

Drainage, soil fertility and fire frequency determine composition and structure of gumland heaths in northern New Zealand

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Abstract: Vegetation and soils were sampled at remaining gumland heath ecosystems in northern New Zealand to determine vegetation patterns, environmental controls and major threats to long-term persistence. Classification and ordination techniques identified six vegetation types reflecting differences in drainage, rainfall, altitude, nutrients, and time since fire. Two modal types reflected opposite ends of the main environmental spectra. *Leptospermum scoparium* (Myrtaceae) shrubland occurred on relatively better drained sites with lower rainfall, altitude, and soil nutrient levels, whereas *Gleichenia dicarpa* (Gleicheniaceae) fernland typically occurred on more poorly drained sites with higher rainfall, altitude, and nutrient levels. Another widespread vegetation type dominated by both *Leptospermum scoparium* and *Gleichenia dicarpa* occupied plots of intermediate drainage, rainfall, altitude and nutrients. The three remaining types were of limited distribution and reflected uncommon combinations of environmental conditions or recent fire. Low soil nutrients in gumlands (mean total N = 0.182%, total P = 0.004%, oven-dry weight) are reflected in low *Leptospermum scoparium* foliage nutrients (mean total N = 0.858%, total P = 0.034%, $\delta^{15}\text{N} = -6.06\text{‰}$, oven-dry weight) and slow growth rates (mean annual height growth rate = 11.90 cm year⁻¹), as in heathlands in Australia and South Africa. Gumlands are threatened by non-native plant species invasion, especially *Hakea sericea* (Proteaceae); habitat destruction for agricultural, industrial, and suburban development; and nutrient enrichment from adjacent agricultural land. Currently, fire is much less common in gumlands (mean time since fire = 18.4 years) than during early European settlement and some communities are apparently reverting to forest. Research to investigate the use of fire as a management tool is recommended for long-term conservation of New Zealand gumlands.

Keywords: drainage gradient; *Gleichenia dicarpa*; *Hakea sericea*; *Leptospermum scoparium*; low nutrient vegetation

Introduction

Heathland ecosystems are characterised by sclerophyllous shrub communities on extremely infertile soils. They may be well drained (dry heathland) or seasonally waterlogged (wet heathland) and are often induced or maintained by regular fire (Specht 1979). Heathlands contain unique and diverse plant and animal communities that are suffering widespread habitat loss and species extinctions in many global strongholds, e.g. north-western European *Calluna* shrublands (Damman 1957; Gimingham 1981), South African fynbos (Taylor 1978; Kruger 1981; de Beer et al. 2005), and Australian heathlands (Specht 1981a; Keith 2004). Agricultural and urban development, and to a lesser extent afforestation, are the main causes (Taylor 1978; Gimingham 1981). Remaining heathlands are typically highly fragmented and isolated, and susceptible to degradation caused by further development, weed invasion, nutrient enrichment, and too frequent fire (Kruger 1981; Specht 1981a; Keith et al. 2002; Darkoh 2009). Many heathlands throughout the world require rehabilitation and restoration to protect and maintain biodiversity values, and ecosystem services such as water production (Higgins et al. 1997).

Understanding ecosystem composition and function is crucial for effective management and restoration of degraded systems (Hobbs 1999; Keddy 2000). European heathlands are well understood (Smith 1902; Gimingham 1981; Maren

et al. 2008), and there is a strong research basis for nature conservation policy and management, e.g. European Union Habitats Directive 1992 (<http://ec.europa.eu/environment/nature/legislation/habitatsdirective/>). More recently, research into pattern and process has been extended to Southern Hemisphere heathlands, often driven by conservation requirements, e.g. biodiversity loss in South Africa (Richardson et al. 1996), fire frequency regime management in Australia (Cheal 1996), and the role of disturbance in New Caledonia (Enright et al. 2001). By contrast, 'gumlands', a threatened wet heathland type confined to northern New Zealand (Wardle 1991), are still poorly understood.

Gumlands occur on flat to rolling lands containing deposits of kauri gum, the subfossil resin of the *Agathis australis* (kauri) forests they supported some hundreds or thousands of years ago (Enright 1989). Soils are strongly podzolised, deficient in nutrients and prone to waterlogging. Gumlands are included in the 'pakihi and gumland' class of the New Zealand wetland classification system (Johnson & Gerbeaux 2004). The vegetation comprises *Leptospermum scoparium* (Myrtaceae; henceforth called *Leptospermum*), *Dracophyllum lessonianum* (Ericaceae) and other ericaceous shrubs, sedges (Cyperaceae, especially *Schoenus*, *Baumea*), and ferns (especially *Gleichenia dicarpa*, Gleicheniaceae; henceforth *Gleichenia*). Although dominated by relatively common, widespread species, gumlands also support at least

24 threatened plant species (<http://www.nzpcn.org.nz/>; de Lange et al. 2009).

In the 1840s New Zealand gumlands covered around 300 000 ha in Northland, Auckland and the Coromandel Peninsula north of latitude c. 37°S (Burrows et al. 1979; Molloy 1993). Some gumlands probably originated after Polynesian settlement (c. AD 1250; Hogg et al. 2003) and were maintained by repeated fires (Taylor & Sutherland 1953; Burrows et al. 1979). Gumlands were further modified and extended by European ‘gum digging’, supporting a large industry c. 1870–1940 exporting gum to Europe and North America, where it was used as a raw material for paints, varnishes, and linoleum (Reed 1972). After the Second World War, improved farming techniques on podzolic soils enabled widespread conversion of gumland to agriculture (Esler & Rumball 1975); as a consequence, only a few thousand hectares of gumlands remain.

As the main New Zealand gumland soils originated from the podsolizing action of an endemic forest (kauri) type (Esler & Rumball 1975), and nearly half of the natural flora comprises endemic species (see Enright 1989), ecosystem development and dynamics may be different from those heathlands elsewhere in the world. Several parallels are apparent in the main controlling factors, i.e. seasonal waterlogging, low nutrients, and occasional fires (Enright 1989), and in the main threats, i.e. site development (Clunie 1983), agriculturally derived nutrient enrichment (Clunie 1983, 1987), and non-native plants (Clunie & Wardle 1983; Clunie 1987; Enright 1989). However, knowledge of the distribution, composition,

ecosystem function, and conservation values of New Zealand gumlands remains limited (Enright 1989). In light of increasing pressures on their ecological integrity, we conducted a systematic survey of remaining gumland ecosystems, to typify vegetation, determine controlling processes, and identify major threats, with the view to informing effective conservation management. Specific questions we addressed were: (1) Are the environmental factors that control wet heathland vegetation generally, i.e. seasonally poor drainage, low nutrients, and fire, also important in New Zealand gumlands? (2) How do environmental factors influence plant community composition in gumlands? (3) Which threats (e.g. non-native plant invasion, agriculture, and nutrient enrichment) are most serious for the long-term integrity of gumlands?

Methods

Study sites

Fifteen sites were selected as encompassing the range of ecological and biogeographic variation in gumland ecosystems based on publications, historical information, local knowledge, and a field reconnaissance survey. These sites were considered to represent the remaining substantial areas of gumland (vegetation height < 2 m) on mainland New Zealand. They were distributed from North Cape to Auckland in the northern North Island, with two clusters centred on Kaitaia and Kaikohe (Fig. 1). Sizes range from 3 ha (Rangiputa) to 500 ha

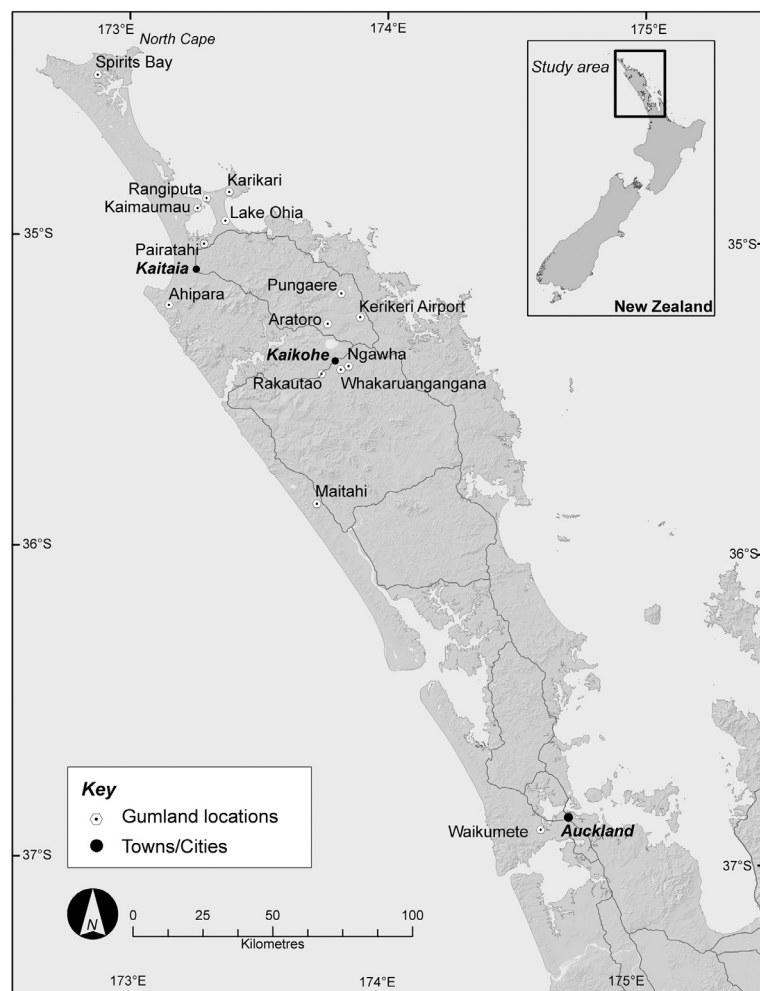


Figure 1. Location of the 15 gumlands sampled in northern New Zealand.

(Lake Ohia; Fig. 2), averaging 90 ha, with the exception of the much larger plateau at Ahipara (1200 ha). Climates are warm and humid, with summer droughts and winter rains. Mean annual temperatures are in the range 14–15°C (New Zealand Meteorological Service 1985). Mean annual rainfalls range from 1200 to 2300 mm (New Zealand Meteorological Service 1985), averaging 1500 mm over all sites, with inland sites centred on Kaikohe being wetter (mean annual rainfall 1845 mm, $n = 6$) than more coastal sites (mean annual rainfall 1338 mm, $n = 7$). Altitudes range from near sea level to just over 300 m a.s.l., with the highest altitude sites being inland near Kaikohe and at Ahipara near Kaitaia.

Soils are mostly Podzols (Te Kopuru sand) or Ultic Soils (Wharekohe silt loam) (Hewitt 1992) derived from deeply weathered consolidated sands, sandstones, and siltstones, with Organic Soils (peaty) in places (Molloy 1993; Hewitt 1992). Both Podzols and Ultic Soils are strongly leached, acidic, seasonally (winter) waterlogged and of low fertility. Podzols have thin topsoil (sometimes humic or peaty) on a pale greyish siliceous layer (E horizon) above a slowly permeable horizon (soil pan) formed from translocated, strongly cemented sesquioxides and organic matter. In contrast, the slowly permeable layer in Ultic Soils is developed in a high-density clay layer.

All sites are likely to have been burnt repeatedly in the past. Polynesian Māori commonly burnt large areas in northern

New Zealand (see Beever 1981) and in the last 150 years gumdiggers frequently burnt gumland vegetation to access the substrate (Reed 1972). Several sites were pockmarked with gum extraction pits and an accidental fire occurred 18 months before sampling at the Lake Ohia east site (P.T. Whaley, DOC, pers. comm.).

Data collection

Gumland boundaries for each site were initially delineated on aerial photographs using colour, pattern, and texture indicative of low-growing heath vegetation or evidence of gum-digging such as pits or exposed soil pans. Boundaries were then ground-truthed and refined in the field based on the following criteria: presence of podzolic soils, evidence of seasonal waterlogging, and vegetation dominated by heath vegetation below 2 m (occasionally up to 3 m). Parallel transects at least 20 m apart were established throughout each gumland with origins located using restricted random numbers. Along each transect, 10 × 10 m plots were placed at random positions, with the constraint of a minimum spacing of 20 m. The number of plots (and transects) was proportional to the size of the site, ranging from five plots for small, homogeneous sites such as Waikumete and Pairatahi to a maximum of 19 plots for larger, more heterogeneous gumlands such as Lake Ohia. One additional plot was established at Ahipara and at Aratoro in vegetation types not or poorly represented in the original



Figure 2. Lake Ohia south gumland showing exposed soil pan and scattered vegetation of *Leptospermum* shrubs and *Campylopus introflexus* moss.

samples. In total, 154 plots were sampled between November 2007 and March 2008, a period suitable for sampling most species apart from early flowering herbaceous perennials (e.g. some orchids).

Vegetation

At each plot, we measured the maximum height of all canopy species with a graduated pole, and estimated the average height of the canopy layer, sensu Atkinson (1985). Percentage covers of species in the canopy layer and the understorey were estimated, with species contributing less than 1% to the canopy being recorded as 0.01%. Additional species within 10 m of the plot in areas with vegetation of similar composition and structure were also recorded.

The height, and diameter at ground level, of the tallest *Leptospermum* in each plot was measured, and a basal stem disc collected for ring counting to determine age and growth rates. *Leptospermum* is killed by fire but rapidly regenerates from seed (Wardle 1991); therefore the putative oldest individual provides an approximation of when the last fire occurred. A small sample (about 5 g) of newly mature terminal foliage was collected, oven-dried for 24 h @ 60°C, and analysed for P, N, and $\delta^{15}\text{N}$. Nitrogen and phosphorus are considered the most important limiting plant nutrients in heathlands of Australia and South Africa (Groves 1983). We used *Leptospermum* because it was present in all plots, and *Leptospermum* foliar nutrients strongly reflect soil nutrient status across nutrient gradients (Clarkson et al. 2004a, b).

Evidence of fire history was scored on a three-point scale as follows: 1 = very recent: <2 years (very short sparse vegetation, *Leptospermum* present only as seedlings, abundant charred standing dead stems); 2 = recent: 2–5 years (short vegetation, sharp boundaries with adjacent taller vegetation, charred wood, charcoal in soil surface layers); 3 = not recent: >5 years (no discernible vegetation differences).

Soil

Using an auger, depths to the bleached siliceous layer and to the impermeable pan were measured at several points within each plot. Predominant soil texture of the upper horizon was classified in four categories (peaty, sandy, silty, clayey). Drainage class was estimated in five categories by soil colour using Munsell® Soil Colour Charts as follows: 1 = very poor, humic, peaty or organic topsoil; 2 = poor, mineral soils with grey colours in top 30 cm (colours chroma 2 or less; chroma 3 or less if value 5 or more); 3 = imperfect, chroma 2 (chroma 3 or less if value 5 or more) first occurs between 30 and 60 cm; 4 = moderate, chroma 2 (chroma 3 or less if value 5 or more) first occurs below 60 cm or ochreous mottling below 30 cm; 5 = good, no mottles (high or low chroma) visible.

Soil samples collected from the uppermost 10 cm (plant rooting layer) from each plot were combined into a composite sample for each site for analysis. On air-dry soil, pH (in water), and on oven-dry soil, total C and total N (using combustion in a Leco CN analyser), total P (by ignition and dissolution in 0.5 M sulphuric acid), and exchangeable cations and cation exchange capacity (CEC), were determined according to Blakemore et al. (1987).

Site characteristics

At each plot we recorded easting and northing using a Garmin 60CSx GPS, altitude, aspect, predominant slope, and an index of mesotopography (sum of slopes measured from plot centre to edges at 45° intervals; McNab 1993). A three-point scale

(low, medium, high) was used in the field to assess the impact of the following threats: weeds, urbanisation, feral mammals, farm mammals, drainage, fire, recreation, and agriculture. Assessment for each threat was based on the overall degree and extent of modification at the gumland site.

Soil types were determined by intersecting plot eastings and northings on the New Zealand soils database within the New Zealand Land Resource Inventory (Newsome et al. 2000). Mean annual rainfalls were determined in a similar manner using data from New Zealand Meteorological Service (1985) within Land Environments of New Zealand (Leathwick et al. 2002). The surrounding land cover within 100 m of the site was estimated by percentage using New Zealand Land Cover Database Version 2 (LCDB2) classes (see <http://www.mfe.govt.nz/issues/land/land-cover-dbase/classes.html>).

Data analysis

Percentage covers for the 66 species recorded in the canopy layer of the 154 plots were analysed using classification (cluster analysis) and ordination techniques to identify vegetation types and examine relationships between vegetation composition and environmental gradients. The programmes used were FUSE (Agglomerative Hierarchical Fusion) and SSH (Semi-Strong-Hybrid Multidimensional Scaling) within the PATN analysis package (Belbin 1995). The SSH hybrid scaling ordination technique implements an improved version of the hybrid scaling, which combines metric and non-metric criteria (Faith et al. 1987). It is considered to be a robust technique for measuring ecological distance because it is flexible and fits output distances to input distances without squaring these distances (Minchin 1987; Belbin 1995). In all analyses we used the Unweighted Pair-Group Method using Arithmetic averages (UPGMA) clustering method (with $\beta = -0.1$) where equal weight is given to objects not groups, and the Bray–Curtis association measure, which consistently performed well in data testing (Faith et al. 1987). A two-dimensional ordination with a stress value of 0.2067 was considered to summarise the data adequately (see Belbin 1995), as solutions of other dimensions did not markedly change ecological interpretability.

The environmental data and plot ordination scores were then analysed using a vector-fitting approach to examine species–environment responses. We implemented Principal Component Correlation (PCC) within PATN, a multiple-linear regression programme designed to see how well a set of environmental attributes can be fitted into an ordination space. Vectors were plotted on the plot ordination to indicate the direction (angle of vector) of best fit for each of the environmental variables and the strength of the correlation (length of vector) in that direction.

Results

Site characteristics

Soil

Soil nutrient levels at all sites (Appendix 1) were rated overall as low (ratings from Blakemore et al. 1987), with individual values ranging from medium to very low. Soils were mostly strongly to extremely acid (pH < 5.3), and total C levels ranged from low to high (2.48–14.19%). There were two main soil types, Te Kopuru sand concentrated in the north (around Kaitaia) and west (Maitahi) of the study area, and Wharekohe

silt loam in central inland areas around Kaikohe. Of the two, Te Kopuru sand generally had higher mean pH (4.7 cf. 4.3; $P < 0.001$) and nutrient levels, particularly total P (34.5 cf. 27.6 mg kg⁻¹, $P < 0.001$), exchangeable Ca (0.9 cf. 0.3 cmol(+) kg⁻¹; $P < 0.001$), exchangeable K (0.24 cf. 0.09 cmol(+) kg⁻¹; $P < 0.001$), and CEC (15.2 cf. 9.2 cmol(+) kg⁻¹ oven-dry soil; $P < 0.001$). Although a minor type, organic soils also had relatively high nutrient levels, particularly total N and total P.

Adjoining land use

The dominant land cover immediately surrounding the gumlands was mānuka and/or kānuka scrub, comprising *Leptospermum* and/or *Kunzea ericoides* respectively, accounting for 57% (SE = 7) mean cover. Exotic grassland (pasture) was next with mean cover of 18% (SE = 5), and closed-canopy exotic plantation was third with 5% (SE = 3). The remaining classes each contributed less than 5% mean cover, although one gumland, Kerikeri Airport, scored highly (45%) for transport infrastructure and another, Karikari, for vineyard (40%).

Weeds

The main threats across all gumlands were non-native weeds (eight sites had medium or high impact scores), and agricultural development (five sites scored medium or high). Weeds were common only on the margins of most gumlands, although *Hakea sericea* and *H. gibbosa*, introduced from Australia, penetrated more deeply. The sites with highest weed threat were small in extent (Rangiputa), within urban settings (Waikumete), or surrounded by pasture or pine plantation (Maitahi). Agricultural (including vineyard) development and vegetation clearance were relatively common around gumland reserves, or in privately owned gumlands (Pairatahi, Pungaere). Residential development was also encroaching on the margins of Pungaere gumland. Large and isolated sites with catchments dominated by native vegetation (Ahipara) had low threats, although remote and extensive Spirits Bay had a weed impact score of medium.

Ahipara, Aratoro, Kerikeri, and Pungaere recorded the lowest percentages (<5%) and smallest numbers (<2) of non-native species, whereas Maitahi and Waikumete had the highest percentages (>20%) and greatest numbers (>5 species). In terms of canopy cover, most sites recorded less than 2% mean non-native species cover, except for Spirits Bay (7%), Karikari (14%) and Maitahi (15%). Apart from *Hakea gibbosa* at Spirits Bay, *H. sericea* was the overwhelmingly dominant non-native species.

Flora

In total, 78 vascular and 12 non-vascular plant species were recorded in the plots (Appendix 2), comprising 69 indigenes, 19 non-natives, and two of uncertain status. For vascular species, indigenous species accounted for 75%, of which 47% (27 species) were endemic, and non-native species contributed 25%. Some early-flowering orchids characteristic of gumlands were either not recorded (e.g. *Pterostylis* spp.) or poorly represented (e.g. *Thelymitra* spp.) because sampling took place later in the growing season.

Seven threatened and uncommon plant species (see de Lange et al. (2009) for lists of threatened plant species) were recorded in the plots: *Anzybas rotundifolius*, *Calochilus paludosus*, *Dianella haemata*, *Kunzea ericoides* var. *linearis*, *Lycopodiella serpentina*, *Phylloglossum drummondii*, and *Utricularia delicatula*. In addition, a new population of the

nationally vulnerable *Baumea complanata* was discovered at Whakaruangangana. All sites contained at least *Dianella haemata* within some of the plots, with Ahipara having the maximum of five threatened or uncommon species. One additional threatened species, *Pomaderris phyllicifolia*, was recorded outside, but close to plots during sampling. Other threatened species are likely to be present; however, a comprehensive flora survey was not the focus of this study.

Fifteen non-native species (79%) had sparse cover (1% or less) and limited distribution, with 14 species being confined to one site each. The remaining four non-native species were more common and/or widespread. Those confined to a single site, but present in most plots therein, were *Erica lusitanica* at Maitahi with maximum cover of 4%, and *Hakea gibbosa* at Spirits Bay with maximum cover of 25%. *Ulex europaeus* was recorded at six of the 15 sites and with very low cover (most plots <1%; maximum of 6%), whereas the most common non-native, *Hakea sericea*, was locally abundant at 10 sites with cover of up to 45%.

Plant analyses

Leptospermum age, height growth rates, and foliar nutrient concentrations showed marked trends, which mainly reflected relatively recent disturbance. Across all sites, *Leptospermum* age ranged from 1 to 43 years, with a mean of 18.4 years (SE = 0.76), and ring widths ranged from 0.40 mm to 3.12 mm, with an overall mean of 0.80 mm. Mean values for *Leptospermum* foliar nutrients were 0.859 N, 0.034 P % dry weight, and -6.06‰ for δ¹⁵N, and 26.9 for N:P ratio. There were strong positive linear relationships between *Leptospermum* height and age ($r^2 = 0.41$, $P < 0.0001$), diameter and age ($r^2 = 0.63$, $P < 0.0001$), and height and diameter ($r^2 = 0.40$, $P < 0.0001$). Height growth rates averaged 11.90 cm year⁻¹ (SE = 0.44 cm year⁻¹). The highest annual height growth rates (mean 17.83 cm year⁻¹, $n = 4$) occurred on the 18-month-old burn site at Lake Ohia east, which had the youngest shrubs and the highest foliar nutrient levels (means 1.30 N, 0.057 P % dry weight, and -1.33‰ δ¹⁵N). The lowest annual height growth rates occurred on the shallow soil pan at Lake Ohia south (mean 5.36 cm year⁻¹, $n = 7$). There, although shrub age (mean 19.4 years) and foliar N and P levels (means 0.847 N, 0.033 P % dry weight) were around the gumland averages, foliar δ¹⁵N (mean -12.6‰) and drainage ('very poor' drainage category for all plots) were the lowest recorded.

For *Leptospermum* height and nutrient correlations, the recently burnt Lake Ohia east plots were omitted, leaving a sample size of 150. This was because mean foliar nutrient levels in these plots were significantly higher for P, N, and δ¹⁵N, and fire has been shown to elevate nutrient levels in wetlands for up to two years (Wilbur & Christensen 1983). Using the reduced dataset, height was positively correlated with foliar N ($r^2 = 0.25$, $P < 0.0001$), P ($r^2 = 0.18$, $P < 0.0001$), and δ¹⁵N ($r^2 = 0.10$, $P = 0.0001$).

Vegetation classification

Six ecologically interpretable groups, delineated by a FUSE dissimilarity value of 2.45, were selected to characterise the gumland vegetation (Fig. 3, Appendix 3). The groups were assigned vegetation type names according to dominant species composition and structure following Atkinson (1985). Two groups, *Leptospermum* shrubland, characteristic of relatively well drained plots, and *Gleichenia* fernland, confined to poorly drained plots, together comprised 70% of all plots.

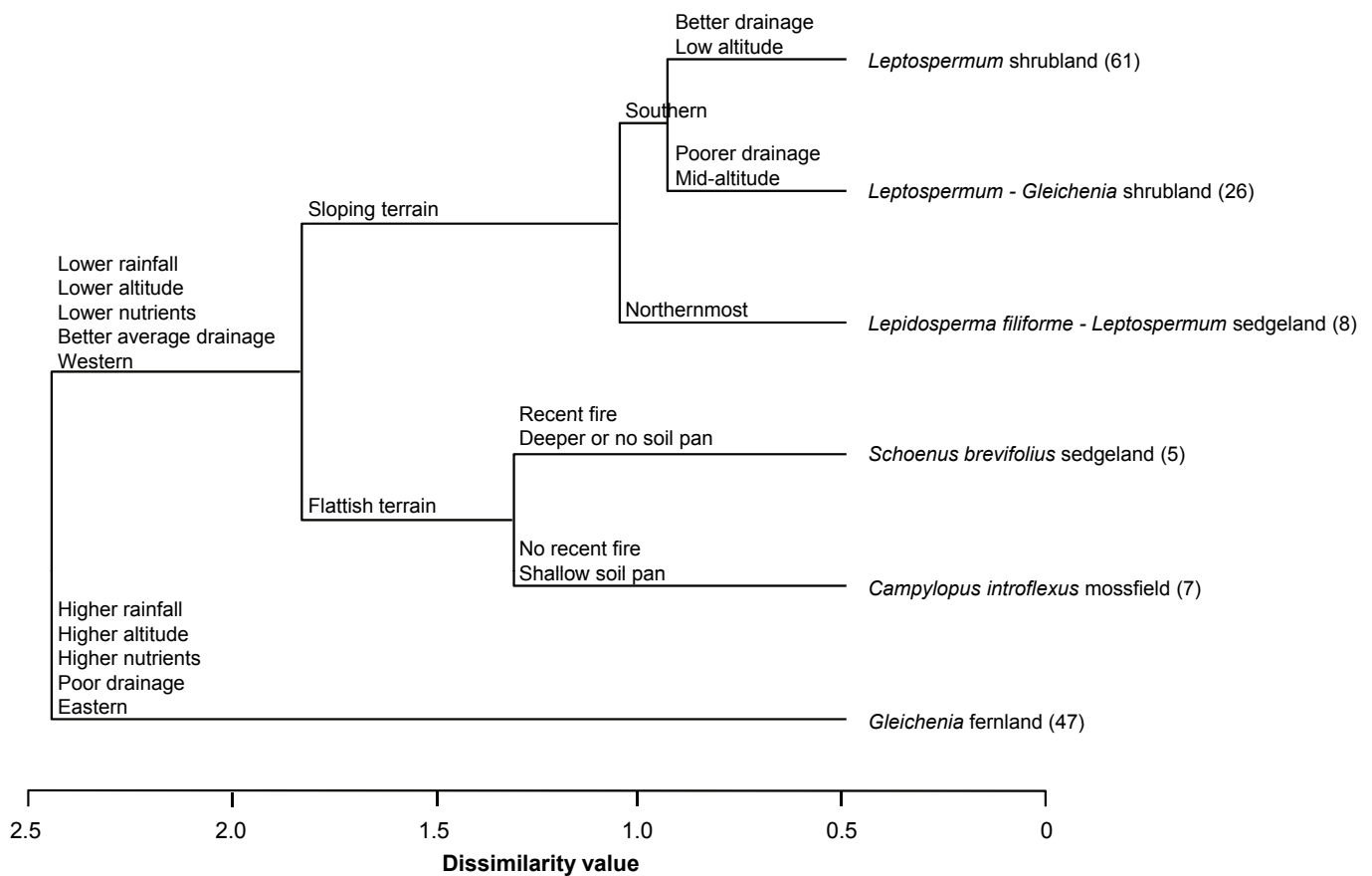


Figure 3. Hierarchical relationships of vegetation types in gumlands and associated environmental contrasts. The number of plots in each type is in parentheses following the type name.

Intermediate between these two was a group containing both *Leptospermum* shrubland and *Gleichenia fernland* species in plots of intermediate drainage (17% of plots). Three small groups comprised a mossfield characterised by surface soil pan exposure, and two sedgelands, one very recently burnt and the other restricted to the northernmost location. Only four indigenous species, *Leptospermum*, *Gleichenia*, *Baumea teretifolia* and *Schoenus brevifolius*, and one non-native species, *Hakea sericea*, were consistently present (in >50% of plots) and contributed >5% of average canopy cover in any vegetation type. Two other species, *Lepidosperma filiforme* and the moss *Campylopus introflexus*, were locally abundant, each contributing >35% of average canopy cover in two different vegetation types. Two further species, *Dracophyllum lessonianum* and *Dianella haemata*, were consistently present but both with low mean cover. The vegetation types together with their environmental characteristics are described below:

Leptospermum shrubland (9 sites, 61 plots)

This group represents the largest and most common gumland vegetation type, dominated by short dense *Leptospermum* (mean height 1.17 m, mean canopy cover 64%), with *Schoenus brevifolius* and *Hakea sericea* as minor associates. *Lepidosperma filiforme*, *Gleichenia*, *Baumea teretifolia* and *Dracophyllum lessonianum* were also locally present. *Leptospermum*, *Hakea sericea* and *Tetraria capillaris*

occurred most commonly in this type. Mean species richness was 10.8 species per 100 m², of which non-native species contributed 1.5. The mean non-native species canopy cover of 7.2%, however, was the highest of any type and nearly twice the second-ranked type (3.8%, *Lepidosperma filiforme* - *Leptospermum* sedgeland). This type was widespread on broad ridges and gently sloping terrain at low altitude (mean = 60 m a.s.l.), particularly in the north and west. Soils were mature podzolic soils, mostly of sandy texture with a shallow E horizon (mean depth 17 cm) above a pan (mean depth 50 cm), and imperfectly to poorly drained. They were extremely low in C and nutrients, especially N, and had low CEC. In addition, the *Leptospermum* foliar N and P levels were among the lowest of all vegetation types. *Leptospermum* ages ranged from 4 to 39 years (mean = 15 years), which suggests a history of relatively recent fires.

Gleichenia fernland (9 sites, 47 plots)

The second largest group was dominated by the fern *Gleichenia* (mean cover 69%), with *Leptospermum* a consistent but minor associate. Other typical species were *Baumea teretifolia*, *Dracophyllum lessonianum* and *Schoenus brevifolius*. Mean vegetation height was 1.13 m, but emergent shrubs up to 3 m tall of *Leptospermum* and, more rarely, *Dracophyllum lessonianum*, were scattered throughout. *Gleichenia*, *Baumea teretifolia*, *Dracophyllum lessonianum* and *Cladia retipora* occurred most commonly in this type. Mean species richness

was 8.9 per 100 m², including 0.2 non-native species, the lowest non-native richness of any group. This type characteristically occurred on flat terrain at relatively high altitudes (mean 230 m a.s.l.) in the east and south. Soils were either organic peats, or podzolic clays (occasionally silts) with deeper E horizons (mean depth 26 cm) and pans (mean depth 61 cm). All were poorly to very poorly drained and acidic (pH 4.01–5.45), and relatively high C, N, and P levels, and *Leptospermum* foliar N and P values were also relatively high compared with other vegetation types. The average age of *Leptospermum* was 26 years (range 7–43 years), indicating that fires are probably less frequent in this vegetation type than in most others.

Leptospermum–*Gleichenia* shrubland (9 sites, 26 plots)

Transitional between the above two types was shrubland of mainly *Leptospermum* (mean cover 40%) interspersed with *Gleichenia* (20%), and *Schoenus brevifolius* (10%). Local admixtures of *Baumea teretifolia*, *Campylopus introflexus*, *Dracophyllum lessonianum* and *Dianella haemata* also occurred. *Leucopogon fasciculatus* occurred most commonly in this type. At 12.4 species (non-native species 0.8) per 100 m², mean species richness was the highest of any type. With the exception of the orchid *Calochilus paludosus*, all threatened species (7) recorded within the plots occurred in the *Leptospermum*–*Gleichenia* shrubland type. This type was scattered over the geographical range of gumlands, and intermediate between *Leptospermum* shrubland and *Gleichenia* fernland in means of altitude, E horizon depth, pan depth, soil and foliar nutrient levels, time since last fire, and vegetation height.

Lepidosperma filiforme – *Leptospermum sedgeland* (1 site, 8 plots)

Confined to the northernmost gumland (Spirits Bay), this type was characterised by large tussocks of *Lepidosperma filiforme* interspersed between *Leptospermum* shrubs. Other canopy associates included *Cassytha paniculata*, *Hakea sericea* and *Schoenus brevifolius*. *Cassytha paniculata*, *Epacris pauciflora*, *Lepidosperma filiforme* and the non-native *Hakea gibbosa* occurred most commonly in this type. Mean species richness of 6.9 per 100 m² was the lowest of any type. Mean non-native richness was 1.4 per 100 m², representing 20% of the total flora, the highest percentage of any type. This type occurred on broad ridge crests and upper slopes (mean slope angle 5.8°, the highest of all vegetation types). The soils were clay and although imperfectly to poorly drained, overall were the best drained in the survey, and typically with no E horizon or pan evident. Values for C, N and P (and *Leptospermum* foliar N and P) were low, but exchangeable Ca, K, Mg, Na were relatively high, probably because of a strong maritime influence. *Leptospermum* age ranged from 8 to 36 years, with a mean of 20 years.

Schoenus brevifolius sedgeland (2 sites, 5 plots)

This was a sparsely vegetated type dominated by short *Schoenus brevifolius* (mean height 32 cm, mean cover 13%), reflecting early stages of recovery from recent fire. Occasional *Leptospermum* were present, along with a variety of short herbs such as *Drosera peltata* subsp. *auriculata*, *Gonocarpus aggregatus*, *Hypochaeris radicata*, *Lycopodiella lateralis*, and *Lycopodium deuterodensum*. *Dianella haemata*, *Drosera* spp., *Gonocarpus aggregatus*, *Lycopodium deuterodensum* and *Schoenus brevifolius* occurred most commonly in this type. Mean species richness was 9.4 per 100 m², including

1.6 non-native species. All except one of the plots were burnt 18 months before sampling (P.T. Whaley pers. comm.), and *Leptospermum* ring widths and foliar N, P and $\delta^{15}\text{N}$ values were the highest recorded in the survey.

Campylopus introflexus mossfield (1 site, 7 plots)

A distinctive moss-dominated type (mean cover 48%) was confined to flat terrain at one gumland (Lake Ohia south). Occasional shrubs of *Leptospermum*, *Kunzea ericoides* var. *linearis*, *Hakea sericea* and *Ulex europaeus* were emergent above the moss carpet. Other species present included *Drosera peltata* var. *auriculata*, *Morelotia affinis*, *Lycopodiella cernua* and *Schoenus brevifolius*. *Campylopus introflexus*, *Kunzea ericoides* var. *linearis* and *Ulex europaeus* occurred most commonly in this type. Mean species richness of 10.9 per 100 m² was relatively high, and mean non-native species of 2 was the highest of any type. Soils were very poorly drained peat over a shallow pan (mean depth 1 cm) that was frequently exposed at the surface. *Leptospermum* foliar nutrient levels were low and $\delta^{15}\text{N}$ signatures were the most depleted of all vegetation types (mean = -12.46‰). *Leptospermum* age ranged from 9 to 24 years, with a mean of 19 years.

Vegetation composition and environment

The plot ordination overlaid with the six vegetation types (Fig. 4A) indicates clear floristic trends. Plots are arranged along Axis 1 from those overwhelmingly dominated by *Leptospermum* (low Axis 1 scores) through those with prominent cover of both *Leptospermum* and *Gleichenia*, to relatively homogeneous plots dominated by *Gleichenia* (high scores). The peripheral plots represent small types which are floristically dissimilar, e.g. those modified by recent fire (*Schoenus brevifolius* sedgeland) on the lower right of the ordination, those with prominent *Lepidosperma filiforme* (*L. filiforme* – *Leptospermum* sedgeland) confined to the northernmost gumland on the left of the ordination, and open-canopied *Campylopus introflexus* mossfields on exposed soil pans with both high and low scores on Axis 2.

There are distinct patterns in environmental variables in this ordination (Fig. 4B). The main trend from left to right along Axis 1 reflects an underlying gradient of increasingly impeded drainage, from imperfectly drained broad sandy ridges to very poorly drained peaty basins. Species centroids show that the three most significant species also reflect this pattern, from *Leptospermum* with low Axis 1 scores to the typical wetland species *Baumea teretifolia* and *Gleichenia* with higher Axis 1 scores. Maximum vegetation height, and *Leptospermum* age (and *Leptospermum* height and diameter), all increase along this gradient, suggesting progressively longer periods since disturbance (less frequent fires) as drainage becomes more impeded. Along the same gradient, total species richness, non-native species richness and non-native cover decrease. Plots with high Axis 1 scores are at higher altitudes and in eastern parts of the gumland range, which typically have higher rainfalls. These plots also have deeper (or no) soil pans and higher plant nutrient concentrations, with %N (N as % dry weight of *Leptospermum* foliage) being the mostly strongly correlated with the plot ordination ($r^2 = 0.329$, $P < 0.0001$, $n = 154$).

Plots that have been very recently burnt (<2 years) are separated out with low Axis 2 scores. These *Schoenus brevifolius* sedgeland plots have short vegetation (mean canopy height <0.5 m), but with relatively high nutrient levels (mean *Leptospermum* foliar N 1.23, P 0.05 % dry weight).

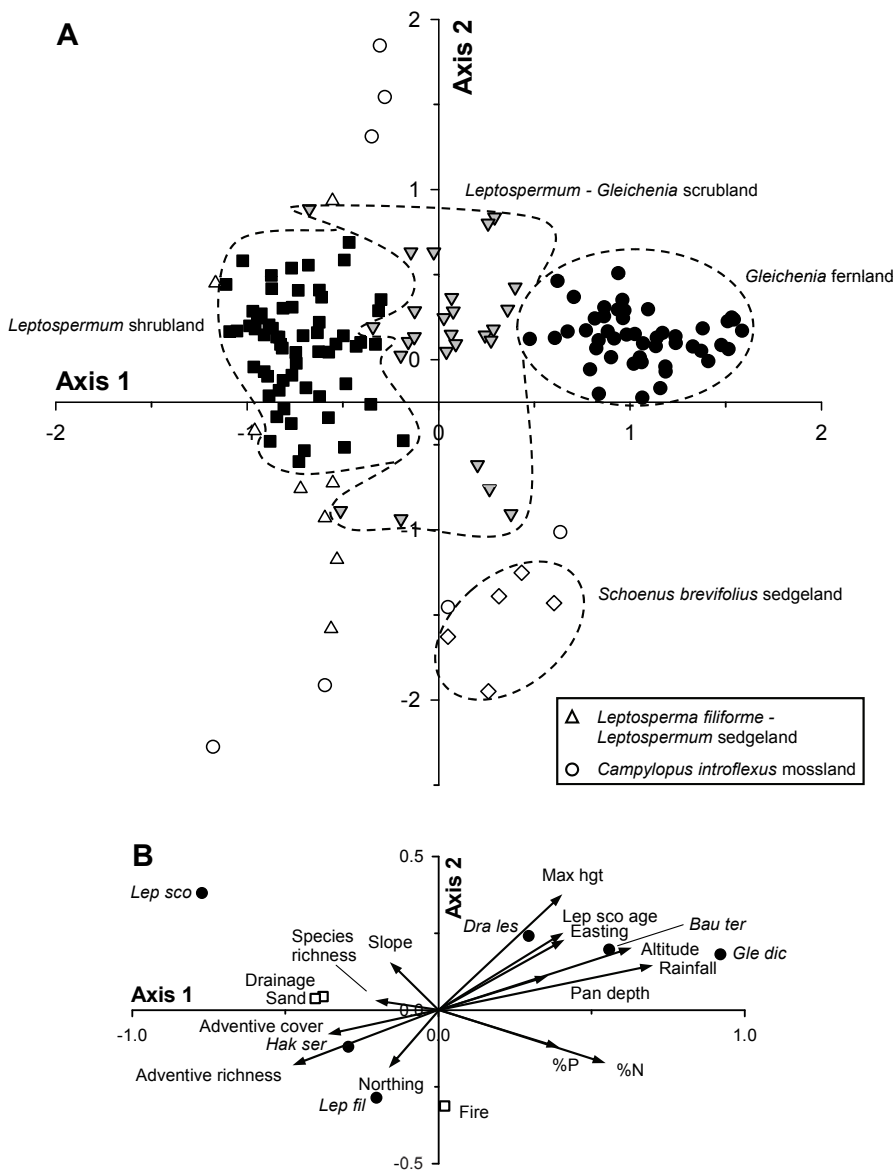


Figure 4. A. Two-dimensional plot ordination of 154 plots based on canopy cover of 66 species in 15 gumlands in northern New Zealand. Plots have been overlaid according to vegetation type derived from the classification. **B.** Significant ($P < 0.01$) fitted vectors, species centroids (circles) and categorical environmental variables (squares). Vectors for *Leptospermum* height and diameter are almost congruent with the vector for *Leptospermum* age and are not shown for reasons of clarity. Dra les = *Dracophyllum lessonianum*, Gle dic = *Gleichenia dicarpa*, Hak ser = *Hakea sericea*, Lep sco = *Leptospermum scoparium*, Lep fil = *Lepidosperma filiforme*. Drainage, Sand and Fire indicate correlation and directional trend for increasing drainage, soil sand component, and recency of fire respectively.

Plots with low scores on Axis 2 tend to be concentrated in low-altitude northern gumlands (<100 m a.s.l.), have been more recently disturbed (vegetation is younger), and are strongholds for *Lepidosperma filiforme* and the non-native shrub *Hakea sericea*. Many of these plots belong to the northern *Lepidosperma filiforme* - *Leptospermum* sedgeland, and a subset of the larger *Leptospermum* shrubland type.

Discussion

Environmental determinants of gumland vegetation

The primary environmental factors related to the structure and composition of gumland vegetation are drainage and nutrients, congruent with those reported for heathlands elsewhere in the world (Specht 1979). Classification and ordination showed the main vegetation types separate out along a drainage gradient from shrubland dominated by *Leptospermum* in relatively better drained plots, through *Leptospermum*-*Gleichenia* shrubland in plots with intermediate drainage, to fernland dominated by *Gleichenia* in poorly drained ones. The drainage pattern has a

geographic component; plots with better drained soils tend to be at lower altitudes and have less rainfall. At the permanently wet end of the gradient, *Gleichenia* fernland merges into fen and bog wetland classes (Johnson & Gerbeaux 2004) in which the restiad *Empodisma minus*, an occasional gumland associate, dominates. Along with deteriorating drainage, soils change from being typically sandy in texture and strongly leached to having an increasing organic component and nutrients, especially N and P, increase. Overall, soil nutrient levels are extremely low (Blakemore et al. 1987), with N (mean = 0.182% oven-dry soil) being higher and P (mean = 0.004%) lower than in Australian heathlands (mean N = 0.082%, P = 0.082%; Groves 1983) and South African coastal fynbos (N = 0.005%, P = 0.06%; Specht & Moll 1983).

Leptospermum mean annual height growth rates of 11.90 cm year⁻¹ also reflect low nutrient availability in gumlands. Even the highest growth rates on gumlands (mean 17.83 cm year⁻¹) are lower than *Leptospermum* mean annual height growth rates of 26.0 cm year⁻¹ on Great Barrier Island lower hill slopes (Perry et al. 2010), 29 cm year⁻¹ on East Coast hill country (Bergin et al. 1993) and 36.6 cm year⁻¹ for Waikato peat bog undergoing restoration (ages 1–6; BRC unpubl. data)

while the lowest (mean 5.36 cm year⁻¹) are similar to shrubland on ridges degraded by repeated fire on Great Barrier Island (5.3 cm year⁻¹; Perry et al. 2010). *Leptospermum* growth rates on gumlands, as determined by mean ring width (0.80 mm), are very similar to pakihi heathlands in Westland, South Island, where the mean ring width was 0.82 mm (Williams et al. 1990). *Leptospermum* foliar nutrient levels of low P (mean = 0.034% dry weight), high N:P ratios (mean = 26.9), and depleted $\delta^{15}\text{N}$ (mean = -6.06‰) suggest that New Zealand gumlands are phosphorus- rather than nitrogen-limited (see Verhoeven et al. 1996; Clarkson et al. 2005). This aligns with other Southern Hemisphere heathlands, as fertilisation experiments in Australia and South Africa showed growth responses to P addition rather than N (Specht 1963; Specht & Groves 1966; Specht et al. 1977; Witkowski 1989). Similar experiments to determine the nature of the nutrient limitation in New Zealand gumlands, however, have yet to be conducted.

Overlying the main vegetation sequence is time since disturbance, mainly by fire, which interacts with the primary gradient in that better drained sites burn more frequently and probably more intensively than poorly drained ones. Fire temporarily increases nutrients (Wilbur & Christensen 1983), and regenerates the system by creating new open habitat and setting back successional processes (Clarkson 1997). This is supported by our study, which showed *Leptospermum* nutrient levels and growth rates in the *Schoenus brevifolius* sedgeland vegetation type were significantly elevated some 18 months after fire. Burning kills fire-sensitive shrubs (= seeders) such as *Leptospermum*, *Dracophyllum* spp. and the prominent non-native invasives *Hakea sericea* and *H. gibbosa*, allowing resistant rhizomatous species to dominate temporarily (= resprouters, e.g. *Schoenus brevifolius* at recently burnt Lake Ohia east), before the shrubs re-establish and eventually reassert dominance via their seed bank (Wardle 1991). Newly created open habitat during the early stages of fire recovery promotes the establishment and survival of rare species such as light-requiring orchids and diminutive species (e.g. the tuberous lycopod *Phylloglossum drummondii*), as well as providing the temporarily nutrient-enriched habitat favoured by non-native herbs and grasses. Different types of disturbances contribute to overall habitat diversity, which helps maintain species richness. The most heavily disturbed areas can be attributed to former gumdigging activities, which included substrate excavation and scouring, resulting in exposed soil pans. This is compounded by further loss of the nutrient pool and degradation of the vegetation through regular fires. Harsh environments such as these enable normally transient heathland communities to maintain themselves as more or less stable communities (Wardle 1991) and retard succession to increasingly distant forest (Perry et al. 2010).

Plant community variation and composition

Soil nutrient availability is the major environmental factor determining the nature and distribution of heathland plant communities throughout the world, with broad vegetation physiognomy controlled by moisture relationships (Groves 1983). This also applies here, with individual gumlands being characterised by mosaics of vegetation reflecting the underlying soil drainage and nutrient levels and to a lesser extent, recent disturbance. The three main vegetation types were present at most gumland sites, particularly the larger ones (>80 ha), but the abundance of types within and between sites was strongly influenced by site rainfall and altitude. Overall, gumlands at coastal or semi-coastal sites in lower rainfall areas had drier

heath communities, whereas inland and higher altitudes sites with higher rainfall had wetter heath communities. Exceptions were caused by local topography and environmental conditions. For example, the *Gleichenia* fernland wetter type occurred on flat, poorly drained terrain at lower-rainfall, semi-coastal Lake Ohia east (mean annual rainfall 1374 mm, mean altitude 9 m), and the *Leptospermum* shrubland drier type covered better drained hillsides at higher rainfall, inland Whakaruangangana (mean annual rainfall >1600 mm, mean altitude 150 m). The three remaining vegetation types were minor and each confined to a single gumland. Two were the result of human-induced modification, i.e. early-successional *Schoenus brevifolius* sedgeland at recently burnt Lake Ohia east, and *Campylopus introflexus* mossfield at Lake Ohia south, heavily impacted by intermittent inundation and by gumdigging activities more than 60 years ago. The final vegetation type, dominated by *Lepidosperma filiforme*, occurred on clay soils only at the northernmost Spirits Bay site.

The gumland flora is dominated by a small but distinctive suite of species. Although they all occur in other heath communities, gumlands are the modal habitat for some, e.g. *Dracophyllum lessonianum* and *Schoenus brevifolius* (Clunie 1983). The four most frequent and abundant, *Leptospermum*, *Gleichenia*, *Baumea teretifolia* and *Schoenus brevifolius*, are widespread on damp, infertile soils in northern New Zealand (Johnson & Brook 1998). *Leptospermum*, present in all plots and with a mean cover of 39%, has a high tolerance of waterlogging, which induces development of aerenchyma and other morphological adaptations (Cook et al. 1980). This may confer a strong competitive advantage over less well adapted species on frequently waterlogged sites (Pryor et al. 2006). *Leptospermum* is also highly tolerant of drought (Burrows 1973), in common with other evergreen sclerophyllous heathland species worldwide (Specht 1981b; Connor & Doley 1981). In addition, it can have dual ectomycorrhizal and arbuscular mycorrhizal associations, which enhance nutrient uptake (Moyersoen & Fitter 1999). The flora is generally consistent between all gumlands, with only minor exceptions. For example, *Lepidosperma filiforme* and the parasitic liane *Cassytha paniculata* were largely confined to northern gumlands (being most prominent at Spirits Bay), and *Dracophyllum lessonianum* was replaced by *D. sinclairii* at the southernmost (Waikumete) site. Species richness at each site depended on size and topographic variation, and local environmental conditions, e.g. the wetter *Gleichenia* fernland had lower species richness (mean = 8.9 per 100 m²) than intermediate-drainage (*Leptospermum*-*Gleichenia* shrubland; mean = 12.4 per 100 m²) or drier (*Leptospermum* shrubland; mean = 10.8 per 100 m²) types. Species richness is low compared with heathlands in South Africa (mean 28.1 per 12.5 m² for fynbos; Kruger 1979) and Australia (mean per 8 m² is 28.3 for dry heaths and 14.5 for wet heaths; Specht & Specht 1989).

Endemic species make up 47% of the indigenous vascular flora, slightly greater than the 40% recorded by Enright (1989) for the Spirits Bay gumland, but low compared with the 82% endemism for the whole New Zealand flora (de Lange et al. 2006). In addition, some 44% of gumland species are also native to Australia, located 2200 km westward (Appendix 2). The relatively low endemism and high percentage of shared species supports the notion of a relatively recent origin of gumland habitats and arrival of gumland species from eastern Australian heathlands (Given 1981; Enright 1989). Further evidence indicates that *Leptospermum*, the heathland dominant,

originated in Australia before the onset of Miocene aridity and was dispersed relatively recently to New Zealand, rapidly colonising open, particularly post-Polynesian, habitats of low available nutrients (Thompson 1989). Many of the species shared with Australian heathlands are orchids (e.g. *Thelymitra cyanea*), ferns (e.g. *Gleichenia*, *Lindsaea linearis*) or other species with light, wind-dispersed spores or seeds suitable for long-distance dispersal (e.g. *Leptospermum*). More species of small, tuberous orchid occur in open heathland (e.g. Esler and Rumball (1975) list 20 orchid species) than any other New Zealand vegetation type, although they represent only a small fraction from the much richer Australian heathlands (Wardle 1991). Several species originating from Australia are very rare in New Zealand (Given 1981; de Lange et al. 2009), notably the lycopods *Phylloglossum drummondii* and *Lycopodiella serpentina*, and the ground orchid *Calochilus herbaceus*. Of the threatened species recorded in our survey, four are also native to Australia, and five are endemic.

Threats to gumlands

The threats to New Zealand gumlands are similar to those influencing heathland conservation elsewhere in the world (e.g. Gimingham 1981; Kruger 1981; Specht 1981a; Keith et al. 2002; Darkoh 2009). Gumlands without statutory protection are particularly at risk from habitat destruction by increased urbanisation, agricultural expansion and subsequent drainage and fertilisation, and potential wind farm development. Perhaps the main threat to legally protected gumlands is invasion by non-native woody plant species, e.g. *Hakea sericea*, *H. gibbosa*, *Erica lusitanica*, and the N-fixer *Ulex europaeus* (McQueen & Forester 2000). Only the highly invasive *Hakea sericea* is currently widespread, being recorded in more than half of the plots. This Australian species was introduced into New Zealand as a hedge plant and was already well established on gumlands by 1940 (Allan 1940). *Hakea* species are particularly adapted to extremely nutrient deficient soils by having proteoid or cluster roots, which function like mycorrhizas in enhancing plant uptake of phosphorus and other nutrients (Lamont 1981; Lambers & Shane 2007). Along with other species of *Hakea*, *Pinus* and *Acacia*, *H. sericea* is also one of the most invasive and problematic species in South African fynbos (Kruger 1981). These species originated in ecosystems with similar climates and infertile soils and thus can immigrate readily into undisturbed fynbos communities. All are adapted to survive regular fire regimes, reproducing profusely and establishing dense populations that can suppress natural communities to the point of extinction (Kruger 1981; Cronk & Fuller 1995).

Relatively few other non-native plant species have been successful in invading the extreme environments of gumlands (Esler & Rumball 1975). However, this may not continue, as increasing pressure from human activities encroaches on gumland ecosystems and their catchments, particularly development for agriculture and other activities, e.g. forestry, viticulture, and residential development (Sullivan et al. 2005). Gumlands without statutory protection are under greatest threat but even sites protected in reserves are subject to pressures from changes in their catchments, e.g. replacement of native species by non-natives and nutrient inputs from fertiliser drift and N-fixing plants such as *Ulex europaeus*. With the upgrading and extension of roads and associated land development, non-native species appear to be encroaching into the gumland ecosystem. Although the majority are still confined to roadsides and gumland margins, they represent potential invaders of the gumland proper. Weediness of wildlands has been positively

correlated with their proximity to roads, which represent linear corridors of disturbed habitat (Sullivan et al. 2009). Although most weed species have habitat requirements dissimilar from the wildland matrix, disturbance, e.g. clearance and nutrient enrichment, can create favourable habitat to facilitate their invasion (Wester & Juvik 1983; Pauchard & Alaback 2004).

Fire is an integral part of heathland ecosystems, and the plants that occupy them are adapted to frequent fire (Specht 1981a). For example, the dominant gumland species, *Leptospermum*, is more strongly serotinous (canopy seed storage) in the northern North Island (where gumlands occur) than in populations growing further south (Harris 2002). Fire frequency in gumlands increased dramatically following human arrival (Enright 1989). However, with the land-clearing phase largely over, statutory protection of most gumlands, and effective rural fire control, fires are now relatively uncommon (mean time since fire = 18.4 years). We do not know the extent to which gumland communities are induced and artefacts of a novel fire regime, as their Holocene history and transience in time and space remain largely unknown. The presence of seral forest species such as *Pteridium esculentum*, *Geniostoma ligustrifolium* and *Weinmannia silvicola* (Appendix 2) and tall mānuka and/or kānuka scrub fringing most sites suggest many are successional communities. They have slow rates of change under low-nutrient and waterlogged conditions exacerbated by retrogression caused by recurrent fire. We did not sample gumlands with vegetation >2 m tall. Our observations suggest that such gumlands tend to contain regenerating trees of early-successional forest species, and to occupy steeper slopes likely to be better drained than our sites, which had a mean slope of less than five degrees. Large areas of the Spirits Bay gumland studied by Enright (1989) were not sampled because their vegetation exceeded 2 m in height and is evidently reverting, albeit slowly, to forest in the absence of fire. Whether the environmental characteristics of these apparently ephemeral gumlands differ substantially from those of our study is unknown and clearly requires study.

Fire has not been used as a management tool in New Zealand gumlands, in contrast to Australian and South African heathlands (Specht 1981a; Keith et al. 2002; Everson et al. 2004). Research on fire frequency and subsequent seedling regeneration produced best-practice guidelines for maintaining species diversity in Australia (Groves 1968) and for controlling *Hakea sericea* invasions in South Africa (e.g. fell *Hakea* and burn within 12 months to kill resultant seedlings; van Wilgen et al. 2001). Too-frequent fire can cause losses in native species richness and diversity, and increase susceptibility to non-native plant invasion and dominance (Fisher et al. 2009). For long-term resilience and maintenance of a flora, a minimum fire-free interval of twice the juvenile period of the slowest maturing species has been suggested (Burrows & Wardell-Johnson 2003). The use of fire in managing gumlands is principally about retarding succession and maintaining early-successional habitats and species. However, non-native serotinous and/or large-seed-bank invasive species such as *Hakea* and *Ulex europaeus* are likely to be also promoted by fire. Research on the judicious use of fire as a management tool is recommended for long-term conservation of gumland community diversity and their threatened species. Future studies should focus on adapting solutions to similar management issues in heathlands overseas to New Zealand conditions, especially in relation to invasive species dynamics.

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Appendix 1. Soil chemical properties of composite samples from 15 gumlands in northern New Zealand, listed from north to south. Ngawha and Lake Ohia have been split into subsites characterised by different soil types. Exch. = exchangeable. Z = Podzol, O = Organic Soil, X = Oxidic Soil, U = Ultic Soil, G = Gley Soil (Hewitt 1992). *Main soil type (more than one type represented over all plots).

Site	Soil type	pH	Total C (%)	Total N (%)	Total P (mg kg ⁻¹)	Exch. Ca (cmol(+) kg ⁻¹)	Exch. Mg (cmol(+) kg ⁻¹)	Exch. K (cmol(+) kg ⁻¹)	Exch. Na (cmol(+) kg ⁻¹)	CEC (cmol(+) kg ⁻¹)	Base saturation (%)
Spirits Bay	Hurewai Clay (U)*	4.84	2.81	0.10	22	1.04	1.33	1.12	0.25	15.3	24
Karikari	Te Kopuru sand (Z)	5.10	3.17	0.11	28	1.36	1.86	0.32	0.48	12.7	32
Rangiputa	Te Kopuru sand (Z)*	4.69	3.97	0.12	22	0.88	0.49	0.14	0.07	10.2	15
Kaunaumau	One Tree Point peaty sand (O)	4.58	13.9	0.50	86	0.90	1.14	0.42	0.43	30.4	9
Lake Ohia east	Ohia sand (Z)	4.65	12.5	0.37	67	1.02	1.03	0.33	0.40	26.6	10
Lake Ohia south	Ruakaka peaty sandy loam (O)	4.68	7.72	0.29	115	0.65	0.39	0.43	0.33	16.3	11
Pairatahi	Te Kopuru sand (Z)	4.01	14.2	0.19	47	1.42	1.05	0.28	0.30	30.3	10
Pungaere	Wharekohe silt loam (U)*	4.41	3.95	0.15	20	0.25	0.30	0.08	0.18	10.4	8
Ahipara	Te Kopuru sand (Z)	4.28	4.73	0.11	36	0.39	0.58	0.39	0.24	15.6	10
Kerikeri Airport	Okaihau clay (X)	4.30	9.72	0.33	77	0.92	0.74	0.38	0.23	19.9	11
Aratoro	Wharekohe silt loam (U)	4.14	3.62	0.12	32	0.26	0.54	0.12	0.14	9.7	11
Ngawha west	Kara silt loam (G)	4.29	4.10	0.17	29	0.87	0.60	0.16	0.14	10.4	17
Ngawha east	Wharekohe silt loam (U)	4.44	2.48	0.08	22	0.47	0.56	0.10	0.10	9.4	13
Rakautao Bush	Wharekohe silt loam (U)	4.14	5.08	0.16	32	0.41	0.57	0.12	0.20	12.3	10
Whakaruangana	Wharekohe sandy loam (U)	4.56	2.51	0.08	26	0.31	0.35	0.05	0.14	7.2	12
Maitahi	Te Kopuru sand (Z)	5.45	2.86	0.09	41	0.48	0.37	0.07	0.11	7.0	15
Waikumete	Mahurangi Clay (U)	5.41	2.70	0.13	27	0.65	0.98	0.21	0.15	11.1	18

Appendix 3. Summary of species and environmental characteristics of the classificatory vegetation types of 15 gumlands in northern New Zealand. The first three are the main types and are ordered to match the dominant gradient (increasingly poor drainage), followed by the minor types that reflect local environmental conditions. Plot (100 m²) means for species percent canopy cover and for site variables are listed separately in decreasing order of significance for partitioning across the groups using the Kruskal–Wallis (KW) statistic, a non-parametric version of the *F*-ratio. A = *Leptospermum* shrubland, B = *Leptospermum–Gleichenia* shrubland, C = *Gleichenia* fernland, D = *Lepidosperma filiforme–Leptospermum* sedgeland, E = *Schoenus brevifolius* sedgeland, F = *Campylopus introflexus* mossfield.

	KW	Gumland vegetation type and number of plots					
		A (n = 61)	B (n = 26)	C (n = 47)	D (n = 8)	E (n = 5)	F (n = 7)
Species							
<i>Leptospermum scoparium</i>	120	64.2	40.4	13.3	32.9	2.8	9.6
<i>Gleichenia dicarpa</i>	118	1.8	20.0	69.3	0.0	0.8	0.0
<i>Baumea teretifolia</i>	86	0.5	5.4	6.8	0.0	0.2	0.0
<i>Hakea sericea</i>	45	5.8	0.8	0.1	1.5	0.2	1.15
<i>Dracophyllum lessonianum</i>	43	1.3	2.4	3.8	0.0	0.0	0.0
<i>Schoenus brevifolius</i>	33	12.9	9.8	3.9	10.8	13.0	0.4
<i>Lepidosperma filiforme</i>	30	1.4	0.4	0.0	39.3	0.0	0.0
<i>Campylopus introflexus</i>	21	0.1	3.4	0.0	0.0	0.0	47.6
Site variables							
Rainfall (mm)	91	1364	1429	1841	1350	1377	1392
Altitude (m a.s.l.)	83	61	140	229	97	51	8
Easting (° ')	75	173 29	173 22	173 48	172 52	173 20	173 22
<i>Leptospermum</i> height (cm)	69	165	173	268	183	33	104
<i>Leptospermum</i> leaf N (%)	68	0.76	0.82	0.97	0.82	1.23	0.85
Non-native canopy cover (%)	64	7.1	0.9	0.1	3.8	0.8	3.3
Maximum veg. height (cm)	61	188	204	285	198	71	147
Non-native species richness (<i>N</i>)	52	1.5	0.8	0.2	1.4	1.6	2
<i>Leptospermum</i> age (years)	47	14.8	16.1	25.6	20.1	3.2	19.4
<i>Leptospermum</i> diameter (cm)	40	2.30	2.53	3.69	3.54	0.64	2.40
<i>Leptospermum</i> leaf P (%)	36	0.030	0.032	0.040	0.030	0.050	0.033
Northing (° ')	35	35 14	35 16	35 20	34 29	35 00	34 59
<i>Leptospermum</i> leaf δ ¹⁵ N (‰)	31	−6.15	−6.78	−5.16	−5.58	−1.55	−12.5
Mean height (cm)	30	117	116	113	138	32	60
Total species richness (<i>N</i>)	30	10.8	12.4	8.9	6.9	9.4	10.9
Slope (degrees)	25	4.8	2.4	3.49	5.8	1.0	0.0
Pan depth (cm)	23	50	55	61	50	55	1