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A Classification of the Geothermal Vegetation of the Taupo Volcanic Zone, New Zealand

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ABSTRACT

We undertook stratified random sampling of vegetation and soil chemical fertility and subsurface temperature at 38 sites on 15 geothermal fields in the Taupo Volcanic Zone, central North Island, New Zealand, to develop the quantitative plot-based classification of geothermal vegetation types and to identify the main environmental drivers of vegetation composition. We used the approach of semi-supervised clustering to allow these new data to be incorporated into a pre-existing classification framework of New Zealand's woody vegetation. We implemented this with the fuzzy classification framework of Noise clustering. Gradients in composition were derived using Detrended Correspondence Analysis ordination and related to soil physical (temperature, surface substrate texture) and chemical (fertility) parameters using correlation. Of 138 vascular plant species, including 58 adventives, 19 moss and nine liverwort species recorded, only seven native species (*Kunzea ericoides* var. *microflora*, *Leucopogon fasciculatus*, *Dianella nigra*, *Pteridium esculentum*, *Campylopus pyriformis*, *Leptospermum scoparium*, *Chiloscyphus novae-zelandiae*) were present in >20% of plots and only four adventive species (*Rubus fruticosus*, *Axonopus fissifolius*, *Prunus serrulata*, *Agrostis capillaris*) in >5% of plots. Subsurface (10 cm depth) soil temperatures ranged from ambient (7 °C) to near-boiling (98.5 °C) and, on average, were nearly 18 °C above ambient. Classification identified 16 vegetation associations in eight structural classes (two mossfield, three fernland, one treefernland, one grassland, four shrubland, three scrub, one forest, one treeland), almost all dominated by indigenous species and unique to geothermal fields. A substantial number of plots (33) were compositional outliers, i.e., did not conform to any of the associations. Of these, a relatively high proportion were in urban or peri-urban areas with high weed pressure. There appear to be distinct regional patterns, with over half the associations observed on only one or two geothermal fields, and none on all of them. Subsurface soil temperature was the main factor controlling vegetation composition. Vegetation composition was less strongly correlated with soil chemical factors: base saturation, cation exchange capacity, pH, total nitrogen, organic carbon and aluminium levels. Geothermal vegetation in the Taupo Volcanic Zone is floristically very simple, dominated by a small suite of species, and occurs across stress gradients that extend well beyond active geothermal features. Most results from earlier site-specific studies in the region apply generally to geothermal vegetation across the Taupo Volcanic Zone. Geothermal vegetation on slightly warm to warm ground is susceptible to weed invasion, particularly in urban and peri-urban areas where weed pressure is high.

1. INTRODUCTION

Geothermal areas throughout the world provide unique habitats for biota through their distinctive combinations of unusual microclimatic and edaphic environments. The former include elevated air temperatures and humidity, the latter elevated soil temperatures, extremes of acidity and alkalinity, and unusually high – even toxic – concentrations of some metals such as aluminium. The high environmental stresses of these extreme environments exclude most vascular plant species and lead to plant communities that are very different from those of the surrounding matrix (e.g., Burns 1997, Convey et al. 2000, Stout and El-Niemi 2002). Thus geothermal vegetation – despite its frequent occurrence within forested bioclimatic zones – is generally dominated by bryophytes (e.g., Iceland: Elmarsdottir et al. 2003; Japan: Glime and Iwatsuki 1994; Antarctica: Convey et al. 2000) which are favoured by the warm, moist environments that prevail, or by grasses and herbs (e.g., Yellowstone National Park, USA: Stout and Al-Niemi 2002). In New Zealand, however, geothermal vegetation is unusual in that it is mostly dominated by woody vegetation (Wardle 1991).

The Taupo Volcanic Zone in the centre of New Zealand's North Island (Wilson et al. 1995) embraces most of New Zealand's surface geothermal features and most of its geothermally-influenced vegetation, with c. 580 ha of vegetation (Burns 1997) occurring at c. 90 sites on c. 25 geothermal fields (Fig. 1). The physical limitations and dangers inherent in active geothermal sites appear to have deterred rigorous quantitative sampling of their vegetation, with one exception, Te Kopia Geothermal Field (Burns 1997). A global classification is needed to provide an overview of the geothermal vegetation of the zone and to allow ready comparisons to be drawn between the vegetation on different geothermal fields in different parts of the zone. This is necessary for priorities to be set for conservation and for allocation of management resources amongst geothermal sites.

2. METHODS

Recent mapping of geothermal vegetation in the Waikato (Wildland Consultants 2011) and Bay of Plenty (Fitzgerald and Smale 2010) regions was used as the basis of stratification into 9 structural classes: soilfield, mossfield, grassland, fernland, shrubland, scrub, treefernland, treeland, and forest (Atkinson 1985). Within mapped areas of each structural class, random locations were generated for potential plot sampling. Sampling aimed to place 20 plots in each of the 9 classes. Thirteen known geothermal sites were excluded from the outset because of physical inaccessibility, access restrictions, small size, wetland nature, or commercial development having obliterated natural vegetation.

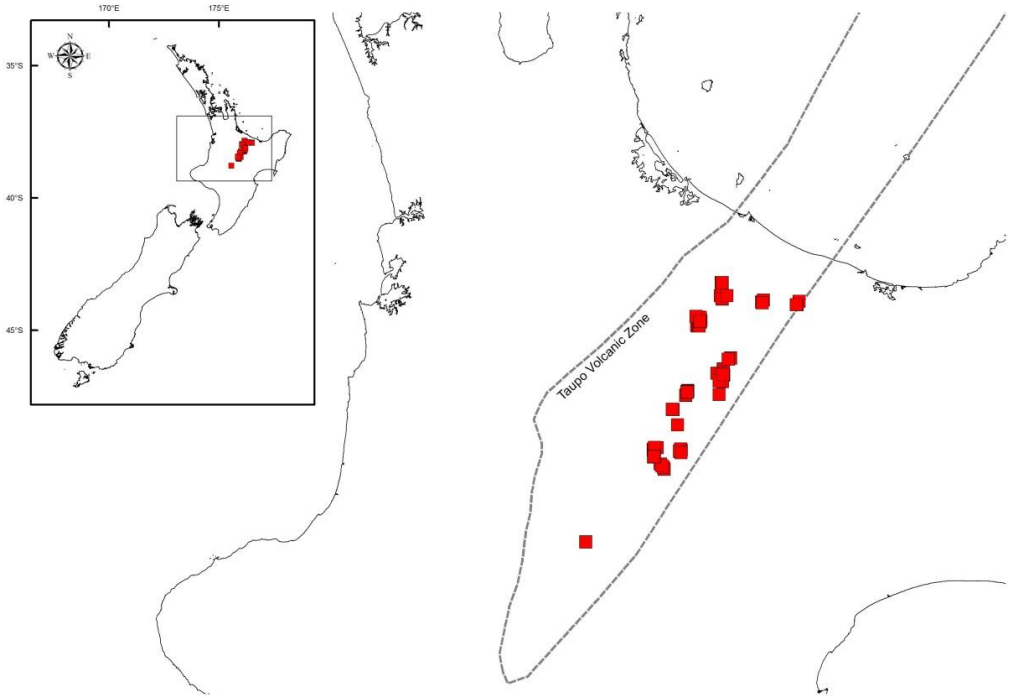

Figure 1 The Taupo Volcanic Zone on North Island, New Zealand, and the location of the geothermal fields sampled.

2.1 Data collection

We used a GPS to locate the pre-selected points. If it was not safe to sample the vegetation at this point, vegetation was sampled at the nearest safe location (using randomly allocated cardinal bearings and fixed distances of multiples of 5 m). After random plot sampling was completed at a site, any under-sampled rare (e.g., mossfield) vegetation types were sampled. Across all sites, 14 such subjectively located plots were sampled.

Varying plot sizes were used, reflecting vegetation stature, and ranging from 1×1-m in soilfield, through 2×2-m in short shrubland and scrub, and 5×5-m in taller shrubland and scrub, to 10×10-m in forest. Within each plot we recorded (Hurst and Allen 2007):

- Observed structural class
- Whether it occurred in an urban (i.e., within an urban area), peri-urban (i.e., on the edge of an urban area), or rural area
- Species abundance in seven fixed height tiers (0–30 cm; >30 cm–2 m; >2 m–5 m; >5 m–12 m; >12 m–25 m; >25 m; epiphyte) using a modified Braun-Blanquet cover-abundance scale (1 = <1%, 2 = 1–5%, 3 = 6–25%, 4 = 26–50%, 5 = 51–75%, 6 = 76–100%; Hurst and Allen 2007)
- All vascular species present, including invasive weeds, bryophytes and lichens
- Physiography, elevation, slope, aspect and drainage
- Subsurface soil temperature at 10 cm depth at 8 systematically-placed locations. In a small number of instances, for example silica terraces, substrates were too impenetrable for soil temperatures to be measured
- Subsurface (10 cm depth) soil temperatures were averaged for each plot and the means compared with ambient long-term soil temperatures (10 cm depth) for the same month (New Zealand Meteorological Service 1973) from the nearest climate station.

Soil samples to 10 cm depth were collected at the same 8 systematic locations within each plot and bulked for later analysis. Soil samples were analysed for pH, electrical conductivity, cation exchange capacity, organic carbon, total nitrogen, Olsen phosphorus, exchangeable bases (calcium, magnesium, sodium, potassium) and water-soluble sulphate following the procedures of Blakemore et al. (1987) and calcium chloride-extractable aluminum following Hoyt and Nyborg (1972). Parameter values were rated according to Blakemore et al. (1987).

2.2 Data analysis

Before classification and ordination cover scores within each height tier were converted to the midpoint of the percentage cover range for that cover class, and summed across tiers (e.g., Wiser et al. 2002). This generated an importance value reflecting the volume occupied by each species rather than its projected cover.

We used the approach of semi-supervised clustering (De Cáceres et al. 2010, Tichý et al. 2014) to allow these new data to be incorporated into a pre-existing classification framework of New Zealand's woody vegetation (Wiser & De Cáceres 2013). We implemented this with the fuzzy classification framework of Noise clustering.. This framework has two distinct advantages. First, it allows plot records that are compositional outliers to be recognized using quantitative criteria (De Cáceres et al. 2010). Secondly, it allows plots that are transitional in composition between defined types (e.g., those occurring on ecotones) to be recognized.

Resemblance between plots was defined using the Chord distance (Orlóci 1967). As a first step, we used this framework to determine whether any of the geothermal vegetation plots were sufficiently similar to woody vegetation associations defined by Wiser et al. (2011, 2013) to be classed as such. We then classified all plots that could not be assigned to the previously defined vegetation types with the constraint that the newly defined types would be as distinct as possible from these. We required a minimum of 2 plots to define a vegetation type. Those plots that were too dissimilar from others in the datasets to be included in a set that defined a vegetation type were designated as 'outliers'.

Once vegetation types (termed 'associations') were defined, we named them based on their dominant species. We defined dominant species for inclusion in the name by ranking the species in the association according to their relative constancy (% frequency in the type) and relative cover. Species were only listed by name if constancy > 85%; if there were more than 5 species with constancy over 85%, only the top 6 were listed. A "/" indicates the species occur in different tiers (working from the top tier down); "–" indicates they occur in the same tier. Within a tier, species are ordered by decreasing constancy. The letter 'GEO' before number below means it is a new association that has been defined only for geothermal areas. An 'a.' means the association has been defined at the national level by Wiser and De Cáceres (2013). Vegetation types were allocated to structural classes following Atkinson (1985).

To understand how vegetation composition related to environment, we derived gradients in composition using Detrended Correspondence Analysis ordination. We then used Spearman rank correlation to determine whether plot positions along these gradients were related to soil physical (temperature, surface substrate texture) and chemical (fertility) characteristics.

3. RESULTS

3.1 Soil chemistry

Soil chemistry varied considerably among plots and to a lesser extent, localities. On average, soils were strongly acidic (mean pH 4.3), with moderate levels of organic carbon (7.2 %) and Olsen phosphorus (25 mg/kg) and moderate cation exchange capacity (19.9 cmol/kg), but low base saturation (24.3 %) and low levels of total nitrogen (0.3%), calcium (2.5 cmol/kg), magnesium (0.6 cmol/kg), potassium (0.5 cmol/kg) and sodium (0.3 cmol/kg). They also had, on average, extremely high levels of aluminium (77 mg/kg) and sulphur (2347 mg/kg).

3.2 Soil subsurface temperature

Mean soil temperatures in plots ranged from ambient (lowest, 7 °C) to near-boiling (highest, 98.5 °C). Most fell in the ambient to slightly heated range of <20 °C (Table 1) and on average, were 17.8 °C above ambient temperatures.

Table 1 Soil temperature classes in 165 random plots in geothermal vegetation across the Taupō Volcanic Zone

Temperature	Thermal range (°C)	Number of plots
Cool (ambient) or slightly heated	<20	66
Warm	20–30	53
Hot	30–60	35
Very hot	>60	11

3.3 Flora

A total of 138 vascular plant species were recorded in plots, comprising 80 native and 58 adventive species. A total of 28 bryophyte species were recorded, comprising 19 moss and 9 liverwort species. Only seven native species were truly widespread, occurring in more than 20% of plots (Table 2). The three shrubby species, *Kunzea ericoides* var. *microflora*, *Leucopogon fasciculatus*, and *Leptospermum scoparium*, are all sclerophyllous and typical of heathlands on infertile soils across the country (Burrows et al. 1979). Only four adventive species (*Rubus fruticosus*, *Axonopus fissifolius*, *Prunus serrulata*, and *Agrostis capillaris*) were at all widespread, occurring in more than 5% of plots.

Table 2 Most widespread native species (occurring in more than 20% of plots) in geothermal vegetation in the Taupō Volcanic Zone.

Species	Frequency of occurrence (% of plots)	Mean cover (%)
Kunzea ericoides var. *microflora*	57	44
Leucopogon fasciculatus	52	25
Dianella nigra	39	3
Pteridium esculentum	28	4
Campylopus pyriformis	25	6

Leptospermum scoparium	25	8
Chiloscyphus novae-zelandiae	22	2

3.4 Vegetation classification

Stratification using existing mapping proved problematic because the structural classes observed at sampling points were not necessarily the same as those indicated by mapping. Over one-third of plots fell in the shrubland class, a reflection of the discord between mapped and actual vegetation classes and the overwhelming predominance (80% in existing mapping) of shrubland in geothermal vegetation.

Classification of the 155 plots (random and systematic) having both vegetation and soil samples identified 16 vegetation types (associations) in seven structural classes (Table 3), all but one of them – *Axonopus fissifolius* grassland – dominated by native species. The definitions of the associations were based on 118 plots; four plots were transitional between two or more defined associations. The associations comprise two mossfield associations dominated by *Campylopus* species, three fernland associations dominated by *Hypolepis* species or *Lycopodiella cernua*, one grassland association dominated by adventive *Axonopus fissifolius*, four shrubland associations dominated by *Leptospermum scoparium* and *Kunzea ericoides* var. *microflora*, three scrub associations dominated by *Kunzea ericoides* var. *microflora*, *Leptospermum scoparium*, or *Leucopogon fasciculatus*, one treefernland association dominated by *Dicksonia squarrosa*, one treeland associated dominated by *Kunzea ericoides*, and one forest association dominated by *Weinmannia racemosa*. Of these, two – *Leptospermum scoparium* shrubland (termed 'successional shrubland' in Wiser et al. 2013) and *Kunzea ericoides*/(*Coprosma–Leucopogon–Leptecophylla*) treeland (termed 'shrubland' in Wiser et al. 2013) – are sufficiently widespread in non-geothermal habitats to have been described in the national-scale plot-based classification of woody vegetation of Wiser et al. (2011, 2013).

A substantial number (33) of plots did not fall within any association, and a further substantial number (4) were transitional in composition between 2 or more defined associations. All unclassified plots were on slightly warm to warm ground (mean = 21 °C), significantly cooler on average than that of classified plots (32 °C). A higher proportion of them (38 %) than of classified plots (24 %) were in urban or peri-urban areas. Most associations appear to be of relatively restricted occurrence, over half recorded on only one or two geothermal fields in the Taupō Volcanic Zone and none on all of them.

Table 3 Vegetation associations of the Taupō Volcanic Zone. Codes beginning with 'GEO' are for associations defined in this project only. Those beginning with 'a.' have been defined at the national level in the shrubland classification of Wiser and de Caceres (2013) and follow the presentation at http://www.landcareresearch.co.nz/publications/factsheets/woody-types/shrublands/list-alliances.

Code	Name
GEOm1	*Campylopus pyriformis* mossfield
GEOm2	*Campylopus introflexus* mossfield
GEOg1	*Axonopus fissifolius* grassland
GEOfe1	*Hypolepis ambigua* fernland
GEOfe2	*Hypolepis distans* fernland
GEOfe3	*Kunzea ericoides var. microflora*/*Lycopodiella cernua* fernland
a: S1	*Leptospermum scoparium* shrubland
GEOsh1	*Leptospermum scoparium–Leucopogon fasciculatus–Kunzea ericoides* var. *microflora/Pteridium esculentum–Dianella nigra–Paesia scaberula* shrubland
GEOsh2	*Kunzea ericoides* var. *microflora–Leucopogon fasciculatus* shrubland
GEOsh3	*Kunzea ericoides* var. *microflora*/*Campylopus pyriformis* shrubland
GEOsc1	*Kunzea ericoides* var. *microflora* scrub
GEOsc2	*Leucopogon fasciculatus* scrub
GEOsc3	*Leucopogon fasciculatus–Kunzea ericoides* var. *microflora*/*Dianella nigra* scrub
GEOtf1	*Dicksonia squarrosa*/*Dianella nigra* treefernland
a: S5	*Kunzea ericoides*/(*Coprosma rhamnoides–Leucopogon fasciculatus–Leptecophylla juniperina*) treeland
GEOf1	*Weinmannia racemosa*/*Leucopogon fasciculatus–Pteridium esculentum–Leptecophylla juniperina*/*Telaranea* species–*Leucobryum javense* forest

Full descriptions follow:

3.4.1 *Campylopus pyriformis* mossfield (Fig. 2)

Structure and composition: Very short mossfield (mean height 5 cm), dominated entirely by *Campylopus pyriformis*. A floristically poor association, with no other species present. Habitat: Very hot (mean temperature at 10 cm depth 72 °C) ground on geothermal sites.

Figure 2. *Campylopus pyriformis* mossfield at Craters of the Moon/Karapiti.

3.4.2 *Campylopus introflexus* mossfield

Structure and composition: Very short (mean 3 cm, range 3-4 cm) mossfield, dominated by *Campylopus introflexus*. No other species are consistently present, i.e. in at least half the samples. Habitat: Hot (44 °C) ground on geothermal sites.

3.4.3 *Axonopus fissifolius* grassland

Structure and composition: Short (mean 0.5 m, range 0.3-0.7 m) grassland, dominated by adventive *Axonopus fissifolius*, with adventive *Agrostis capillaris* and the moss *Campylopus introflexus* also consistently present. Habitat: Warm (26 °C) ground on the margins of geothermal sites. This is the only association dominated by an adventive species.

3.4.4 *Hypolepis ambigua* fernland

Structure and composition: Tall (mean 2.1 m, range 1.4-6 m) fernland, dominated almost entirely by *Hypolepis ambigua*. No other species are consistently present, although *Histiopteris incisa* and *Pteridium esculentum* occur commonly. Habitat: Warm (21 °C) ground on the margins of geothermal sites.

3.4.5 *Hypolepis distans* fernland

Structure and composition: Tall (mean 2.8 m, range 1-9 m) fernland, dominated almost entirely by *Hypolepis distans*. *Histiopteris incisa* and *Pteridium esculentum* are also consistently present. Habitat: Warm (21 °C) ground on the margins of geothermal sites.

3.4.6 *Kunzea ericoides* var. *microflora/Lycopodiella cernua* fernland (Fig. 2)

Composition: Short (mean 0.6 m, range 0.2-1.3 m) fernland, dominated by *Lycopodiella cernua*, with scattered *Kunzea ericoides* var. *microflora* above it. No other species are consistently present. Habitat: Very hot (68 °C) ground on geothermal sites.

Figure 2. *Kunzea ericoides var. microflora/Lycopodiella cernua* fernland at Ohaaki.

3.4.7 *Leptospermum scoparium* successional shrubland

Structure and composition: Moderately tall (mean 3 m, range 0.3-6 m) shrubland, dominated by *Leptospermum scoparium*. *Kunzea ericoides* var. *microflora*, *Leucopogon fasciculatus* and *Histiopteris incisa* are consistently present. Habitat: Warm (24 °C) ground on the margins of geothermal sites.

3.4.8 *Leptospermum scoparium–Leucopogon fasciculatus–Kunzea ericoides* var. *microflora/Pteridium esculentum–Dianella nigra–Paesia scaberula* shrubland

Structure and composition: Tall (mean 9 m, range 6-19 m) shrubland, dominated by *Leptospermum scoparium*, *Leucopogon fasciculatus*, *Kunzea ericoides* var. *microflora* and *Pteridium esculentum*, over a ground layer dominated by *Dianella nigra* and *Paesia scaberula*. Adventive *Cytisus scoparius* is also consistently present. Habitat: Slightly heated (17 °C) ground on the margins of geothermal sites.

3.4.9 *Kunzea ericoides* var. *microflora–Leucopogon fasciculatus* shrubland

Composition: A variable association of widely varying height (mean 5 m, range 1-12 m) and structure (mostly shrubland, with some scrub, forest and treeland), dominated by *Kunzea ericoides* var. *microflora* and *Leucopogon fasciculatus*. *Dianella nigra* is also consistently present in the ground layer. Habitat: Warm (25 °C) ground on the margins of geothermal sites.

3.4.10 *Kunzea ericoides* var. *microflora/Campylopus pyriformis* shrubland

Structure and composition: Short (mean 0.4 m, range 0.2-1 m) shrubland, dominated by *Kunzea ericoides* var. *microflora* with a *Campylopus pyriformis* ground layer. No other species are consistently present, although *Lycopodiella cernua* is moderately widespread in the ground layer. Habitat: Hot (50 °C) ground on geothermal sites.

3.4.11 *Kunzea ericoides* var. *microflora* scrub

Composition: Short (mean 1 m, range 0.6-2.3 m) scrub, dominated almost entirely by *Kunzea ericoides* var. *microflora*. No other species are consistently present, although a range of bryophytes (*Chiloscyphus novae-zelandiae*, Telaranea praenitens, *Isopterygium* species) commonly occur. Habitat: Hot (39 °C) ground on geothermal sites.

Figure 3. *Kunzea ericoides* var. *microflora* scrub at Craters of the Moon/Karapiti.

3.4.12 *Leucopogon fasciculatus* scrub

Composition: Moderately tall (mean 3 m, range 1-10 m) scrub and shrubland, dominated by *Leucopogon fasciculatus*. No other species are consistently present. Habitat: Slightly heated (17 °C) ground on the margins of geothermal sites.

3.4.13 *Leucopogon fasciculatus–Kunzea ericoides* var. *microflora/Dianella nigra* scrub

Composition: Tall (mean 5.5 m, range 2-9 m) scrub, dominated by *Leucopogon fasciculatus* and *Kunzea ericoides* var. *microflora*, with a ground layer dominated by *Dianella nigra*. *Weinmannia racemosa*, *Myrsine australis*, and *Leptecophylla juniperina* are also consistently present, along with bryophytes (*Chiloscyphus novae-zelandiae*, *Lepidozia* species, *Telaranea* species, and *Dicranoloma robustum*). Habitat: Warm (24 °C) ground on the margins of geothermal sites.

3.4.14 *Dicksonia squarrosa/Dianella nigra* treefernland

Structure and composition: Short (mean 9 m, range 7-12 m) treefernland, dominated almost entirely by *Dicksonia squarrosa*, with a ground layer dominated by *Dianella nigra*. *Weinmannia racemosa*, *Pseudopanax arboreus*, *Myrsine australis* and *Leucopogon fasciculatus* are also consistently present. Habitat: Slightly heated (19 °C) ground on the margins of geothermal sites.

3.4.15 *Kunzea ericoides/(Coprosma rhamnoides–Leucopogon fasciculatus–Leptecophylla juniperina)* treeland

Structure and composition: Short (mean 9 m, range 8-9 m) treeland, dominated by *Kunzea ericoides* with an understorey dominated by *Coprosma rhamnoides*, *Leucopogon fasciculatus*, and *Leptecophylla juniperina*. *Knightia excelsa*, *Myrsine australis*, *Coprosma*

lucida, *Dianella nigra* and *Ptychomnion aciculare*, along with adventive *Cotoneaster glaucophyllus* and *Prunus serrulata*, are consistently present. Habitat: Warm (22 °C) ground on the margins of geothermal sites.

3.4.16 *Weinmannia racemosa/Leucopogon fasciculatus–Pteridium esculentum–Leptecophylla juniperina/Telaranea praenitens–Leucobryum javense* forest

Structure and composition: Short (mean 9 m, range 5-16 m) forest, dominated by *Weinmannia racemosa*, with an understorey dominated by *Leucopogon fasciculatus*, *Leptecophylla juniperina* and *Pteridium esculentum*, and a ground layer dominated by bryophytes (especially *Telaranea praenitens* and *Leucobryum javense*). A range of other trees and shrubs – *Pseudopanax arboreus*, *Myrsine australis*, *Leptospermum scoparium*, *Coprosma lucida*), megaherb (*Astelia solandri*), fern (*Dicranopteris linearis*, *Lycopodium deuterodensum*), and bryophyte (*Chiloscyphus novae-zelandiae*, *Ptychomnion aciculare*) species – are also consistently present. Habitat: Slightly heated (18 °C) ground on the margins of geothermal sites.

3.5 Relationships between vegetation and environment

The DCA ordination showed that compositional patterns largely reflect a single dominant vegetation gradient (Figs. 3, 4). This gradient is strongly related to a complex gradient reflecting changes in both soil temperature (Fig. 5) and soil chemistry (Table 4). Soil temperature, pH and base saturation decrease and aluminium, cation exchange capacity, total nitrogen and organic carbon increase from left to right along the compositional gradient. Boulders are more prevalent on cooler soils as well. A secondary compositional gradient shows a relationship with the amount of litter present. Species such as lichens, *Lycopodiella cernua*, *Campylopus pyriformis*, *Kunzea ericoides* var. *microflora* and *Campylopus introflexus* tend to occur at the warmer end of the primary gradient, whereas species such as *Pteridium esculentum*, *Histiopteris incisa*, *Dicksonia squarrosa*, *Pseudopanax arboreus*, *Rubus fruitcosus*, *Coprosma lucida* and *Kunzea ericoides* tend to occur at the cooler end (Fig. 3). Overlaying the association identities with the ordination shows how each association is restricted to a relatively small portion of this gradient (Fig. 4). The degree to which this reflects soil temperature is illustrated in Figure 3. Shorter associations dominated by mosses and by geothermal endemics (*Campylopus pyriformis*, *Kunzea ericoides* var. *microflora*) occur on the left side of the plot ordination (Fig. 4) and taller associations dominated by mesic species such as *Weinmannia racemosa* and *Dicksonia squarrosa* on the right side. The exceptions to this stature pattern are short fernland associations dominated by *Hypolepis ambigua* and *H. distans* on the right side of the ordination. Associations in which *Leucopogon fasciculatus* is prominent occur in the centre of the ordination. Adventive species occur across the entire compositional gradient, but are most diverse on the end of the compositional gradient on cooler sites with higher total nitrogen and organic carbon (Fig. 6).

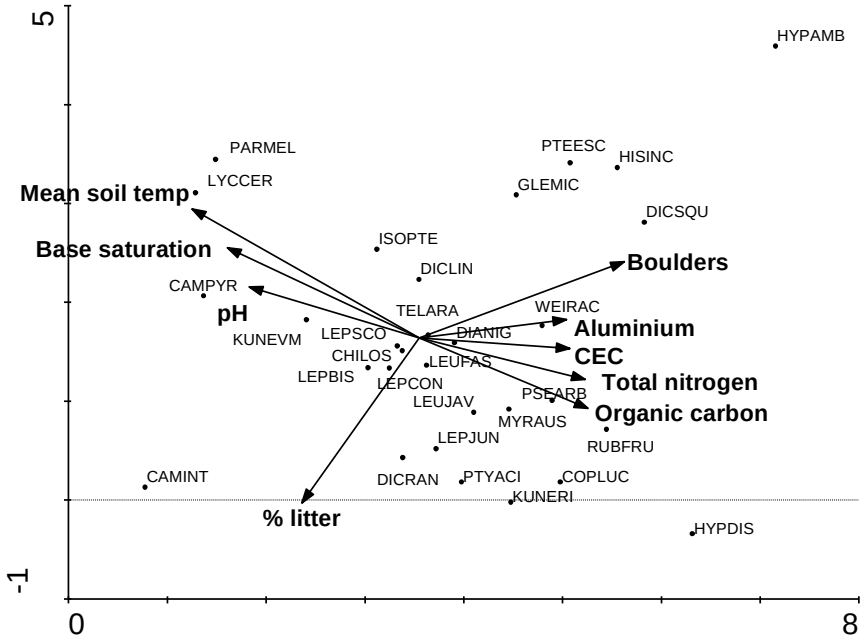

Figure 3 Species by environment biplot displaying results of DCA ordination of 155 plots with both vegetation and soil data in the Taupō Volcanic Zone. To simplify interpretation, only the most influential species and environmental variables are displayed. For environmental variables, those having R^2 with one or more axes > 0.18 are shown. For species, those 34 having a weight in the ordination > 4 are displayed. Species codes (* denotes adventive): CAMINT *Campylopus introflexus*; CAMPYR *Campylopus pyriformis*; CHILOS *Chiloscyphus* spp.; COPLUC *Coprosma lucida*; DIANIG *Dianella nigra*; DICLIN *Dicranopteris linearis*; DICRAN *Dicranoloma* spp.; DICSQU *Dicksonia squarrosa*; GLEMIC *Gleichenia microphylla*; HISINC *Histiopteris incisa*; HYPAMB *Hypolepis ambigua*; HYPDIS *Hypolepis distans*; ISOPTE *Isopterygium* spp.; KUNERI *Kunzea ericoides*; KUNEVM *Kunzea ericoides* var. *microflora*; LEPBIS *Lepidozia bisbifida*; LEPCON *Lepidozia concinna*; LEPJUN *Leptecophylla juniperina*; LEPSCO *Leptospermum scoparium*; LEUFAS *Leucopogon fasciculatus*; LEUJAV *Leucobryum javense*; LYCCER *Lycopodiella cernua*; MYRAUS *Myrsine australis*; PARMEL *Parmelia* spp; PSEARB *Pseudopanax arboreus*; PTEESC *Pteridium esculentum*; PTYACI *Ptychomnion aciculare*; RUBFRU **Rubus fruticosus*; TELARA *Telaranea* spp.; WEIRAC *Weinmannia racemosa.*

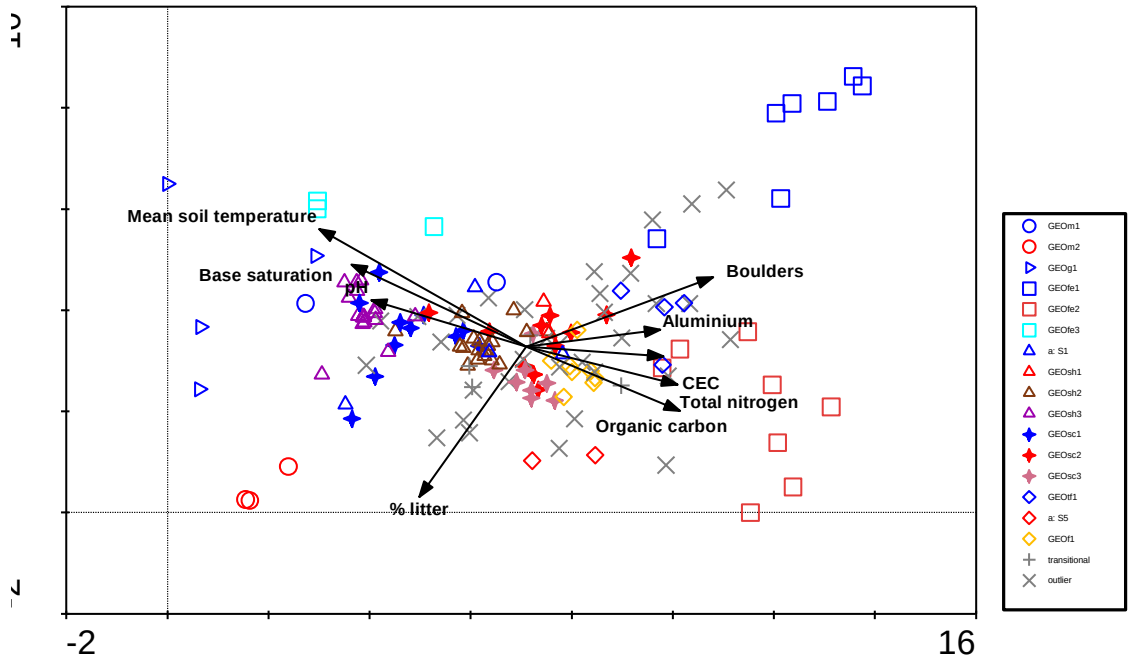

Figure 4 Plot by environment biplot displaying results of DCA ordination of 155 plots with both vegetation and soil data in the Taupō Volcanic Zone. To simplify interpretation, only the most influential environmental variables are displayed—i.e. those having R^2 with one or more axes > 0.18 are shown. Plots are coded by association with codes as in Table 3. The shapes of the association symbols reflect vegetation structure.

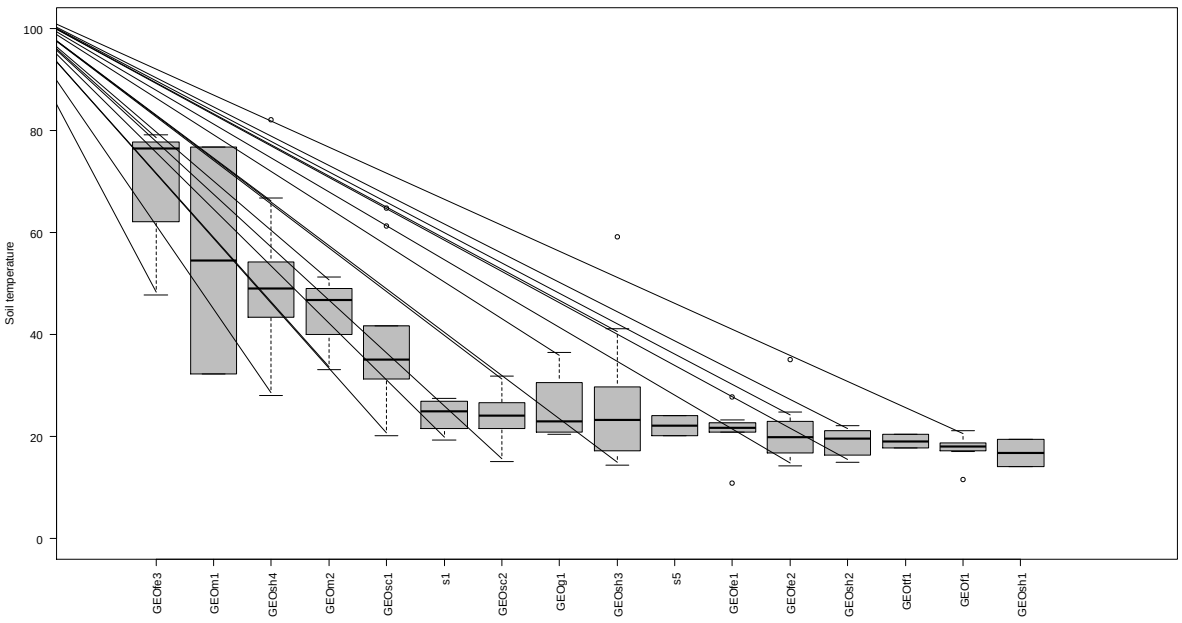

Figure 5 Box plot of soil temperature (10 cm depth) by vegetation association, ordered by descending median temperature. Horizontal bars represent median temperature; the top and bottom of the boxes represent the 75th and 25th quartile respectively; the dashed vertical lines show the maximum and minimum values. Association codes as in Table 3.

Table 4 Correlations of DCA axes with environmental parameters in geothermal vegetation associations of the Taupō Volcanic Zone. ** significant at p < 0.01.

Parameter	Axis 1	Axis 2
Soil temperature	-0.6**	0.3**
pH	-0.4**	0.2

Base saturation	-0.4**	0.2
Aluminium	0.5**	-0.1
CEC	0.5**	0.01
Total nitrogen	0.6**	-0.1
Carbon	0.6**	-0.2
Boulders	0.7**	0.1
Litter cover	-0.6**	-0.3**

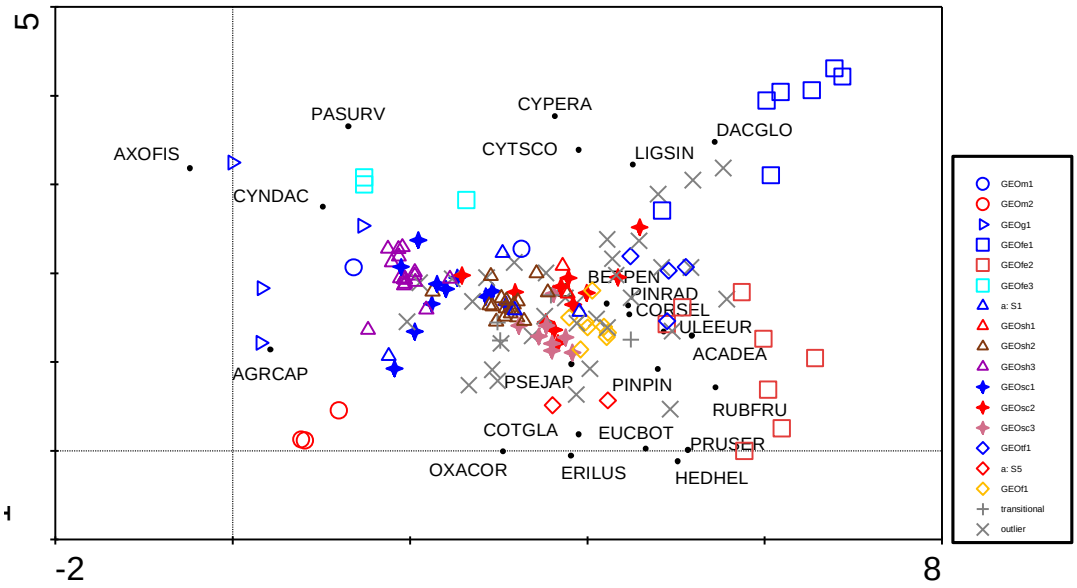

Figure 6 Adventive species by plot biplot displaying results of DCA ordination of 155 plots with both vegetation and soil data in the Taupō Volcanic Zone. Species occurring on 3 or more plots are shown. Plots are coded by association with codes as in Table 3. The shapes of the association symbols reflect vegetation structure. Species codes: ACADEA *Acacia dealbata*; AGRCAP *Agrostis capillaris*; AXOAFF *Axonopus fissifolius*; BETPEN *Betula pendula*; CORSEL *Cortaderia selloana*; COTGLA *Cotoneaster glaucophyllus*; CYND|AC *Cynodon dactylon*; CYPERA *Cyperus eragrostis*; CYTSCO *Cytisus scoparius*; DACGLO *Dactylis glomerata*; ERILUS *Erica lusitanica*; EUCBOT *Eucalyptus botryoides*; HEDHEL *Hedera helix*; LIGSIN *Ligustrum sinense*; OXACOR *Oxalis corniculata*; PASURV *Paspalum urvillei*; PINPIN *Pinus pinaster*; PINRAD *Pinus radiata*; PRUSER *Prunus serrulata*; PSEJAP *Pseudosasa japonica*; RUBFRU *Rubus fruticosus*; ULEEUR *Ulex europaeus.*

Vegetation height is strongly inversely correlated (r^2 = -4, $p < 0.01$) with soil temperature, with mean association height reducing dramatically at mean subsurface temperatures above 30 °C. Although varying plot size precludes analysis of species richness here, a similar trend appears likely.

4. CONCLUSIONS

Geothermal vegetation in the Taupō Volcanic Zone is floristically very simple, dominated by a small suite of tree (*Weinmannia racemosa*), shrub (*Kunzea ericoides* var. *microflora*, *Leucopogon fasciculatus*, *Leptospermum scoparium*, *Leptecophylla juniperina*, *Coprosma rhamnoides*), liane (adventive *Rubus fruticosus*), herb (*Dianella nigra*), grass (adventive *Axonopus fissifolius*), fern (*Dicksonia squarrosa*, *Hypolepis ambigua*, *H. distans*, *Pteridium esculentum*, *Paesia scaberula*), fern-ally (*Lycopodiella cernua*), and bryophyte (*Campylopus pyriformis*, *C. introflexus*, *Chiloscyphus novae-zelandiae*, *Telaranea praenitens*, *Leucobryum javense*) species. Of these, only seven native species (*Kunzea ericoides* var. *microflora*, *Leptospermum scoparium*, *Leucopogon fasciculatus*, *Dianella nigra*, *Pteridium esculentum*, *Campylopus pyriformis*, *Chiloscyphus novae-zelandiae*) are widespread. Apart from two species endemic to geothermal sites (*Kunzea ericoides* var. *microflora* and *Campylopus pyriformis*), the dominant species are all widespread in other mesic habitats. A small number of other tree (*Pseudopanax arboreus*, *Myrsine australis*, *Knightia excelsa*), shrub (*Coprosma lucida*), megaherb (*Astelia solandri*), and fern (*Histiopteris incisa*, *Dicranopteris linearis*) species are consistently or commonly present in some associations, along with a very small suite of weedy adventives (*Prunus serrulata*, *Cotoneaster glaucophyllus*, *Cytisus scoparius*, *Agrostis capillaris*). This floristic poverty reflects the highly stressed edaphic environment of geothermal sites.

Our study generalises specific results from three sites on two geothermal fields – Wairakei (Given 1980; van Manen and Reeves 2012) and Te Kopia (Burns 1997) – in the Taupo Volcanic Zone. Geothermally-influenced vegetation and geothermally-influenced

soils extend well beyond active geothermal features. A range of communities mostly unique to geothermal fields occurs across the spectrum of soil temperatures and chemistries present, most of them – including two that are widespread beyond them – on the extensive slightly heated soils surrounding geothermal features, with a small number on the smaller areas of markedly heated soils. Soil chemical fertility is generally low, with high acidity and high levels of sulphur and aluminium, the latter at levels that are normally toxic for plants.

Vegetation pattern appears to be controlled by a complex stress gradient reflecting variation in both soil temperature and possibly soil chemistry as well. Other features of the stress gradient at Te Kopia – decreasing canopy height, plant stature, leaf size, litter ground cover and probably species richness (although our methodology precludes analysis of this) with increasing soil temperature – also apply generally to vegetation on geothermal fields across the Taupo Volcanic Zone. There appear to be distinct regional patterns, with some associations – for example, *Leucopogon fasciculatus* scrub in the northern part of the zone – more common or apparently restricted to parts of the Taupo Volcanic Zone, and others – for example, *Kunzea ericoides* var. *microflora*/*Campylopus pyriformis* shrubland at Wairakei – apparently more-or-less restricted to one geothermal field.

Soil temperature is the main factor controlling vegetation pattern on geothermal fields elsewhere in the world, for example Ponponyama, Japan (Glime and Iwatsuki 1994), Iceland (Elmarsdottir et al. 2003), Yellowstone National Park, USA (Sheppard 1971), Mt Melbourne, Antarctica (Broady et al. 1987) and the South Sandwich Islands, Antarctica (Convey et al. 2000). Vascular floras are universally depauperate at geothermal sites, as here. In Iceland, as here, bryophytes dominate hotter soils and vascular plants cooler ones (Elmarsdottir et al. 2003).

Geothermal vegetation presents particular difficulties for classification and mapping because of the highly dynamic nature of the environment in both space and time. This is reflected in the substantial amount of discord between mapped and actual structural classes at sampling locations, and in the relatively large number of samples that were so dissimilar from all other samples that they did not conform to any defined association. However, a higher proportion of unclassified (38 %) than classified (24 %) samples were in urban or peri-urban areas, and generally had higher proportions of adventive species, reflecting the greater weed 'pressure' on them (Timmins and Williams 1991) and the apparently unpredictable successional trajectories of the mixed communities of indigenous and adventive species that are becoming ever more common in New Zealand. The one association dominated by an adventive species, *Axonopus fissifolius* grassland, seems likely to become more widespread in future.

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