mountain toatoa. Leathwick et al. (2004) (Fig. 10) predicted a widespread upland, dryland forest type of Hall's totara and broadleaf (Community 7), which we see as broadly equivalent of our dry conifer forest type (we note that mountain toatoa was not included in the data underlying the Leathwick et al. reconstruction). We suggest that dry conifer forest occupied similar hill-country topography to dry *Nothofagus* forest, but extended beyond the moisture deficit limitations of *Nothofagus*, as well as areas beyond its post-glacial spread. Accordingly, western inland Marlborough supported *Nothofagus* forest, whereas the driest central-eastern interior was dominated by conifer forest (Basher 1990; McGlone & Basher 1995). It was extensive in the dry interior of Otago (Burrell 1965; Wells 1972; Walker, Lee et al. 2003a) and in western Canterbury's hill-country (Burrows et al. 1993).

6.3.5 Dry *Nothofagus* forest

Nothofagus was still undergoing its post-glacial expansion into potentially suitable southern dryland environments when humans arrived, and it is often not clear today where it was time, and where it was climate, that limited its spread. Extant stands and predictive models of tree species distributions (Wardle 1984, 2001a, b; Leathwick 2001; Walker, Lee et al. 2003a; Leathwick et al. 2004) indicate there were extensive stands of beech (both *N. solandri* and *N. menziesii*)-dominated forests along the eastern flanks of the Main Divide that extended into the dryland zone. Leathwick et al. (2004) (Fig. 10) predicted widespread cover of two *Nothofagus* forest types: mountain beech and mountain beech with matai and totara in dryland South Island. Those stands of mountain beech that remain in eastern New Zealand drylands typically have

monospecific canopies and depauperate understoreys (Wardle 1984), while more diverse canopies and understoreys are typical of the mesic (wetter) *Nothofagus* forests that occur further west.

6.3.6 Tall podocarp forest

Higher-fertility alluvial and colluvial toeslopes and floodplains supported tall podocarp forest, principally matai-kahikatea-totara forest (Fig. 10) (Community 4 of Leathwick et al. 2004). This community had its greatest expression on the Canterbury Plains but would have included the lower Wairau Valley of Marlborough, the Hurunui and other North Canterbury basins, the lower Waitaki Valley, and isolated pockets through Central Otago. Insight into its community composition comes from Putaringamotu-Riccarton Bush (Molloy 1995). Matai, kahikatea and totara dominated the canopy or emergent tier. Kahikatea were dominant on the poorly drained, gleyed soils, while matai and totara dominated well-drained soils. Miro (*Prumnopitys ferruginea*) was also important, but rimu was probably less so because of its comparative drought intolerance. A rich array of hardwood trees complemented the canopy, the diversity of which declined southward.

Floodplains are characterised by subtle variations in relief that produce striking edaphic and vegetation composition changes; forest composition is often largely also determined by patterns of hydrology and frost. The community composition of floodplain forests is therefore often more complex than that on hillslopes, making it more difficult to generalise a summary reconstruction here. However, we suggest that oxbows, flood channels and winter-water-ponding depressions behind levees supported low hardwood forest and shrubland usually bereft of podocarps. One derivative of the wide soil variations that influenced tall podocarp forest is kanuka forest or woodland on recent stony soils (Cox & Mead 1963). However, the few relict examples of this community are early successional, showing high forb and grass diversity in the understorey (e.g. Eyrewell, Medbury, Culverden).

6.3.7 Grassland

Pre-settlement grassland in the eastern dryland zone was an early successional feature, which followed, for example, very occasional local fires or floodplain disturbances. In general, where seral grassland established, it was subsequently rapidly reduced as shrubs and trees re-asserted dominance, spreading from abundant surrounding seed sources. For example, rare coincidences in pollen diagrams between charcoal peaks and Poaceae peaks suggest that non-*Chionochloa* grasses temporarily expanded then contracted in response to infrequent natural fires (average intervals > 1500 y) over the Holocene. We expect that the short tussocks hard tussock (*Festuca novae-zelandiae*), silver tussock (*Poa cita*) blue tussock (*P. colensoi*), and brittle tussock (*Rytidosperma setifolia*) were major components of the seral grasslands of floodplains, and of the rare early successional grasslands that followed fire.

Grasses were certainly present as a more-or-less stable component of the vegetation across the eastern dryland zone, for example on peneplain landforms (such as near Clarks Junction; McGlone 2001) and on lower hillslopes and basin floors (e.g. Duncan Stream and Idaburn Valley; McGlone & Moar 1998; McGlone et al.

2001). Similarly, *Chionochloa* grasses were certainly important within shrub-tussockland or tussock-shrubland above the treeline (i.e. largely outside the dryland zone). In section 6.2, we suggested that in the dryland zone, as above treeline, grasses occurred as locally important floristic components in a range of stressed ecosystems, and as ground cover components of light-canopied dryland forest. In non-forest habitats and woody understoreys, dryland grasses probably included *Ryttidosperma* spp., *Elymus* spp., *Dichelachne* spp., *Puccinellia* spp., *Deyeuxia* spp., *Microlaena* spp., *Australopyrum calcis*, *Echinopogon ovatus*, *Simplicia laxa* and *Achnatherum petriei*.

Pre-settlement dryland grassland (in the sense of areas continuously dominated by Poaceae with few woody plants) was a rare, disturbance-dependent feature of drylands. Today's grasslands are artificial analogues of the pre-settlement grassland condition because fire has differentially removed competing woody plants, and domestic stock have replaced browsing and grazing birds.

6.3.8 Intergrades

Compositional consistency characterises some of these proposed communities such as in mountain beech forest and Hall's totara-mountain totoa forest. However, because each species responds uniquely to environmental factors that determine pattern, species associations will vary continuously across the landscape. Accordingly, community composition, which is a human construct, varies, and gradations between communities are always evident in extensive, continuous forest and shrubland.

6.4 ANTHROPOGENIC DEFORESTATION

The arrival of Polynesians in New Zealand ushered in a phase of deforestation fires unprecedented in the Holocene (McGlone 1983; McGlone et al. 1994). Possible reasons for the early fires include Maori improving access for rock prospecting, hunting, navigation and travel, with the first the strongest reason for fire in the initial phase of coastal settlement, Forest clearance for the defence of settlements became important later. Various sources of evidence suggest that fires began 800–550 y BP and that clearance was rapid and comprehensive (McGlone 2001). Fire frequency and magnitude appear not to have been related to human population density (McGlone & Wilmschurst 1999); vast, virtually uninhabited areas of vegetation were burned in both the North Island and South Island (Rogers & McGlone 1989; McGlone & Basher 1995). Information on the rate of vegetation clearance by fire at a regional scale is relatively scarce. In the Moawhango Ecological District of the central North Island, there is evidence for just two regional conflagrations (550–430 y BP), which removed much of the primary forest cover (Rogers 1987) across a region 40 km by 30 km. Because transiting Maori repeatedly fired woody regrowth, secondary fires were frequent, perhaps more than one per decade (M. McGlone, pers. comm.). These fires probably caused little change in the pattern of the relict forest created by the initial conflagrations because fuel loads in the secondary vegetation were low (Rogers 1987). So complete was the loss of New Zealand's rain-shadow or eastern forests that regional climates may have become more summer dry, with lower annual precipitation due to the loss of convective rainfall.

7. Changes in disturbance regimes

Human settlement of New Zealand cannot have changed the disturbance effects of vulcanism, tectonic-seismic processes and extreme weather events such as snow break, hailstorms and windthrow. However, there may have been significant changes in other disturbances, as detailed below.

7.1 LANDSLIDE, FLOODING AND SEDIMENTATION

In naturally vegetated catchments in New Zealand, most landsliding and sediment production is related to parent material, tectonic uplift and rainfall intensity. Deforestation by humans can substantially increase the frequency and intensity of flood events in fluvial systems, and substantially increase gully erosion (Trustrum et al. 1999). In upland catchments, vegetation clearance probably also increased the frequency and magnitude of landslide events. Overall, the loss of forest from fires lit by the first Polynesians increased storm-water erosion, as cleared forest soils adjusted to loss of tree-root strength and soil cohesion. Siltation of the lowlands correspondingly increased.

A second peak in soil erosion rates occurred with the arrival of European pastoralists who increased the frequency of fire and commenced sheep grazing, greatly reducing vegetation cover. McSaveney & Whitehouse (1989) showed that sheet erosion is more than 10 times greater from bare soils than from those with intact tussock, scrub or scree cover. In dry Central Otago, topsoil erosion in the European era has locally redistributed A-horizons from exposed sites to leeward sites (Hewitt 1986).

Today, alluvial floodplains are most at risk of flooding at the point where rivers disgorge from their mountain catchments and in their coastal deltas. Although peak flows have been intensified by forest clearance in the upper reaches of catchments since human settlement, the containment of rivers with stopbanks and dams has regulated peak flows and somewhat mitigated this effect. Nevertheless, in flood-prone riparian areas, flooding and sedimentation remain key ecosystem disturbance processes in eastern New Zealand drylands, furnishing fresh substrates that rejuvenate soil fertility, redistributing organic matter and stimulating plant regeneration.

7.2 AOLIAN

Since European settlement, many New Zealand dune systems have undergone stabilisation through the establishment of introduced sand-binding plants and the area of naturally unstable sand has substantially reduced (Hilton et al. 2000). This has modified the natural dynamic of sandy coasts, and many early successional plants of sand hollows are consequently threatened (Johnson & Rogers 2002).

7.3 FIRE

Fire first became a significant anthropogenic disturbance factor in New Zealand following human settlement (Molloy et al. 1963; McGlone 1983; Basher 1990; Ogden et al. 1998). Over 750 years, it has progressively promoted a somewhat less fire sensitive grass-and-forb vegetation and flora over woody vegetation and its flora. Little of the study area is untouched by anthropogenic fire; relict forests with old-growth structures (including cliffs) now occupy only 1.1% of those areas in the South Island that we classify as drylands, and Wilson (2002) estimated that 0.8% has remained unburned on Banks Peninsula since the arrival of humans.

A very few woody species have increased their range since the destruction of old-growth shrubland and forest by anthropogenic fires. For example, although kanuka and matagouri are fire-sensitive, they are exceptional in the native woody flora for their ability to invade disturbed sites relatively rapidly, and to function as early successional species (Allen et al. 1992). Applications of farm fertiliser has probably also fostered the spread of matagouri in some areas. However, the majority of woody species have virtually disappeared from their former extensive dryland ranges, probably because they had limited ability to recover from fire, and because seed sources were destroyed by intense conflagrations in the early years of human settlement (Walker, Lee et al. 2003a).

Topography and rainfall appear to have affected the pattern of clearance of dry forest and shrubland by anthropogenic fire, and the subsequent response of seral species in eastern New Zealand drylands. In the dry, gently sloping intermontane basins and piedmont floodplains of the driest interior basins, woody vegetation rarely survived initial conflagrations. Virtually all woody vegetation was eliminated from the summer-dry mountains of the interior (e.g. Arrowsmith Range) (Burrows et al. 1993) and the dry floodplains. Only on the steepest relief in the most broken catchments of the dry mountains have small and often secondary relicts survived. Thus, a few forest remnants survive in steep, shady sites, particularly in North Otago and North Canterbury, and across eastern Marlborough.

Today, the frequency of fire in eastern New Zealand drylands is relatively low, because biomass is depleted relative to pre-settlement and early European states at low elevations, and hence fuel loads are modest. Moreover, land uses such as viticulture, horticulture and lifestyle blocks are progressively replacing traditional pastoralism at low altitudes, and there is an increasing social resistance to the use of fire as a land management tool. The incidence of accidental burns on land managed for nature conservation across New Zealand is also quite low: between 1987 and 1998, fires on land administered by DOC covered 28 000 ha in 2000 fires (R. McColl, pers. comm. 2002). This equates to a yearly average of 143 fires, each of which burned 14 ha on average (i.e. 2333 ha/y).

7.4 SEABIRD PERTURBATION

Millions of burrow-nesting petrels were eliminated from sites on the New Zealand mainland at the time of human colonisation (McGlone et al. 1994; Worthy & Holdaway 2002). This substantially reduced the extent and intensity of local soil perturbation on escarpments, spurs and ridges that afforded topography

suitable for bird take-off and on relatively deep soils for burrowing across much of the lowland and montane land area of the eastern New Zealand dryland zone. In addition, nutrient enrichment regimes and the biogeochemistry of waters downstream of former colonies have probably been considerably altered (Hawke & Holdaway 2003). Little is known of the effects of these changes on the indigenous inland vegetation. The loss of both seabirds and marine mammals from the coastal zone may be a factor in the decline of six threatened indigenous herbaceous plants in the *Lepidium* genus (Norton et al. 1997).

7.5 HERBIVORY

Selective consumption by herbivores, and their mode of feeding can accelerate, slow or fundamentally alter the course of vegetation succession (Connell & Slatyer 1977; Bond et al. 2004). Different modes of herbivory act as very different selection filters in a flora, and result in considerably different vegetation structure and composition (Caughley 1989; Bond et al. 2004). Adaptations to browsing incur resource costs, and a change in a herbivory regime may disadvantage plants that have evolved browse-resistance and confer advantages on more browse-sensitive or non-adapted species (e.g. McGlone 1989). In New Zealand, a c. 500-year period of very low levels of herbivory followed Polynesian fires. Thereafter, a suite of domestic and feral grazing and browsing mammals were introduced (including deer, possums, goats, rabbits, pigs, hares and sheep). Also since that time, a limited suite of self- or human-introduced bird herbivores (finches, ducks, geese, rooks and rosellas) have been substituted for the exceptionally diverse pre-settlement herbivorous fauna.

The fundamental changes occurring in herbivore assemblages since human settlement have probably altered successional pathways and trajectories in dryland vegetation, just as they have in forest communities (Coomes et al. 2003). Therefore, inevitably, surviving woody vegetation, and future compositions of seral woody communities, will differ from pre-settlement compositions. Between Polynesian and European settlement, it seems likely that, among the woody elements that survived fires, broadleaved species would have enjoyed an advantage over divaricate species in forest relicts protected from fire and in secondary woody successions between fires. Mammalian herbivores then ushered in a new phase of herbivory, exerting different pressure upon plants and propagules from that of indigenous herbivorous birds (Caughley 1989). We note that the early years of exploitative pastoralism were marked by a combination of frequent clearance fires and intense mammalian grazing (exceptionally high stocking rates, followed by plagues of rabbits). The synergistic combination of the two novel disturbance types led to unparalleled transformations in the flora and fauna (Mather 1982). In the few surviving relicts of primary or secondary woody vegetation, mammalian herbivory ended a brief period of advantage for palatable broadleaved shrubs and trees, and variously affected bird-adapted species, depending on how well their particular suite of bird-browse adaptations equipped them for mammalian browsing.

Today's seral woody communities are dominated by browse-tolerant or browse-avoiding species such as kanuka, manuka, matagouri, small-leaved coprosmas, *Melicytus* spp., *Ozothamnus leptophyllus*, *Muehlenbeckia* spp., *Rubus* spp. and mountain toatoa. For instance, kanuka has regenerated to form extensive

woodlands in the presence of grazing mammals and a 60-year absence of fire at Bendigo in Central Otago, but browse-intolerant shrubs are restricted to inaccessible rock outcrops (see also Allen et al. 1992). Consequently, the full woody potential of grazed drylands is not realised. For instance, Walker, Wilson et al. (2003) showed significant decreases, both in relict tussock and *Carmichaelia petriei* shrubs with grazing in an Otago short-tussock grassland (of *Festuca novae-zelandiae*) over 12 years. There are many examples where late successional trees such as mountain totara are reduced to individuals on fire-deflecting rock outcrops. Such trees often have little prospect for recruitment in the surrounding grassland, because they may be browse-sensitive or require a shrub nurse for establishment. Overall, the browse-sensitivity of dryland shrubs and trees is a complex issue in terms of herbivore species, their density, land use history, and community composition that is beyond the scope of this review.

Dryland vegetation has also been affected by the spread of carnivorous mammals since human settlement. Predation by rats, mice, cats, stoats and ferrets has eliminated or reduced populations of many animal species with roles in ecosystem processes (including lizards and large invertebrates such as weta); many of these species are now confined to disjunct, relict distributions. Campbell & Atkinson (2002) showed that on northern nearshore islands, present forest composition differs significantly from that of forests before rats (*Rattus* spp.) were present. They suggested that rats have probably substantially altered the composition of mainland forests by reducing populations of certain tree species through seed consumption, and that they have indirectly affected birds such as kiwi through consumption of some invertebrates. Arboreal geckos are abundant on rat-free nearshore islands, and the collapse or elimination of their populations on the mainland through predation by rats, cats and mustelids will have altered pollination and seed dispersal processes, and hence changed the population dynamics of trees and other plants (Worthy & Holdaway 2002).

Current mammalian herbivory may have significant flow-on and feedback effects for mammalian pests and dryland biodiversity (Ruscoe et al. in press). For instance, it appears that sheep grazing promotes open vegetation through limiting woody recruitment, which in turn limits litter accumulation and soil-moisture retention and transfers nutrients out of the ecosystem. These changes in turn create conditions favourable for an increase in rabbit numbers, which not only impose additional limitations on the recruitment of woody species, but also determine numbers of predators such as cats and ferrets, with adverse consequences for already reduced native lizard populations.

7.6 A GRASS BIOME

While our understanding of the biome (or ecological community) transformation that has accompanied human settlement is increasing (McGlone 2001), it is difficult to separate the respective influences of fire and mammalian herbivory in the latter phase of the process. It is clear that the transformation process had two phases. The first phase of fire selected for more fire-tolerant grass and herb species and grassland vegetation over the fire-intolerant woody plants and vegetation. Repeated fire was the principal limitation on the progress of secondary succession to woody plants, since levels of herbivory

were probably lower than at any earlier time in evolutionary history. The second phase, associated with European pastoralism, involved a further check to the competitive re-expression of shrubs and trees over grasses and progressively degraded the secondary grasslands to mixed exotic-indigenous communities.

The spread of tall tussocks onto previously forested soils of eastern New Zealand also occurred in two stages. Pollen diagrams from the interior indicate an initial rise in grass pollen of non-*Chionochloa* grasses, representing among others *Festuca*, *Poa*, *Rytidosperma*, *Dichelachne* and *Elymus* grasses. Percentages of larger pollen types (like *Chionochloa*) peaked somewhat later, although their expansion was probably advanced by the time of European settlement (McGlone 2001). There was probably an elevational and therefore climatic / edaphic separation on the relative successional performance of the two grass types. *Chionochloa* grasses principally rose to dominate all elevations in humid zones but were limited to montane areas in the driest interior. The smaller grasses rose to dominate the driest lowlands, but across dryland South Island this pattern is now culturally modified.

8. Rare plants' ecosystems and pre- and post-settlement disturbances

8.1 INTRODUCTION

The latest environmental modelling techniques and tools have proved effective for mapping broad-scale patterns, but they are less usefully applied to the prediction of landform-driven, small-scale changes in edaphic patterns, because that detail is not yet incorporated in digital databases. Several non-forest ecosystems are defined by environmental factors that are not available as mapped surfaces, or occur at smaller spatial scales than present digital data support. These non-forest ecosystems include the inland saline ecosystem (Rogers et al. 2000), coastal dunes (Hilton et al. 2000), coastal turfs (Rogers 1999), cliffs (especially limestone), permanent wetlands, turfs of ephemeral wetlands (Johnson & Rogers 2002) and hydrothermal sites. These are regulated by extremes of hydrology, geochemistry, disturbance and topography, rather than by the climate and soil parameters used in the national environmental classification (LENZ).

In this section, we list the ecosystems of dry eastern New Zealand. These are preliminary, subjective ecosystem categories that complement and supplement our LENZ-based dryland classification. We then list threatened and data-deficient plants (hereafter, for convenience, simply 'rare plants') that occur in each ecosystem category, and consider whether they are disturbance dependent. We discuss the disturbance regimes that applied to each ecosystem and its flora before and after human settlement. We also consider, in the broadest terms only, the life-history strategies of different rare plants, and whether these appear to confer early or late successional fitness in relation to disturbance.

8.2 METHODS

We listed 18 ecosystem categories based on the physiography of dry eastern New Zealand (after Rogers & Walker 2002). We then compiled a list of rare plants that occur in the 18 ecosystem classes. This list includes 227 threatened plants in the New Zealand Threat Classification System list (Hitchmough 2002). We included a further eight plants that are categorised as data deficient or taxonomically indeterminate, or that are diseased: *Brachyscome* (b) (CHR 518295; Pareora River); *Colobanthus* (a) (CHR 515133; Pareora River); *Colobanthus* 'Tengawai'; cabbage tree (*Cordyline australis*); *Hebe pimeleoides* var. *glauco-caerula* (J.B. Armstr.) Cockayne et Allan (CHR 462377); *Hydrocotyle pterocarpa* F. Muell.; *Ileostylus micranthus* (Hook. f.) Tiegh.; and *Stackhousia minima* Hook. f. In a few instances, listed species occur outside the geographical limits of our defined eastern dryland zone, but occupy drought-prone habitats such as coastal sands and inland and coastal cliffs within more mesic matrix ecosystems. Each of the 235 listed species was allocated to one of the 18 ecosystem categories of Rogers & Walker (2002). We then examined the spatial extent and magnitude of impact of the various disturbances across the 18 ecosystem classes.

8.3 RESULTS

8.3.1 Ecosystems of dryland rare plants

The 244 rare plants (Table 8) of eastern South Island drylands represent a large portion (25%) of the approximately 1000 New Zealand plants in those categories of the threat classification system (Hitchmough 2002). The distribution of rare plants across the different types of South Island dryland ecosystems is strongly skewed (Table 8). At the higher level of ecosystem classification (i.e. ecosystem groups), inland non-forest ecosystems (excluding wetlands) have the highest proportions of rare plants, followed by non-forest coastal ecosystems and wetlands. High numbers of rare plants occur in the inland cliff and talus ecosystem, and in the alluvial terrace, fan and outwash basin ecosystem. These plants also occur frequently in the dry hill-country ecosystem and coastal cliff, talus and terraced headland ecosystem. This pattern of distribution of rare plants across ecosystem groups is very similar to that of the entire rare flora of New Zealand (Rogers & Walker 2002), i.e. non-forest ecosystems support a high proportion of rare plants, of which the majority occur in coastal and inland cliff habitats.

8.3.2 Disturbance of dry alluvial terraces, fans and basin floors; wet / dry frosty hollows; and dry hill-country

The first three inland ecosystem classes—(1) dry alluvial terrace, fan and outwash basin floor, (2) dry hill-country and (3) wet / dry frosty hollow—on alluvial floodplains and terraces are considered together because they form a functionally integrated mosaic of landforms and account for much of the dry eastern New Zealand environment. Ninety-nine (41%) rare plants occur within at least one of these three ecosystems (Table 8). In pre-settlement times, scree-creep, flooding

and sedimentation and natural fire were local disturbances (Table 9). In hill-country areas with steeper relief, landslide, snow break, windthrow and seabird bioturbation were further disturbances. On alluvial floodplains, gravel, sand and silt deposition on riparian terraces was the dominant disturbance. Wet / dry and frosty hollows within alluvial floodplain ecosystems support a distinct woody flora, where tall trees are less competitive, and low trees and shrubs adapted to flood disturbance and winter water-ponding and frost predominate. Because all of these disturbances were limited in spatial extent and severity, they resulted in mainly small patches of secondary succession within the dominant forest and shrubland. Primary successions were generated only on the denuded surfaces of landslides in hill-country or on the deepest floodplain alluvium. Bioturbation and herbivory processes did not, in themselves, create primary or secondary vegetation. At any

TABLE 8. FREQUENCY OF RARE PLANTS (AFTER HITCHMOUGH 2002)* OF DRY EASTERN SOUTH ISLAND BY ECOSYSTEM TYPE† AND PLANT TYPE.

The sum of total plants (last row) in ecosystems exceeds 244 because some taxa are categorised as occupying more than one ecosystem (see Appendix 4).

ECOSYSTEM	DTOF	DHC	W/DH	CT	BR	ISE	HT	LZEW	MIRE	SW	AQM	F/S	R/SB	CCLTH	SGB	CDHSP	CD	EL
Fern	2	2																
Psilopsid, lycoid or or quillwort		1																
Non-composite dicotyledonous herb	17	8	5	27	1	4		12	2	2		1	2	14	4	5		3
Composite dicotyledonous herb	15	3	1	4	1			4					3	6	1	3		
Dicotyledonous tree or shrub	17	18	4	26	1							1	1	9	1	4		
Dicotyledonous liane	6	4	1												1	1		
Grass	5	4		12		1		2						6	1			2
Sedge	6	2		2				6	2	2		1	2	1		1	1	1
Rush or allied plant	1			1	1			1							1	1		
Orchid	2	1							1									
Other mono- cotyledonous herb sedge, rush and allied plant	2	2		1				1	1			1						
Monocotyledonous tree or shrub		1								1								
Total rare plants in ecosystem (244 total)	71	46	11	75	4	5	0	26	6	5	0	4	8	36	9	15	1	6

* No gymnosperm trees or shrubs or monocotyledonous lianes were found in the ecosystem types.

† Abbreviations used for ecosystem types are: DTOF = dry, alluvial terrace, fan, and outwash basin floor; DHC = dry hill-country; W / DH = wet / dry frosty hollow on alluvial floodplains and terraces; CT = cliff and talus; BR = braided riverbed; ISE = inland saline ecosystem; HT = hydrothermal; LZEW = littoral zone of ephemeral wetland; SW = swamp; AQM = aquatic macrophyte; F / S = flush / seepage; R / SB = river and stream bank; CCLTH = coastal cliff, talus, and terraced headland, SGB = sand and gravel beach; CDHSP = coastal dune hollow and sand plain; CD = coastal dune; EL = estuary and lagoon.

one time, primary and secondary vegetation generated by disturbance was concentrated either throughout the riparian margins of gullies, streams and rivers in the uplands; along oxbows and meandering channels of flood-prone parts of alluvial floodplains; or on hill-country landslide scars and about wind-exposed ridges and spurs.

The spatial extent, frequency and magnitude of the post-human settlement disturbance regime are different from that of pre-settlement times.

- Landsliding has probably increased as a result of land clearance in steep, soft rock country but not in other more cohesive substrates.
- The incidence of snow break, hailstorm and windthrow disturbance has dramatically declined since the large-scale clearances of forest by fire. Soil disturbance in the form of root-plate rejuvenation of soil surfaces on exposed topography has also been lost as a consequence. Although vegetation clearance has increased the magnitude of storm-water runoff, flood containment by dams and stopbanks has dramatically reduced the

TABLE 9. SPATIAL EXTENT AND MAGNITUDE OF IMPACT OF TYPES OF PRE-SETTLEMENT DISTURBANCE WITHIN ECOSYSTEM CLASSES IN DRY EASTERN SOUTH ISLAND.

Disturbance effects are classed as: 1, local-minor; 2, local-major; 3, widespread-minor; 4, widespread-major.

Symbols indicate post-settlement changes in each disturbance: -, now absent; >, increased; <, reduced; =, equivalent.

DISTURBANCE	LAND-SLIDE	SCREE-CREEP	FLOODING & SEDIMENTATION	SNOWBEAK, HAILSTORM, WINDTHROW	TRANS-GRESSIVE SAND MVMT.	NATURAL FIRE	SEABIRD BIOTURBATION	HERB-IVORY
NO. ECOSYSTEM TYPE								
1 Dry, stony, alluvial terrace, fan and basin floor *		1 =	3 =		2 <	2 <		3 >
2 Dry hill-country †	2 >	1 =	1 >	1 <		2 <	2 -	3 >
3 Wet / dry frosty hollow on alluvial floodplains and terraces ‡			3 <	1 <		2 <		3 >
4 Inland cliff and talus	2 =	1 =		1 <		2 -	1 -	3 >
5 Braided riverbed	1 >	1 =	4 >		2 -	1 <		3 =
6 Inland saline ecosystem						1 -		3 >
8 Littoral zone of ephemeral wetland			1 <			1 <		3 >
9 Mire	1 =					1 <		3 =
10 Swamp	1 =		1 <			1 <		3 >
11 Aquatic (macrophyte)			2 <					3 >
12 Flush / seepage	1 =	1 =				1 <		3 >
13 River and stream bank	1 =	1 =	4 >					3 >
14 Coastal cliff, talus and terraced headland	2 >	1 =		1 <		2 <	2 -	3 >
15 Sand-and-gravel beach								3 >
16 Coastal dune hollow and sand plain					2 <			3 >
17 Coastal dune					2 <	1 <	2 -	3 >
18 Estuary and lagoon			2 >			1 <	2 -	3 >

* Originally diverse shrubland with grass-and-forb understoreys and glades.

† Originally conifer-hardwood or *Notbofagus* forest with shrubland and grassland glades.

‡ Meanders and oxbows producing light gaps and margins to forest.

frequency of flooding disturbance of the riparian terrace zone. Soil erosion from storm-water and drying winds on hill-country probably had two peaks, one corresponding to the period following the arrival of Maori, and the second following the commencement of European pastoralism. However, in the intervening and subsequent periods there is little evidence for substantial erosion as vegetation was transformed and recovered from the initial clearances (Whitehouse 1978, 1980).

- Fire frequency substantially increased following human settlement, depleting the pools of volatile nutrients for soils and plants, the vegetation biomass, and reducing the natural ranges of plants and animals.
- Seabird bioturbation has all but disappeared, and vertebrate herbivory modes have profoundly changed, as farm stock, lagomorphs and feral ungulates have replaced birds and reptiles.

The frequency of threatened and data-deficient plants varies across these three ecosystem types (Table 8). Rare herbaceous species are concentrated in the dry alluvial terrace and fan ecosystem, although they are also relatively common in the dry hill-country ecosystem (Table 8). Thirty-five rare trees and shrubs occur with more-or-less equal frequency in these two ecosystems. In contrast, few rare grasses occupy this ecosystem group.

8.3.3 Disturbance of inland cliffs and talus

The pre-settlement disturbance regime of the inland cliff and talus ecosystem differed from that of its surrounding hill-country and alluvial terrace landforms (Table 8). Only the talus zone of cliffs may be exposed to flooding and sedimentation. Landsliding or rock-avalanching was regulated by seismic activity and rock cohesion (the former is important only in the greywacke mountains with high uplift rates and is determined by the cohesion of the rock). Cliffs of massive sandstone, limestone and schist were extremely stable, whereas the less cohesive greywacke was more prone to rock avalanches. However, across all substrate types, the main disturbance agent appeared to be the fretting of cliff faces. Fretting produced patches of slowly accumulating blocky talus or, more commonly, the build-up of finer-grained sediment at the cliff base. Water erosion, solution weathering (of calcareous substrates) and roosting and nesting birds constituted constant, ubiquitous background ecosystem processes that allowed soil to accumulate only on the convex creepslope, ledges, crevices and fringing toeslopes. Natural fire and herbivory were minor because of relatively low vegetation biomass and inaccessibility, respectively.

Since the arrival of humans, introduced mammalian herbivores have been able to gain access to greater areas of steep topography than did pre-settlement bipedal birds. Moreover, fringing vegetation has been cleared, and the vegetation of cliffs and talus is no longer buffered from extreme weather events. Therefore, seasonal extremes of humidity have replaced more equable microclimates, soils have been eroded by increased storm-water and wind ablation, and exfoliation of rock surfaces has probably increased with greater exposure to frost. We therefore expect that erosion has increased overall in the inland cliff and talus ecosystem.

The inland cliff and talus ecosystem supports the largest group of threatened plant species in the dryland zone. Since cliffs and talus provide natural refuges from fire, we cannot discount the possibility that some of the species now restricted to this ecosystem were more widespread prior to human settlement. Certainly, many are highly palatable and / or fire-sensitive. The present-day rare flora of the inland cliff and talus ecosystem consists mainly of non-composite herbs, dicotyledonous trees and shrubs and several grasses (Table 8). Long-lived or late-successional life strategies predominate, with forbs and grasses being perennial rather than annual, often with taproots as storage organs (e.g. *Leptidium sisymbrioides* subsp. *sisymbrioides*). Traits conferring longevity may be an advantage in difficult situations for seedling establishment or, alternatively, may simply be advantageous in relatively stable habitats such as these. Moreover, there seems to have been selection for layering and low stature, i.e. for subshrubs rather than erect, tall growth forms. In the genus *Carmichaelia*, *C. astonii*, *C. hollowayi*, *C. compacta* and *C. curta* are currently restricted to cliff and talus, and have these growth strategies, which confer longevity.

8.3.4 Disturbance of braided riverbeds

The arrival of humans has changed the magnitude of braided riverbed disturbances, although flooding and sedimentation remain the key physical drivers of this dynamic ecosystem (Table 9). In rivers that have not been dammed, sediment bedloads have probably increased with the construction of stopbanks, and the proliferation of riparian willow corridors that contain floods. However, in dammed rivers, the energy to transport sediment is diminished and the debris is contained in reservoirs. As a consequence, transgressive dunes that formed in the fresh sand and silt of frequently flooded terraces have disappeared, as at Cromwell in Central Otago (McKinlay 1997). Migrational changes in riverbeds on the floodplains will be less in dammed catchments but similar in intact systems. Herbivory was probably prominent in the pre-settlement braided riverbed ecosystem because landform heterogeneity and elevated fertility selected for a diverse array of waterfowl and terrestrial birds. However, bird-bioturbation was inconsequential, since the flat topography did not lend itself to use as take-off sites.

The pre-human vegetation of braided riverbeds was probably a mosaic of early- to mid-successional lichenfield, sparse herbfield, sedgeland, rushland, grassland and shrubland, with the pattern of communities and successional stages determined by the dynamic pattern of watercourses and the degree of flushing, scouring and sedimentation across the mosaic of braids and riparian terraces. Since human settlement, the proportion of mid-successional vegetation has probably decreased because stopbanks and fringing willows have contained floods within riverbeds and the frequency of fire has increased. In addition to willows, other introduced plants such as gorse (*Ulex europaeus*), broom (*Cytisus scoparius*) and lupin (*Lupinus arboreus*) are overtly competitive in riverbeds and often out-compete early-successional indigenous communities.

Braided riverbeds support a relatively small number of rare plants, most of which are shared with other ecosystems. For instance, braided riverbed broom, *Carmichaelia juncea*, also occurs on lakeshores and coastal cliffs and talus.

8.3.5 Disturbance of inland saline ecosystems

The inland saline ecosystem of Central Otago and the Waitaki River valley around Otematata was comparatively stable in pre-settlement times (Table 9). The main physical disturbances were surface ablation from wind, storm-water and bird movement, since flooding and sedimentation are inimical to salt accumulation in soils. Infrequent natural fire may have been of less consequence than elsewhere in dry, eastern New Zealand because of the inherently low biomass. We suggest that bird movement was the dominant disturbance agent, but because it was a constant ecosystem process, it did not produce distinct secondary communities.

Today, areas of the most extreme soil chemistry have a sparse vegetation cover, and the flora comprises mostly forbs and grasses (Rogers et al. 2000). Saline areas with lower salinity and alkalinity, and transition soils to the surrounding dry terrace and hill-country landforms, probably supported shrubland and grassland mixes in the past, but are now cleared and in exotic pasture, with declining native content. Farm stock and rabbits are now the main disturbance agents. Both consume native plants, and farm stock foster increased erosion, since their hooves fracture surface crusts, while rabbits alter nutrient pools through the concentration of their faeces in patches. Weeds, particularly *Plantago coronopus* and *Puccinellia distans*, threaten native plant cover. The overall change in the disturbance regime has seen:

- The soft trampling of cursorial birds replaced by the sharp-hoofed, surface-fracturing trampling of farm stock; and
- The plucking of plant foliage and stems by birds replaced by the cropping by stock and lagomorphs.

The rare flora of the saline ecosystem is relatively small, and comprises mainly herbs and grasses, which rely upon asexual rather than sexual reproduction (Table 8). This suggests a late-successional and disturbance-independent life-history strategy.

8.3.6 Disturbance of wetland ecosystems

Wetland ecosystems (including littoral zone of ephemeral wetland, mire, swamp, aquatic (macrophyte), flush / seepage, and river- and streambank) were concentrated on floodplains, basin floors, low hill-country and coastal sand plains. Flooding and sedimentation would have affected most river- and streambanks, swamps on flood-prone parts of alluvial floodplains, and flushes on steeper hill-country (Table 9). However, ephemeral wetlands and mires had seasonally fluctuating water tables, and probably experienced few floods. In some mires and swamps, the presence of sclerophyllous shrubs may have promoted a somewhat higher fire frequency than the inherently low fire frequency of the surrounding terraces and hill-country.

We suggest that apart from infrequent natural fire, flooding and sedimentation were the only disturbances that promoted early successional vegetation in wetland ecosystems, and that these disturbances were mainly confined to river- and streambanks and the most flood-prone swamps of alluvial floodplains. The seasonal fluctuation in water tables in ephemeral wetlands was of sufficient duration to promote early- to mid-successional turf vegetation and may be regarded as a surrogate for irregular flooding and sedimentation in other wetland ecosystems. The succulent vegetation of all wetland margins provided

a rich array of food sources for prehistoric birds, and was probably heavily impacted by several groups of birds, e.g. waterfowl, ratites and rails. Bird herbivory would have been of some evolutionary significance on wetland margins but did not necessarily foster early-successional communities. Johnson & Rogers (2002) point out that the turf growth form of plants around ephemeral wetlands is so internationally unusual, and the turf flora is so large, that the growth form may have evolved in New Zealand partly in response to grazing and trampling pressure by birds.

Has the disturbance regime of wetlands changed following human settlement? In general, we suggest that flooding and sedimentation are now less influential in the wetlands of riparian terraces than in pre-settlement times. Across farmland, water tables have been lowered by drains, nutrient pools have been boosted by the addition of fertilisers and substrate structure has been pugged or compacted by repeated stock trampling. Turf vegetation surrounding ephemeral wetlands appears to be resilient to the grazing and browsing of sheep and rabbits, but is highly vulnerable to cattle trampling (Johnson & Rogers 2002); the impacts of sheep hooves may have some broad equivalence to those of prehistoric birds on spongy turfs, but the browsing, grazing and footprint pressures of cattle are highly disruptive.

Forty-nine species in the dryland rare flora (21%) occur in the five wetland-ecosystem types (Table 8). The majority of the wetland species are herbs and sedges, which are concentrated in the two ecosystems with fluctuating water margins—ephemeral wetlands and river- and streambanks. These two ecosystem types are probably the most regionally specialised (e.g. kettlehole ephemeral wetlands are highly distinctive in Canterbury).

8.3.7 Disturbance of coastal ecosystems

Although coastal ecosystems (coastal cliff, talus and terraced headland; sand-and-gravel beach; dune hollow and sand plain; dune; and estuary and lagoon) are affected by the actions of wind, water and salt, these may be viewed as more or less continuous background processes in the normal functioning of the ecosystem. Nevertheless, infrequently, wind and salt events are of such magnitude that they reset some coastal ecosystems to primary or early secondary stages, and may therefore be classed as disturbances (Tables 2, 9). Transgressive dunes periodically inundate coastal plains and embayments, creating primary vegetation sequences on the fresh sand. Accordingly, a substantial proportion of the dune, hollow and sandplain flora is early successional. Infrequent transgressive dunes are of such magnitude that they engulf bordering coastal forest and shrubland or cause forest dieback. However, in periods of dune quiescence, vegetation succession proceeds toward various associations of late-successional podocarp-hardwood forest, lakes or swamp communities such as those dominated by raupo (*Typha orientalis*). In the coastal cliff and talus ecosystem, the primary disturbance is landsliding or rock avalanche, particularly on aggrading coastal platforms formed in soft sedimentary rock, e.g. along the Kaikoura Coast. Therefore, the flora and vegetation of cliffed-coastlines are selected for survival of frequent disturbance, and communities are often early- to mid-successional. Tiny relict seabird populations remain to suggest their former influence on soil physical and chemical properties around the coast.

The rejuvenation of coastal dune ecosystems by fresh sand has been considerably reduced by dune stabilisation following European colonisation. A major cause has been the deliberate and unintentional establishment of a suite of mid-successional, sand-binding, salt-tolerant introduced plants. These have overwhelmed vast areas of coastal dunelands, modifying the niche of the specialist early-successional native plants of foredunes, reardunes and sandplains. Although the frequency of landslides on coastal cliffs today is similar to that in pre-settlement times, aggressive introduced plants now threaten many of the early- to mid-successional native plant species there.

Low-stature herbs, grasses and shrubs dominate the threatened flora of coastal dryland ecosystems, reflecting replacement by taller and more aggressive exotic plants and the artificial stabilisation of sand (Table 8). Farm stock graze extensively through coastal ecosystems, and, as elsewhere, this has little equivalence with the browsing and disturbance regime imposed by the extinct avifauna.

8.4 SUMMARY AND DISCUSSION

8.4.1 Changes in disturbance regimes

Equivalent or slightly increased levels of landsliding through deforestation were experienced by all dryland ecosystems with the advent of settlement (Table 9). Because scree formation is largely a natural process, we judge its impacts as largely unaltered by settlement. In recent years, flooding and sedimentation may have had greater impacts in the hill-country parts of drainage catchments but less impact on alluvial floodplain ecosystems because of the mitigating effects of stopbanks and dams. Snow break, hailstorm and windthrow are substantially less now in the hill-country ecosystem with deforestation. Transgressive sand movement has been reduced by various human development activities and by invasion of sand-stabilising exotic species. Across much pastoral land, defoliation levels from mammalian herbivory may substantially exceed those brought about by the extinct avifauna because fertiliser supplements have greatly increased carrying capacity (Table 9). Apart from herbivory and trampling, most natural disturbances still operate. Today, sward grasses stabilise soils on all but the most arid stony terraces.

8.4.2 Rare plants and disturbance

Species' disturbance relationships are individualistic. For rare dryland species, researchers have seldom studied disturbance responses in detail and, instead, have simply interpreted disturbance relationships from field observations (e.g. *Hebe cupressoides*, Widyatmoko & Norton 1997; *Olearia hectorii*, Rogers 1996). Much more knowledge is available on the responses of the common constituents of seral grasslands to fire and grazing by farm stock. Threat categories applied to all New Zealand's threatened plants show they have had adverse responses to anthropogenic disturbances such as habitat destruction and grazing by farm stock (Given & Norton 1993; Dopson et al. 1999: 19). Dryland threatened plants are no exception. The patchy nature and low frequency of natural disturbance in pre-settlement drylands suggests that our forb and grass floras have life-history traits suited to mid- to late-successional roles. Few appear obligately early successional. Because the characteristic

intervals between most pre-settlement disturbances probably greatly exceeded the lifespan of most dryland perennial forbs and grasses, their reproductive strategies employ both vegetative and seed recruitment. By clonal reproduction, individuals can be very long lived. The behaviour of many dryland herbs in garden cultivation suggests their clonal spread would be stimulated by animal (bird) trampling, which would scarify and rejuvenate the soil surfaces the herbs exploit in their vegetative spread. In addition, birds would have transferred nutrients about the landscape, which would have stimulated plant reproductive responses. *Acaena*, *Leptinella*, *Epilobium*, *Myosotis*, *Chenopodium*, *Etinardia* and *Convolvulus* are species-rich genera with low-growing dryland species that include vegetative perpetuation and reproduction strategies. In contrast, exotic sward-forming grasses and forbs appear early successional in their adaptation to disturbance, which explains their dominance in today's frequently burnt, degraded tussock grasslands.

Nevertheless, some rare species in those dryland ecosystems that experienced frequent natural disturbance seem to require natural disturbances to stimulate seedling establishment today. For instance, coastal dunes require mobile sand to stimulate seedling establishment of several native sand-binders. The wet/dry and frosty hollow ecosystem supports several rare, small-leaved trees and shrubs and herbs that appear to be dependent upon flooding and sedimentation to maintain gleyed soils or rejuvenate nutrient budgets.

Smothering sward grasses are a significant threat in degraded rare-plant habitats. What solutions are available? For convenience, dryland rare-plant habitats might be divided into those that were predominantly woody and those that were more open, the latter either from environmental stress or frequent disturbance. In the former, restoring mid- to late-successional approximations to the original woody communities should reduce the vigour of ground-smothering weeds, with benefits for the recruitment of rare plants. There is a paucity of trial information on this scenario (e.g. see the case study of *Muehlenbeckia astonii* below), although anecdotal evidence exists for substantially reduced vigour of sward grasses in semi-shaded understoreys of dry shrubland and forest. Forested, limestone cliff communities in Canterbury with the threatened grass *Australopyrum calcis* subsp. *calcis* have been little invaded by exotic herbs and grasses, and the rare native grass shows perpetuation in semi-shade. There are several examples of rare dryland shrubs successfully recruiting beneath woody canopies. For example, *Helicbrysum dimorphum* has successful recruitment within relict dry shrublands of the Waimakariri River catchment. These few field examples suggest that a reconstitution of dryland woody communities should be trialled in dryland threatened species recovery programmes, even in the absence of experimental evidence for seedling recruitment of each rare-plant species.

Restoration of woody vegetation is not appropriate for more open or non-woody ecosystems such as some saline patches, some wetlands and some dune ecosystems. There, hand weeding and herbicides are two methods under trial to suppress exotic weeds, but it is too early to form generalisations on their effectiveness or efficiency at different scales of application. Early attempts at herbicide suppression of marram grass (*Ammophila arenaria*) in coastal dunes at Masons and Doughboy Bays, *Plantago coronopus* in Otago's saline patches, and a raft of weeds in ephemeral wetlands (Champion 2000) provide encouraging results.

Is disturbance equivalent to that provided by extinct birds necessary to promote the seed regeneration of rare plants in the understorey of woody communities? We have no evidence for this; rather, we have limited evidence that a range of dryland species recruit successfully beneath woody canopies without such disturbance. If it becomes apparent that such disturbances are, in fact, necessary for the restoration of threatened species in dryland environments, we think it unlikely that mammals will be appropriate substitutes for avian guilds, since a high proportion of eastern dryland threatened species are susceptible to grazing, browsing and / or trampling by stock and feral animals (Dopson et al. 1999). Moreover, we contend that the rebuilding of dryland woody communities is vital to restoring the habitat and ecosystem processes required by many rare species, and both experimental and anecdotal evidence shows that mammalian grazing and browsing may have various effects on restoration pathways: antagonistic, benign or beneficial depending on circumstances and goals.

9. Case study: *Muehlenbeckia astonii*

9.1 BACKGROUND AND OBJECTIVE

We chose the threatened shrub *Muehlenbeckia astonii* to test the utility of insights into the pre- and post-settlement disturbance regime and likely community structure and composition of its pre-settlement ecosystems to aid recovery planning for the species. This plant is one of the most studied of New Zealand's threatened plants, and there is a substantial body of literature and recovery planning providing background information (Petrie 1911; Jenkins 1930; Baird 1990; de Lange & Silbery 1993; de Lange & Pitt 1998; de Lange & Jones 2000; Given 2001; Norton 2001; Partridge 2001).

Intact benchmark communities containing *M. astonii* plants are no longer present in eastern South Island. Most populations of *M. astonii* grow in highly modified, short-statured exotic grassland, and contain few or no juvenile plants. The reasons for this apparent recruitment failure are not well understood, and the question has been raised of whether the species might depend upon disturbances now missing to initiate recruitment. Better knowledge of the characteristics of the original plant communities, and their pre-settlement disturbance regimes, is required to guide appropriate conservation management and community restoration goals for the species.

In this section, we review current knowledge of the biology and ecology of *M. astonii*. We use national environmental surfaces to assess its environmental envelope and therefore its likely minimum pre-settlement distribution. We apply our understanding of pre-settlement ecosystem disturbance regimes, and the structure, composition and function of pre-settlement *M. astonii* communities, to recovery planning.

9.2 METHODS

9.2.1 Current distribution and habitat characteristics

We collected 44 sample plot records from populations of *M. astonii* that cover its geographical and environmental range. The RECCE method of Allen (1992) was used to typify site physiography and community composition. Plot size varied from 100 m² (10 × 10 m) to 8000 m² (c. 90 × 90 m) according to the land area covered by the population.

In order to better characterise the environmental envelope of the species, we added a further 20 grid-referenced locations that were sourced from historical records, including former sites of plants that are believed to have died, and those at sites yet to be resurveyed. The full set of 64 sites (44 surveyed sites + 20 previous and yet to be surveyed sites) occur in 24 LENZ Level IV land environments (Leathwick et al. 2003) representing 14 of the 40 eastern dryland environmental types as separately classified in this report (see Sections 3.2 & 3.3).

9.2.2 Environmental envelope

We examined the current distribution of *M. astonii* in relation to LENZ and the dryland environments separately classified in this paper. Since the distribution of *M. astonii* reflects the fact that it exists as a relict, its distribution is likely to be largely determined by anthropogenic disturbance rather than by environment. Therefore, predictions of its potential distribution using regression models (GRASP; Lehmann et al. 2002) may be misleading. To provide a landscape-scale estimate of its likely former range, we built on a method developed for rare-plant species in the Waikato District (Rutledge et al. 2004) to define an environmental envelope based on the species' present distribution. Our method erects a wide environmental space based on maxima and minima of a suite of environmental factors, then progressively refines this envelope using, firstly, further environmental factors and, secondly, potential vegetation communities (see also Fig. 11).

Step 1: For each Level IV land environment with at least one *M. astonii* record, the maxima and minima of maximum and minimum values for each of 30 environmental factors were extracted. All Level IV land environments in dry eastern New Zealand that fall within these limits (i.e. for all of the 30 environmental factors) were included in the broad regional environmental envelope of the species.

Step 2: To refine this envelope, we selected those areas within the regional environmental envelope that fall within one of the geological classes intercepted by the *M. astonii* plot co-ordinates on the NZLRI top-rock geological surface (see Appendix 1, Table A1.1, for details). We refer to this as the 'environment+geological envelope'.

Step 3: A second refinement produces an even more conservative estimate of the likely geographic distribution of *M. astonii*. For this, we selected all areas within the regional environment+geological envelope that are classified within any one of the nine potential vegetation zones that *M. astonii* sites presently cover in a vegetation reconstruction map for pre-settlement New Zealand (Leathwick et al. 2004).

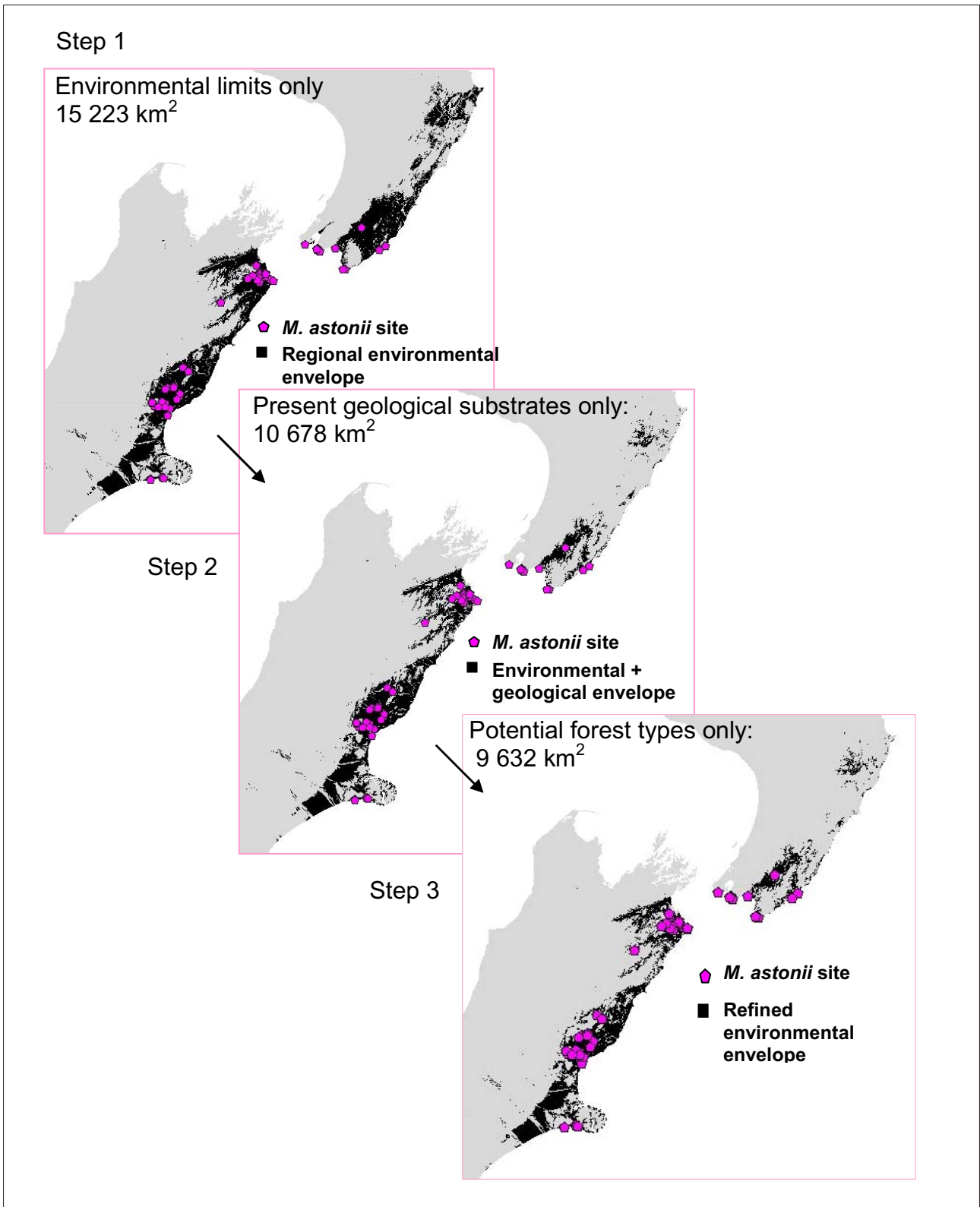


Figure 11. Steps (described in Section 9.2.2) in determining the refined environmental envelope of *Muehlenbeckia astonii* within the eastern dryland zone.

9.2.3 Current communities

To identify the range of plant communities currently occupied by *M. astonii*, we used the multivariate techniques of classification (cluster analysis, Canberra distance measure, flexible sorting strategy, β set to -0.25; Clifford & Stephenson 1975). After inspection, we terminated this classification at the arbitrary level of four groups (i.e. plant communities). Tukey's test was used to identify significant differences between these communities in average environmental characteristics and the abundance of component plant species.

9.2.4 Current demography

To assess the demographic characteristics of each population, we measured the maximum canopy height and diameter (length and breadth dimensions) of each *M. astonii* plant in each of the 44 sampled populations. We arbitrarily defined plants of height < 0.2 m as seedlings. We calculated the volume (m³) of each plant based on the assumption that average shape approximates a half sphere, with the widest circumference at or near ground level. We calculated the average height and volume of plants, and average height:radius ratio characteristic for each plot, for each plant community and for each population size class.

9.3 RESULTS

9.3.1 Current distribution and habitat characteristics

Half of the 64 known *M. astonii* sites are below 75 m elevation, and all but one are from below 380 m a.s.l. (one historical record from Winterton River in the Awatere River valley, Marlborough, is recorded at 850 m a.s.l.). All populations were recorded on well-drained soils. Geological parent materials recorded in the field were: greywacke (Wellington / Wairarapa); calcareous sandstone, greywacke gravels, sandstone and siltstone with or without loess cover, sandstone gravels, coastal mixed sand and gravel (Marlborough); basalt colluvium, limestone colluvium, greywacke colluvium, sandstone gravels, and coastal sand (Canterbury). Populations grow across the full range of aspects from sunny to shady, and occupy slopes from flat to escarpments of 55° (average slope 23°, median 21°).

Muehlenbeckia astonii occupies a wide range of landforms. Although its national and local distribution is clearly one of a relict species, the diversity of sites suggest that it was a versatile species and capable of occupying a wide range of habitats. Around the coast, it occurs on uplifted wave-cut platforms veneered with sand or gravel, on escarpments, on toeslope talus, and on sand plains behind foredunes. Inland, it is found on rolling downland or low hill-country, on stony alluvial floodplains and on escarpments bordering incised rivers. We found no landform-climate combinations in its distribution that would have supported open or non-forest or non-shrubland vegetation in pre-settlement times. In essence, it occupies most landforms in edaphically and climatically dry environments that would have supported tall shrubland or low forest communities. Such communities would either have been of a stature compatible with the height capabilities of *M. astonii*, or low forest with light or broken canopies that enabled *M. astonii* to survive as an understorey or light-

gap component. Although *M. astonii* is typically present in open, mostly introduced short-statured vegetation today, one population occurs within a mid-successional, 7-12-m-high kanuka forest on an edaphically dry river escarpment near Martinborough in inland Wairarapa. Further, the species recruits freely via bird dispersal of seed from cultivated adults within the understorey of low kowhai-kanuka forest in the grounds of Landcare Research, at Lincoln, on the Canterbury Plains (P. Heenan, pers. comm.; pers. obs. 2004). These two situations are strong evidence that *M. astonii* is not an obligate occupant of open vegetation with a high light requirement. Rather, we believe its habitat in pre-settlement times was almost entirely closed-shrubland to low-forest.

9.3.2 Environmental envelope

Distribution in relation to environment

The broad regional environmental envelope of 15 223 km² includes land as far north as Cape Kidnappers in eastern North Island. Further restricting this area with respect to geology and potential vegetation type reduces the area to 9632 km² (i.e. the refined environmental envelope; Fig. 11). The latter represents a substantial extension of the current range of *M. astonii* onto the dry Heretaunga Plains of southern Hawke's Bay, into the lower Wairau Valley in Marlborough, and onto the eastern plains of mid-Canterbury. The environmental envelope also suggests that *M. astonii* might have occupied a larger number of land environments within its geographic range than it does at present, especially in north Canterbury's coastal hill-country and inland Wairarapa.

The refined environmental envelope suggests that *M. astonii* may have occurred within seven of the eight dryland environmental types. It occurs in six of these today (Fig. 12; Table 10). The refined environmental envelope covers all or part of 69 Level IV land environments (*M. astonii* occurs in 24 of these today).

TABLE 10. DRYLAND ENVIRONMENTS INCLUDED IN THE REFINED ENVIRONMENTAL ENVELOPE OF *Muehlenbeckia astonii*.

DRYLAND ENVIRONMENT	AREA (%) (km ²)	No. OF <i>M. astonii</i> SITES	LEVEL IV LENZ* (No. OF SITES)
B	1586 (18%)	13	B3.1A (1), B8.1B (2), F4.1B (1), F1.2C (8), F4.1D (1)
C	1106 (43%)	11	J4.1c (2), J4.3b (8), J4.2c (1)
D	819 (80%)	14	B9.1a (4), B9.1b (2), B9.2a (2), B6.1a (1), B7.1a (1), B7.1b (3), B6.1c (1)
E	2092 (39%)	10	E1.2a (1), B8.1c (1), B3.2b (8)
F	3479 (30%)	13	N1.1a (1), J2.1b (2), N1.1b (8), F3.1a (2)
G	385 (4%)	3	J2.1c (2), J2.2c (1)
H	166 (2%)	0	
Total	9632 (19% of the 50 555-km ² dryland zone)	64	

* Land environments (Leathwick et al. 2003) with site records of *M. astonii*.

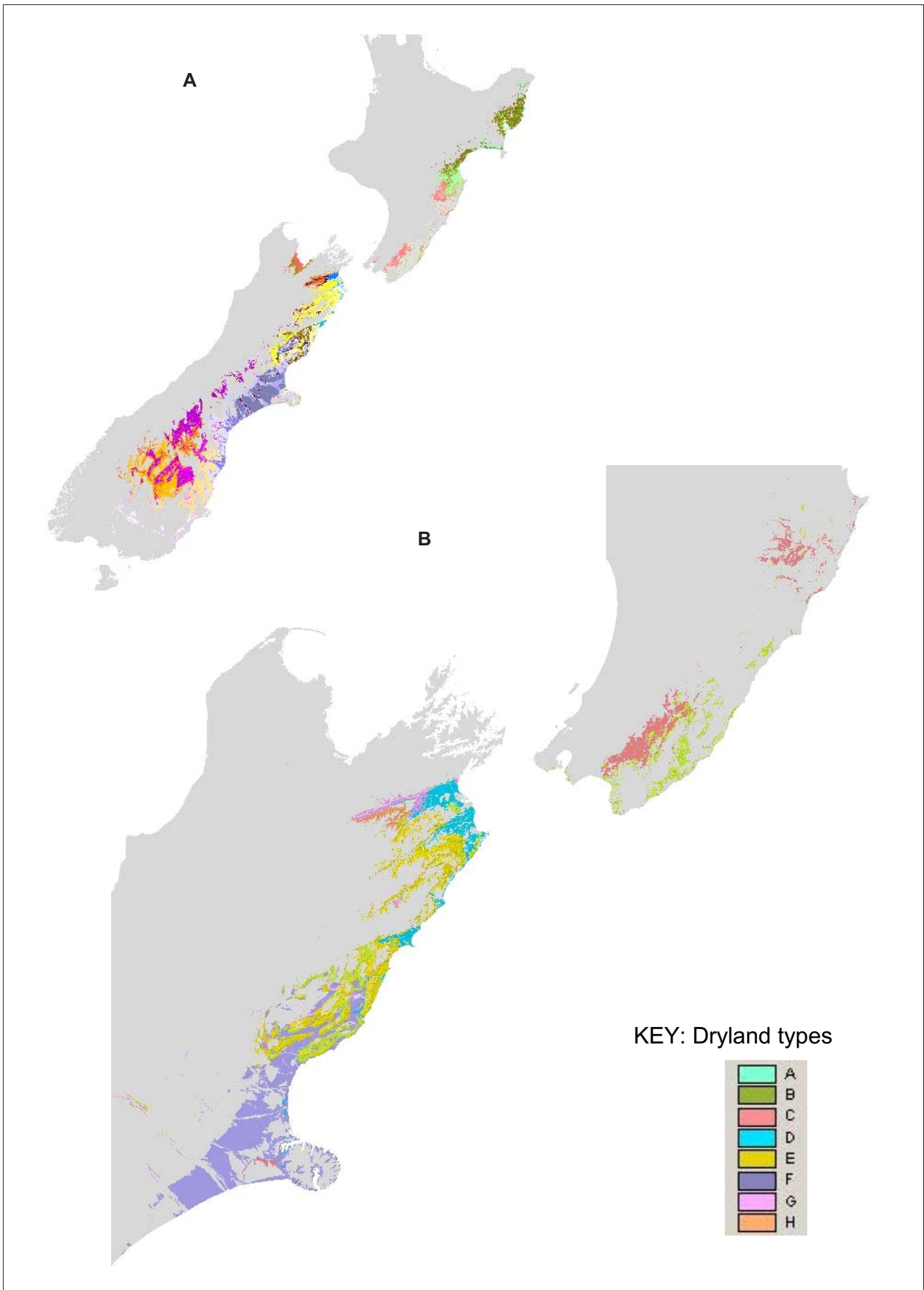


Figure 12. Environmental envelope of *Muehlenbeckia astonii* in relation to the national dryland classification. **A.** National dryland classification. **B.** Refined predicted environmental envelope of *M. astonii*.

Distribution in relation to potential vegetation type

Vegetation plots containing *M. astonii* fall within nine of the potential vegetation types of Leathwick et al. (2004) (i.e. dunelands and eight forest types; Table 11). A high proportion of the environmental envelope covers the matai-kahikatea-totara, kahikatea-pukatea-tawa, and matai-totara / black /mountain beech forest zones. The environmental envelope covers smaller areas of the kahikatea-matai / tawa-mahoe (*Melicytus ramiflorus*) and mountain beech forest zones, and overlaps very small portions of the kauri / taraire (*Beilschmiedia tarairi*)-kohekohe (*Dysoxylum spectabile*)-tawa, rimu / tawa-kamahi and Hall's totara / broadleaf potential forest zones.

9.3.3 Current *M. astonii* communities

Muehlenbeckia astonii grows in short-statured communities (Table 12) spanning a range of dryland environments from the coast to at least 50 km inland. The tallest plants recorded with *M. astonii* were low trees up to 7 m high, such as kanuka and *Cordyline australis* (5–12 m tall; Tier 3). A rich variety of shorter shrubs co-occur with *M. astonii*. The communities are very poorly distinguished by environment, probably because modification has tended to homogenise the vegetation.

Community A: Northern South Island grasslands

Six plots in North Marlborough (Te Hau, Blind River, The Waterfall and Seddon Vineyard) and one in North Canterbury (Balmoral Reserve) are included in this species-poor, low-statured exotic grassland community (Table 12). Each plot contains a single, relatively large *M. astonii* plant (average height 2.1 m, volume 14.6 m³). The vegetation is distinguished by the presence of *Melicytus* sp. unnamed and *Rosa rubiginosa* and a dense ground layer of introduced grasses. Occasional shrubs of matagouri, pohuehue (*Muehlenbeckia complexa*) and box thorn (*Lycium ferossimum*) are present. The community occurs in two of the

TABLE 11. POTENTIAL FOREST TYPES (FROM LEATHWICK ET AL. 2004) INCLUDED IN THE REFINED ENVIRONMENTAL ENVELOPE OF *Muehlenbeckia astonii*.

POTENTIAL FOREST TYPE	No. OF <i>M. astonii</i> SITES	LAND AREA (km ²) AND % OF POTENTIAL ENVIRONMENTAL ENVELOPE	PERCENTAGE OF THIS FOREST TYPE INCLUDED
1. Kauri / taraire-kohekohe-tawa forest	1	18 (0.2)	0.1
2. Rimu / tawa-kamahi forest	5	256 (2.7)	0.5
3. Kahikatea-pukatea-tawa forest	18	2055 (21.3)	10.7
4. Matai-kahikatea-totara forest	6	3003 (31.2)	21.3
5. Kahikatea-matai / tawa-mahoe forest	12	1137 (11.8)	22.6
7. Hall's totara / broadleaf forest	1	125 (1.3)	1.1
19. Mountain beech forest	7	647 (6.7)	5.5
20. Matai-totara / black / mountain beech forest	8	2296 (23.8)	45.9
23. Dunelands	2	95 (1.0)	5.8
Unclassified	4	na	na
Total	64	9632 (100)	

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