

# Changes in western Waikato frost-flat heathland, 2013/14–2021

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Manaaki Whenua  
Landcare Research

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Prepared for: Waikato Regional Council

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*Contract Report: LC4052*

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# Summary

## Project and client

- Permanent vegetation monitoring plots were established in the remaining substantial frost-flat heathlands in the western Waikato Region in January–May 2013 and in January 2014, and remeasured from April to June 2021. Changes in vegetation composition and structure over this period were assessed for Waikato Regional Council.

## Objectives

- To identify changes in the condition of the substantial frost-flat heathlands remaining in the western Waikato Region.

## Methods

- Fifteen permanently marked 2 × 2 m plots were established at pre-selected random sites at the four largest intact frost flat sites remaining in the western Waikato Region in 2013 and 2014 and remeasured in 2021. One large site, Whenuakura Plain (72 ha), and two smaller sites, Pokaiora Clearing (38 ha) and Taparoa Clearing (23 ha), in Pureora Forest Park, were sampled, along with another smaller one, Kuratau (0.8 ha), in Waituhi-Kuratau Scenic Reserve, giving a total of 60 plots over all sites.
- Within plots we recorded cover estimates of each species in standard height tiers, as well as prominent bryophytes and lichens. Physical parameters such as slope, altitude and aspect, height of the tallest individual of the dominant vascular species, and height of the tallest *Dracophyllum subulatum* (if present) were measured. Any apparent human and introduced mammal impacts were also noted.
- We tested for significant changes in the proportion of plots occupied between surveys, and changes in cover between surveys (within plots) for species assigned to three groups: diagnostic frost-flat species, forest precursor species, and invasive exotic species that occurred at least 15 times across both surveys. We used generalised linear mixed-effect models to test the significance of changes in the proportion of plots occupied, and a non-parametric test statistic recording the net direction of changes in cover and height of paired differences between surveys. Significant results are obtained when the proportion of plots experiencing an increase or decrease is greater than expected by chance ( $p < 0.05$ ).

## Results

- The most widespread diagnostic frost-flat species in both surveys were *Dracophyllum subulatum* (97% of plots occupied in both surveys), *Rytidosperma gracile* (67% of plots occupied in 2013/14 and 60% in 2021), *Cladia retipora* (48% and 47%), *Cladonia confusa* (38% and 50%), and *Hypochoeris radicata* (38% and 28%)
- The most widespread forest precursors were *Leptospermum scoparium* (17% of plots occupied in 2013/14 and 20% in 2021), *Phyllocladus alpinus* (17% and 27%), and *Pseudopanax crassifolius* (17% and 22%)

- The most widespread invasive exotics were *Holcus lanatus* (27% of plots occupied in 2013/14 and 17% in 2021), *Cytisus scoparius* (23% and 22%), *Anthoxanthum odoratum* (18% and 13%), and *Agrostis capillaris* (17% and 3%)
- Only *Phyllocladus alpinus*, a forest precursor species, and *Holcus lanatus*, an invasive exotic, showed significant changes in frequency between surveys. *P. alpinus* increased in presence from 17% of plots in 2013/14 to 27% in 2021, while *H. lanatus* reduced in presence from 27% of plots to 17% in 2021
- The proportion of plots experiencing an increase in cover was greater than expected by chance for two forest precursors, *Phyllocladus alpinus* (mean total cover 1% in 2013/14 and 4% in 2021) and *Raukaua anomalus* (0.2% and 1.4%), another native shrub, *Coprosma propinqua* (5% and 9%), and an invasive exotic, *Calluna vulgaris* (22% and 23%)
- The proportion of plots experiencing an increase in a) total cover of forest precursor species, b) maximum vegetation height (mean 2.37 m in 2013/14 and 2.6 m in 2021), and c) maximum height of *Dracophyllum subulatum* (mean 2.17 m and 2.37 m) between surveys was greater than expected by chance.

## Conclusions

- The diagnostic frost-flat species *Dracophyllum subulatum* was the most widespread and abundant species in both surveys, indicating a high level of species occupancy and native dominance.
- The increase in total cover of forest precursor species, along with total vegetation and *Dracophyllum subulatum* height, in a significant proportion of plots indicates a slow but inexorable natural succession to forest in many plots.
- The increase in cover of the invasive exotic *Calluna vulgaris* in a significant proportion of plots where it is already present is cause for serious concern. *Calluna vulgaris* is an ecological analogue of *Dracophyllum subulatum* and can outcompete it, as has already happened at Kuratau.

## Recommendations

- Maintain and remeasure the plots again in 2026 to monitor the response of frost-flat species to a warming climate.
- Analyse existing and future data in light of the potential existence of incipient successional pathways towards two different forest types.
- Establish annual surveillance and removal plans for *Calluna vulgaris* at Whenuakura.
- Introduce heather beetle to Kuratau frost flat and monitor its establishment success annually for 5 years from the second year after release.

## 1 Introduction

Permanent vegetation monitoring plots were established in the remaining substantial frost-flat heathlands in the western Waikato Region by Manaaki Whenua – Landcare Research (MWLR) in January–May 2013 and in January 2014 for the Waikato Regional Council. The plots were remeasured between April and June 2021 and compared against the baseline measurements for change in species cover and other indicators of condition.

## 2 Background

Frost-flat heathlands comprise short, sclerophyllous shrublands dominated by the ericaceous shrub monoao (*Dracophyllum subulatum*).<sup>1</sup> These heathlands occur on well-drained, infertile volcanic soils, where monoao often dominates because it is tolerant of very infertile soils due to its mycorrhizal association (McNabb 1961). Frost flats were once characteristic of shallow basins on the North Island Volcanic Plateau, mantled by deep deposits of infertile rhyolitic tephra (Smale 1990). Despite their occurrence well below the regional treeline under climates that are generally amenable to plant growth, the most ecologically stressed sites are subject to a year-round frost regime resulting from cold air ponding, which maintains the treeless community. The potential additional role of soil infertility in excluding native forest from frost flats remains unexplored.

The region has a long history of human burning, which has undoubtedly played a major role here – as elsewhere – in reducing taller woody vegetation and replacing it with shorter woody vegetation and grassland. The taller shrub component of frost-flat heathland – bog pine (*Halocarpus bidwillii*) and mountain toatoa (*Phyllocladus alpinus*) – has been severely reduced by burning and now survives only as scattered remnants, mostly on sites like dongas (deep, steep-sided erosion gullies) that are protected from fire. The floristic affinities of frost-flat heathland with the largely fire-induced short tussock grasslands of the eastern South Island (Smale 1990) emphasise the role fire may have played in helping form and maintain these communities.

Some colder sites at west Taupo and elsewhere on the Volcanic Plateau are occupied by short forest dominated by mountain toatoa, mentioned in passing by McKelvey (1963). It is so limited in extent that it has missed local vegetation classifications but is analogous to the bog pine, mountain celery pine scrub/forest that occurs on acidic infertile soils in intermontane basins in the eastern South Island (Singers & Rogers 2014). This may have been the pre-human vegetation type on the coldest sites at west Taupo now occupied by frost flat heathland.

The long-term persistence of non-forest communities on well-drained sites under reasonable rainfall is unusual in New Zealand, and frost flats provide habitat for a suite of

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<sup>1</sup> Common and scientific names of all plants and lichens are given in Appendix 1.

species that would otherwise be absent from these landscapes. As a historically rare ecosystem, frost-flat heathland falls within National Priority 3 ('To protect indigenous vegetation associated with "originally rare" terrestrial ecosystem types') of the National Biodiversity Strategy (DOC & MfE 2000; MfE & DOC 2007) and is now a Critically Endangered ecosystem (Holdaway et al. 2012).

The pre-European extent of frost-flat heathland is estimated to have been several tens of thousands of hectares (Smale 1990), but this has been reduced by an order of magnitude since c. 1930 by land development for agriculture and forestry to a few thousand hectares, mostly at one extreme site (Rangitaiki Conservation Area, Bay of Plenty). The few intact remaining frost flats are highly fragmented and susceptible to a range of threats, such as weed invasion (especially contorta pine, *Pinus contorta*), climate change leading to a lighter and less frequent frost regime, and nutrient enrichment through topdressing drift. The influence of the surrounding matrix on survival prospects is unknown but is likely to be significant.

### 3 Objectives

To identify changes in the vegetation structure and composition of the substantial frost-flat heathlands remaining in the western Waikato Region.

## 4 Methods

### 4.1 Permanent plots

Fifteen permanently marked 2 × 2 m plots were established during 2013/14 (Smale et al. 2013) in major vegetation types reflecting different structural classes (grassland, shrubland) and fire history across the four substantial frost-flat sites remaining in the western Waikato Region (Figure 1). The structural classes, such as grassland and shrubland, represent both community developmental stages of and site (e.g. fertility) variation.

Within plots we recorded the following attributes, following Hurst and Allen (2007):

- all vascular species present, including invasive weeds, as well as prominent bryophytes and lichens
- quantitative cover estimates of each species in standard height tiers (<0.3 m, 0.3–<2 m, 2–<5 m, 5–<12 m)
- physical parameters such as slope, altitude and aspect
- maximum height of *Dracophyllum subulatum*, and the height of the tallest individual of the dominant vascular species if this was not *Dracophyllum*
- human impact (e.g. off-road vehicle tracks)
- introduced mammal impact, including the presence of faecal pellets and trampling, and presence and degree of browsing by species.

Photographs were taken from each plot corner, from approximately 1.4 m above ground level, with the opposite corner approximately centred in the image.

The sampled sites include one larger, intact site with apparently good prospects for survival – Whenuakura Plain (Pureora Forest Park, 72 ha, within native forest matrix) – and three smaller sites with apparently poorer prospects for survival – Pokaiora Clearing (38 ha, Pureroa Forest Park, native forest matrix), Taparoa Clearing (23 ha, Pureora Forest Park, native forest matrix), and Kuratau (0.8 ha, Waituhi-Kuratau Scenic Reserve, native forest and scrub matrix).



## 4.2 Data analysis

We used a repeated-measures design to assess changes in cover between surveys (but within plots) for species assigned to three groups:

- diagnostic frost flat species
- forest precursor species
- invasive exotic species that occurred at least 15 times across both surveys.

Mean cover was calculated as the sum of the total cover (sum across all tiers) in all plots, divided by the total number of plots for each sample year. Statistical significance testing was based on a non-parametric test statistic, recording the net direction of paired differences:

$$T_{dir} = [N(t_2 > t_1) - N(t_1 > t_2)] / N_{plots}$$

where  $N(t_2 > t_1)$  is the number of plots where sample 2 is greater than sample 1, and  $N_{plots}$  is the total number of pairs.

The advantage of this test is that by only documenting the direction of shifts between samples (but within pairs) it provides equal power to detect increases or decreases, even in data sets where values are constrained by fixed upper or lower values. For cover values, the lower bound is generally zero, and many cover data sets exhibit extremely right-skewed distributions (many small value, few large values). For such data sets, test statistics incorporating both the size and direction of shifts within pairs have lower power to detect decreases than increases (Mason & Bellingham 2018). We used randomisation tests to test whether observed values of  $T_{dir}$  differed significantly from those expected by chance. These tests randomly allocate data between samples but within pairs (see Mason & Bellingham 2018 for details).

Using this method, we tested for changes in the maximum cover score recorded in any height tier for each species in each plot, as well as the sum of cover scores across height tiers within plots. Both measures gave very similar results. Here we present results for the sum of cover scores across height tiers. We also used generalised linear mixed-effects models (GLMMs) to test for significant changes in the proportion of plots occupied by species occurring in at least five plots in each survey using the `GLMMadaptive` package in the R statistical computing environment version 3.6.2 (R Core Team 2020).

As well as testing for changes in the cover of individual species, we also tested for changes in the total cover of our three groups: diagnostic frost-flat species, forest precursors, and invasive exotic species. Diagnostic frost-flat species are 12 key species previously identified as being present in more than 50% of frost-flat plots (Smale 1990). We also tested for change in total cover of non-frost-flat species (both forest precursors and invasive exotic species). Finally, we tested for changes in the maximum height of vegetation in each plot, as well as changes in the maximum height of *Dracophyllum subulatum* in each plot.

## 5 Results

All species recorded in monitoring plots and their mean cover estimates in both surveys are listed in Appendix 1.

### 5.1 Species occupancy

The most widespread diagnostic frost-flat species in both surveys were the diagnostic species *Dracophyllum subulatum* (97% of plots occupied in both surveys), *Rytidosperma gracile* (67% in 2013/14 and 60% in 2021), *Cladia retipora* (48% and 47%), *Cladonia confusa* (38% and 50%), and *Hypochoeris radicata* (38% and 28%; Table 1).

The most widespread forest precursors were *Leptospermum scoparium* (17% of plots occupied in 2013/14 and 20% in 2021), *Phyllocladus alpinus* (17% and 27%), and *Pseudopanax crassifolius* (17% and 22%).

The most widespread invasive exotics were *Holcus lanatus* (27% of plots occupied in 2013/14 and 17% in 2021), *Cytisus scoparius* (23% and 22%), *Anthoxanthum odoratum* (18% and 13%), and *Agrostis capillaris* (17% and 3%).

Only two species, *Phyllocladus alpinus* (a forest precursor) and *Holcus lanatus* (an invasive exotic grass) showed significant changes in frequency between surveys. *Phyllocladus alpinus* increased in presence from 17% of plots in 2013/14 to 27% in 2021, and *Holcus lanatus* reduced in presence from 27% of plots to 17% in 2021.

**Table 1. Proportion of plots occupied in 2012 ( $P_{occ}$  2012) and 2018 ( $P_{occ}$  2018) and GLMM P values for species occurring in at least five plots in both survey years**

Group	Species	$P_{occ}$ 2013/2014 ( $N = 60$ )	$P_{occ}$ 2021 ( $N = 60$ )	P
Diagnostic frost flat species				
	<i>Celmisia gracilentia</i>	0.13	0.12	0.603
	<i>Cladia retipora</i>	0.48	0.47	0.712
	<i>Cladonia capitellata</i>	0.08	0.10	0.674
	<i>Cladonia confusa</i>	0.48	0.50	0.682
	<i>Deyeuxia avenoides</i>	0.05	0.07	
	<i>Dracophyllum subulatum</i>	0.97	0.97	0.999
	* <i>Hypochoeris radicata</i>	0.33	0.28	0.071
	<i>Leucopogon fraseri</i>	0.25	0.23	0.706
	<i>Pimelea prostrata</i>	0.07	0.08	
	<i>Poa cita</i>	0.12	0.03	
	<i>Racomitrium lanuginosum</i>	0	0.10	
	<i>Rytidosperma gracile</i>	0.67	0.60	0.291

Forest precursor species			
<i>Cordyline australis</i>	0	0.03	
<i>Elaeocarpus hookerianus</i>	0.05	0.03	
<i>Griselinia littoralis</i>	0.03	0.03	
<i>Leptospermum scoparium</i>	0.17	0.20	0.355
<i>Melicope simplex</i>	0.02	0	
<b><i>Phyllocladus alpinus</i></b>	<b>0.17</b>	<b>0.27</b>	<b>0.018</b>
<i>Phyllocladus trichomanoides</i>	0.07	0.13	
<i>Podocarpus laetus</i>	0.03	0.05	
<i>Podocarpus totara</i>	0.03	0.05	
<i>Prumnopitys taxifolia</i>	0.05	0.10	
<i>Pseudopanax arboreus</i>	0.03	0	
<i>Pseudopanax crassifolius</i>	0.17	0.22	0.171
Invasive species			
* <i>Agrostis capillaris</i>	0.17	0.03	
* <i>Anthoxanthum odoratum</i>	0.18	0.13	0.266
* <i>Calluna vulgaris</i>	0.25	0.27	0.708
* <i>Cytisus scoparius</i>	0.23	0.22	0.669
* <i>Festuca rubra</i>	0.03	0.08	
<b>*<i>Holcus lanatus</i></b>	<b>0.27</b>	<b>0.17</b>	<b>0.043</b>
* <i>Lotus pedunculatus</i>	0.05	0.07	
* <i>Pilosella officinarum</i>	0.03	0.07	
* <i>Rubus fruticosus</i>	0.08	0.13	0.140
* <i>Trifolium repens</i>	0.02	0.02	
* <i>Trifolium sp.</i>	0.02	0	

Notes: Significant changes ( $p < 0.05$ ) are in bold; \* denotes exotic

## 5.2 Vegetation cover and height

The diagnostic frost-flat species *Dracophyllum subulatum* had by far the highest mean cover (mean total cover 57% in 2013/14 and 58% in 2021) of any diagnostic species in both surveys (Appendix 2). Of the invasive exotics, *Calluna vulgaris* had by far the highest mean cover (mean total cover 22% and 23%) of any exotic species in both surveys.

The total cover of forest precursor species combined increased in a significant proportion of plots between surveys (Table 2). Neither the total cover of diagnostic frost-flat species nor that of invasive exotic species increased in a significant proportion of plots.

Both maximum vegetation height (mean 2.37 m in 2013/14 and 2.6 m in 2021) and maximum height of *Dracophyllum subulatum* (mean 2.17 m and 2.37 m) increased in a significant proportion of plots between surveys at all sites except Kuratau.

Cover of two forest precursors, *Phyllocladus alpinus* (mean total cover 1% in 2013/14 and 4% in 2021) and *Raukaua anomalus* (mean total cover 0.2% and 1.4%); a shrub, *Coprosma propinqua* (mean total cover 5% and 9%); and an invasive exotic, *Calluna vulgaris* (mean total cover 22% and 23%), increased in a significant proportion of plots between surveys (Table 3). The dominance and change in *Calluna vulgaris* cover were a result of one site, Kuratau, where it was present in every plot in both surveys and increased in 11 of them. *Calluna vulgaris* was only recorded in one other plot, at Whenuakura in 2021.

**Table 2. Mean and 95% confidence intervals of cover values and significance test results for the proportion of plots in which total cover for each species group, maximum vegetation height, and maximum height of *Dracophyllum subulatum* (DRAsub) increased or decreased between surveys**

Group	Mean (95% CI)		Tdir		P obs	
	2013/14	2021	Observed	Expected	≥ exp	≤ exp
Diagnostic frost-flat species	75.1 (84.6)	75.3 (89.4)	-0.067	0.001	0.744	0.346
<b>Forest precursors</b>	<b>3.0 (14.4)</b>	<b>6.5 (29.4)</b>	<b>0.317</b>	<b>-0.001</b>	<b>0.001</b>	1
Invasive exotics	28.8 (96.9)	28.3 (94.6)	-0.017	-0.001	0.619	0.5
Non-frost-flat species	31.8 (95.7)	34.8 (94.6)	0.25	-0.001	0.029	0.986
<b>Max height all</b>	<b>2.37 (0.03)</b>	<b>2.6 (0.03)</b>	<b>0.517</b>	<b>0.0004</b>	<b>0</b>	1
<b>Max height DRAsub</b>	<b>2.17 (0.03)</b>	<b>2.37 (0.03)</b>	<b>0.579</b>	<b>0.001</b>	<b>0</b>	1

Notes: Tdir expected is the mean value of the test statistic across randomisations. P obs ≥ exp is the probability that the observed value of the test statistic is greater than expected (cover increased in more plots than expected). P obs ≤ exp is the probability that the test statistic is less than expected (cover decreased in more plots than expected). Significant changes ( $p < 0.05$ ) are in bold.

**Table 3. Significance test results for the proportion of plots in which total cover for individual species increased or decreased between surveys. Tests were only performed for species with a total of at least 15 occurrences across both surveys.**

Species	Group	Tdir observed	Tdir expected	P obs ≥ exp	P obs ≤ exp
<i>Androstoma emperifolia</i>		-0.017	-0.002	0.513	0.718
* <i>Anthoxanthum odoratum</i>	Invasive species	-0.133	0.001	0.02	0.997
<i>Blechnum penna-marina</i>		0.067	-0.001	0.930	0.189
Bryophytes		0.133	-0.0002	0.98	0.057
* <i>Calluna vulgaris</i>	<b>Invasive species</b>	<b>0.133</b>	<b>0.001</b>	<b>0.991</b>	<b>0.038</b>
<i>Carex minor</i>		0.083	0.001	0.95	e0.137
<i>Carex punicea</i>		0.033	-0.001	0.867	0.361
<i>Celmisia gracilentia</i>	Diagnostic frost-flat species	-0.05	-0.0001	0.224	0.938
<i>Chaerophyllum ramosum</i>		-0.017	-0.0001	0.5	0.688
<i>Cladonia confusa</i>	Diagnostic frost-flat species	-0.083	0.001	0.217	0.883
<i>Cladonia retipora</i>	Diagnostic frost-flat species	-0.117	-0.002	0.129	0.934
<i>Coprosma dumosa</i>	Forest precursor	0.05	-0.0004	0.815	0.328

Species	Group	Tdir observed	Tdir expected	P obs ≥ exp	P obs ≤ exp
<b><i>Coprosma propinqua</i></b>		<b>0.267</b>	<b>-0.001</b>	<b>0.999</b>	<b>0.005</b>
* <i>Cytisus scoparius</i>	Invasive species	-0.133	0.001	0.026	0.994
<i>Dicranoloma billardieri</i>		-0.4	-0.001	0	1
<b><i>Dichondra</i> species</b>		<b>0.25</b>	<b>0.001</b>	<b>1</b>	<b>0.0001</b>
<i>Dracophyllum subulatum</i>	Diagnostic frost-flat species	-0.067	-0.0003	0.342	0.751
<i>Geranium potentilloides</i>		-0.25	-0.0001	0	1
<i>Gonocarpus aggregatus</i>		-0.067	0.001	0.201	0.914
<i>Gonocarpus micranthus</i>		-0.083	-0.001	0.09	0.98
* <i>Holcus lanatus</i>	Invasive species	-0.217	0.001	0.001	1
<i>Hymenophyllum sanguinolentum</i>		0	-0.0002	0.756	0.749
<i>Hypnum cupressiforme</i>		0.017	0.0002	0.744	0.5
* <i>Hypochoeris radicata</i>	Diagnostic frost-flat species	-0.067	-0.0005	0.27	0.847
<i>Lepidosperma australe</i>		0.017	0.001	0.694	0.509
<i>Leptospermum scoparium</i>	Forest precursor	0.1	0.001	0.98	0.075
<i>Leucopogon fraseri</i>	Diagnostic frost-flat species	-0.017	-0.0001	0.501	0.688
<i>Lycopodium fastigiatum</i>		-0.017	-0.001	0.504	0.701
<b><i>Phyllocladus alpinus</i></b>	<b>Forest precursor</b>	<b>0.183</b>	<b>-0.0002</b>	<b>1</b>	<b>0.004</b>
<i>Polytrichum juniperinum</i>		-0.183	0.0004	0.014	0.996
<i>Pseudopanax crassifolius</i>	Forest precursor	0.1	0.001	0.971	0.092
<b><i>Raukaua anomalus</i></b>	<b>Forest precursor</b>	<b>0.2</b>	<b>0.001</b>	<b>1</b>	<b>0.001</b>
<i>Rytidosperma gracile</i>	Diagnostic frost-flat species	-0.167	-2.333	0.089	0.951

Notes: Tdir expected is the mean value of the test statistic across randomisations. P obs ≥ exp is the probability that the observed value of the test statistic is greater than expected (cover increased in more plots than expected). P obs ≤ exp is the probability that the observed value of the test statistic is less than expected (cover decreased in more plots than expected). Significant changes ( $p < 0.05$ ) are in bold. \* denotes exotic species

## 6 Discussion

The diagnostic frost-flat species *Dracophyllum subulatum* was the most widespread and abundant species in both surveys, indicating a high level of species occupancy and native dominance. However, the increase in total cover of forest precursor species in a significant proportion of plots indicates a slow but inexorable natural succession to forest in many plots. Increases in the maximum height of vegetation and of *Dracophyllum subulatum* in a significant proportion of plots between surveys also lend support to our earlier conclusion (Smale et al. 2013) that succession to native forest is likely in the foreseeable future on much of the west Taupō frost-flat heathland. The intriguing possibility exists that two successional pathways may be incipient on west Taupō frost flats, one on somewhat

milder sites towards tall conifer or conifer/broadleaved forest, the other on colder sites towards short mountain toatoa forest similar to extant remnants in the region.

The overall significant increase in cover of the invasive exotic *Calluna vulgaris* is cause for serious concern. *Calluna* is an ecological analogue of *Dracophyllum subulatum* and can largely oust it. Comparing between sites was beyond the scope of the current project, but the increase in *Calluna* was clearly dominated by change at Kuratau, where it was present in every monitoring plot and the total cover of diagnostic frost-flat species (30%) is already much lower than at other sites (84–97%). Across the other sites, *Calluna* was present in only one plot at Whenuakura in 2021. Dense stands of *Calluna* slow the succession back to native forest on flatter sites (Rogers 1996). The efficacy of the recent introduction of biological control for *Calluna* elsewhere on the Volcanic Plateau (Peterson et al. 2020) suggests that, if introduced, heather beetle (*Lochmaea suturalis*) may reduce *Calluna* considerably at Kuratau – where it is now beyond practical control by other methods – in the foreseeable future. Heather beetles are weak fliers and do not readily colonise isolated sites (PG Peterson, MWLR, pers. comm. June 2021). Pioneering populations of *Calluna* at Whenuakura need to be removed before control there becomes impracticable.

Although little plant browse was seen in plots, feral pig (*Sus scrofa*) rooting was observed frequently at Pokaiora and Whenuakura, particularly under tall *Dracophyllum subulatum* and *Coprosma propinqua* (Figure 2).



**Figure 2. Feral pig rooting under tall *Dracophyllum subulatum* at Pokaiora.**

Recent changes at six frost-flat heathlands on the southern Kaingaroa Plateau provide an interesting comparison with those occurring over a similar period at west Taupō. At southern Kaingaroa, where diagnostic frost-flat species are far more widespread and forest precursor species far less widespread, cover of two diagnostic frost-flat species (*Cladia retipora* and *Rytidoperma gracile*) increased and one (*Deyeuxia avenoides*) decreased in a significant number of plots over a similar period (Fitzgerald et al. 2019). No forest precursor species occurred frequently enough to be included in significance tests. The slow but detectable progress of succession to forest in many plots at west Taupō is in stark contrast to the virtual absence of it at southern Kaingaroa and indicates the essentially ephemeral nature of much of the west Taupō frost-flat heathland.

## **7 Conclusions**

Slow but inexorable natural succession to native forest is occurring in many plots in the monitored plots in frost-flat heathland at west Taupō. Increasing cover at Kuratau of the invasive exotic *Calluna vulgaris*, an ecological analogue of the quintessential frost-flat species *Dracophyllum subulatum*, indicates an urgent need to remove pioneering populations where they have established at Whenuakura before their control becomes impractical.

## **8 Recommendations**

- Maintain and remeasure the plots again in 2026 to monitor the response of frost-flat species to a warming climate and exotic weed pressure.
- Analyse existing and future data in light of the potential existence of incipient successional pathways towards two different forest types.
- Establish surveillance and removal plans for *Calluna vulgaris* at Whenuakura
- Introduce heather beetle to Kuratau frost flat and monitor its establishment success annually for 5 years from the second year after release.

## **9 Acknowledgements**

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## 11 Appendix 1 – Species recorded in frost-flat monitoring plots

Mean of total cover (summed across height tiers within plots) taken across plots and 95% confidence intervals of the mean estimates (calculated as 1.96 x standard error) of plants and lichens recorded in Waikato frost-flat vegetation monitoring plots in 2013/14 and 2021 (60 plots). Taxonomy follows Allan Herbarium 2000.

Scientific name	Common name	2013/14		2021		Origin	Group
		Mean cover	95% CI	Mean cover	95% CI		
<i>Acaena agnipila</i>	sheep's bur	0.025	0.028	0.033	0.046	Exotic	
<i>Acaena anserinifolia</i>	bidibid	0	0	0.008	0.016	Endemic	
<i>Agrostis capillaris</i>	browntop	0.451	0.751	0.177	0.343	Exotic	Invasive
<i>Androstoma empetrifolia</i>	bog mingimingi	0.343	0.231	0.29	0.235	Endemic	
<i>Anthoxanthum odoratum</i>	sweet vernal	1.46	1.173	0.25	0.237	Exotic	Invasive
<i>Aporostylis bifolia</i>	odd-leaved orchid	0.003	0.005	0	0	Endemic	
<i>Aristotelia fruticosa</i>	mountain wineberry	0.717	0.889	0.535	0.734	Endemic	
<i>Blechnum penna-marina</i>	little hard fern	1.5	1.702	1.952	1.812	Native	
<i>Calluna vulgaris</i>	heather	21.55	11.017	22.975	11.239	Exotic	Invasive
<i>Campylopus sp.</i>	moss	0.037	0.066	0	0	Native	
<i>Carex dipsacea</i>		0.017	0.033	0.383	0.751	Endemic	
<i>Carex horizontalis</i>		0.317	0.416	0.417	0.526	Endemic	
<i>Carex minor</i>		0.367	0.378	0.28	0.201	Endemic	
<i>Carex punicea</i>	red hook sedge	0.129	0.103	0.115	0.077	Endemic	
<i>Celmisia gracilentia</i>	common mountain daisy	0.059	0.051	0.072	0.075	Endemic	Diagnostic frost flat
<i>Centaurium erythraea</i>	centuary	0	0	0.002	0.003	Exotic	
<i>Centella uniflora</i>	centella	0.025	0.036	0.02	0.033	Native	
<i>Chaerophyllum ramosum</i>		0.127	0.081	0.142	0.106	Endemic	
<i>Chionochloa rubra</i>	red tussock	0.307	0.32	0.433	0.666	Endemic	

Scientific name	Common name	2013/14		2021		Origin	Group
		Mean cover	95% CI	Mean cover	95% CI		
<i>Cladia aggregata</i>	lichen	0.085	0.067	0.168	0.175	Native	
<i>Cladonia capitellata</i>	lichen	0.068	0.075	0.293	0.355	Native	Diagnostic frost flat
<i>Cladonia confusa</i>	reindeer lichen	6.003	3.271	4.447	2.538	Native	Diagnostic frost flat
<i>Cladia retipora</i>	coral lichen	6.06	3.228	6.295	3.711	Native	Diagnostic frost flat
<i>Cladia sullivani</i>	lichen	0.003	0.007	0	0	Native	
<i>Clematis quadribracteolata</i>	clematis	0.01	0.017	0.003	0.007	Endemic	
<i>Coprosma cheesemani</i>		0.733	1.024	0.687	1.145	Endemic	
<i>Coprosma dumosa</i>		0.9	0.904	1.435	1.394	Endemic	
<i>Coprosma propinqua</i>	mingimingi	4.848	2.576	9.034	4.15	Endemic	
<i>Coprosma ×cunninghamii</i>		0.008	0.016	0	0	Endemic	
<i>Cordyline australis</i>	Cabbage tree	0	0	0.005	0.007	Endemic	Forest precursor
<i>Corokia cotoneaster</i>	korokio	0.053	0.098	0.083	0.163	Endemic	
<i>Crepis capillaris</i>	smooth hawksbeard	0.058	0.057	0.012	0.017	Exotic	
<i>Cytisus scoparius</i>	broom	3.663	2.401	2.727	2.709	Exotic	Invasive
<i>Deyeuxia avenoides</i>	mountain oat grass	0.067	0.103	0.084	0.085	Endemic	Diagnostic frost flat
<i>Dicranoloma billardierei</i>	moss	8.635	3.842	3.168	3.064	Endemic	
<i>Dichondra brevifolia</i>	dichondra	0.008	0.016	0.052	0.069	Endemic	
<i>Dicranoloma sp.</i>	moss	0	0	3.137	2.459		
<i>Dracophyllum subulatum</i>	monoao	57.23	10.003	57.733	10.302	Endemic	Diagnostic frost flat
<i>Elaeocarpus hookerianus</i>	pökākā	0.037	0.065	0.1	0.145	Endemic	Forest precursor
<i>Erigeron sp.</i>		0.008	0.016	0	0		
<i>Festuca rubra</i>	Chewing's fescue	0.185	0.331	0.333	0.495	Exotic	Invasive
<i>Gaultheria antipoda</i>	bush snowberry	0.167	0.327	0.05	0.098	Endemic	

Scientific name	Common name	2013/14		2021		Origin	Group
		Mean cover	95% CI	Mean cover	95% CI		
<i>Geranium microphyllum</i>	small-leaved cranesbill	0	0	0.055	0.056	Endemic	
<i>Geranium potentilloides</i>		0.132	0.082	0	0	Native	
<i>Gleichenia alpina</i>	alpine tangle fern	4.233	2.805	6.6	3.917	Native	
<i>Gleichenia dicarpa</i>	tangle fern	0.917	1.388	2.417	3.371	Native	
<i>Gnaphalium sp.</i>	cudweed	0.037	0.065	0.025	0.036	Exotic	
<i>Gonocarpus aggregatus</i>		1.094	1.064	0.589	0.686	Endemic	
<i>Gonocarpus micranthus</i>		0.15	0.149	0.179	0.327	Native	
<i>Griselinia littoralis</i>	broadleaf	0.018	0.033	0.002	0.003	Endemic	Forest precursor
<i>Halocarpus bidwillii</i>	bog pine	1.887	3.691	1.533	2.94	Endemic	
<i>Helichrysum filicaule</i>	creeping everlasting daisy	0.047	0.035	0.07	0.064	Endemic	
<i>Hierochloa redolens</i>	holy grass	1.31	1.982	0.148	0.189	Native	
<i>Histiopteris incisa</i>	water fern	0.083	0.163	0.05	0.098	Native	
<i>Holcus lanatus</i>	Yorkshire fog	1.295	1.12	0.527	0.821	Exotic	Invasive
<i>Hydrocotyle moschata</i>	hairy pennywort	0.142	0.189	0.003	0.005	Endemic	
<i>Hydrocotyle novae-zeelandiae var. montana</i>		0.008	0.016	0.002	0.003	Endemic	
<i>Hymenophyllum sanguinolentum</i>		0.002	0.003	0	0	Endemic	
<i>Hypnum cupressiforme</i>		1.002	1.127	1.158	1.395	Native	
<i>Hypericum perforatum</i>	Saint John's wort	0.045	0.053	0.175	0.209	Exotic	
<i>Hypochaeris radicata</i>	catsear	0.285	0.143	0.512	0.391	Exotic	Diagnostic frost flat
<i>Jacobaea vulgaris</i>	ragwort	0.001	0.002	0.008	0.016	Exotic	
<i>Lagenophora pumila</i>	papatāniwhaniwha	0.017	0.033	0.003	0.005	Endemic	
<i>Lepidosperma australe</i>	square sedge	0.936	1.312	0.199	0.159	Endemic	
<i>Leptospermum scoparium</i>	mānuka	1.328	1.406	1.635	1.6	Endemic	Forest precursor

Scientific name	Common name	2013/14		2021		Origin	Group
		Mean cover	95% CI	Mean cover	95% CI		
<i>Leptostigma setulosum</i>	nertera	0.695	0.944	1.45	2.465	Endemic	
<i>Leucopogon fraseri</i>	pātōtara	0.408	0.328	0.55	0.432	Endemic	Diagnostic frost flat
<i>Lichen species</i>		0.017	0.033	0	0	Native	
<i>Lobelia angulata</i>	pānakenake	0.15	0.128	0.032	0.037	Endemic	
<i>Lotus pedunculatus</i>	lotus	0.03	0.037	0.112	0.182	Exotic	Invasive
<i>Luzula decipiens</i>		0.008	0.016	0	0	Endemic	
<i>Luzula picta</i>		0.177	0.343	0	0	Endemic	
<i>Luzula sp.</i>	woodrush	0.01	0.017	0.008	0.016	Native	
<i>Lycopodium fastigiatum</i>	alpine clubmoss	0.725	0.697	0.587	0.422	Native	
<i>Melicope simplex</i>	poataniwha	0.008	0.016	0	0	Endemic	Forest precursor
<i>Microlaena stipoides</i>	meadow rice grass	1	0.899	1.405	1.994	Native	
<i>Moss species</i>	moss	0.767	0.955	0	0	Native	
<i>Muehlenbeckia axillaris</i>	creeping pōhuehue	0.242	0.334	0.202	0.329	Native	
<i>Myrsine divaricata</i>	weeping māpou	0.217	0.268	1.008	1.59	Endemic	
<i>Olearia virgata</i>	twiggy tree daisy	0.05	0.098	0.217	0.233	Endemic	
<i>Oreobolus pectinatus</i>	combsedge	0.357	0.653	0.383	0.656	Endemic	
<i>Paesia scaberula</i>	hard fern	0	0	0.002	0.003	Endemic	
<i>Phyllocladus alpinus</i>	mountain toatoa	0.987	0.856	3.637	2.991	Endemic	Forest precursor
<i>Phyllocladus trichomanoides</i>	tānekaha	0.408	0.575	0.24	0.225	Endemic	Forest precursor
<i>Pilosella officinarum</i>	mouse-ear hawkweed	0.025	0.036	0.028	0.036	Exotic	Invasive
<i>Pimelea prostrata</i>	New Zealand daphne	0.725	1.276	0.469	0.818	Endemic	Diagnostic frost flat
<i>Pittosporum tenuifolium</i>	kōhūhū	0.15	0.263	1.025	1.963	Endemic	
<i>Pittosporum turneri</i>		0.025	0.049	0.067	0.131	Endemic	

Scientific name	Common name	2013/14		2021		Origin	Group
		Mean cover	95% CI	Mean cover	95% CI		
<i>Poa sp.</i>	meadow grass	0.025	0.028	0	0	Native	
<i>Poa anceps</i>	broad-leaved poa	0	0	0.017	0.033	Endemic	
<i>Poa cita</i>	silver tussock	0.428	0.541	0.092	0.18	Endemic	Diagnostic frost flat
<i>Podocarpus laetus</i>	mountain totara	0.018	0.033	0.005	0.006	Endemic	Forest precursor
<i>Podocarpus totara</i>	tōtara	0.042	0.067	0.117	0.198	Endemic	Forest precursor
<i>Polytrichum juniperinum</i>	moss	0.583	0.51	0.239	0.192	Native	
<i>Prumnopitys taxifolia</i>	mataī	0.043	0.067	0.27	0.434	Endemic	Forest precursor
<i>Prunella vulgaris</i>	self-heal	0.018	0.033	0.067	0.079	Exotic	
<i>Pseudopanax arboreus</i>	five-finger	0.017	0.023	0	0	Endemic	Forest precursor
<i>Pseudopanax crassifolius</i>	lancewood	0.082	0.073	0.469	0.661	Endemic	Forest precursor
<i>Pterostylis sp.</i>	greenhood	0.002	0.003	0	0	Native	
<i>Racomitrium lanuginosum</i>	woolly moss	0	0	2.033	2.53	Native	Diagnostic frost flat
<i>Raukaua anomalus</i>		0.217	0.236	1.427	1.283	Endemic	
<i>Rubus australis</i>	bush lawyer	0.008	0.016	0	0	Endemic	
<i>Rubus fruticosus</i>	blackberry	0.142	0.153	1.17	1.256	Exotic	Invasive
<i>Rumex acetosella</i>	sheep's sorrel	0.035	0.065	0	0	Exotic	
<i>Rytidosperma gracile</i>	dainty bristle grass	3.749	1.576	2.75	1.631	Native	Diagnostic frost flat
<i>Simpliglottis cornuta</i>	green bird orchid	0.042	0.067	0.002	0.003	Endemic	
<i>Sphagnum sp.</i>	sphagnum moss	0	0	0.033	0.065	Native	
<i>Stereocaulon sp.</i>	lichen	0.008	0.016	0	0	Native	
<i>Taraxacum officinale</i>	dandelion	0	0	0.002	0.003	Exotic	
<i>Thuidiopsis furfurosa</i>		2.428	2.358	0.55	0.692	Native	
<i>Trifolium sp.</i>	clover	0.002	0.003	0	0	Exotic	Invasive

Scientific name	Common name	2013/14		2021		Origin	Group
		Mean cover	95% CI	Mean cover	95% CI		
<i>Trifolium repens</i>	white clover	0.002	0.003	0	0	Exotic	Invasive
<i>Uncinia sp.</i>	hook grass	0.245	0.249	0.033	0.065	Native	
<i>unidentified bryophyte species</i>	bryophytes	2.247	1.681	3.95	2.568	Native	
<i>Veronica stricta</i>	koromiko	0.075	0.09	0.175	0.266	Endemic	
<i>Viola cunninghamii</i>	mountain violet	0.008	0.016	0	0	Native	
<i>Viola filicaulis</i>	forest violet	0.017	0.033	0	0	Endemic	