Manaaki Whenua
Landcare Research

Contrasting the ecological integrity of naturally unforested ecosystems and deforested ecosystems on public conservation land throughout New Zealand

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Contrasting the ecological integrity of naturally unforested ecosystems and deforested ecosystems on public conservation land throughout New Zealand

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Summary

Project and client

The Department of Conservation (DOC) monitors the ecological integrity of natural ecosystems across all public conservation land using the Tier 1 permanent sampling point network. In 2023 DOC commissioned Manaaki Whenua – Landcare Research to develop a framework for:

- analysing and interpreting ecological integrity in non-forest ecosystems
- understanding the drivers of non-vascular plant communities in non-forest ecosystems

with a focus on contrasting naturally unforested ecosystems and those that have been historically deforested.

Objectives

The aim was to assess ecological integrity in non-forest ecosystems using data from the Tier 1 permanent plot network. Manaaki Whenua – Landcare Research was asked to:

1 develop a framework for analysing and interpreting ecological integrity in non-forest ecosystems

2 evaluate key interrelationships among measures from non-forest ecosystems using the framework developed in (1), contrasting naturally unforested and deforested ecosystems

3 determine the potential for spatial interpolation across sampling locations to derive maps of ecological integrity and change in ecological integrity, contrasting naturally unforested and deforested ecosystems

4 test for interrelationships between three measures of non-vascular plant communities and measures of vegetation structure, ungulate abundance, and non-native plant (weed) abundance, contrasting naturally unforested and deforested ecosystems.

Develop a framework for analysing and interpreting ecological integrity in non-forested ecosystems

Method: We built a framework to differentiate non-forested ecosystems from forested ecosystems, and then to distinguish, within non-forested ecosystems, those that are naturally unforested from those that were historically deforested.

Results: A framework was developed to evaluate each sample point according to: (i) mechanistic drivers of tree growth (climate, distance to regional treeline); (ii) direct evidence (presence of canopy trees at the sample point, observed land cover); and (iii) corroborative evidence (land cover, modelled environmental limits, modelled potential natural vegetation).

Discussion: Most of the Tier 1 plots that we consider to be in *naturally unforested* ecosystems are above or at treelines delineated in previous studies. Most of the Tier 1 plots in *deforested ecosystems* on public conservation land are in the eastern South Island, but others are scattered nationally. This framework can be applied to evaluate monitoring efforts in non-forested ecosystems nationally, and results given in subsequent sections show how it might influence local (Tier 2) monitoring to evaluate the effects of management in unforested and deforested ecosystems.

Evaluate key interrelationships among measures of ecological integrity, contrasting naturally unforested ecosystems and deforested ecosystems

Method: We used data from Tier 1 plots to compare the interrelationships between native vegetation, weeds, and ungulates in naturally unforested and deforested ecosystems, and changes over time in these variables, using a hierarchical Bayesian modelling approach. Models also included environmental predictors (climate, elevation), soil nutrients, and features of the surrounding landscape.

Results: Ungulates were more abundant in deforested ecosystems relative to unforested ecosystems. Native vegetation cover in both unforested and deforested ecosystems increased with mean annual temperature. Increasing weed cover was related to mean annual temperature in deforested ecosystems, but not in naturally unforested ecosystems. There were no clear relationships between ungulate abundance and weed cover.

Discussion: It was surprising that, at a wide scale, there was no clear relationship between ungulate abundance and either native vegetation cover or weed cover, or changes in weed cover. There were some interrelationships between some components of native vegetation and weeds, but the predominant drivers at the scale we examined were climatic, especially mean annual temperature and, to a lesser extent, mean annual precipitation.

Determine the potential for spatial interpolation of ecological integrity measures

Method: We used species distribution models based on Bayesian additive regression trees to produce spatial maps of weed presence and changes in weed cover, and of ungulate presence, in both naturally unforested and deforested ecosystems.

Results: Weeds were widespread across unforested and deforested ecosystems and had the lowest probability of occurrence in the wettest regions. The greatest likelihood of increases in weed cover were across the deforested ecosystems of the eastern South Island. Ungulate presence was modelled as nearly ubiquitous across unforested and deforested ecosystems.

Discussion: The results point to a need for managers to focus widely on ungulate management across all non-forested ecosystems, but to focus on weed management mostly on deforested ecosystems of the eastern South Island and central and eastern North Island.

Evaluate key interrelationships between non-vascular plant communities and measures of ecological integrity, contrasting naturally unforested ecosystems and deforested ecosystems

Method: We compared the community composition of non-vascular plant species from Tier 1 plots between unforested and deforested ecosystems using non-metric multi-dimensional scaling, and we quantified the interrelationships between non-vascular plants, native plant cover, weed cover, and ungulate and lagomorph abundance using generalised linear models.

Results: Unforested and deforested ecosystems differed in their non-vascular plant communities, with mosses and lichens the most widespread, common species in both (liverworts were localised). While bryophyte and lichen cover and species richness were positively related to total vegetation cover, bryophyte species richness and lichen cover declined with increasing weed cover. There were no significant relationships between ungulate and lagomorph abundance and bryophyte and lichen cover and species richness.

Discussion: Bryophyte and lichen cover and richness can be used to assess ecological integrity in unforested and deforested ecosystems, especially in relationship to weed cover. Interpretation of their responses to pressures such as weed invasion will be enhanced if we better characterise the functional roles of species or genera of non-vascular plants.

Conclusions

- While rates of change in New Zealand's naturally unforested ecosystems are often slow, we can ill afford to be complacent about measuring changes in their ecological integrity. This is because they are subject to climate change, including rapid deglaciation, which creates new areas for plants to colonise; and because of biological invasions, including trees such as lodgepole pine that can invade above the treeline, and ongoing pressures from mammalian herbivores such as tahr. Tier 1 and Tier 2 networks will be needed to measure the effects of these changes, and of management actions.
- Deforested ecosystems can change rapidly in response to pressures such as climate change and altered disturbance regimes (notably fire disturbance). Biological invasions and successional trajectories within them are poorly understood. There is an opportunity to integrate ongoing measurement of change in deforested ecosystems using the Tier 1 network by reinstating and remeasuring Tier 2 plot networks, some established in the 1970s and even earlier, which can provide essential interpretive background.
- Interpreting change in response to management in New Zealand's forests is underpinned by critical ecological trait data that are largely lacking from unforested and deforested ecosystems. A structured investment in determining the traits of vascular plants would help overcome current issues of interpretation that result from high geographical species turnover in these ecosystems.
- We are not yet in a position to determine whether the non-vascular flora on Tier 1 plots affords novel insights into ecological integrity and the effects of pressures, such that these insights add value above that obtained from vascular plants.

Recommendations

- Appraise and prioritise Tier 2 networks in unforested and deforested ecosystems for their remeasurement. This would enhance understanding of state and trends in Tier 1 plots by providing fine-scale spatial resolution and temporal resolution that extends over several decades. Include in this assessment Tier 2 networks of plots in ecosystems adjacent to unforested and deforested ecosystems.
- Build effective partnerships with key stakeholders and neighbours adjoining public conservation land to evaluate changes in deforested ecosystems and the pressures on them, such as Land Information New Zealand and the New Zealand Defence Force, and mana whenua[1] (e.g. Ngāi Tahu, Ngāti Tūwharetoa).
- Build partnerships with researchers who maintain and measure change in unforested and deforested ecosystems, especially in universities.
- Design a programme to quantify the traits linked with pressures from climate change and herbivory in the vascular flora across deforested and unforested ecosystems. This would include a prioritisation process based on species' relative abundance and biomass contribution, information about sensitivity to pressure, and, for some genera with a high species diversity in architecture and leaf size (e.g. *Aciphylla*, *Brachyglottis*, *Dracophyllum*, *Myosotis*, *Ranunculus*, *Veronica*), a representative range. Linking these traits to quantitative studies of the dietary preferences of a range of mammalian herbivores would add further value.
- Do not remeasure the non-vascular plant communities until we have adequate information on their ecology and function, and confidence in our capacity to quantify change, so that repeat-measures data from these plants can be interpreted to report on state and change in ecological integrity. A caveat to this recommendation is that there is merit in establishing new Tier 1 plots in areas that have become deglaciated or are no longer in permanent snow or ice since the network was established in 2011, and, in these new plots, record cover and the identity of non-vascular plants, which we could expect to be the first colonists.

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[1] (Māori) territorial rights, power from the land, authority/jurisdiction over land or territory, power associated with possession and occupation of tribal land. Sometimes used (as here) to describe those associated with such rights/authority; or (more loosely) with tribal links to a specific area.

1 Introduction

The Department of Conservation (DOC) monitors the ecological integrity of natural ecosystems across all public conservation land using the Tier 1 permanent sampling point network. DOC uses the network to sample vegetation, birds, and some non-native mammals (ungulates, brushtail possums, hares, and rabbits) on a regular 8 km grid, visiting each sample point every 5 years. In 2023 DOC commissioned Manaaki Whenua – Landcare Research to develop a framework for analysing and interpreting ecological integrity, and changes in it, in non-forest ecosystems, focusing on whether there are differences between naturally *unforested* ecosystems, which have never supported forests, and those that have been *deforested*.

2 Background

The Tier 1 network sampling approach was developed during 2011 and 2012 and implemented at a national scale in 2013 (Bellingham et al. 2020; Wright et al. 2020). Two full measures of the Tier 1 network have now been completed across all public conservation land, which allows quantification of key aspects of ecological integrity; i.e. the full potential of indigenous biotic and abiotic features and natural processes, functioning in sustainable communities, habitats, and landscapes (McGlone et al. 2020).

The comprehensive nature of Tier 1 data enables DOC to determine the status and trend of ecological integrity across both forest and non-forest ecosystems using a wide set of measures, and to evaluate interrelationships among those measures (Figure 1). Better understanding of the interrelationships among various ecological integrity measures allows us to identify key drivers of ecosystem change and determine how different components, such as vegetation structure, ungulate abundance, and the presence of weeds, are interconnected (Bellingham et al. 2020). This knowledge is crucial for developing effective conservation and management strategies (Wurtzebach & Schultz 2016; McGlone et al. 2020).

This report focuses on the non-forested ecosystems on public conservation land and how information on measures of ecological integrity derived from sample points on the Tier 1 network can inform their management. Until now most of the focus on results from the Tier 1 network has been on forested ecosystems, which is understandable because some of the time-series data from forested ecosystems derive from measurements taken since 2002. Time-series data from forests now show interrelationships at a national scale between forest dynamics and the abundance of ungulates (Hawcroft et al. 2024), and the influence of disturbance, native plant abundance, and non-native mammal abundance on weed invasions in forests (Jo et al. 2024).

In contrast, the extension of the Tier 1 network to include non-forested ecosystems began in 2011, and only since 2020 have there been sufficient time-series data to determine trends in ecological integrity. National-scale investigations of non-forested ecosystems in New Zealand can build on past studies of weed invasions and effects of ungulates in these ecosystems, most of which have been conducted at catchment scales (e.g. Mills et al. 1989; Cruz et al. 2017; but see Walker & Lee 2002, and Day & Buckley 2011).

An earlier appraisal of Tier 1 data, including data from non-forested ecosystems nationally but lacking time-series data, showed that the degree of invasion by non-native plants (weeds), birds, and mammals was highly variable, but that some non-forested ecosystems on public conservation land showed high spatial aggregation in terms of invasion, especially in the northeastern South Island (Bellingham et al. 2020). This report investigates the interrelationships among measures of ecological integrity in non-forested ecosystems in greater detail to determine the consequences of high degrees of biological invasion on ecological integrity. In particular, it evaluates whether any interrelationships found in those parts of public conservation land that are naturally *unforested* (i.e. have never had extensive woody cover) differ from those that have been *deforested* and remain so.

Our approach to evaluating inter-relationships in non-forested ecosystems and the consequences for ecological integrity follows a model that underpinned the development of methods for the Tier 1 network and the rationale for collecting particular data and measures (Figure 1).

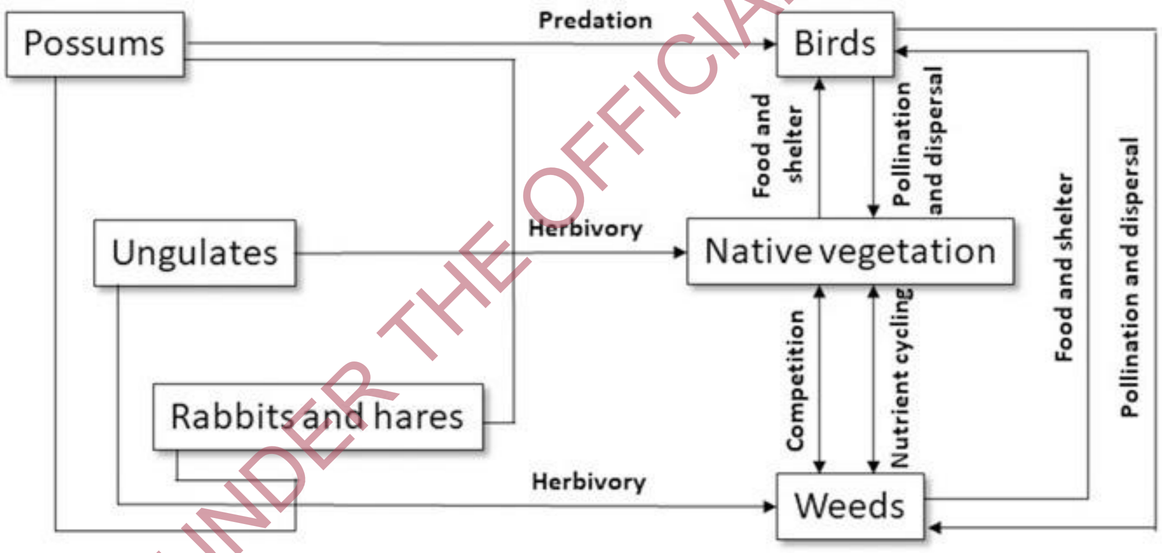

Figure 1. Interrelationships among measures of ecological integrity.
(Source: Marburg & Allen 2010; Bellingham et al. 2020)

This report compares and contrasts ecological integrity in naturally unforested and deforested ecosystems, as well as evaluating the interrelationships among the measures that assess ecological integrity. An essential first step is to conduct a reproducible, defensible means of distinguishing the two ecosystems, based mostly on quantifying the limits to forest growth throughout New Zealand.

Reconstruction of human-induced disturbances that were agents of deforestation – especially fire – has a bearing on distinguishing the two ecosystems, but there will be future value in further evaluating how historical disturbances – not only fire, but also grazing – affect current ecological integrity. For example, fire and grazing were practised over decades not just in deforested ecosystems but also in some naturally unforested ecosystems (e.g. Kepler Range in Fiordland National Park, Lockett Range in Kahurangi National Park). A foundation for distinguishing naturally unforested and deforested ecosystems allows for these to be suitable reporting units at a range of scales, suitable for national evaluation (Tier 1 networks) and local evaluation (Tier 2 networks).

Having established a quantitative basis for distinguishing the two non-forested ecosystems, we then quantified the interrelationships shown in Figure 1, and compared and contrasted them between naturally unforested and deforested ecosystems. We used hierarchical models to include the effects of likely environmental drivers, including climatic and soil nutrient variables, and likely anthropogenic drivers, such as nearby land use, to enhance understanding of the interrelationships.

While a national evaluation of the drivers of ecological integrity in naturally unforested and deforested ecosystems is valuable, decisions about managing pressures that could prevent decline in ecological integrity or enhance it will be easier if there are spatial patterns in some of those pressures. We therefore further evaluated ecological integrity across the two non-forested ecosystems to determine whether there are spatial patterns, especially in terms of pressures on the two ecosystems, that could make management decisions about where to act strongly evidence based.

Finally, we explore the value of non-vascular plant species as indicators of ecological integrity in both naturally unforested and deforested ecosystems and their interrelationships with native and non-native components of ecosystems (per Figure 1) as a case study that can be repeated for other measures in the future. We focused on non-vascular plants because little is known about their distribution and drivers of their distribution in non-forested ecosystems in New Zealand.

3 Objectives

The aim was to assess ecological integrity in non-forest ecosystems using data from the Tier 1 permanent plot network. Manaaki Whenua – Landcare Research was asked to:

1. develop a framework for analysing and interpreting ecological integrity in non-forest ecosystems
2. evaluate key interrelationships among measures from non-forest ecosystems (based on Figure 1) using the framework developed in (1)
3. determine the potential for spatial interpolation across sampling locations to derive maps of ecological integrity and change in ecological integrity
4. test for interrelationships between three measures of non-vascular plant communities and measures of vegetation structure, ungulate abundance, and non-native plant (weed) abundance.

4 Developing a framework for analysing and interpreting ecological integrity in non-forest ecosystems

4.1 Background

New Zealand was overwhelmingly forested before human arrival in the 13th century, with as much as 90% of its area in tall, woody ecosystems (McGlone 1989). Naturally non-forested ecosystems were found only in alpine areas (c. 9–10% of New Zealand; this is now almost entirely public conservation land), and in very small areas where temperature inversions, infertile or toxic soils, fire, or coastal sea spray precluded the growth of tall, woody plants.

After human settlement, fire and clearance for agriculture removed 77% of the forest cover, and deforested ecosystems now account for c. 60% of New Zealand's area (Allen et al. 2013; Perry et al. 2014). Deforestation has been greatest in drier regions, and at lower elevations where people settled (Perry, Wilmshurst, McGlone, & Whitlock 2012; Perry, Wilmshurst, McGlone, & Napier 2012). Some deforested landscapes are managed as public conservation land, particularly in the eastern South Island (Bellingham et al. 2020).

A nationally representative sampling framework (the Tier 1 plot network) provides data to underpin assessments of ecological integrity throughout New Zealand, sampling a diverse range of ecosystems from indigenous forests to, more recently, agricultural ecosystems (Bellingham et al. 2020). Ecosystems other than indigenous forests or shrublands on public conservation land have previously been grouped as non-forested ecosystems. However, this broad category could limit understanding of state and trends in ecological integrity in a changing environment, because important historical context is not taken into consideration (Clark 2007).

Ecosystems that are naturally non-forested and those that have been deforested through anthropogenic activities are likely to differ in successional trajectories, and may also differ in their resilience to climate change because they differ in their environmental conditions, influences of surrounding landscapes and land uses, and legacies of past disturbances. It is therefore necessary to carefully group these diverse ecosystems to better reflect their historical contexts. In this report we developed a defensible, repeatable method to differentiate ecosystems that were historically never forested (unforested ecosystems) from those previously dominated by indigenous forest (deforested ecosystems).

4.2 Methods

Vegetation data sets used to classify plots

We obtained vascular plant data for each plot surveyed between 2012 and 2022 under the DOC Tier 1 monitoring project from the National Vegetation Survey Databank (NVS) (https://nvs.landcareresearch.co.nz/). Plots were measured under the New Zealand Biodiversity and Indigenous Carbon Monitoring System, the New Zealand Biodiversity Monitoring System, Greater Wellington state of the environment monitoring, and the DOC Tier 1 projects. For each Tier 1 plot all vascular plant species are identified and given a cover class (1: <1%; 2: 1–5%; 3: 6–25%; 4: 26–50%; 5: 51–75% and 6: 76–100%) across six height tiers (Tier 1: >25 m, Tier 2: 12–25 m, Tier 3: 5–12 m, Tier 4: 2–5 m, Tier 5: 0.3–2 m, Tier 6: 0–0.3 m); vascular epiphytes (Tier 7) are not assigned cover classes (Allen 1993; Hurst et al. 2022).

We used the NVS plant name list ('CurrentNVSNames') in combination with New Zealand flora native and non-native growth form data sets (Brandt, Maule et al. 2020; Brandt, McGlone et al. 2020) to correct synonyms and to source biostatus (i.e. native, weeds species) and growth form for each species. We calculated plant species richness and cumulative cover for weed species, all native species, and native species that were present at over 5 m in height. Cumulative cover was calculated by converting the cover class midpoints to proportion of cover and summing them across height tiers using the Fischer function, which corrects for overlaps in height tiers, giving a percentage of cover ≤100 % (Fischer 2015; Holdaway et al. 2017). We also used plot-level descriptions measured in the field, such as canopy cover (%), observed land-cover type, and mean top height (m).

Currently forested ecosystems (both forests and shrublands) will have a predominant cover of measurable woody stems, for which the NVS stem diameter data set provides the diameter and unique identification ('ItemObsIdentifier') of plant individuals having a diameter at breast height (DBH, measured at 1.35 m height) of ≥2.5 cm. For each Tier 1 plot, to distinguish forested from non-forested ecosystems we estimated the total stem density, the mean and maximum stem diameter, and the tree basal area. We included trees, shrubs, cabbage trees, and tree ferns based on the plant species growth form data in NVS. The stem diameter data were then used to identify large trees (≥30 cm DBH). Stems below 30 cm DBH were classified into two size categories: small (≥2.5 and <10 cm DBH), medium (≥10 and <30 cm DBH) to provide extra information about the vegetation structure when manually checking plot classification into ecosystem type. Then we calculated the stem density by size category.

These data allowed us to create a framework that distinguishes between non-forested and forested ecosystems, and further categorises non-forested ecosystems into those that have been historically deforested and those that are naturally unforested.

Climate and landscape data sets used to classify plots

We extracted the mean annual temperature (MAT, ˚C) and mean annual precipitation (MAP, mm) for each Tier 1 plot using the New Zealand Environmental Data Stack (McCarthy et al. 2021), which is publicly available on the Land Resource Information Systems portal (https://lris.scinfo.org.nz/group/nzenvds/data/).

The location of Tier 1 plots with respect to the regional treeline was estimated based on treeline positions calculated separately for the North and South Islands, and on measurements from Cieraad et al. (2014). We used a quantile regression model predicting the elevation of the treeline from latitude using data from Cieraad et al. (2014) with a 0.95 quantile using the 'quantreg' package (Koenker 2023) in R (R Development Core Team 2023). We used the model coefficients to predict the elevation of the treeline on each island as a function of latitude, and then categorised each Tier 1 plot as 'above' or 'below' that treeline, based on their measured elevation. Plots that were within 100 m of the predicted treeline were considered 'around' treeline (Figure 2a).

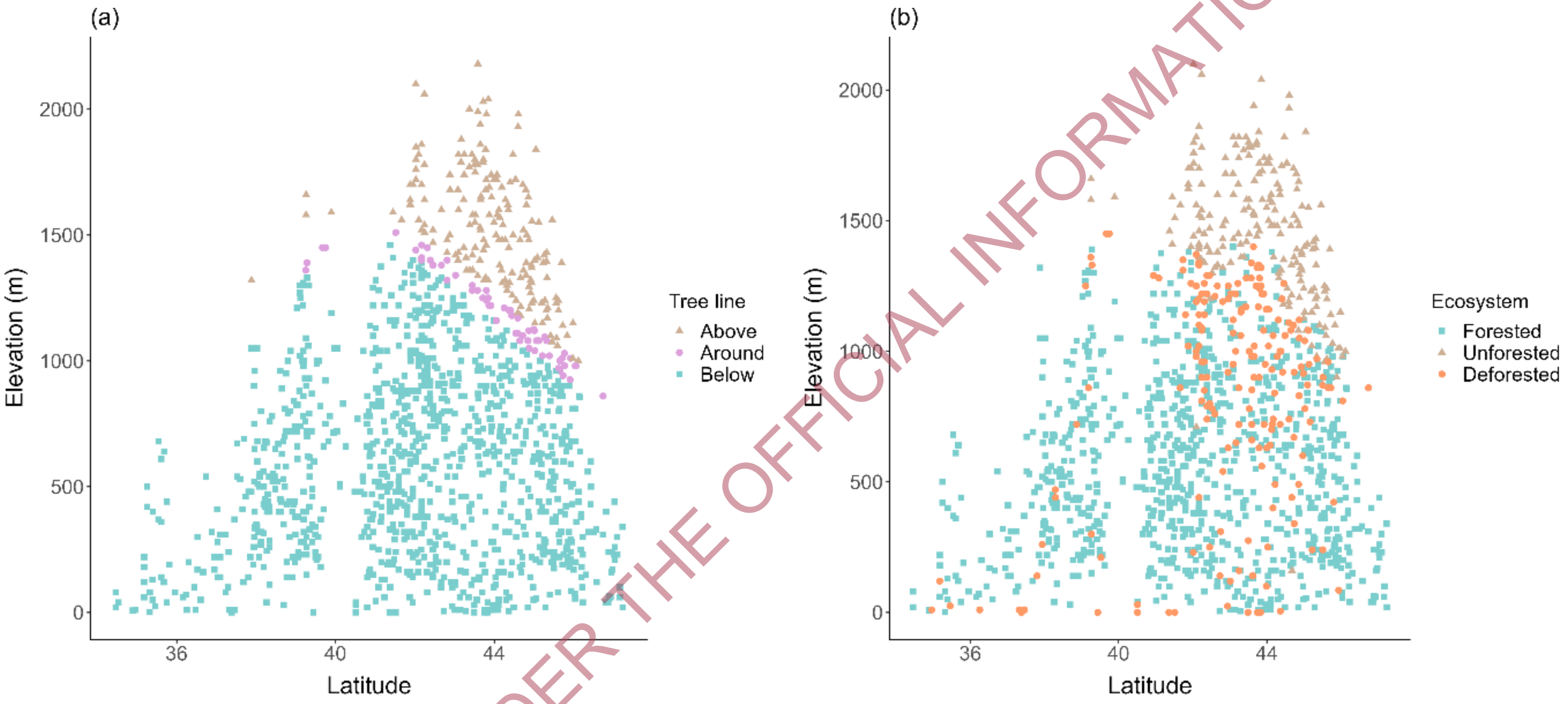

Figure 2. Classification of all Tier 1 plots by: (a) treeline, based on Cieraad et al. 2014, (b) framework, based on mean annual temperature, observed land cover, and measured weed species dominance (ratio between weed and native cover >1).

For each Tier 1 plot we extracted the most recent land-cover classes from the New Zealand Land Cover Database version 5 (Manaaki Whenua – Landcare Research 2020). To summarise the landscape surrounding each plot, we calculated the number of land-cover classes and the proportion of each land-cover class within a 4 km radius to account for the potential maximum dispersal distance for 97% of vascular plant species (Tamme et al. 2014; Jo et al. 2024). We aggregated the 33 land-cover classes into six vegetation cover classes: native woody, native grassland, non-native woody, non-native grassland, disturbed land, and non-vegetated lands, following Rossignaud et al. (2022) (see Appendix 1). We calculated the distance to the nearest road, river, and track using New Zealand Road Centrelines (1:50,000 scale), River Centrelines (1:50,000 scale), and Track Centrelines (1:50,000 scale), all from the LINZ Data Service (Land Information New Zealand 2024).

For each Tier 1 plot we obtained the predicted environmental limiting factors (Newsome et al. 2011; MfE Data Service 2012). This spatial layer maps environmental conditions (e.g. low temperatures, saline soils) that preclude the growth of tall, woody vegetation (Newsome et al. 2011). We also obtained the predicted potential forest composition for each plot (LRIS Portal 2020). Predicted composition is based on correlative models of tree abundance from plot-based data and environmental variables (Leathwick 1995). All climatic and landscape feature information was obtained using ArcGIS Pro version 3.2.0.

Framework

We developed a method to categorise Tier 1 plots based on a sequence of elements that determine whether a plot could have supported tall, woody (forest) vegetation prior to human settlement. The aim was to provide a simple but reliable method that could be applied to vegetation plot networks in New Zealand. Elements considered for our classification included:

- mechanistic drivers of tree growth – climate, distance to regional treeline (Cieraad et al. 2014)
- direct observations – the presence of canopy tree species on the plot (tree basal area and tree density), observed land cover on the plot
- corroborative research – mapped land-cover type from the LCDB, environmental limiting factors (Newsome et al. 2011), potential natural vegetation (Leathwick 1995).

We considered plots to be unforested when they were located in areas where native tree species would not grow naturally, such as above the regional alpine treeline or in areas with a MAT less than 5.5˚C (Leathwick 1995; Ewers et al. 2006; Cieraad et al. 2014). Deforested plots were identified as those in areas that provide favourable conditions to forest growth but where native tree species above 30 cm DBH are absent (McGlone 1989; Allen et al. 2023).

We combined all elements associated with each Tier 1 plot and identified the sequence in which these should be applied to obtain a reliable list of forested, unforested, and deforested plots. The first filter applied was based on MAT and the observed land cover.

1. Plots with an MAT ≥5.5˚C and an observed land cover of indigenous forest or shrubland were classified as the forested ecosystem type.
2. Plots with an MAT <5.5˚C and an observed land cover of bare ground, grassland or scree were classified as the unforested ecosystem type.
3. All plots not classified as forested or unforested were classified as the deforested ecosystem type.

We then applied manual verification and reclassification. For plots located near the treeline (i.e. MAT was 5.5 ± 1.5˚C or classified as 'around', using the analysis based on Cieraad et al. 2014), we used measures of vegetation structure (e.g. canopy cover, tree diameter) to detect the presence of tall trees indicative of a forested or deforested ecosystem type. For plots identified as deforested, we used tree diameter and native canopy cover to identify the presence of native trees, suggesting that the plot should be assigned to forested ecosystem. Plots initially identified as forested but showing a ratio between weed and native cover of >1 (e.g. a plot dominated by gorse, *Ulex europaeus*) were reclassified as deforested. Lastly, we checked vascular species composition on plots near the treeline to check for the presence of woody species that reach >5 m at maturity (following McGlone et al. 2010).

We used 1,326 plots for which information was available for all vegetation and environmental elements (n = 1,005 in the South Island, n = 25 on Stewart Island / Rakiura, and n = 296 in the North Island) (Figure 3).

Statistical analysis

To identify differences between each ecosystem type (i.e. unforested, deforested, and forested ecosystem) we used generalised linear models (GLMs) predicting each vegetation, climate, and landscape variable from ecosystem type using the 'glmmTMB' package (Brooks et al. 2017) in R. Depending on the variable, a binomial, beta binomial, Gaussian, Poisson or negative binomial error distribution was used (Table 2). GLMs with beta binomial error distributions were used for proportion and vegetation cover data, as recommended by Damgaard and Irvine (2019).

Vegetation cover was converted into proportion of cover and transformed to avoid zeroes and ones, following the method described by Smithson and Verkuilen (2006). This transformation was also applied to the proportion of each land cover class within a 4 km radius. Distance to nearest road, river, and track as well as mean annual precipitation were log transformed and analysed using a Gaussian error distribution.

The significance of ecosystem type was identified using Wald χ^2 tests on each GLM model with the 'Anova' function from the 'car' package (Fox & Weisberg 2019). The R^2 (coefficient of determination) for each GLM model was obtained using the 'MuMIn' package (Barton 2022). Pearson's χ^2 tests were conducted alongside a contingency table to assess whether there were differences between the two different classification frameworks (i.e. based on treelines or based on mean annual temperature and observed land cover).

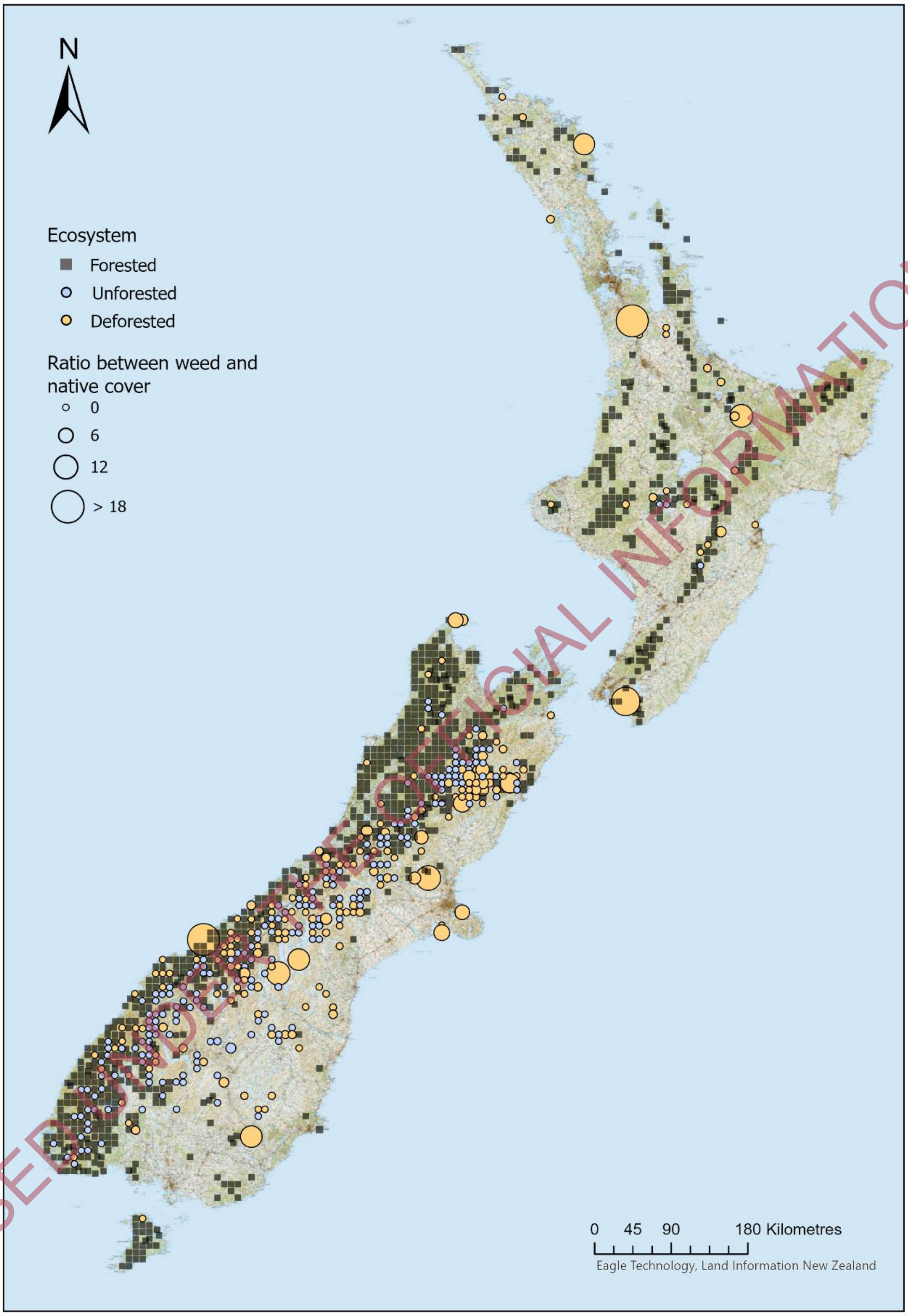

Figure 3. Map showing the location of Tier 1 plots (*n* = 1,326) based on their ecosystem (forested, unforested, deforested), with the size of the circles proportional to the ratio of weed and native plant species cover.

4.3 Results

Overall, both methods, relying either on the estimated treeline (based on Cieraad et al. 2014) or on MAT and observed land cover, showed a relatively similar number of plots classified either as forested or as non-forested (Table 1). The method based on estimated treeline identified 174 plots above the treeline that were considered non-forested, with 59 around the treeline and 1,093 below the treeline considered forested (Table 1). The method based on MAT and observed land cover classified 200 plots as unforested and 1,126 as forested.

The use of observed land cover and vegetation information allowed us to further classify forested plots as either deforested (190 plots) or forested (936 plots), which may explain the significant difference between the two frameworks (Pearson's χ^2 = 1039.2, $P < 0.001$, Table 1). Corroborative measures were kept in the data set as a last resort for manual checking but proved unnecessary: direct observations and mechanistic drivers of tree growth were sufficient to categorise plots as forested, unforested or deforested.

Table 1. Contingency table showing the number of Tier 1 plots classified using the treeline framework based on Cieraad et al. 2014 (i.e. above, around, or below treeline) and the framework based on mean annual temperature, observed land cover, and measured weed species dominance (ratio between weed and native cover >1) (i.e. forested, unforested or deforested ecosystem type)

	Above	Around	Below
Forested	7	14	915
Unforested	161	23	16
Deforested	6	22	162
Total	174	59	1,093

Notes: Pearson's χ^2 = 1039.2, $P < 0.001$.

Among the variables considered, mean native cover and the proportion of native woody vegetation best explained the differences between each ecosystem type ($R^2 > 0.80$, Table 2). MAT and elevation were the next best explanatory variables ($R^2 > 0.40$), which is to be expected given that MAT was used to distinguish whether plots were located in unforested or deforested ecosystems, and that elevation and MAT are correlated (Table 2).

Plots in deforested ecosystems had higher weed plant species richness and cover than either unforested or forested ecosystems (Table 2). Although more Tier 1 plots in unforested ecosystems had at least one weed species (45% of plots) compared to forested ecosystems (32%), weed species richness and cover were similarly low in unforested and forested ecosystems (mean weed richness <2 and mean weed cover c. 2%) (Table 2).

Unsurprisingly, there was greater tree basal area (mean = 50.6 m^2/ha) in forested plots than in unforested and deforested ecosystems (Table 2). Most plots in unforested ecosystems had no woody stems with a DBH ≥ 2.5 cm (only three plots had measurable tree basal area, with a maximum of 3.5 m^2/ha). Of the 190 plots in deforested ecosystems, 48 (25.2%) had woody stems with DBH ≥ 2.5 cm. Tree basal area measurements ranged from 0.01 to 83.9 m^2/ha, reflecting the diversity within deforested ecosystems that included bare ground, grassland, inland wetlands, pastures, and coastal sands, which had few woody plants, to shrublands and planted forests that had more woody plants.

MAT was used to categorise the three ecosystem types, so, unsurprisingly, MAT was significantly different between ecosystem types, from the warmer forested ecosystem (9˚C) to the coolest unforested ecosystem (4˚C) (Table 2). The mean value of MAP was significantly higher in unforested ecosystems relative to deforested ecosystems (Table 2), but MAP ranged widely within those two ecosystems (1,071–8,705 mm in unforested ecosystems; 635–9,304 mm in deforested ecosystems), which might explain the low R^2 (0.04).

Unforested plots were further from roads and tracks than deforested or forested ecosystems (Table 2). Deforested plots were the closest to tracks. The land-cover types surrounding Tier 1 plots were mainly native woody and grassland vegetation, followed by non-native grassland vegetation (Table 2). Forested ecosystems had the highest proportion of surrounding native woody cover with 0.74, followed by unforested and deforested ecosystems, which were both c. 0.32 (Table 2). Unforested ecosystems had the highest proportion of surrounding native grassland with 0.40, followed by deforested ecosystems (0.30) and forested ecosystems (0.11) (Table 2).

Table 2. Summary of vegetation attributes, environment, and surrounding land cover for Tier 1 plots in forested, unforested, and deforested ecosystems

Variable	Units	Forested	Unforested	Deforested	Error distribution	Transformation	R^2	χ^2	*P*
Number of plots	Count	936	200	190					
Percentage of plots with a weed species present	%	32 (a)	45 (b)	80 (c)	binomial	-	0.15	126.42	<0.001
Mean native richness	Count	50.6 ± 18.5 (a)	42.1 ± 24.7 (b)	36.5 ± 21.4 (c)	negative binomial	-	0.05	75.62	<0.001
Mean native cover (%)	% total cover	92.9 ± 7.0 (a)	52.3 ± 33.4 (b)	58.5 ± 31.6 (c)	beta binomial	Smithson	0.89	708.95	<0.001
Mean weed richness	Count	1.5 ± 4.3 (a)	1.7 ± 2.9 (a)	10.3 ± 10.1 (b)	negative binomial	-	0.02	135.81	<0.001
Mean weed cover (%)	% total cover	2.0 ± 7.9 (a)	2.4 ± 7.3 (a)	28.1 ± 32.2 (b)	beta binomial	Smithson	0.10	194.25	<0.001
Mean basal area	m^2/ha	53.6 ± 30.1 (a)	1.2 ± 2.0 (b)	7.7 ± 15.4 (b)	Gaussian	-	0.11	119.63	<0.001
Mean tree density	number/ha	139.6 ± 109.6 (a)	7.7 ± 9.9 (b)	61.3 ± 62.0 (c)	negative binomial	-	0.08	95.11	<0.001
Mean annual temperature	˚C	9.3 ± 2.1 (a)	4.2 ± 0.9 (b)	8.0 ± 2.5 (c)	Gaussian	-	0.44	1041.8	<0.001
Mean annual precipitation	mm	2,735 ± 1,373 (a)	3,331 ± 1,769 (b)	2,566 ± 1,933 (c)	Gaussian	log	0.04	52.242	<0.001
Elevation	m	560 ± 335 (a)	1,464 ± 264 (b)	822 ± 421 (c)	Gaussian	-	0.47	1175.1	<0.001
Distance to nearest road	km	8.46 ± 10.6 (a)	11.20 ± 8.5 (b)	6.94 ± 7.1 (a)	Gaussian	log	0.04	59.48	<0.001
Distance to nearest track	km	3.08 ± 4.4 (a)	3.79 ± 3.6 (b)	2.27 ± 2.8 (c)	Gaussian	log	0.03	41.50	<0.001
Distance to nearest river	km	0.224 ± 1.0 (a)	0.298 ± 0.2 (b)	0.304 ± 0.7 (a)	Gaussian	log	0.03	45.66	<0.001
Native woody vegetation	Proportion	0.74 ± 0.22 (a)	0.32 ± 0.25 (b)	0.32 ± 0.29 (b)	beta binomial	Smithson	0.80	738.35	<0.001
Non-native woody vegetation	Proportion	0.03 ± 0.08 (a)	0.004 ± 0.02 (b)	0.03 ± 0.09 (a)	beta binomial	Smithson	0.01	14.88	0.001
Native grassland	Proportion	0.11 ± 0.14 (a)	0.40 ± 0.20 (b)	0.30 ± 0.24 (c)	beta binomial	Smithson	0.38	554.71	<0.001
Non-native grassland	Proportion	0.07 ± 0.12 (a)	0.05 ± 0.09 (a)	0.21 ± 0.24 (b)	beta binomial	Smithson	0.04	55.32	<0.001
Disturbed land	Proportion	0.001 ± 0.01 (a)	0.0003 ± 0.00 (a)	0.001 ± 0.002 (a)	beta binomial	Smithson	0.002	3.97	0.137
Non-vegetated land	Proportion	0.05 ± 0.09 (a)	0.23 ± 0.21 (b)	0.14 ± 0.18 (c)	beta binomial	Smithson	0.19	318.64	<0.001
Number of land-cover types	Count	10.2 ± 3.2 (a)	8.9 ± 2.4 (b)	9.4 ± 3.1 (c)	Poisson	-	0.01	16.42	<0.001

Notes: Data are means with ± standard deviations. Values within rows that share a letter in parentheses are not significantly different from each other, based on generalised linear models (GLMs) with binomial, negative binomial, beta binomial, Gaussian or Poisson errors and data transformation when necessary. The χ^2 and *P* values are from an analysis of variance (Anova), and R^2 (coefficient of determination) are based on each GLM. Vegetation attributes are based on the most recent measurement of each plot. The proportion and number of surrounding land-cover types are taken from a 4 km radius around each plot.

4.4 Discussion

Considering the historical legacy when characterising ecosystem types is important to accurately assess trends in biodiversity and improve our understanding of the interrelationships between ecosystem integrity measures and non-native species and environmental factors (Clark 2007; Bellingham et al. 2020). Distinguishing between unforested ecosystems that were historically never forested and deforested ecosystems that historically had indigenous forests but experienced strong anthropogenic disturbances will inform appropriate ecosystem-based management programmes (Bellingham et al. 2020).

We used two different methods to establish a reliable way to classify Tier 1 plots as being located in unforested, deforested or forested ecosystems. The first method relied on an estimated position of the treeline, and the second was based on a combination of mechanistic drivers and direct observations. The first method separated unforested ecosystems from other ecosystems, but the second method, using MAT as a mechanistic driver and direct observations of woody vegetation, provided a more comprehensive classification as we were also able to separate deforested ecosystems from forested ecosystems.

Both methods still required some manual checking, especially for Tier 1 plots located on the edge of the treeline or with an MAT around 5.5 ± 1.5˚C, where some plots may have woody species that reach >5 m height at maturity and thus qualify as tree species (McGlone et al. 2010). After applying the second method, some woody species were still present in Tier 1 plots located in unforested ecosystems, but these plots had a low basal area. When focusing on the vascular plant community in unforested ecosystems, some tall, native, woody plant species were present, but they were not recorded in height tiers >5 m (e.g. *Macrolearia colensoi*, *Dracophyllum longifolium*). One woody weed species known to grow taller than 5 m, *Pinus contorta*, was found in unforested plots; it is known to invade unforested ecosystems above New Zealand treelines (e.g. Wardle 2008). This highlights the importance of considering native and non-native woody species separately when classifying plots as either unforested or deforested to account for woody species such as *P. contorta*, which can colonise unforested ecosystems.

5 Contrasting key interrelationships among measures of ecological integrity in naturally unforested ecosystems and deforested ecosystems

5.1 Background

Studying the interrelationships among measures of ecological integrity is important if we are to develop a comprehensive understanding of how different factors interact to influence the health of ecosystems (Capmourteres et al. 2018; Bellingham et al. 2020). In this section we compare and contrast interrelationships among specific measures of ecological integrity in naturally unforested ecosystems and deforested ecosystems. We compare these ecosystems in terms of how ungulates affect native vegetation and weed invasion, and how native vegetation affects weed invasion (Figures 1 and 4). We assess native vegetation and weeds in terms of plant functional traits, and we also incorporate environmental variables and measures of soil fertility as covariates to examine how these factors affect the interrelationships.

5.2 Methods

Vascular plant data

For each non-forested plot we selected data from the first census (T1) and the most recent census (T2). The mean interval was 4.7 years (± 1.0 SD for unforested and ± 1.2 SD for deforested plots). We then calculated the proportional cover of native and weed vascular plant species on each plot using the approach described in section 4.2 (above).

We used two categorical plant functional traits – woodiness and the ability to fix atmospheric nitrogen – to describe the functional composition of each vegetation plot. Species' woodiness (i.e. woody vs non-woody) information was compiled primarily from McGlone et al. 2010 and McGlone & Richardson 2023, with additional unpublished data collated by the authors. Nitrogen (N)-fixation information was obtained using data from the Global Inventory of Floras and Traits (GIFT) databank, which is accessible through the 'GIFT' R package (Weigelt et al. 2020; Denelle et al. 2023). This provided information for 28% of the plant species (518 out of 1,852 species). Further N-fixation information was added based on higher taxonomic level (i.e. order or family) of each species with no available information, based on Santi et al. 2013, which allowed us to reach 30% (548 species) of plant species with N-fixation information.

Ungulate data

The relative abundance of non-native herbivorous ungulates is estimated on each Tier 1 plot using faecal pellet counts in up to 120 circular subplots, evenly spaced along up to four transects radiating from the four corners of the 20 m × 20 m permanent vegetation plot (Department of Conservation 2020; Moloney et al. 2021). We used the proportion of measured subplots that had ungulate faecal pellets collected from 2012 to 2018 (Moloney et al. 2021) as a proxy for the relative abundance of ungulates (Bellingham et al. 2020). These include deer, goats (*Capra hircus*), Himalayan tahr (*Hemitragus jemlahicus*), chamois (*Rupicapra rupicapra*), and sheep (*Ovis aries*).

Environmental variables and surrounding landscape information

We compiled plot-level environmental variables (MAP, MAT) (McCarthy et al. 2021), and landscape attributes (distance to the nearest road, composition of the landscape within a 4 km radius of the plot) using the LCDB5 (Manaaki Whenua – Landcare Research 2020) and LINZ (Land Information New Zealand 2024). Details are given in section 4.2, above.

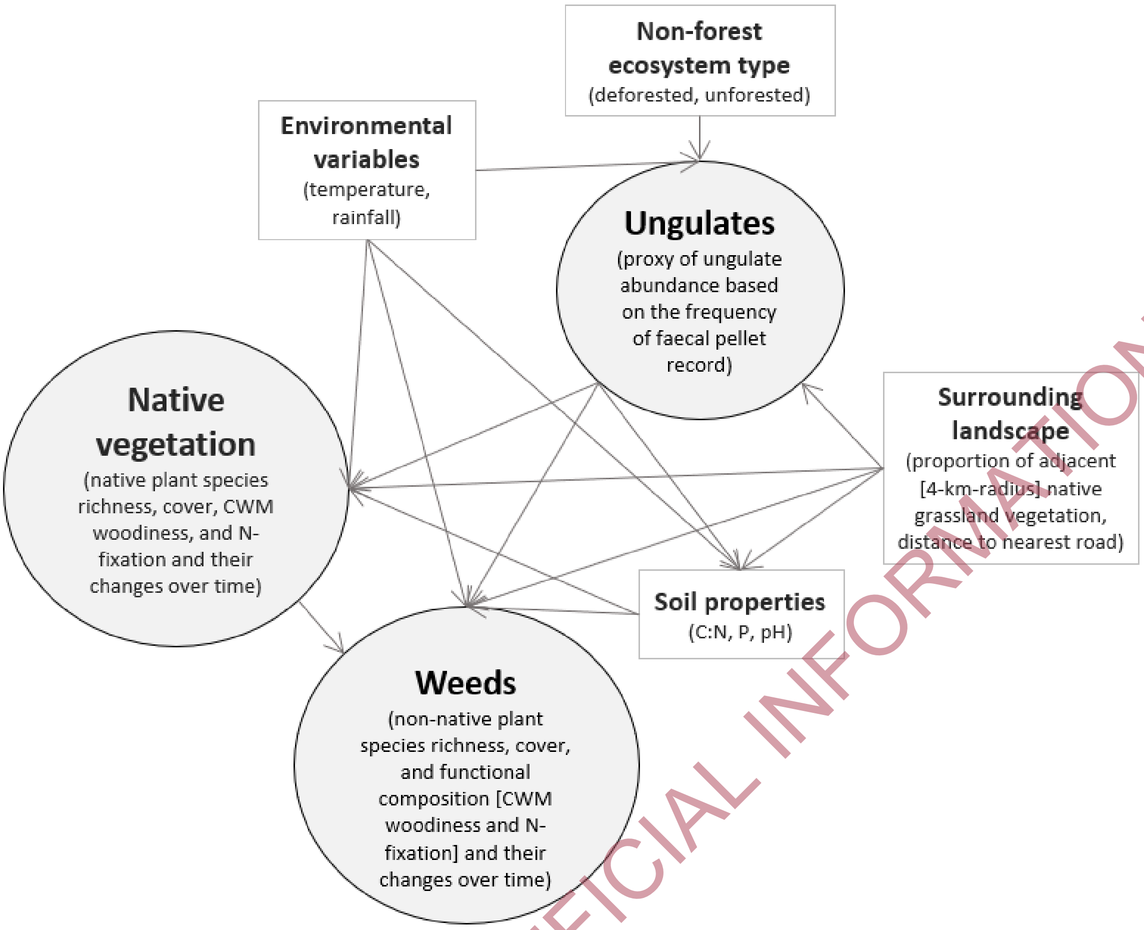

Figure 4. Hypothesised relationships between measures of weed invasion and other related ecological integrity measures (native vegetation and ungulates).
Notes: Ecological integrity measures are circled and other potential covariates are in squares. CWM = community-weighted mean; C:N = carbon:nitrogen ratio; P = phosphorus.

Statistical analysis

We tested relationships between selected measures of ecological integrity (i.e. ungulates, native vegetation, and weeds) using a Bayesian hierarchical modelling approach. We included plots in the analysis where all predictor variables were available, resulting in 111 unforested plots and 97 deforested plots. We modelled each ecological integrity metric at the first census (T1) and its changes between two censuses (T1 and T2) as a function of other ecological integrity measures and related environmental variables, which include climate, soil properties, and surrounding landscape information (Figure 4, Table 3). Native vegetation and weed measures include species cover and community-weighted mean (CWM) values for woodiness and N-fixation. The CWM woodiness and N-fixation values were transformed to avoid having zero or one in the model with a beta distribution (Table 3). This transformation was done using the formula $y' = \frac{y(N-1)+0.5}{N}$, where N is the sample size, following Averill et al. (2018). Model structure and specifications are available in Table 3.

Change in vegetation cover values was simplified to a binary response variable (1 = increase, 0 = no change or decrease) to focus on testing the drivers of increasing native vegetation and weed cover.

Models predicting vegetation cover and CWM values at T1 used all plots for native species, and only plots where weeds were present for weed species at T1. For models of change in vegetation cover and CWM values, only plots where weeds were present at *both* times could be included.

Except for one categorical variable (for non-forest ecosystem [deforested = 1, unforested = 0]), all continuous predictor variables were standardised by subtracting their mean and dividing by two SDs to make effect size comparable between predictors. Non-informative priors were used for fixed-effect coefficients of the relationships from a normal distribution of mean = 0 and variance = 10,000, and the models were fitted using Markov chain Monte Carlo methods (MCMC) in JAGS in R 4.3.2, with three parallel MCMC chains for 2,000 iterations with a 1,000-iteration burn-in (Plummer 2003; Su & Yajima 2021; R Development Core Team 2023).

To further understand how native species and weed cover were related to ungulate relative abundance at T1 and T2 in deforested and unforested plots, we plotted box plots of native species and weed cover across binned proportions of ungulate pellets. Most plots (>70% in both ecosystem types) had a very low proportion of subplots with ungulate pellets (<0.05), so we binned the data to explicitly compare vegetation measures under low ungulate relative abundance (<0.05), with vegetation measures under four other categories of ungulate relative abundance (0.05–0.1, 0.1–0.2, 0.2–0.4, and >0.4 proportion of subplots with ungulate pellets).

Table 3. Summary of specifications of model components illustrated in Figure 4

Response variable (*y*)	**Predictor variable** (*x*)	**Model structure**
Ungulate abundance (proportion of measured subplots that had ungulate faecal pellets collected)	Mean annual precipitation (MAP); mean annual temperature (MAT); neighbourhood native grassland (proportion of surrounding native grasslands within 4 km radius); distance to nearest road; deforested ecosystem (deforested = 1, unforested = 0)	• $y \sim Beta\ (a, b)$ $a = \mu \times \tau;\ b = (1 - \mu) \times \tau$ $logit(\mu) = \beta_0 + \ \beta_1 x_1 \ldots + \beta_n x_n + R$
Soil C:N ratio; soil P; soil pH	MAP; MAT; neighbourhood native grassland; distance to nearest road; ungulate abundance	• $y \sim Normal\ (\mu, \sigma^2)$ $\mu = \beta_0 + \ \beta_1 x_1 \ldots + \beta_n x_n + R$
Native vegetation at T1 (cover, CWM woodiness, CWM N-fixation)	MAP; MAT; neighbourhood native grassland; distance to nearest road; ungulate abundance; soil C:N ratio; soil P; soil pH	• $y \sim Poisson\ (\mu)$ [cover] $\ln(\mu) = \beta_0 + \ \beta_1 x_1 \ldots + \beta_n x_n + R$ • $y \sim Beta\ (a, b)$ [CWM woodiness, CWM N-fixation] $a = \mu \times \tau;\ b = (1 - \mu) \times \tau$ $logit(\mu) = \beta_0 + \ \beta_1 x_1 \ldots + \beta_n x_n + R$
Changes in native vegetation between T1 and T2 (changes in cover [increase = 1, decrease or no change = 0], CWM woodiness, CWM N-fixation)	MAP; MAT; neighbourhood native grassland; distance to nearest road; ungulate abundance; soil C:N ratio; soil P; soil pH	• $y \sim Bernoulli\ (p)$ [cover change] $ln(p) = \alpha_0 + \alpha_1 x_1 \ldots + \alpha_n x_n + R$ • $y \sim Normal\ (\mu, \sigma^2)$ [CWM woodiness and N-fixation change] $\mu = \beta_0 + \ \beta_1 x_1 \ldots + \beta_n x_n + R$
Weeds at T1 (cover, CWM woodiness, CWM N-fixation for the plots where weeds were present)	MAP; MAT; neighbourhood native grassland; distance to nearest road; ungulate abundance; soil C:N ratio; soil P; soil pH; native vegetation richness, cover, CWM woodiness, and CWM N-fixation	• $y \sim Poisson\ (\mu)$ [cover] $ln(\mu) = \alpha_0 + \alpha_1 x_1 \ldots + \alpha_n x_n + R$ • $y \sim Beta\ (a, b)$ [CWM woodiness, CWM N-fixation] $a = \mu \times \tau;\ b = (1 - \mu) \times \tau$ $logit(\mu) = \beta_0 + \ \beta_1 x_1 \ldots + \beta_n x_n + R$
Changes in weeds between T1 and T2 (changes in cover [increase = 1, decrease or no change = 0], CWM woodiness, and CWM N-fixation for the plots where weeds were present)	MAP; MAT; neighbourhood native grassland; distance to nearest road; ungulate abundance; soil C:N ratio; soil P; soil pH; native vegetation richness, cover, CWM woodiness, and CWM N-fixation	• $y \sim Bernoulli\ (p)$ [cover change] $ln(p) = \alpha_0 + \alpha_1 x_1 \ldots + \alpha_n x_n + R$ • $y \sim Normal\ (\mu, \sigma^2)$ [CWM woodiness and N-fixation change] $\mu = \beta_0 + \ \beta_1 x_1 \ldots + \beta_n x_n + R$

Notes: See Figures 5, 6 and 10–12 for the estimated coefficients ($\boldsymbol{\beta_s}$). Intercept (α_0) and slope ($\alpha_1, \ldots, \alpha_n$) estimates; random intercept (β_0) and slope ($\beta_1, \ldots, \beta_n$) estimates for unforested and deforested plots; R = random intercept for the geographical locations of plots (i.e. the North Island or the South Island); μ = mean; σ^2= variance; p = the probability of a plot having non-zero values for y; a, b = shape parameters for beta distribution; CWM = community-weighted mean.

5.3 Results

Ungulate abundance

In unforested ecosystems ungulates were detected by faecal pellets in 48.6% of 111 plots. For those plots with faecal pellets, the proportion of subplots containing ungulate faecal pellets (a proxy for ungulate abundance) was 0.09 ± 0.02 (mean ± SE).

In deforested ecosystems, ungulates were detected by faecal pellets in 57.7% of 97 plots. For those plots with faecal pellets, the proportion of subplots containing ungulate faecal pellets was 0.11 ± 0.02.

Overall, ungulate abundance was negatively associated with MAP and positively associated with distance to the nearest road (Figure 5). Ungulate abundance was higher in deforested ecosystems than in unforested ecosystems (Figure 5).

Soil chemistry

Unforested ecosystems

Soil phosphorus (P) concentrations were negatively associated with MAP (Figure 6). The soil carbon:nitrogen (C:N) ratio was positively associated with MAT, while soil P concentrations and soil pH were negatively associated with MAT. Soil P concentrations were negatively associated with distance to nearest road, and with the proportion of native grassland within a 4 km radius (Figure 6). Soil P concentrations were positively associated with ungulate abundance (Figure 6).

Deforested ecosystems

In deforested ecosystems, soil P concentrations and soil pH were both negatively associated with MAP (Figure 6). In contrast to unforested ecosystems, soil C:N ratio was negatively associated with MAT, while soil pH was positively associated with MAT. Soil P concentrations were positively associated with the proportion of native grassland within a 4 km radius. Soil pH was negatively associated with the proportion of native grassland within a 4 km radius. As in unforested ecosystems, soil P concentrations were negatively associated with distance to nearest road. Soil P concentrations were positively associated with ungulate abundance (Figure 6).

Native vegetation cover and functional composition at T1

Unforested ecosystems

Native vegetation cover per plot was positively associated with MAT (Figure 7). The CWM of native vegetation woodiness in plots was also positively associated with MAT. Native vegetation cover and CWM native vegetation woodiness were both positively associated with soil C:N ratio. Native vegetation cover per plot was positively associated with soil P concentrations and negatively associated with soil pH (Figure 7).

Native vegetation cover and CWM native vegetation woodiness per plot were both negatively associated with ungulate abundance (Figure 7 and Figure 8a,b). Native vegetation cover was negatively associated with distance to the nearest road (Figure 7).

Deforested ecosystems

Native vegetation cover per plot was positively associated with both MAP and MAT (Figure 7). As in unforested ecosystems, native vegetation cover and CWM native vegetation woodiness were both positively associated with soil C:N ratio. In addition, CWM native vegetation N-fixation in plots was positively associated with soil P concentrations, whereas CWM native vegetation woodiness was negatively associated with soil P concentrations. Native vegetation cover per plot was negatively associated with soil pH, but CWM native vegetation woodiness and CWM native vegetation N-fixation were positively associated with soil pH (Figure 7).

As in unforested ecosystems, native vegetation cover per plot was negatively associated with ungulate abundance (Figure 7 and Figure 9a,b). In contrast to unforested ecosystems, native vegetation cover in plots was positively associated with both the proportion of native grassland within a 4 km radius and distance to nearest road, but their effect sizes were small (Figure 7).

Predictors of whether native vegetation cover increased, and changes in CWM native vegetation woodiness and N-fixation, between T1 and T2

Unforested ecosystems

The probability of native vegetation cover increasing on a plot between the two censuses (T1 and T2) was negatively associated with MAP (Figure 10). None of the other predictor variables were strongly associated with the probability of native vegetation cover increasing (all 90% credible intervals [CIs] overlapped with zero, Figure 10). The change in the CWM of native vegetation woodiness was positively associated with ungulate abundance and soil P concentrations, although their 90% CIs overlapped with zero (Figure 10). The change in the CWM N-fixation had no strong associations with any of these predictor variables (Figure 10).

Deforested ecosystems

As in unforested ecosystems, the probability of native vegetation cover increasing on a plot was negatively associated with MAP, although its 90% CI slightly overlapped with zero (Figure 10). The change in CWM native vegetation woodiness was not significantly associated with any of the predictor variables, similar to the pattern observed in unforested ecosystems. However, unlike unforested ecosystems, the change in CWM native vegetation N-fixation was positively associated with ungulate abundance and negatively associated with soil P and soil pH (Figure 10).

Weed cover and functional composition at T1

Unforested ecosystems

In unforested ecosystems, 46 plots (41.4% of plots in unforested ecosystems) had weed species present. Across the plots where weed species were present in unforested ecosystems, weed cover was 4% ± 1.1% (mean ± SE) and weed species richness was 3.7 ± 0.5 species per 400 m^2. Weed cover per plot was negatively associated with MAP and positively associated with MAT (Figure 11). Weed cover was negatively associated with soil C:N ratio.

Weed cover per plot was not significantly associated with ungulate abundance (Figure 11), but there was a weak positive association, indicating that weed cover tended to be greater on plots with higher ungulate abundance (Figure 8c,d). Weed cover per plot was negatively associated with soil C:N ratio and CWM native vegetation N-fixation. Surprisingly, weed cover per plot was positively associated with the proportion of native grassland within a 4 km radius and distance to nearest road. CWM weed woodiness and CWM weed N-fixation did not have significant associations with any of the predictor variables included in the model (Figure 11).

Deforested ecosystems

In deforested ecosystems, 76 plots (78.4% of plots in deforested ecosystems) had weed species present. Across the plots where weed species were present in deforested ecosystems, weed cover was 52% ± 7.6% (mean ± SE) and weed species richness was 13 ± 1 species per 400 m^2. Weed cover per plot at T1 was positively associated with MAT (Figure 11). In addition, CWM weed N-fixation was positively associated with MAT. Weed cover per plot was positively associated with soil P concentrations (Figure 11). CWM weed N-fixation was also positively associated with soil pH.

In contrast to unforested ecosystems, weed cover per plot was negatively associated with ungulate abundance, but the effect size was small (Figure 11 and Figure 8c,d).

Weed cover per plot was negatively associated with native vegetation species richness per plot (Figure 11). Weed cover was also positively associated with CWM native vegetation woodiness and CWM N-fixing native vegetation per plot (Figure 11). CWM weed woodiness did not have significant associations with any of the predictor variables included in the model. CWM weed N-fixation was positively associated with CWM native vegetation N-fixation per plot. In contrast to unforested ecosystems, weed cover per plot was negatively associated with the proportion of native grassland within a 4 km radius, although the effect size was small (Figure 11).

Predictors of whether weed cover increased, and the changes in CWM weed woodiness and N-fixation, between T1 and T2

Unforested ecosystems

The probability of weed cover increasing on a plot was positively associated with CWM native vegetation N-fixation (Figure 12). Also, native vegetation species richness and cover were negatively associated with the probability of weed cover increasing, although their 90% CIs overlapped with zero (Figure 12). All other predictor variables had no significant associations with the probability of weed cover increasing.

Change in CWM of weed woodiness was positively associated with MAP and soil C:N ratio. It was also negatively associated with soil P concentrations, native vegetation species richness, native vegetation cover, and CWM native vegetation woodiness. The change in CWM weed N-fixation was negatively associated with the proportion of native grassland within a 4 km radius and soil P concentrations, although their 90% CIs overlapped with zero (Figure 12).

Deforested ecosystems

The probability of weed cover increasing on a plot between the two censuses (T1 and T2) was positively associated with MAT (Figure 12). The probability of weed cover increasing was not significantly associated with ungulate abundance, the proportion of native grassland within a 4 km radius, or distance to the nearest road. Changes in CWM weed woodiness and CWM weed N-fixation also showed no strong associations with these variables (Figure 12).

The probability of weed cover increasing and the changes in CWM weed woodiness and CWM weed N-fixation were not significantly associated with native vegetation species richness and cover. Change in CWM weed N-fixation per plot was negatively associated with CWM native vegetation woodiness (Figure 12).

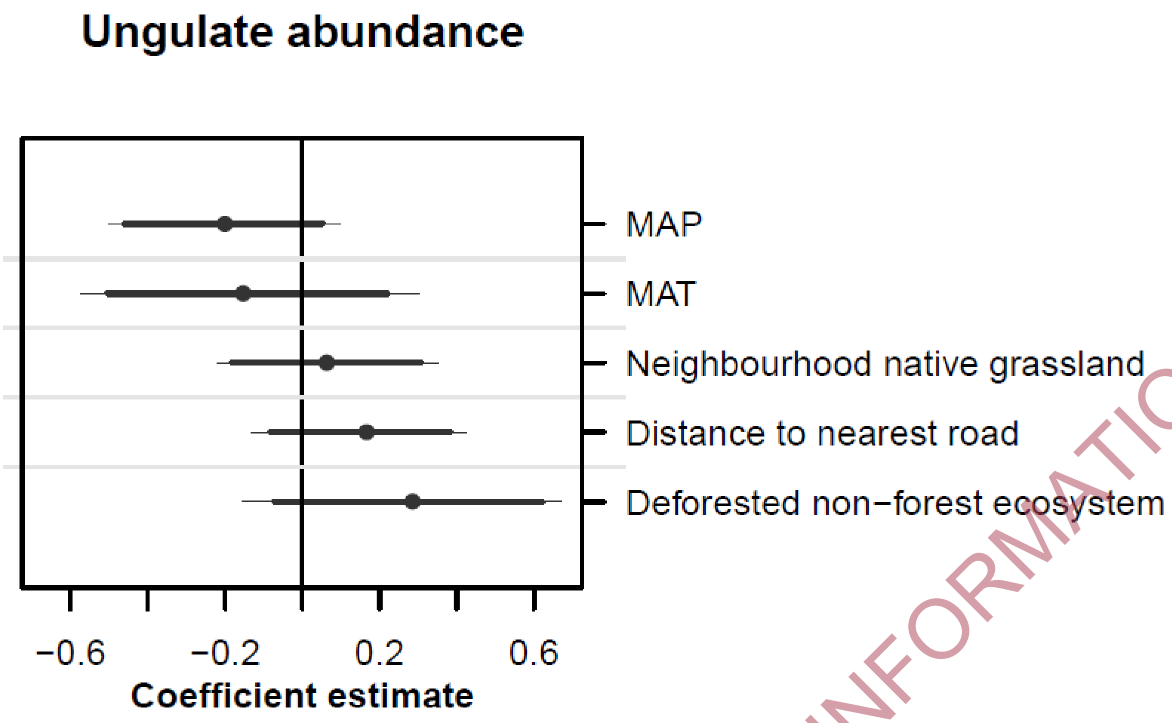

Figure 5. Effects of environmental variables, surrounding landscape, and non-forest ecosystem type on ungulate abundance, based on faecal pellet index.

Notes: The coefficient 'deforested non-forest ecosystem' is the effect of the deforested ecosystem type relative to the unforested ecosystem type. Error bars are 90 (thick line) and 95% (thin line) credible intervals.

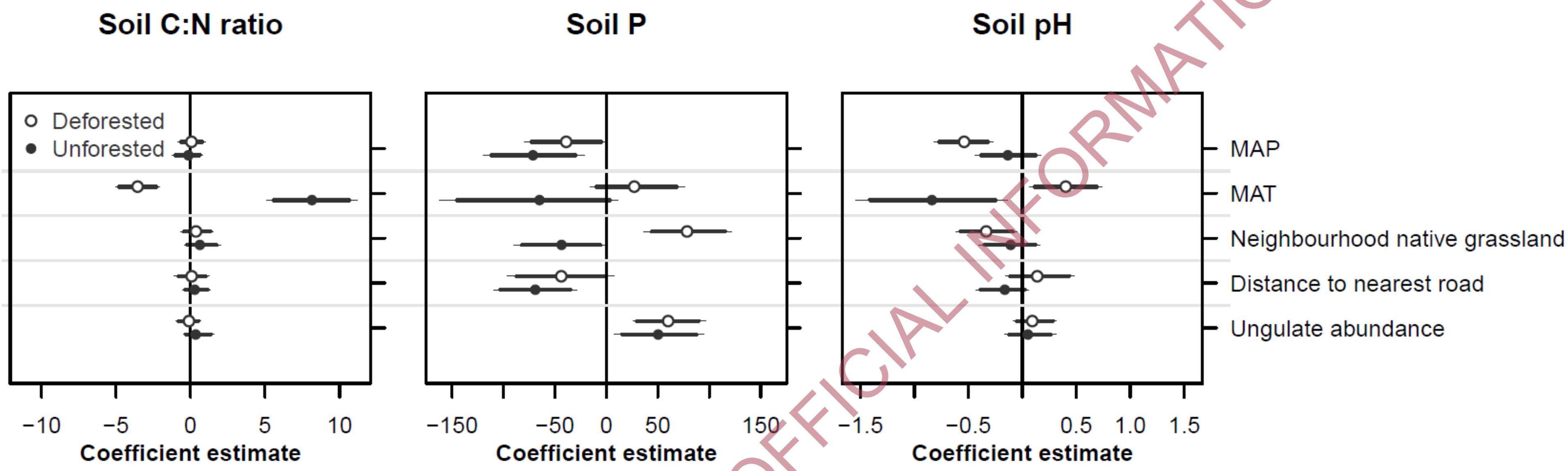

Figure 6. Effects of environmental variables and ungulate abundance on soil properties (soil C:N ratio, soil P, and soil pH).
Note: Error bars are 90 (thick line) and 95% (thin line) credible intervals.

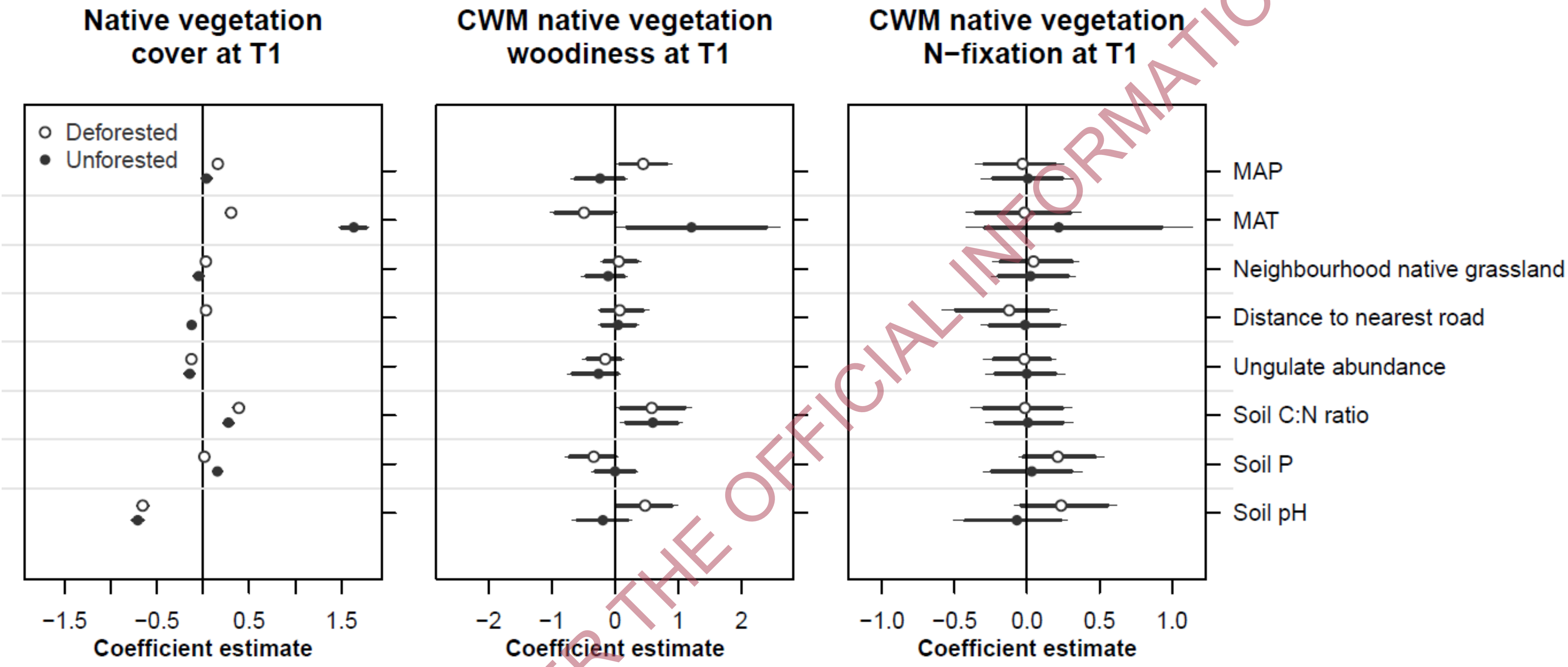

Figure 7. Effects of environmental variables, surrounding landscape, ungulate abundance, and soil properties on native vegetation (i.e. cover, community-weighted mean [CWM] woodiness and N-fixation) at T1.
Note: Error bars are 90 (thick line) and 95% (thin line) credible intervals.

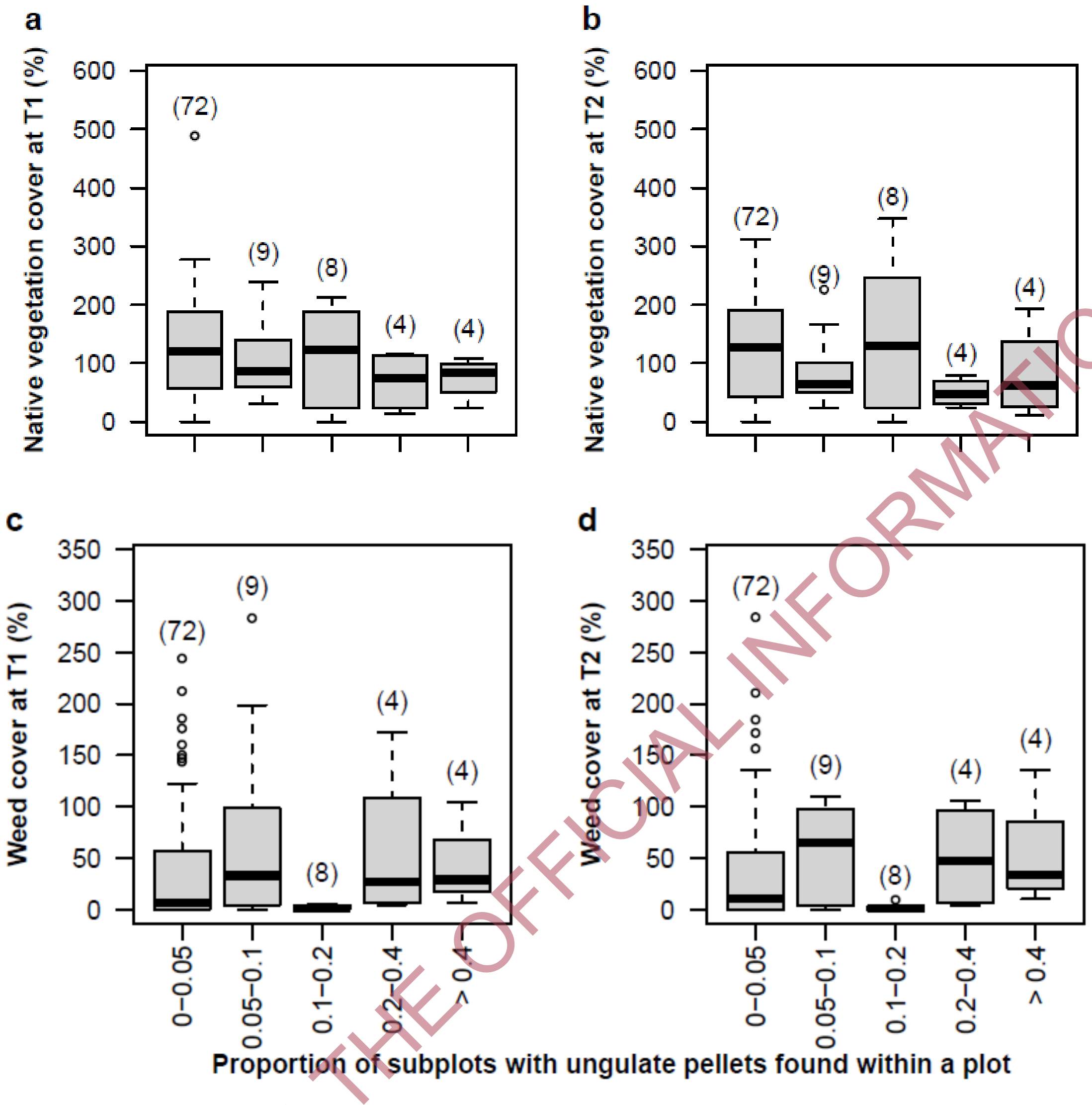

Figure 8. Native vegetation and weed cover at T1 and T2 in deforested non-forest plots across different ungulate abundance gradients (proportion of subplots with ungulate pellets found within a plot).

Note: Numbers within parentheses represent number of plots.

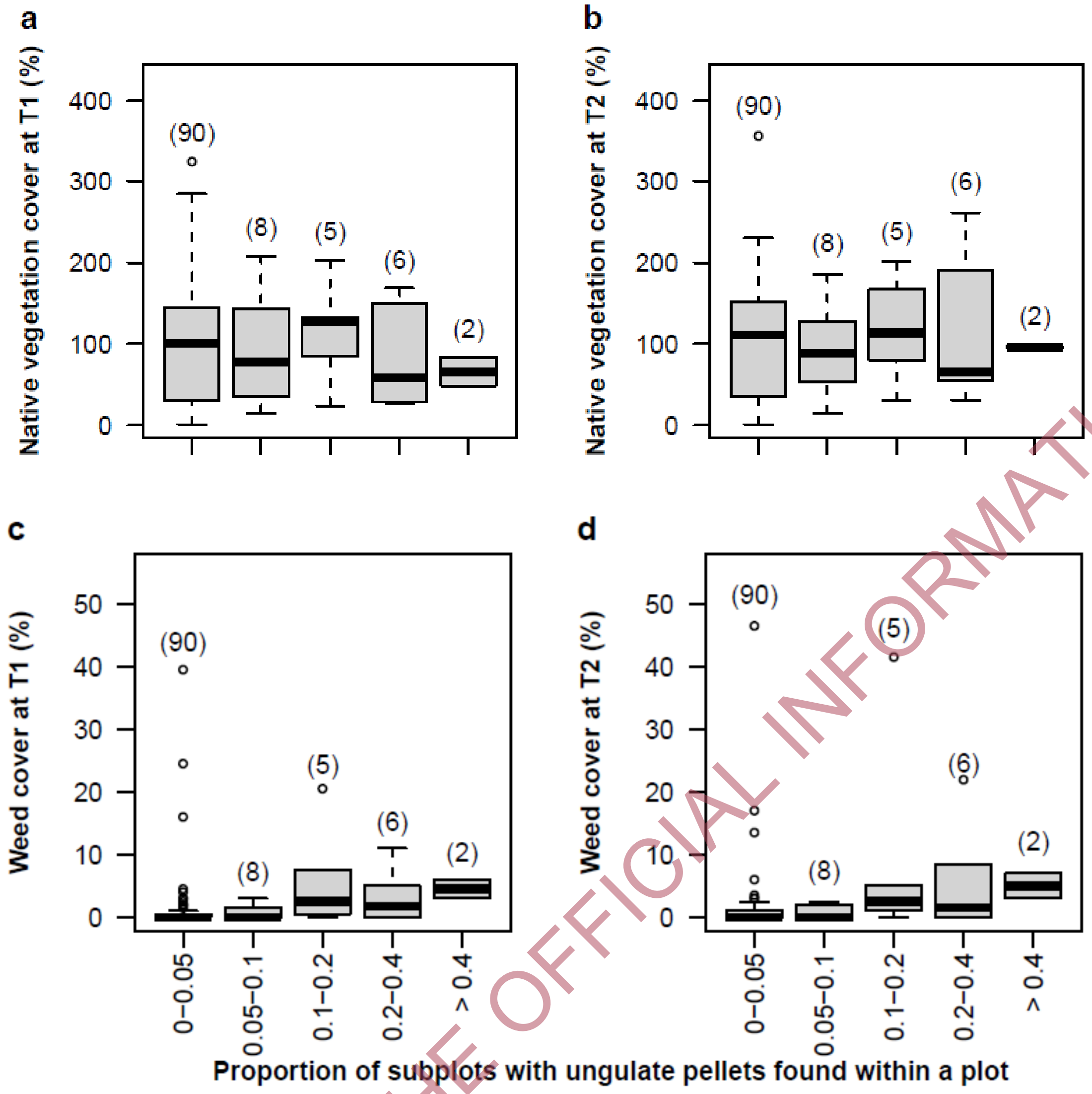

Figure 9. Native vegetation and weed cover at T1 and T2 in unforested non-forest plots across different ungulate abundance gradients (proportion of subplots with ungulate pellets found within a plot).

Note: Numbers within parentheses represent number of plots.

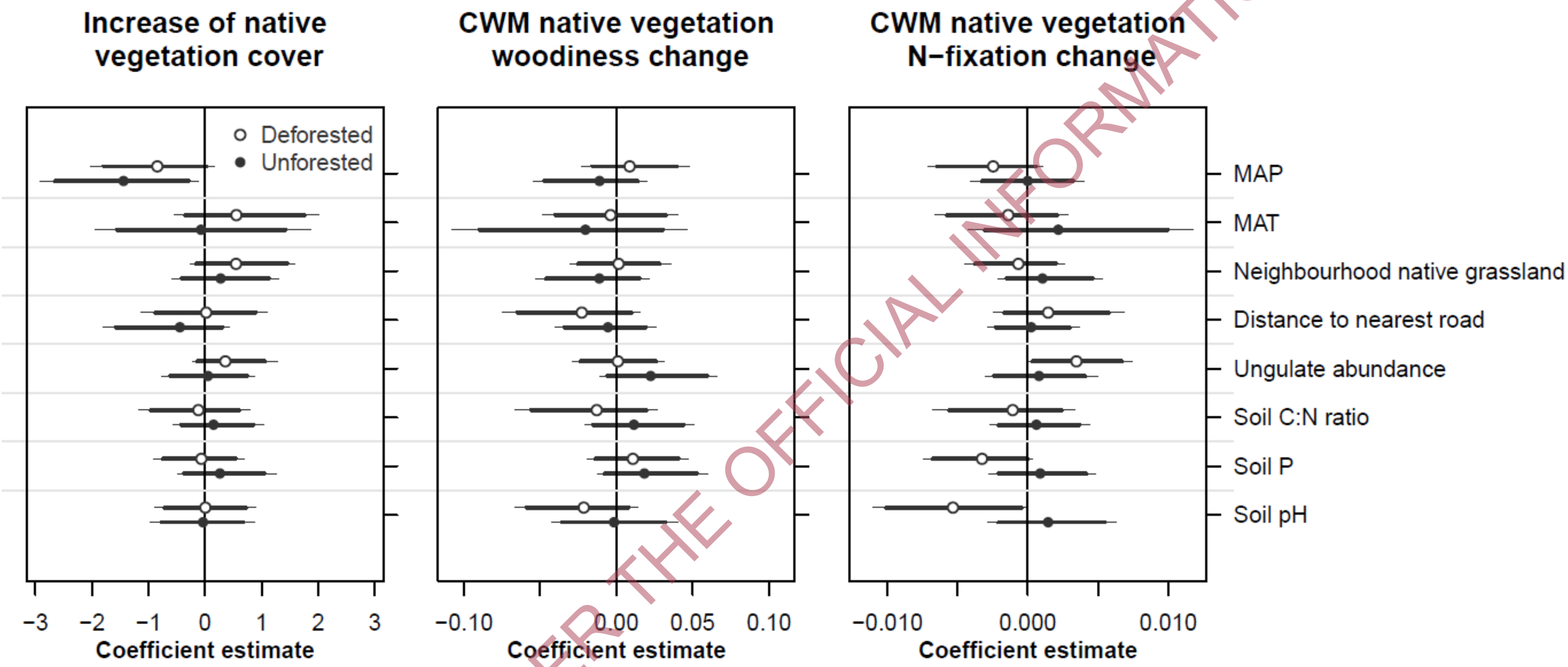

Figure 10. Effects of environmental variables, surrounding landscape, ungulate abundance, and soil properties on changes in native vegetation (i.e. cover, community-weighted mean [CWM] woodiness, and N-fixation) between T1 and T2.

Note: Error bars are 90 (thick line) and 95% (thin line) credible intervals.

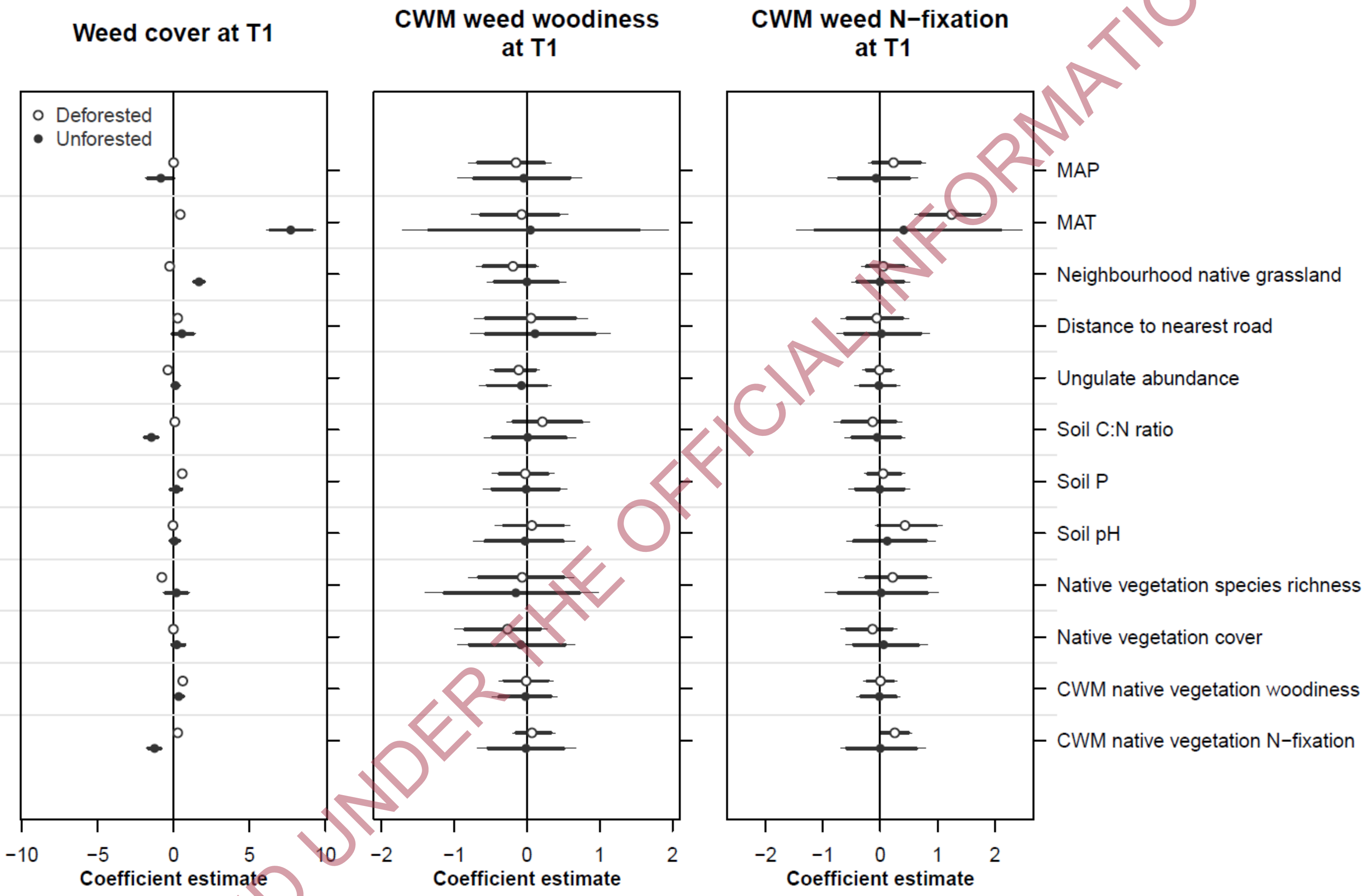

Figure 11. Effects of environmental variables, surrounding landscape, ungulate abundance, soil properties, and native vegetation on weeds (i.e. cover, community-weighted mean [CWM] woodiness, and N-fixation) at T1 in unforested and deforested plots where weeds were present.
Note: Error bars are 90 (thick line) and 95% (thin line) credible intervals.

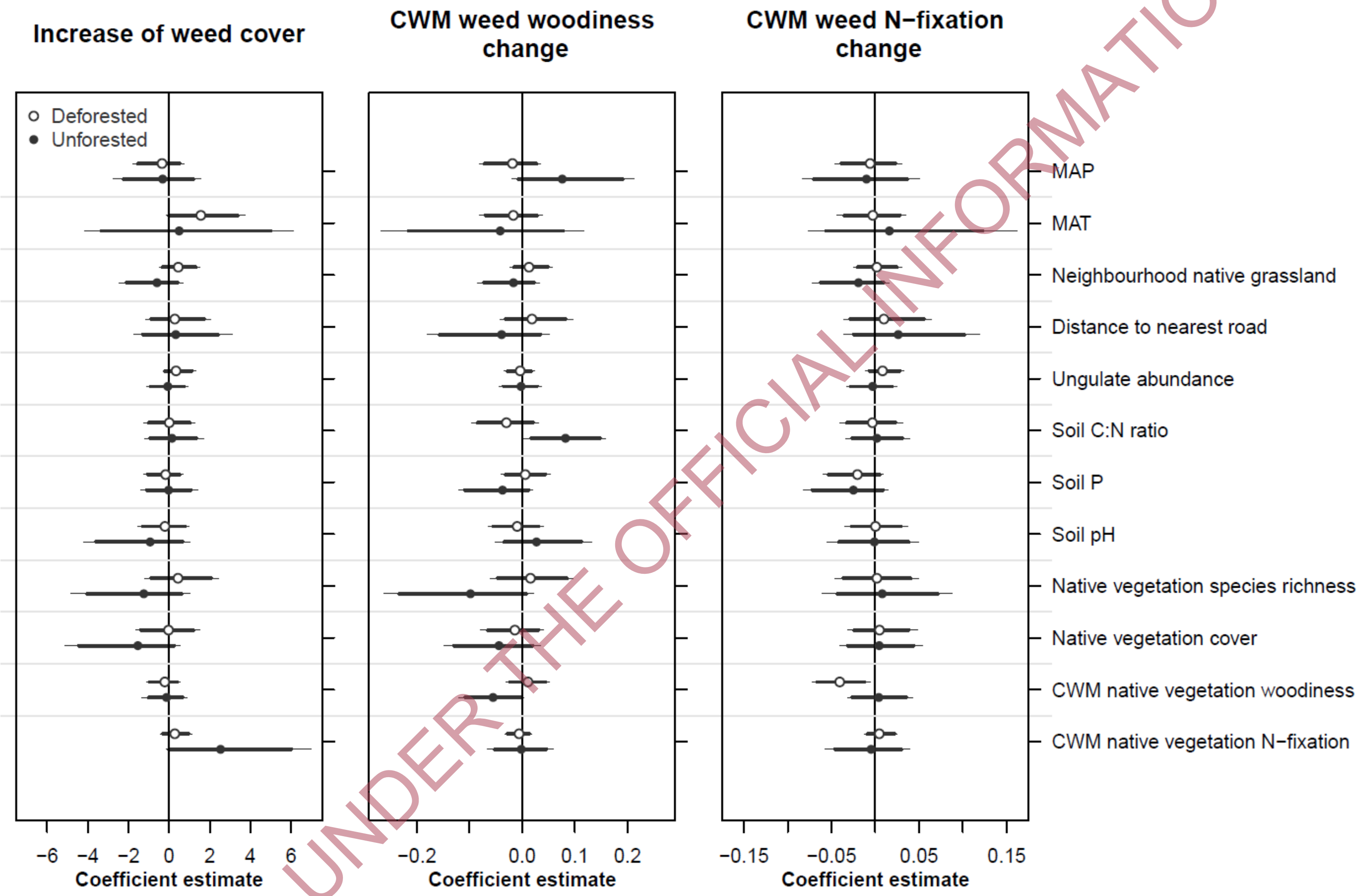

Figure 12. Effects of environmental variables, surrounding landscape, ungulate abundance, soil properties, and native vegetation on the increase of weed cover and changes in community-weighted mean (CWM) woodiness and N-fixation between T1 and T2 in unforested and deforested plots where weeds were present.

Note: Error bars are 90 (thick line) and 95% (thin line) credible intervals.

6 Discussion

Understanding the interrelationships among ecological integrity measures is crucial for effective ecosystem management and conservation efforts (Kandziora et al. 2013; Bellingham et al. 2020). Our findings underscore the importance not only of interrelationships among ecological integrity measures but also their relationships with environmental variables.

Since key environmental factors (especially MAT) distinguish deforested and unforested ecosystems, it is unsurprising that these, along with MAP, have different effects on components of ecological integrity in these two ecosystem types. For example, above the treeline, unforested ecosystems are dominated, in terms of biomass, by native grasses adapted to alpine environments, whereas deforested ecosystems below the treeline comprise not only grasses that have expanded in range beyond alpine environments (McGlone 2001), but also a mixture of woody and non-woody species driven by disturbances such as periodic fire and herbivory (Mark & Dickinson 2003; Mark & McLennan 2005).

There is substantial evidence that ungulates are responsible for compositional changes in forest understoreys by reducing the regeneration of palatable woody species (Wardle & Hayward 1970; Hawcroft et al. 2024). Likewise, negative associations between ungulate abundance and native vegetation biomass have been noted in New Zealand alpine unforested ecosystems (Rose & Allen 1990). Walker and Lee (2002) reported lower biomass and species richness of native species in response to grazing in deforested grasslands on alluvial sites across the eastern South Island. Native plant species cover and biomass increased when cattle were excluded from deforested ecosystems in Molesworth, in the northeastern South Island (Husheer & Moore 2024).

Consistent with these studies we found a negative association between native vegetation cover (a proxy for biomass) and ungulate abundance in both unforested and deforested ecosystems, presenting a *prima facie* case that higher ungulate abundance may be linked to a decrease in native vegetation cover above and below the treeline in New Zealand. However, we did not find significant relationships between ungulate abundance and weed measures, except for a weak negative association with weed cover in deforested non-forest plots. Removing grazing had no effect on invasion by widespread common weeds (*Hieracium* spp.) in deforested ecosystems (short-tussock grasslands; Rose et al. 1995; Rose & Frampton 2007), which was attributed to the aggressiveness of their invasion and the depleted site condition resulting from grazing. Ungulate effects on native vegetation and weeds in both naturally unforested and deforested ecosystems were often not significant and were similar in both ecosystem types.

However, ungulate abundance was greater in deforested ecosystems (Figure 5), which suggests that the effects of ungulates may be influenced directly by environmental conditions, and potentially indirectly through related differences in primary productivity and food resource quality (Fenner et al. 1993; Lloyd et al. 2010), including the contribution of weeds to ungulate diets. A comprehensive approach to disentangling ungulate–vegetation–environment interrelationships will help us better understand ungulate impacts across both naturally unforested and deforested ecosystems.

Relationships between native vegetation and weed invasion varied between unforested and deforested ecosystems. While there was a negative association between native vegetation richness and weed cover in deforested ecosystems, indicating the potential for native vegetation to suppress weed establishment and growth, there were no significant relationships between native vegetation cover and weed cover in both types of non-forested ecosystems, suggesting limited evidence of biotic resistance to invasions in either deforested or unforested ecosystems (Levine et al. 2004).

Consistent with our results, previous studies in deforested ecosystems in the eastern South Island found no evidence that native vegetation cover or abundance was related to widespread invasion by *Hieracium* spp. (Duncan et al. 2001; Day & Buckley 2013). The negative association between CWM native N-fixation and weed cover in unforested ecosystems and the positive associations between CWM values of native vegetation woodiness and native N-fixation and weed cover in deforested ecosystems (Figure 9) suggest that vegetation functional composition may play an important role in weed invasions in non-forest ecosystems (Gross et al. 2013).

However, that role varied between unforested and deforested ecosystems. Species-level analyses can help to test how functional differences between co-occurring native and weed species affect weed invasions in non-forest ecosystems (Gross et al. 2015). Further, we found that CWM native N-fixation was positively associated with the probability of weed cover increasing in unforested ecosystems (Figure 10), which may be linked to enhanced N availability, which in turn can facilitate weed invasions (González et al. 2010; Keser et al. 2015).

Examining the interactions among various environmental variables associated with the Tier 1 monitoring programme, including soil properties and environmental factors, enhances our understanding of how these elements collectively influence native vegetation and weed dynamics. Recognising these complex interactions is crucial in the management of conservation efforts and weed control in non-forest ecosystems.

Previous research has shown that soil properties and climatic factors significantly influence community composition in non-forested ecosystems in New Zealand. For instance, in alluvial deforested ecosystems, high native species abundance was associated with high precipitation, and with soils that have low pH and low P concentrations but high organic matter content (Walker & Lee 2002). The importance of these variables changed across different sites, but also within sites (e.g. in response to different landscape positions and grazing history). By comprehensively understanding these factors, conservation strategies can be tailored more effectively to maintain native vegetation and mitigate weed invasions.

The census interval between the repeat-measured inventory data used in this study is relatively short (mean 4.9 yr ± SD 1), which may limit the ability to detect trends and effects on changes in native vegetation and weed measures. For example, in Tier 1 plots where weed cover increased, weed cover increased by 4% (SD 8%) in plots in unforested ecosystems, and 27% (SD 51%) in plots in deforested ecosystems. Also, where weed cover decreased over the two census periods, it declined by 2% (SD 5%) in unforested ecosystems and by 24% (SD 40%) in deforested ecosystems.

The high variability in weed cover changes in deforested ecosystems – whether increases or decreases – suggests a need for targeted sampling strategies to determine why the changes are so variable. It could reflect localised, rapid invasion by high-biomass woody invaders (e.g. invasive conifers or Scotch broom) in the case of some increases, or control efforts that rapidly reduce weed biomass (e.g. removing wilding conifers) in the case of some decreases. Further sampling could investigate whether there is spatial aggregation of Tier 1 plots that show significant changes in weed cover (cf. section 6). If there is such spatial aggregation, employing Tier 2 plot networks could help determine the underlying causes and more accurately assess the spatial dynamics of weed cover changes.

The complexity of ecological processes (especially in deforested ecosystems with strong legacy effects) and the variability in responses to environmental changes necessitate longer monitoring periods to accurately capture these dynamics (Lindenmayer et al. 2012). Continued long-term monitoring on the permanent Tier 1 monitoring plots is essential for predicting and mitigating the impacts of environmental change on ecological integrity and its dynamics, providing valuable insights into ecosystem responses over time and informing adaptive management practices.

7 Spatial interpolation to derive maps of ecological integrity and changes in ecological integrity

7.1 Background

Weeds and ungulates are critical components of ecological integrity measures in New Zealand (Bellingham et al. 2020) and have significant implications for biodiversity and ecosystem health (Vavra et al. 2007; Vilà et al. 2011; Moloney et al. 2021). In this report we spatially interpolate selected ecological integrity measures based on weeds and ungulates across unforested and deforested ecosystems. This approach allows us to visualise ecological integrity measures across a landscape and to identify spatial patterns and trends that are not apparent from raw data alone (Turner 1989). By illustrating the spatial distribution of ecological integrity measures, these maps can facilitate planning for targeted conservation efforts, efficient allocation of resources, and the development of site-specific management plans (Xie et al. 2023; Zhang et al. 2024).

7.2 Methods

Statistical analysis

We used species distribution models based on Bayesian additive regression trees (BARTs; Carlson 2020) to produce spatial interpolations of the two non-forest ecosystem types (unforested and deforested) and three measures of ecological integrity (weed species presence/absence at T1, the probability of an increase in weed cover between T1 and T2, and ungulate presence) (Table 4).

We used 72 predictor variables that were available as spatial layers, encompassing climate, topography, geographical distance, soil attributes, and terrain (Table 4). These were sourced from McCarthy et al. 2021. The spatial predictor variables were used in the BART model to identify the subset of variables that are most important for correctly predicting the observed values, and then to produce a spatial interpolation of predicted values. All spatial analyses were performed on a 1 km resolution to facilitate model execution.

Table 4. Summary of data used for spatial interpolation of ecological integrity measures

Model	Ecological integrity measure	Data format*
Model 1	Unforested/deforested ecosystems	Binary (1 = unforested; 0 = deforested)
Model 2	Weed species presence at T1	Binary (1 = presence; 0 = absence)
Model 3	Increase of weed species cover from T1 to T2	Binary (1 = increased; 0 = decreased or no change)
Model 4	Ungulate presence	Binary (1 = presence; 0 = absence)

***** Data need to be binary to be implemented in the BART model.

Table 5. List of the 72 predictor variables used for spatial interpolation of ecological integrity measures

Category	Variable
Climate	Annual potential incoming solar radiation
	Annual temperature amplitude
	Annual temperature variability
	Annual temperature variation
	Annual water deficit
	FAO Penman
	FAO Penman PET
	Forest Penman
	Growing degree days (16°C base)
	Growing degree days (5°C base)
	Maximum monthly temperature
	Mean annual daily sunshine ratio (actual/potential)
	Mean annual humidity
	Mean annual solar radiation
	Mean annual temperature
	Mean annual vapour pressure deficit
	Mean annual windspeed
	Mean monthly temperature range
	Mean temperature of the coldest quarter
	Mean temperature of the driest quarter
	Mean temperature of the warmest quarter
	Mean temperature of the wettest quarter
	Minimum temperature of July (winter)

Category	Variable
Climate (cont.)	Minimum temperature of the coldest month
	Normalised minimum winter temperature
	October vapour pressure deficit
	Precipitation of the coldest quarter
	Precipitation of the driest month
	Precipitation of the driest quarter
	Precipitation of the warmest quarter
	Precipitation of the wettest month
	Precipitation of the wettest quarter
	Precipitation seasonality
	Priestley Taylor
	Rainfall to potential evapotranspiration ratio
	Temperature isothermality
	Total annual precipitation
	Winter (June) solar radiation
	Winter potential incoming solar radiation
	Winter/summer precipitation ratio
Geographical distance	Distance to the coast
	Distance to the nearest road
	Horizontal distance to the nearest river
	Latitude
	Longitude
	Vertical distance to river
Soil	Chemical limitations to plant growth
	Soil age
	Soil calcium
	Soil drainage capacity
	Soil induration (hardness)
	Soil particle size
	Soil pH (0–10 cm depth)
	Soil phosphorus
Topographic/terrain	Aspect (degrees)
	Aspect (radians)
	Eastness
	Eastness, incorporating slope
	Elevation
	Flow direction of water
	Geomorphons
	Normalised height
	Northness
	Northness, incorporating slope
	Slope (degrees)
	Slope (radians)

Category	Variable
Topographic/terrain (cont.)	Topographic position index
	Topographic roughness index
	Topographic ruggedness index
	Topographic wetness index
	Valley depth
	Wind exposition index

Notes: FAO Penman = Annual sum of any monthly rainfall deficits in comparison to monthly potential evaporation as estimated from monthly estimates of temperature, solar radiation, humidity and wind for the years 1950–1980 using the FAO (Food and Agriculture Organization)-Penman method appropriate for grasslands; FAO Penman PET (potential evapotranspiration) = Annual sum of monthly potential evaporation as estimated from monthly estimates of temperature, solar radiation, humidity and wind for the years 1950–1980 using the FAO-Penman method appropriate for grasslands; Forest Penman = Annual sum of monthly potential evaporation as estimated from monthly estimates of temperature, solar radiation, humidity and wind for the years 1950–1980 using the FAO-Penman model of evaporation as appropriate for a forest canopy; Details on all of the variables are available from McCarthy et al. 2021, Appendix S1.

7.3 Results

The probability of being categorised as an unforested ecosystem was very high in alpine regions, whereas the probability of being categorised as a deforested ecosystem was high across much of New Zealand (Figure 13). Topography and temperature variables were identified as key determinants in the model predicting the probability of being categorised as an unforested ecosystem (AUC[2] = 0.99, Table 6).

The probability of a weed species being present was high in most regions, except for the west coast of the South Island (Figure 14). The model predicting weed species presence at T1 (AUC = 0.943) identified valley depth, aspect, elevation, and precipitation of the driest month as the most influential variables (Table 6).

The probability of an increase in weed cover between T1 and T2 was particularly high in the Canterbury region (Figure 15) and along the east coast of the North Island (Figure 15). Models predicting the probability of an increase in weed cover (AUC = 0.881) highlighted the importance of precipitation and temperature variables (Table 6).

The probability of ungulate presence was estimated to be high along the west coast of the South Island and in the Southern Alps (Figure 16), with the model (AUC = 0.893) indicating key variables such as mean temperature of the wettest quarter and slope (Table 6).

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[2] AUC = area under the receiver-operator curve. A high AUC value indicates that the model has done an adequate binary classification: fair if AUC ≥ 0.7, good if AUC ≥ 0.8, and excellent if AUC ≥ 0.9 (Swets 1988)

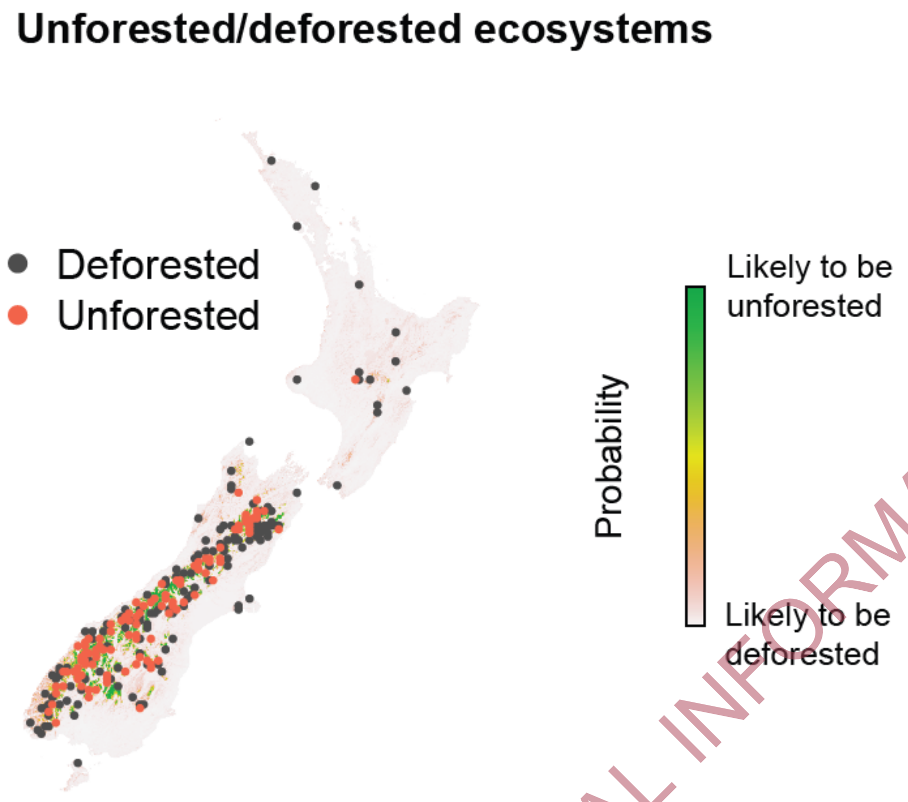

Figure 13. A map of probability of unforested and deforested ecosystems, constructed using spatial distribution modelling with Bayesian additive regression trees (see 6.2 Methods).
Notes: Each dot represents a plot. Only non-forest plots were used for the analysis.

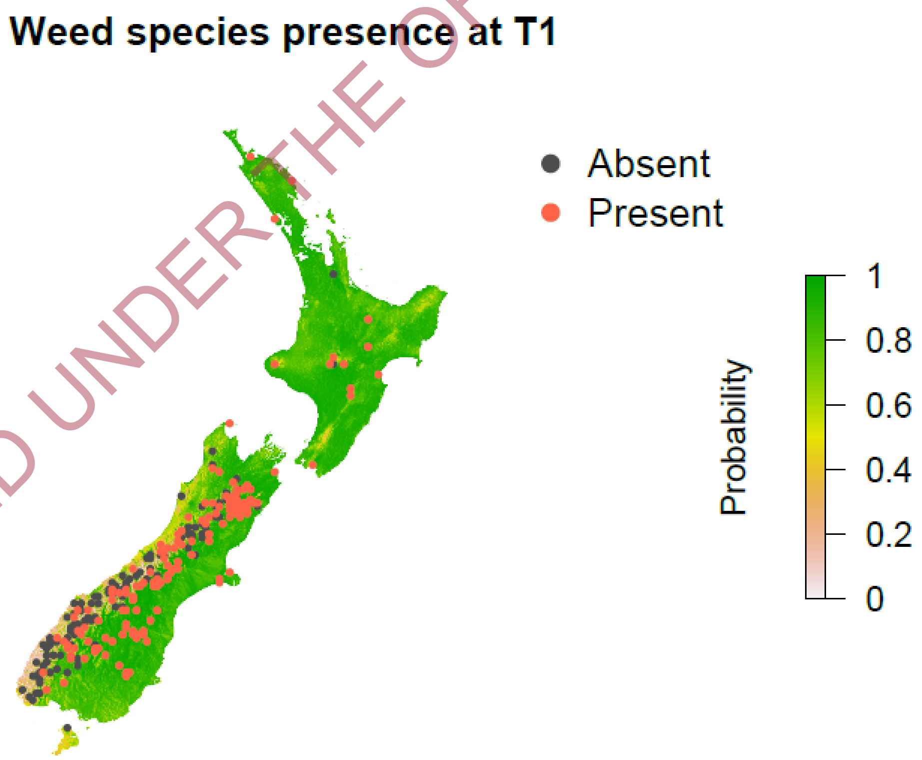

Figure 14. A map of probability of weed species presence at T1, constructed using spatial distribution modelling with Bayesian additive regression trees (see 6.2 Methods).
Notes: Each dot represents a plot. Only non-forest plots were used for the analysis.

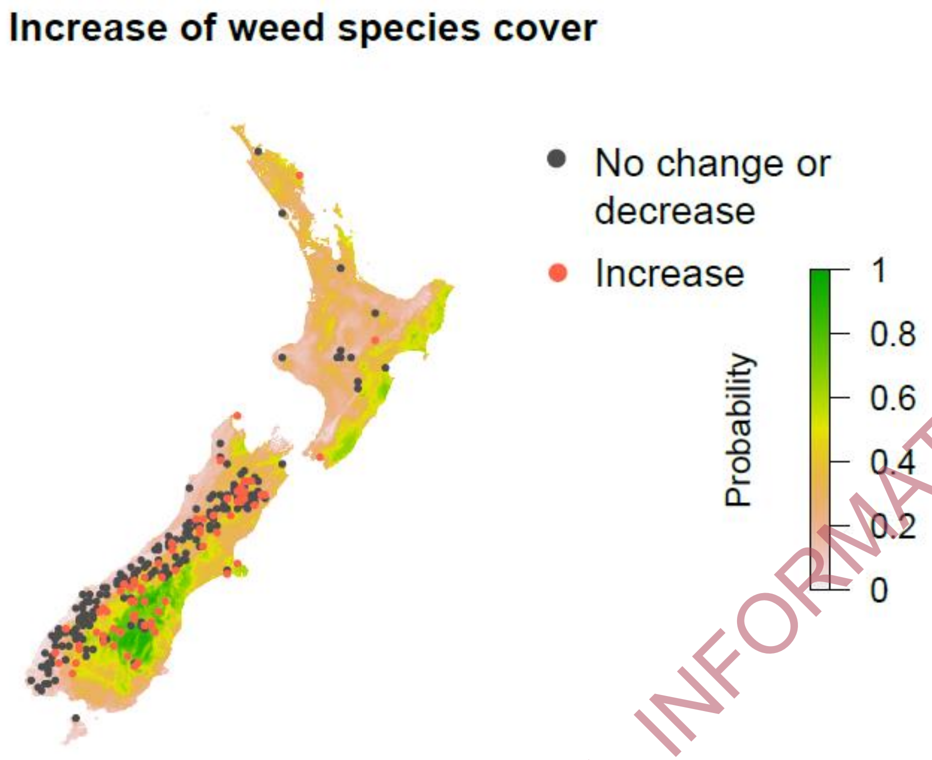

Figure 15. A map of probability of increase of weed species cover during the census interval between T1 and T2, constructed using spatial distribution modelling with Bayesian additive regression trees (see 6.2 Methods).
Note: Each dot represents a plot. Only non-forest plots were used for the analysis.

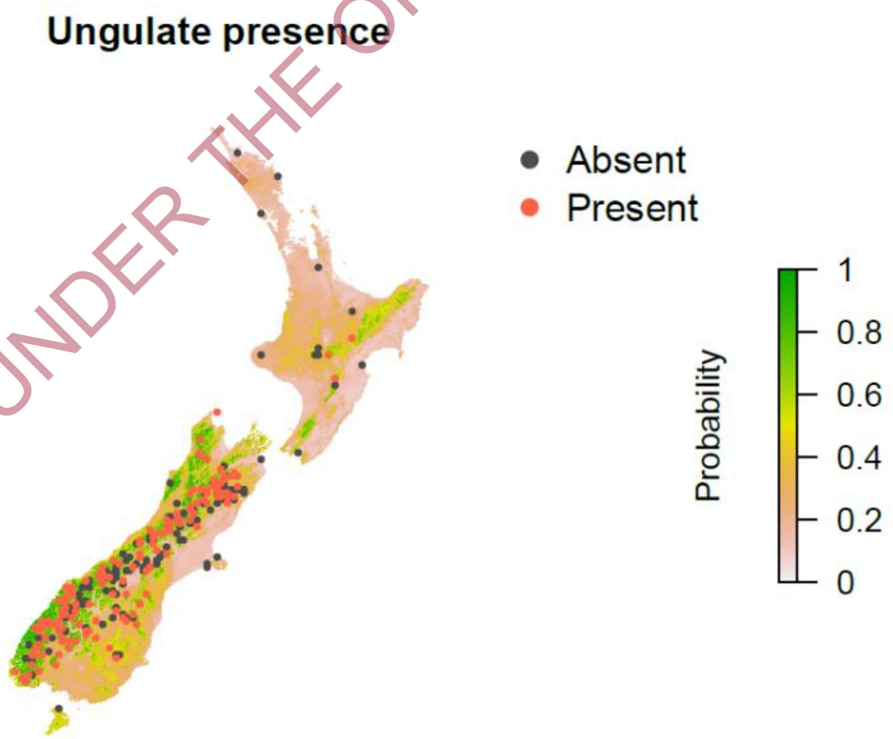

Figure 16. A map of probability of ungulate presence, constructed using spatial distribution modelling with Bayesian additive regression trees (see 6.2 Methods).
Notes: Each dot represents a plot. Only non-forest plots were used for the analysis.

Table 6. Importance of environmental variables selected for the spatial distribution models and model performance statistics (AUC, area under the receiver-operator curve). The importance value is measured by counting how many times a given variable is used in splits across all trees in Bayesian additive regression trees models.

Model	Ecological integrity measure	AUC	Environmental variables used in the model after variable selection process	Importance
Model 1	Unforested ecosystems	0.99	Flow direction of water	0.116
			Aspect (radians)	0.115
			Mean annual temperature	0.115
			Mean temperature of the coldest quarter	0.113
			Annual temperature variability	0.112
			Mean monthly temperature range	0.11
			Temperature isothermality	0.108
			Maximum monthly temperature	0.106
			Topographic position index	0.105
Model 2	Weed species presence at T1	0.943	Valley depth	0.132
			Aspect (radians)	0.129
			Elevation	0.128
			Precipitation of the driest month	0.126
			Mean annual daily sunshine ratio (actual/potential)	0.122
			Mean monthly temperature range	0.122
			Temperature isothermality	0.121
			Precipitation of the warmest quarter	0.120
Model 3	Increase in weed cover from T1 to T2	0.881	Precipitation of the driest month	0.145
			Distance to the coast	0.144
			Mean annual humidity	0.144
			Annual temperature amplitude	0.143
			Mean temperature of the driest quarter	0.143
			Precipitation seasonality	0.141
			Annual temperature variation	0.141
Model 4	Ungulate presence	0.893	Mean temperature of the wettest quarter	0.130
			Slope (radians)	0.130
			Winter potential incoming solar radiation	0.126
			Winter:summer precipitation ratio	0.126
			Elevation	0.123
			Temperature isothermality	0.122
			Forest Penman	0.122
			Mean annual vapour pressure deficit	0.120

Notes: A high AUC value indicates that the model has done an adequate binary classification: fair if AUC ≥ 0.7, good if AUC ≥ 0.8, and excellent if AUC ≥ 0.9 (Swets 1988). Details on the environmental variables can be found in McCarthy et al. 2021.

7.4 Discussion

The spatial interpolation of ecological integrity measures presented in this study offers insights into the spatial dynamics of non-forest ecosystems in New Zealand. By employing Bayesian additive regression trees (BARTs) for spatial modelling (Carlson 2020), we produced detailed maps that highlight the distribution and changes in weed species measures and ungulate presence. These maps offer a visual representation of ecological data across landscapes, facilitating the identification of spatial patterns and trends that are not immediately evident from raw data.

Here we show the contrasting spatial patterns that distinguish deforested and unforested ecosystems; i.e. naturally unforested ecosystems are mostly alpine, concentrated mostly in the South Island, with a mean annual temperature below 5.5˚C (as outlined in section 4.3), whereas deforested non-forest ecosystems span the nation, except for the elevated alpine regions. The spatial distribution of deforested ecosystems closely mirrors that of weed species presence, indicating a correlation between habitat alteration and weed proliferation in these ecosystems (Rose et al. 1998; Peltzer 2018).

The spatial interpolation results also reveal several key findings about the distribution and dynamics of weeds and ungulates across the landscape. The high probability of weed species presence in most regions, except for the west coast of the South Island, underscores the widespread challenge of weed management (Brandt et al. 2021). The spatial patterns for the increase in weed species richness and cover, which is particularly high in the Canterbury region, highlight areas that may require intensified management efforts. Also, the high probability of increased weed species richness in the central volcanic plateau of the North Island and increased weed species cover along the east coast of the North Island suggest specific regional vulnerabilities that need to be addressed.

High estimated ungulate presence along the west coast of the South Island and in the Southern Alps is consistent with previous findings (Bellingham et al. 2020; Moloney et al. 2021), and presents another dimension of ecological impact. The model for ungulate presence identified key environmental variables, such as the mean temperature of the wettest quarter and slope. These factors may be helpful for understanding ungulate habitat preferences and their potential impact on ecosystem dynamics.

The spatial interpolation of ecological integrity measures not only reveals spatial patterns and trends, but also provides valuable assistance for conservation planning, resource allocation, and the formulation of efficient management strategies (Watkins et al. 1997; Aspinall & Pearson 2000). Given the ongoing alterations in environmental conditions and species distributions under climate change (Pecl et al. 2017; Keegan et al. 2022), continuous monitoring and updating of these maps are essential for maintaining the ecological integrity of New Zealand's non-forest ecosystems.

8 Non-vascular plant communities in non-forest ecosystems

8.1 Background

Non-vascular plant species include bryophytes (mosses, liverworts and hornworts), lichens, and green algae. They are characterised by the lack of a vascular system to transport nutrients and water, which limits their per-individual height and biomass. Non-vascular species can play a significant role in water availability and carbon cycling in habitats less favourable to vascular plant species (e.g. DeLucia et al. 2003; Michel et al. 2013; Street et al. 2013). However, only a restricted number of studies have focused on the ecology of non-vascular species in New Zealand, resulting in important knowledge gaps, such as their species distributions, their conservation status (Rolfe et al. 2016), and their functional roles across different ecosystem types.

Ecological studies in New Zealand of non-vascular species plant species have focused on forested ecosystems and shrublands, including their contribution to ecosystem functioning and distributions of some species at small to large scales (e.g. Michel et al. 2011; Rolfe et al. 2016; Kentjens et al. 2023). There have been fewer studies in non-forested ecosystems (Wilson & Meurk 2011; Michel et al. 2013).

Non-vascular species respond strongly to changes in environmental conditions associated with light and moisture availability (e.g. Bates 1998; Pharo et al. 2005). However, responses may differ between bryophytes and lichens (Pharo & Beattie 1997), or even among species (Michel et al. 2011). For example, in Tasmania bryophytes, especially liverworts, are more diverse in wet habitats whereas lichens are more diverse in dry ecosystems (Pharo & Beattie 1997; Ferguson et al. 2009).

Ungulates are known to influence communities of non-vascular species (e.g. Bernes et al. 2018; Speed et al. 2020). Ungulates can reduce the abundance of non-vascular species (Boudreau & Payette 2004; Bernes et al. 2018), but they can also favour bryophyte richness by reducing competition with vascular species (Chollet et al. 2013; Bernes et al. 2018). However, Ferguson et al. (2009) found no relationship between grazing by introduced ungulates and non-vascular species in non-forested ecosystems in Tasmania.

The lack of data available on bryophytes and lichens constrains investigation on non-vascular communities to higher taxonomic levels (e.g. overall bryophyte richness) rather than ecological subgroups (e.g. species richness by growth form) (Michel et al. 2011; Bernes et al. 2018). This makes disentangling the direct impact of ungulates (i.e. browsing, trampling) or weed invasions from the indirect impact (e.g. change in microhabitat, alteration of relationship with vascular plant species) of non-vascular plant communities challenging.

Multiple methods have been established to measure changes in non-vascular communities, but they have yet to be carefully assessed. For example, Payton et al. (2004) developed methods to record non-vascular communities on permanent plots as part of biodiversity monitoring protocols for LUCAS (Land Use and Carbon Analysis System). They focused on abundant non-vascular species occurring on a subset of understorey subplots and on the entire 20 m × 20 m plot. The DOC Tier 1 plot network attempts to generate a more detailed inventory of bryophytes (mosses and liverworts) and lichen species (Department of Conservation 2019). This information aims to support future conservation projects by providing suitable data to assess biodiversity trends at a national scale, which can be presented alongside vascular measurements.

Here we assess how the data collected on non-vascular plant species in the Tier 1 plot network provides a case study to inform estimates of ecological integrity in non-forested ecosystems, and how they compare between naturally unforested and deforested ecosystems. We test for interrelationships between measures of non-vascular plant communities and measures of vegetation structure, ungulate abundance, and non-native plant abundance. We use the term 'non-vascular' to refer to bryophyte and lichen species.

8.2 Methods

Non-vascular plant survey

We obtained non-vascular plant data collected between 2002 and 2020. Non-vascular species were recorded according to the Recce method and the DOC Tier 1 field protocol, which outlines a plot-based method for systematically searching and managing the collection of non-vascular plant individuals (Department of Conservation 2019). Of 1,326 Tier 1 plots, 153 in non-forested ecosystems had data for non-vascular plants: 67 in unforested ecosystems and 86 in deforested ecosystems (Table 8). Because only two plots in unforested ecosystems and 16 plots in deforested ecosystems had remeasurements, this precluded any analyses of change over time.

In all plots in unforested and deforested ecosystems, each non-vascular plant specimen (apart from crustose lichens) was collected and assigned a height tier: ground level (<30 cm, i.e. Tier 6) or epiphytic (Tier 7), for which the search area was from ground level to 2 m height. Within Tier 6, each specimen was assigned a cover class using a modified Braun–Blanquet cover-abundance scale (i.e. 1: <1%; 2: 1–5%; 3: 6–25%; 4: 26–50%; 5: 51–75%; and 6: 76–100%); epiphytic plants were not assigned a cover class. Each specimen was also ascribed one of four substrates: litter (growing on humus, fine woody debris, leaf litter); soil (growing on mineral soil); coarse woody debris (growing on logs and stumps with a diameter >10 cm); rock (growing on rocky outcrops). Some specimens were described only as 'terrestrial', which precludes, for those specimens, evaluation of substrate associations (i.e. they were not assigned to 'litter' or 'soil'). Specimens with no tier or substrate information were removed from the data set.

Non-vascular plant list

We focused our analysis on differences between taxon groups (lichen vs bryophytes) and collected further information on major groups (i.e. lichens: crustose, fruticose or foliose; bryophytes: mosses, liverworts, hornworts). The combination of both taxon and major groups can be associated with ecosystem characteristics such as light and moisture availability. While a trait-based approach could be valuable for determining how non-vascular plants (Bates 1998) can inform measures of ecological integrity, data to inform such an approach in New Zealand are currently available only for a very limited number of species.

We updated the list of non-vascular plant species obtained from the NVS. This list initially provided species names and some of their synonyms with information on taxonomic classification (i.e. family, genus) and biostatus (e.g. indigenous endemic, exotic, unknown). The higher taxonomic level (i.e. phylum, class, order) as well as supplementary information about the biostatus of bryophyte species was obtained from the checklist of the New Zealand flora – hornworts, liverworts and mosses from 2023 (Allan Herbarium 2023). Where possible, missing information on lichens and unknown bryophytes was sourced from Biota NZ (Manaaki Whenua — Landcare Research 2024), the New Zealand Plant Conservation Network (NZPCN 2024), and *Lichens of New Zealand: An introductory illustrated guide* (Knight 2014).

Non-vascular plants only identified to the genus, family, or higher taxonomic level (e.g. phylum, order) were assigned to a major group and biostatus associated with the nearest identified taxonomic level. If the taxon included other known species with various major groups and biostatus, this non-vascular plant was considered as 'unknown'. For instance, all species from the Bryopsida class can be assigned to the major group 'moss'. However, not all species from the Parmeliaceae family (lichen) belong to the 'foliose' major group, so this non-vascular plant was assigned as 'unknown'.

The final list of non-vascular plant species with their characteristics was checked and edited by Dr David Glenny (botanist at Manaaki Whenua – Landcare Research with an expertise in bryophytes). However, this was only done for the non-vascular species identified in unforested and deforested plots, as these ecosystems are the key focus of this study. The updated non-vascular species list was later merged with the Tier 1 data.

Deriving measures of ecological integrity based on non-vascular plant species

Multiple measures of non-vascular plant communities were considered for the analysis. We calculated, at taxon and major group level, the non-vascular species richness and cumulative cover at each Tier 1 plot. Non-vascular species found in tiers 6 and 7 were combined to calculate the non-vascular species richness. Non-vascular species cumulative cover (hereafter referred to as non-vascular cover) was only calculated for species found at tier 6, since epiphytic (tier 7) taxa were listed only as present (in the data set referred to 'P' as present). The non-vascular cover was calculated by converting the cover classes to the midpoint of the percentage cover and summing the cover of all non-vascular plants by taxon groups (lichen vs bryophytes) and by major groups within those (i.e. lichens: crustose, fruticose or foliose; bryophytes: mosses, liverworts, hornworts). Non-vascular richness and cover per biostatus were only calculated for bryophytes, as little is known about the biostatus of lichens.

Biotic and environmental variables

The final non-vascular data set, including Tier 1 plots located in either unforested or deforested ecosystems, was merged with vascular plant community information, plot characteristics, and climatic variables (i.e. MAT and MAP) used in sections 4 and 5 and highlighted in previous studies as being key drivers of non-vascular plant community structure (e.g. Pharo & Beattie 1997; Ferguson et al. 2009; Kentjens et al. 2023).

Vascular plant community composition and vegetation structure have been shown to influence non-vascular plants through competition for resources (e.g. light, space) or by providing micro-habitats (Pharo & Beattie 1997; Kentjens et al. 2023). We used the vascular plant vegetation information from the Tier 1 plots to calculate the total vascular plant cumulative cover (later referred to as vascular plant cover) using the approach described in section 4. We also included the weed cover calculated in the previous sections (see method in section 4 – Framework).

The Tier 1 plot network also provides relevant information describing each plot, which can contribute to understanding the level of light and moisture available. For each Tier 1 plot we obtained data for latitude, longitude, elevation (in metres), aspect (measured in degrees, with values ranging from 1 to 360), slope (measured in degrees from the horizontal), angle to the horizon (measured in degrees), and mean top height of the dominant vegetation on the plot (>25% cover), as well as the surface cover of bedrock and broken rock (in %) (Hurst et al. 2022). Because moisture availability has previously been found to be an important factor in explaining non-vascular species distribution (especially for liverworts, Pharo & Beattie 1997), we included distance to the nearest river using New Zealand River Centrelines (1:50,000 scale) (Land Information New Zealand 2024).

Latitude, aspect, and slope were used to calculate solar radiation for each plot, following Kaufmann & Weatherred 1982. We calculated the landform index for each as the mean angle to the horizon in eight cardinal and intercardinal directions (McNab 1993). We generated a new variable called 'rocky cover' by summing the percentage cover of bedrock and of broken rock.

To estimate the potential impact of ungulates or lagomorphs on non-vascular plants, we used the ungulate, hare (*Lepus europaeus*) and rabbit (*Oryctolagus cuniculus*) faecal pellets index (FPI) values for each Tier 1 plot (Moloney et al. 2021). The index is expressed as the number of intact faecal pellets along each of the four transects established at the corners of each Tier 1 plot (Moloney et al. 2021). The ungulate pellet index includes deer, goats (*Capra hircus*), Himalayan tahr (*Hemitragus jemlahicus*), chamois (*Rupicapra rupicapra*), and sheep (*Ovis aries*).

Among the 154 Tier 1 plots with non-vascular information, 116 had all the environmental data required for further analysis. Discarded plots were missing measures such as elevation, aspect or slope.

Statistical analysis

We investigated how non-vascular community composition differed between unforested and deforested ecosystem types using non-metric multi-dimensional scaling (NMDS) with the 'metaMDS' function (999 iterations) from the vegan package in R (Oksanen et al. 2019). We ran the NMDS based on 116 plots, with 63 plots in unforested ecosystems and 75 in deforested ecosystems. We generated a Bray–Curtis dissimilarity matrix from the presence or absence of each non-vascular species present in at least four plots of one of the two ecosystem types, giving a total of 149 non-vascular species. With three dimensions and a maximum of 100 iterations, we achieved an NMDS solution with a satisfactory stress of 0.14. Then we used the 'envfit' function with 999 permutations to test for a difference in the centroids of plots from unforested and deforested ecosystems, and a goodness of fit (R^2) associated with non-vascular species. We tested for homogeneity of group variance between unforested and deforested ecosystems by calculating the beta dispersion using the 'betadisper' function, followed by an analysis of variance (Anova).

We tested for interrelationships between measures of non-vascular plant communities and measures of vegetation structure, ungulate abundance, weed cover, and environmental covariables across naturally unforested and deforested ecosystems. We first investigated the level of correlation between each variable using the 'Hmisc' package in R (Harrell 2021). To prevent autocorrelation, only variables with a correlation of <0.7 were included in models (Appendix 2, Tables A1 and A2). We ran generalised linear models (GLMs) with the 'glmmTMB' package (Brooks et al. 2017) in R (R Development Core Team 2023). We predicted bryophyte, liverwort (as a subset of bryophyte), or lichen species richness using a negative binomial distribution, while models predicting bryophyte or lichen cover were fitted using a beta distribution, as this is recommended when analysing proportion data (Damgaard & Irvine 2019). Non-vascular cover was converted into proportion of cover and transformed to avoid zeroes and ones, following the method described by (Smithson & Verkuilen 2006).

The predictors in each GLM model included ecosystem type (unforested or deforested) and a combination of covariates associated with vegetation composition and structure (vascular plant and weed cover, mean top height), climate (MAT, MAP), environment (elevation, rocky cover, solar radiation, landform index), and herbivore pellet index (ungulate, hare, rabbit). Models predicting liverwort richness also included distance to nearest river. To account for differences in climatic and site conditions between unforested and deforested plots, we also included an interaction term between ecosystem and either MAP, rocky cover, lichen richness, lichen cover, bryophyte richness or bryophyte cover. We did not include an interaction term with temperature because it was used in the framework to identify unforested ecosystems.

We kept the best-fitting models with the lowest AICc[3] values, which were obtained with the 'MuMIn' package (Barton 2022). Significant covariates were identified using Wald chi-square tests with the 'Anova' function from the 'car' package (Fox & Weisberg 2019).

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[3] AICc is the corrected Akaike information criterion, a mathematical method for evaluating how well a model fits the data from which it was generated.

8.3 Results

Information available on non-vascular plant communities

Across the 200 Tier 1 plots in unforested ecosystems, 67 plots had non-vascular plant information, with all these plots having non-vascular plants at ground level (tier 6) and 29 having non-vascular plants that were epiphytes (tier 7). Among the 190 Tier 1 plots in deforested ecosystems, 86 had non-vascular plant information, with 85 plots having non-vascular plants at ground level (tier 6) and 49 having non-vascular epiphytes (tier 7). Non-vascular plant species found in the epiphyte tier can also occur in the ground-level tier, and sometimes occurred within the same Tier 1 plot.

Overall, 739 non-vascular species (i.e. either bryophyte or lichen) were identified in non-forested ecosystems, with 418 species (57%) only present in one of the two ecosystem types (16% in unforested and 41% in deforested ecosystems) (Table 7). There were more species of bryophytes (481) than lichens (258; Table 7 and Table 8). Seven bryophyte species were non-native mosses (Table 8). The 10 most frequent bryophyte and lichen species were very similar between unforested and deforested ecosystems. As examples, the fruticose lichen *Cladia aggregata* occurred in 39% of the unforested plots and 49% of the deforested plots, and the moss *Racomitrium crispulum* occurred in 55% of the unforested plots and 37% of the deforested plots (Table 9).

Table 7. Summary of the number of non-vascular species in non-forested ecosystem types (i.e. overall, unforested, and deforested), showing the percentage of unique species (species only found in one of the ecosystem types) in each ecosystem types and only found in one Tier 1 plot (singletons)

Ecosystem	Taxon group	Description	No species
Non-forested	*Non-vascular*	*Total*	*739*
	Bryophyte	All species	481 (65%)
	Lichen	All species	258 (35%)
Unforested	Bryophyte	*Total*	*294*
		Unique	72 (15%)
		Singletons	55 (11%)
	Lichen	*Total*	145
		Unique	46 (10%)
		Singletons	34 (13%)
Deforested	Bryophyte	*Total*	*409*
		Unique	187 (39%)
		Singletons	132 (27%)
	Lichen	*Total*	*212*
		Unique	113 (44%)
		Singletons	74 (29%)

Table 8. Number of non-vascular species summarised by ecosystem, taxon group, major group, and biostatus, with the number of plots where the species was identified (Freq.) and its mean and maximum cover (%)

Non-forested ecosystem	Taxon group	Major group	Biostatus	No. species	Freq.	Mean cover (%)	Max cover (%)
Unforested	Bryophyte	*Total*		*294*	*66*	*0.7*	*15*
(No. plots = 67)		Hornwort	Native	1	1	0.5	0.5
		Liverwort	Native	155	44	0.7	15
			Unknown	1	2	-	-
		Moss	Non-native	4	6	0.8	3
			Native	133	66	0.7	15
	Lichen	*Total*		*145*	*58*	*0.6*	*3*
		Crustose	Native	15	23	0.5	0.5
		Foliose	Native	53	43	0.6	3
			Unknown	1	2	0.5	0.5
		Fruticose	Native	58	55	0.6	3
		Unknown	Native	18	29	0.5	3
Deforested	Bryophyte	*Total*		*409*	*83*	*1*	*63*
(No. plots = 86)		Hornwort	Native	3	2	0.5	0.5
		Liverwort	Native	209	56	0.7	15
			Unknown	2	2	3	3
		Moss	Non-native	6	11	0.9	3
			Native	188	83	1.2	63
			Unknown	1	1	-	-
	Lichen	*Total*		*212*	*77*	*0.5*	*3*
		Crustose	Native	19	27	0.6	3
		Foliose	Native	111	66	0.5	3
			Unknown	1	8	0.5	0.5
		Fruticose	Native	62	69	0.5	3
		Unknown	Native	18	22	0.6	3
			Unknown	1	2	0.5	0.5

Note: Information was based on the most recent survey conducted at each plot.

Table 9. List of the 10 most common non-vascular species per ecosystem, with number of plots where the species was identified (Freq.) and mean and maximum cover

Ecosystem	Taxon group	Major group	Species name	Biostatus	Freq.	Mean cover (%)	Max cover (%)
Unforested	Bryophyte	Moss	*Bartramia papillata*	Native	39	0.6	3
	Bryophyte	Moss	*Racomitrium crispulum*	Native	37	0.7	3
	Bryophyte	Moss	*Dicranoloma robustum*	Native	29	1.0	15
	Bryophyte	Moss	*Racomitrium pruinosum*	Native	27	1.0	15
	Lichen	Fruticose	*Cladonia* species	Native	27	0.5	0.5
	Lichen	Fruticose	*Cladia aggregata*	Native	26	0.5	0.5
	Bryophyte	Moss	*Polytrichum juniperinum*	Native	22	0.5	0.5
	Lichen	Foliose	*Hypogymnia lugubris*	Native	20	0.6	3
	Bryophyte	Moss	*Andreaea mutabilis*	Native	20	0.5	0.5
	Bryophyte	Moss	*Notoligotrichum australe*	Native	20	0.5	0.5
Deforested	Lichen	Fruticose	*Cladia aggregata*	Native	42	0.5	3
	Lichen	Fruticose	*Cladonia* species	Native	38	0.6	3
	Bryophyte	Moss	*Racomitrium crispulum*	Native	32	0.9	15
	Bryophyte	Moss	*Dicranoloma robustum*	Native	31	1.7	15
	Bryophyte	Moss	*Hypnum cupressiforme*	Native	30	0.6	3
	Bryophyte	Moss	*Polytrichum juniperinum*	Native	27	1.0	15
	Bryophyte	Moss	*Racomitrium pruinosum*	Native	24	3.2	63
	Bryophyte	Moss	*Breutelia pendula*	Native	21	1.1	3
	Bryophyte	Moss	*Thuidiopsis furfurosa*	Native	19	0.6	3
	Lichen	Foliose	*Hypogymnia lugubris*	Native	19	0.5	0.5

Note: Information was based on the first survey done at each plot, as very few plots provided non-vascular data across multiple surveys.

Variation in non-vascular community composition

The vector analysis of the NMDS showed that the non-vascular plant communities differed between unforested and deforested ecosystems (R^2 = 0.10, P = 0.001, Figure 17). An analysis testing for a difference in the dispersion among sample plots indicated that there was no difference between unforested and deforested ecosystems (function betadisper in the R package 'vegan', F = 2.29, P = 0.13). Of the 149 non-vascular species across the 116 plots considered in this analysis, 37 significantly contributed to the difference in the non-vascular community composition of the Tier 1 plots (Appendix 2, Table A3).

The non-vascular plant species with R^2 of at least 0.10 and P = 0.001 were all bryophytes with *Bartramia papillata* (BARPAP, Bartramiaceae, moss), *Sphagnum cristatum* (SPHCRI, Sphagnaceae, moss), and *Racomitrium crispulum* (RACCRI, Grimmiaceae, moss), presenting an R^2 above 0.20 (Appendix 2, Table A3). The vector of *Bartramia papillata* was associated with unforested ecosystems (present in 39 unforested plots and 14 deforested plots), whereas *Sphagnum cristatum* was associated with plots in deforested ecosystems (present in three unforested plots and 10 deforested plots) (Figure 17). *Racomitrium crispulum* was present in both non-forested ecosystem types (Figure 17, Table 9).

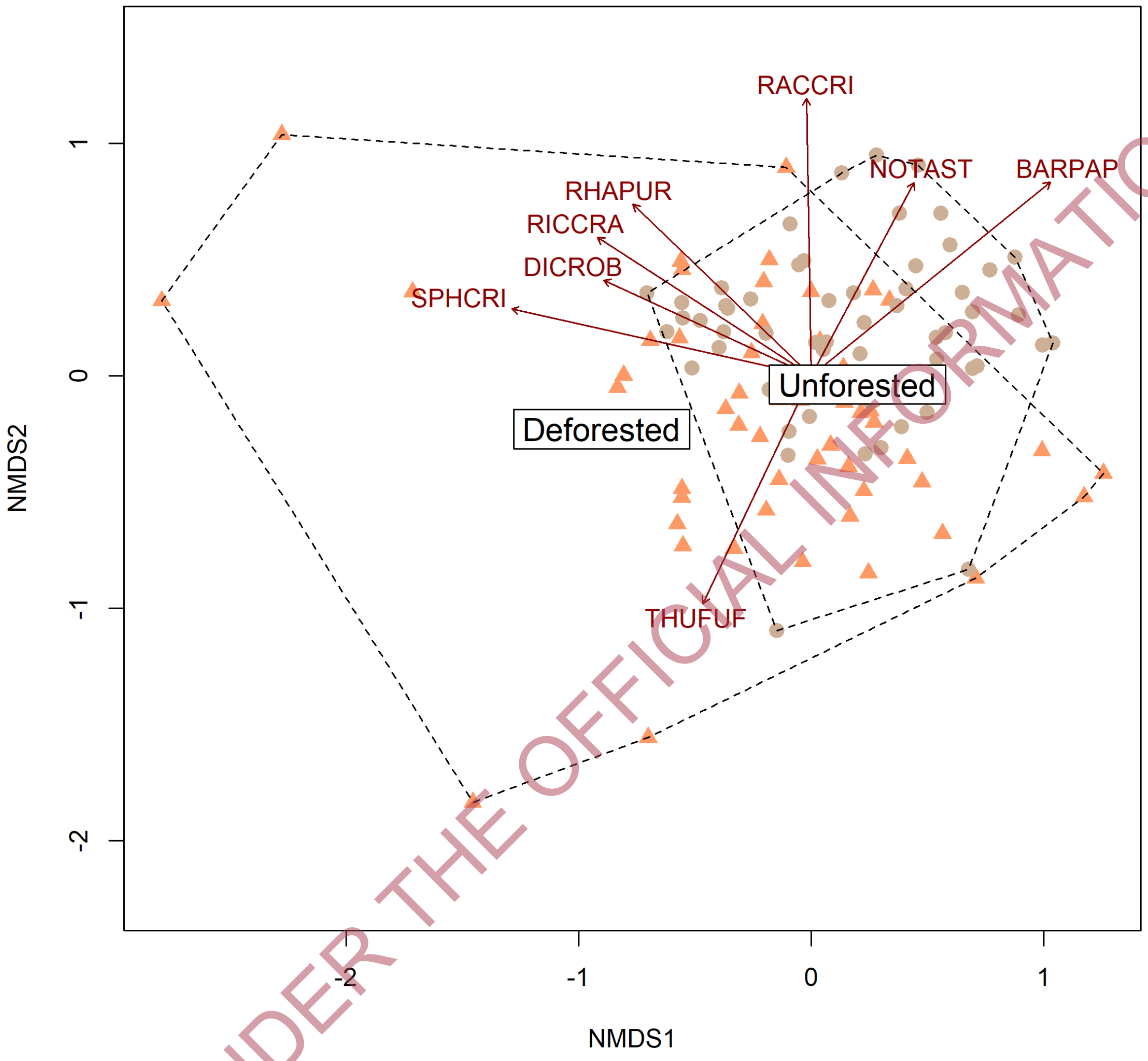

Figure 17. Non-metric multi-dimensional scaling (NMDS) of non-vascular community composition across plots, based on non-vascular species present in at least four plots (no. species = 149, no. plots = 116, stress = 0.14).

Notes: Arrows represent non-vascular species driving these differences, with P ≤ 0.001 (see Appendix 2, Table A3 for NMDS output and full species names). Composition was significantly different between unforested (brown circles) and deforested (orange triangles) ecosystems (R2 = 0.096, P = 0.001).

Bryophyte and lichen richness relationships

The best GLM model predicting bryophyte richness included weed cover, vascular cover, landform, and MAP, and the interaction between ecosystem type and lichen richness (Appendix 2, Table A4a). Although the raw means suggested a lack of differences between ecosystem types, we found that once other variables were accounted for there was greater bryophyte species richness in plots in unforested than deforested ecosystems (Figure 18; Table 11; Appendix 2, Table A5a).

Bryophyte and lichen richness were positively associated across both ecosystem types, more strongly so in deforested ecosystems (Figure 19a). Although bryophyte richness increased with vascular plant cover, it was negatively associated with increasing weed cover (Table 10; Table 11; Appendix 2, Table A4a). Among the climate and environmental variables considered in this analysis, bryophyte richness increased with landform index; i.e. bryophyte richness was lowest on ridge crests and highest in gullies (Table 10; Table 11; Appendix 2, Table A4a). Even though bryophyte richness and MAP were not significantly related, the latter contributed significantly to the model (Table 10; Table 11; Appendix 2, Table A5a).

The best GLM model predicting lichen species richness included bryophyte species richness, vascular plant cover, rocky cover, and MAP (Appendix 2, Table A4b). Lichen species richness did not differ between naturally unforested and deforested ecosystems (Figure 18a). Lichen species richness increased with greater rocky cover and vascular plant cover (Table 10; Table 11; Appendix 2, Table A5b). In contrast to bryophyte species richness, lichen richness declined with increasing MAP (Table 10; Table 11; Appendix 2, Table A5b). There was no significant relationship between weed cover and lichen species richness (Appendix 2, Table A4b).

For both bryophyte and lichen richness, there were no significant relationships with pellet indices of either ungulates or lagomorphs; these variables were removed early from the final model (Appendix 2, Table A4).

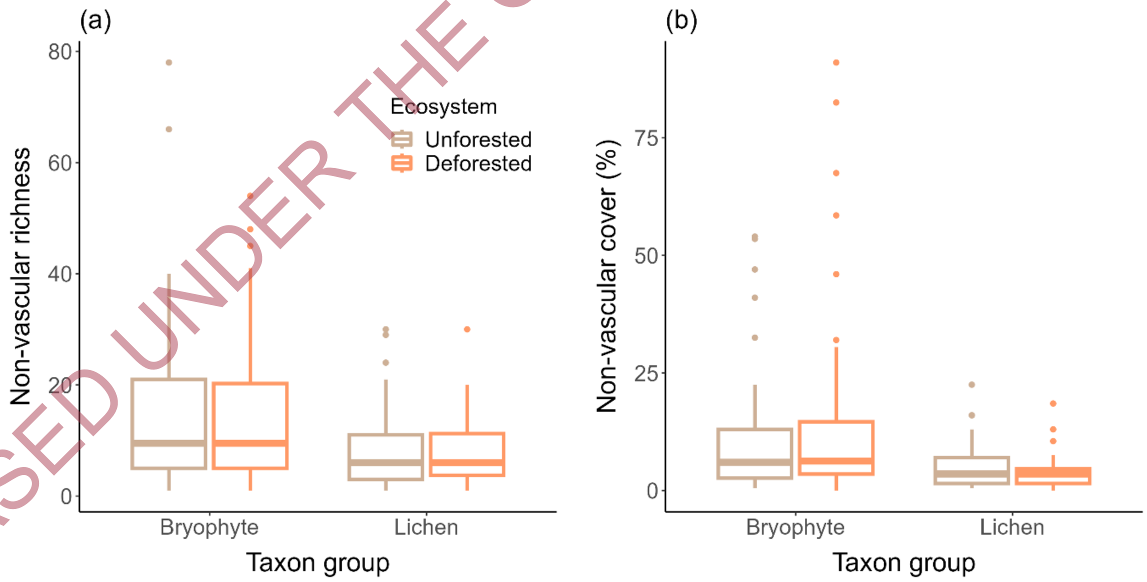

Figure 18. Boxplot showing (a) the non-vascular species richness, and (b) the non-vascular cover (%) by taxon group (i.e. bryophyte or lichen), by ecosystem type (unforested or deforested).

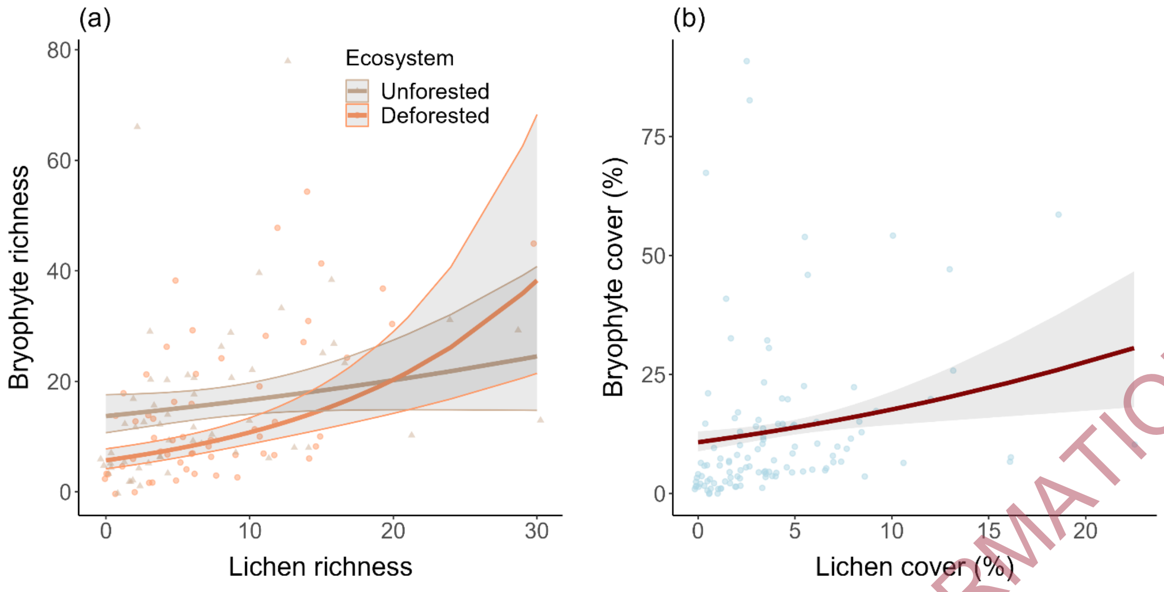

Figure 19. Predicted mean relationship between (a) bryophyte and lichen species richness by ecosystem type (unforested: brown triangles, deforested: orange dots), and (b) bryophyte and lichen cover (%), with each relationship predicted with the other covariables held to their mean.

Notes: Grey areas represent 95% confidence intervals and blue points raw values. See Appendix 2, Table A5, for detailed outputs.

Bryophyte and lichen cover relationships

The best GLM model predicting bryophyte cover included lichen cover, weed cover, vascular plant cover, landform index, and MAP (Appendix 2, Table A4c). Bryophyte cover did not differ between naturally unforested and deforested ecosystems (Figure 18b). Bryophyte and lichen cover were positively related (Figure 19b). As for bryophyte species richness, bryophyte cover increased with greater vascular plant cover and MAP, and decreased with greater weed cover (Table 10; Table 11; Appendix 2, Table A4c). Although landform index was non-significant, this variable still contributed to the model fit (Table 12; Appendix 2, Table A4c).

The best GLM model predicting lichen cover included bryophyte cover, vascular plant cover, weed cover, rocky cover, MAP, and MAT (Appendix 2, Table A4d). There were no significant differences in lichen cover between unforested and deforested ecosystems: the mean lichen cover in both was 4% (Figure 18b). As with lichen species richness, lichen cover increased with rocky cover and vascular plant cover, and declined with greater weed cover (Table 10; Table 11; Appendix 2, Table A5d). Greater MAP and MAT was associated with lower lichen cover (Table 10; Table 11; Appendix 2, Table A5d).

There were no significant relationships between ungulate and lagomorph faecal pellet indices and either bryophyte or lichen cover (Appendix 2, Table A4d).

Table 10. Variables considered for the generalised linear model analyses of bryophyte and lichen richness and cover, indicating the direction of significant relationships: positive relationship (+, green shading), negative relationship (-, orange shading), and non-significant relationship (ns, no shading) (see Table 11 and Appendix 2, Table A5, for detailed models output).

	Bryophyte richness	**Bryophyte cover**	**Lichen richness**	**Lichen cover**
Vegetation				
Vascular cover	+	+	+	+
Weed cover	-	ns	ns	-
Mean top height	ns	ns	ns	ns
Climate				
MAP	ns	ns	-	-
MAT*	-	ns	ns	-
Site description				
Rocky cover	ns	ns	+	+
Solar radiation	ns	ns	ns	ns
Landform index	+	ns	ns	ns
Herbivore pellet index				
Ungulates	ns	ns	ns	ns
Hares	ns	ns	ns	ns
Rabbit	ns	ns	ns	ns

* Mean annual temperature (MAT) and elevation were highly correlated (Appendix 2, Table A1) so only MAT was used as a variable.

Table 11. Variables influencing (a) bryophyte richness, (b) bryophyte cover, (c) lichen richness, and (d) lichen cover, with χ^2 and P values extracted from analysis of variance (Anova) for each final GLM model. Interaction terms are denoted using ×.

Response variable	**Predictors**	χ^2	***P***
a) Bryophyte richness	MAP	2.85	0.091
	Elevation	7.82	0.005
	Ecosystem	9.84	0.002
	Lichen richness	19.89	<0.001
	Weed cover	6.74	0.009
	Vascular cover	30.05	<0.001
	Landform index	6.57	0.010
	Ecosystem × Lichen richness	6.75	0.009
*b) Bryophyte cover**	MAP	3.29	0.070
	Lichen cover	8.63	0.003
	Weed cover	3.53	0.060
	Vascular cover	15.72	<0.001
	Landform index	2.58	0.108

Response variable	Predictors	χ^2	*P*
c) Lichen richness	MAP	11.33	0.001
	Bryophyte richness	20.36	<0.001
	Rocky cover	2.51	0.113
	Vascular cover	7.33	0.007
d) Lichen cover	MAP	5.23	0.022
	MAT	9.58	0.002
	Bryophyte cover	3.74	0.053
	Weed cover	4.26	0.039
	Rocky cover	3.96	0.047
	Vascular cover	27.00	<0.001

Liverwort richness relationships

The best GLM model predicting liverwort richness included weed cover, vascular plant cover, MAP, elevation, and the interaction between distance to nearest river and ecosystem type (Table A5). Liverwort richness did not differ between naturally unforested and deforested ecosystems (Table 12). The relationship between liverwort richness and distance to nearest river was only significant in deforested ecosystems, with a greater liverwort richness found near rivers (Table 13; Appendix 2, Table A6; Figure 20). Liverwort richness increased with greater vascular plant cover and decreased with greater weed cover (Table 12 and Table 13; Appendix 2, Table A6). Greater liverwort richness was found in wetter areas and at lower elevation (Table 12 and Table 13; Figure 20).

There were no significant relationships between ungulate and lagomorph faecal pellet indices and liverwort richness (Table 13; Appendix 2, Table A5).

Table 12. Variables influencing liverwort richness with χ^2 and *P* values from analysis of variance (Anova) based on final GLM

Predictor variables	χ^2	*P*-value
Vascular cover	37.45	<0.001
Weed cover	23.88	<0.001
Elevation	18.42	<0.001
Ecosystem	10.40	0.001
MAP	10.06	0.002
Ecosystem × Distance to river	7.01	0.008
Distance to river	6.83	0.009

Table 13. Variables considered for the analysis predicting liverwort richness with the direction of significant relationships: positive relationship (+, green shading), negative relationship (-, orange shading), and non-significant relationship (ns, no shading) (see Table 12, and Appendix 2, Table A6, for detailed models output)

Variable group	Variable	Direction of effect on liverwort richness
Vegetation	Vascular cover	+
	Weed cover	-
	Mean top height	ns
Climate	MAP	+
	MAT*	-
Site description	Rocky cover	ns
	Solar radiation	ns
	Landform index	ns
	Distance to nearest river**	-
Herbivore Pellet index	Ungulates	ns
	Hares	ns
	Rabbit	ns

* Mean annual temperature (MAT) and elevation were highly correlated (Appendix 2, Table A1) so only MAT was used as variable.

** Relationship only significant in deforested ecosystem (Appendix 2, Table A6).

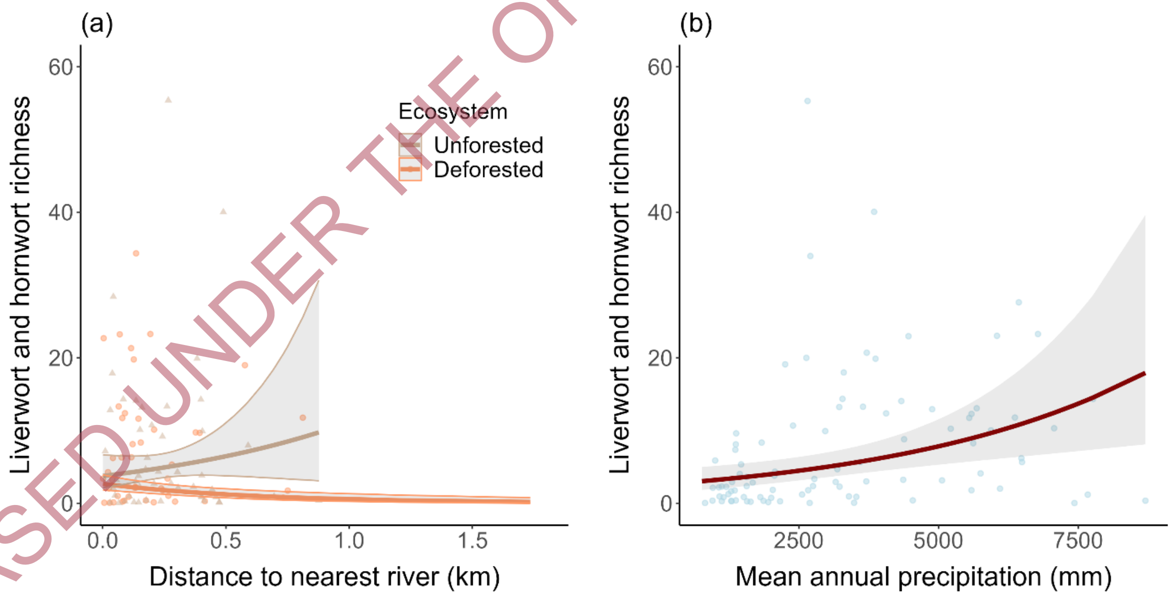

Figure 20. Predicted mean relationship between liverwort and hornwort richness and (a) distance to nearest river (km), by ecosystem type (unforested: brown triangles, deforested: orange dots), and (b) mean annual precipitation (mm), with each relationship predicted with the other covariables held to their mean.

Notes: Grey areas represent 95% confidence intervals, and points raw values. See Appendix 2, Table A6, for detailed outputs. (a) showed a shorter range of predicted means for unforested ecosystems as no liverwort species were found beyond 1 km distance in this ecosystem type, giving very wide confidence intervals.

8.4 Discussion

The presence or absence of 30 bryophyte species (22 species of mosses and eight liverworts) and seven lichen species explained differences in the non-vascular species community composition between naturally unforested and deforested ecosystems. None of those species was a hornwort or a crustose lichen (see Appendix 2, Table A2). All the most frequent bryophytes in unforested and deforested ecosystems were mosses – none were liverworts. Liverworts (also including hornworts) were most species-rich close to rivers in deforested ecosystems, consistent with a Tasmanian study that showed greatest liverwort species richness in wetter ecosystems (Pharo & Beattie 1997).

Among individual non-vascular species, the widespread common moss *Sphagnum cristatum* was strongly associated with deforested habitats. Palaeoecological studies have shown this species increased substantially in abundance after historical deforestation and a coincident increase in water availability (McGlone & Wilmshurst 1999). Its local dominance can be promoted by ongoing disturbance that results in impeded drainage (Whinam et al. 2003), or it may form peats colonised by vascular plants (Wardle 1991). The mosses *Dicranoloma robustum* and *Polytrichum juniperinum* were frequent in both unforested and deforested ecosystems (Table 10), and both were classified by Kentjens et al. (2023) as 'generalist' species; they are also widespread, common species in forests (Michel et al. 2011). More information is needed to understand why some non-vascular species are more associated with unforested or deforested ecosystems.

For example, the moss *Bartramia papillata* was the most frequent species in naturally unforested ecosystems (Table 10), but other studies emphasise its occurrence across diverse habitats (Fife 2020). Although it was present in a study of community ecology in *Chionochloa*-dominated grasslands in Otago (Wilson & Gitay 1999), that study provides insufficient detail to determine whether its study sites were in communities we would classify as unforested or deforested. Interestingly, only bryophyte richness seemed to vary between non-forested ecosystem types, and solely after accounting for multiple covariables. The use of species richness and cover at the taxon level may not be nuanced enough to detect variation of interrelationships. Relying on more ecologically meaningful measures such as growth form may provide further information necessary to comprehend ecosystem integrity (Bates 1998).

Climatic influences on bryophytes and lichens were similar in unforested and deforested ecosystems. Consistent with other studies, lichens had higher richness and greater cover in drier sites (Pharo & Beattie 1997; Ferguson et al. 2009). In deforested regions of the eastern South Island, in short-tussock grasslands, the lichens in the genera *Cladia* and *Cladonia*, which were the most frequent species in Tier 1 plots in deforested ecosystems, are characteristic of well-drained, stony soils that are likely to be nutrient-poor (Wardle 1991).

However, we found only positive trends between bryophytes richness or cover and MAP, which may have been less important than other variables included in the model. For instance, the second-best model predicting bryophyte richness without an interaction term showed a significant positive relationship with MAP (Appendix 2, Table A3a).

We also found that liverworts had a greater species richness in plots located in wetter areas. *Polytrichum juniperinum* and *Breutelia pendula* (the latter common in deforested ecosystems, Table 9) are drought-tolerant moss species (Kentjens et al. 2023); further investigations between drought indices of plots and their community composition may reveal relationships between particular bryophyte and lichen taxa and drought tolerance. Lichen richness and cover were positively related to the percentage of rocky surface, which is consistent with previous studies or botanical records showing the association between rocks and various saxicolous (a term describing lichens living on rocks and other bare surfaces like roads or metal) lichen species (e.g. Orwin 1970; Galloway & Ledingham 2006; Knight 2014). Similarly, lichens and mosses are dominant components of the vegetation of very high elevation sub-nival rock areas of New Zealand's alpine unforested ecosystems, such as in Aoraki / Mount Cook National Park (Wilson 1976).

Bryophyte and lichen cover were positively related in both unforested and deforested ecosystems, as were, bryophyte and lichen species richness. These results are the opposite to relationships between bryophytes and lichens in Tasmanian and New Zealand natural forests (Pharo & Beattie 1997; Kentjens et al. 2023). Kentjens et al. (2023) suggested that the negative relationship between lichen and bryophyte cover they found in montane New Zealand forests and shrublands could be associated with the lichen and those bryophyte species more tolerant to drought competing for resources.

Bryophyte and lichen richness and cover were strongly associated with greater vascular vegetation cover in both unforested and deforested ecosystems, which is consistent with relationships found for a range of bryophyte species throughout New Zealand's indigenous forests (Michel et al. 2011), but contrasts with a local-scale study from New Zealand forests, where there was a decrease in bryophyte cover with greater vascular plant cover (Kentjens et al. 2023). More research is necessary to investigate further the relationship between non-vascular and vascular plants in unforested and deforested ecosystems in New Zealand, and the mechanisms that underpin them.

Weed cover in both unforested and deforested ecosystems reduced bryophyte cover and richness and lichen cover. Similarly, in semi-arid grasslands in western North America, weed species cover (of *Bromus tectorum*, Poaceae) reduced the cover of bryophyte and lichen communities, in contrast to native vascular plant species cover, which increased alongside mosses and lichen cover (Belnap et al. 2006). In that case, disentangling the relationship with weed invasion from the effects of other environmental drivers or extreme events (e.g. droughts) was feasible because of repeated measurements over 8 years.

Although the final number of Tier 1 plots (n = 116) allowed us to test interrelationships between measures of non-vascular plant communities and measures of vegetation structure and weed cover, we were not able to detect any influence of ungulate or lagomorph populations on non-vascular plant communities in either naturally unforested or deforested ecosystems. Ungulates and lagomorphs have been documented (mostly in the northern hemisphere) to directly affect bryophyte and lichen richness and cover (Bernes et al. 2018; Speed et al. 2020). Although a study of non-forested ecosystems in Tasmania found no relationships between grazing by introduced ungulates and non-vascular species' cover or richness (Ferguson et al. 2009), more evidence is needed in New

Zealand to evaluate the impacts of ungulates and lagomorphs on non-vascular plant communities in both unforested and deforested ecosystems.

There was an increase in moss and lichen cover over 30 years in mid-elevation tussock grassland (a deforested ecosystem) after grazing by livestock ceased (Mark & Dickinson 2003). However, a study in English grasslands from which rabbits were excluded showed significant increases in grass biomass but significantly less biomass of mosses and lichens (Watt 1960). Equivalent studies are needed on the effects of hares in unforested ecosystems in New Zealand, where they are common, and of rabbits in deforested ecosystems, where they are locally abundant, to determine the effects on non-vascular plant communities in New Zealand (Bellingham et al. 2020). The limited number of Tier 1 plots with repeated measurements also makes it challenging to disentangle the influences of ungulates or lagomorphs on non-vascular plant communities from those of other covariables.

Further research is required to fill the multiple gaps in knowledge on non-vascular plant species in New Zealand if we are to interpret current state and future trends in non-vascular plant communities in Tier 1 plots. For instance, there is currently no non-vascular plant trait data set that could provide growth form or life strategy traits. These non-vascular plant traits might be more relevant when testing ecological hypothesis (Bates 1998). Comparing non-vascular plant communities between plots fenced to exclude ungulates and lagomorphs and unfenced control plots in unforested and deforested communities would allow better determination of their effects.

Such studies could shed light on the positive relationship we found between vascular plant cover and non-vascular plant cover, which contrasts with studies at high latitudes in Europe, where experimental warming resulted in increased vascular plant biomass and reduced lichen cover (Cornelissen et al. 2001). Similarly, measurement of effects of weed control on non-vascular plant communities could determine their utility in assessing the recovery of ecological integrity. For example, the removal of wilding *Pinus contorta* in deforested ecosystems in New Zealand resulted in biomass increase of grasses, mostly non-native species, and the consequences for bryophyte and lichen communities is unknown.

9 Conclusions

This study, showing state and trends in non-forested ecosystems on public conservation land throughout New Zealand assessed using the systematic network of Tier 1 plots, provides strong support for delineating those ecosystems that are naturally unforested from those that have been historically deforested, and reporting them (and, by implication, managing them) separately.

9.1 Naturally unforested ecosystems

Most of New Zealand's naturally unforested ecosystems are in the alpine zones above the treeline. These ecosystems are internationally important areas of high endemism of plants and animals (e.g. Mark 2012). They are subject to pressures from climate change and invasions by non-native mammals, including herbivores (Himalayan tahr, chamois, deer, and brown hares) and predators (including stoats, cats, hedgehogs, and pigs) (O'Donnell et al. 2017). All these pressures affect native biodiversity and require ongoing measurement of their state and trends. Changes in vegetation in response to these pressures are likely to be slow because of the low primary productivity of most alpine ecosystems. For example, changes in vegetation cover and species composition alpine ecosystems at Arthur's Pass (measured from 1931 to 2018) have been slow after a fire that burned them in 1890 (Burge et al. 2020).

Nonetheless, we can ill afford to be complacent about measuring change in New Zealand's naturally unforested – mostly alpine – ecosystems. Climate change is altering alpine ecosystems worldwide, affecting species distributions, the physiology of resident species, and their distributions (Yoccoz et al. 2010). New primary successions are occurring where deglaciation in New Zealand is occurring apace (Dykes et al. 2011; Abrahim et al. 2023). Major structural changes to alpine ecosystems caused by plant invasions have been uncommon so far, but some invasive trees such as lodgepole pine (*Pinus contorta*) can already establish above natural treelines (Ledgard 2001), and it is likely that altered growing seasons may favour wider invasions by this species and potentially others.

Altered alpine climatic conditions, coupled with potentially longer growing seasons for plants, could, in turn, alter the energetics, foraging behaviour, and breeding success of introduced mammalian herbivores, with consequences for the composition of plant communities. It is clear from the rapid declines of endemic alpine birds such as kea (*Nestor notabilis*) and rock wren *(Xenicus gilviventris*) within the last two decades that rapid action is needed to ensure the ecological integrity of unforested, alpine ecosystems is maintained or restored, and monitoring is required to provide the evidence that management effects change.

Ongoing evaluation of widespread change in unforested, alpine ecosystems and assessments of the effectiveness of management will bring the greatest benefits if local evaluations, using Tier 2 plot networks, are made in addition to widespread Tier 1 assessments. For example, this approach was recommended to evaluate how the management of tahr changes vegetation (Bellingham et al. 2018), and it could be extended to other management actions. Moreover, understanding of effects of introduced herbivores such as deer, which range across forested and naturally unforested alpine ecosystems and the shrub ecotones between them, is critical if we are to maintain and restore ecosystem integrity. Studies of long-term change in ungulate abundance and vegetation using Tier 2 plot networks across forests, subalpine shrublands, and alpine vegetation in the Murchison Mountains is an exemplar of how this can be done effectively (Tanentzap et al. 2009) and should be maintained in the long term.

9.2 Deforested ecosystems

Because of their lower elevation, and the fact that they once supported forest, deforested ecosystems can change rapidly in response to pressures such as climate change, altered disturbance regimes (notably fire disturbance), and biological invasions. This is especially apparent in the case of invasions by ecosystem-transforming 'wilding conifers', which rapidly accrue biomass and return deforested ecosystems dominated by native plants to forested ecosystems dominated by non-native trees within one to two decades (Ledgard 2001; Peltzer 2018), altering the composition of soil biota (Dickie et al. 2017) and catchment hydrology (Fahey & Payne 2017).

Successional trajectories are poorly understood in New Zealand's deforested ecosystems. While it is easy to focus on some deforested ecosystems returning rapidly to forest, others don't show a return to forest at multiple decadal scales. Many are invaded heavily by low-biomass invasive species. In some cases, low-biomass invaders can have strong ecosystem effects and dominate deforested ecosystems, depressing native species, such as thyme (*Thymus vulgaris*) in Central Otago (Nielsen et al. 2015). For others, like *Hieracium* species, after several decades of investigation it is unclear whether their local dominance and low native species diversity is a consequence of their invasion, or they invaded nutrient-poor ecosystems with low native species richness and have remained in constant abundance since (Scott et al. 2001; Day & Buckley 2011, 2013). Legacies of grazing, periodic use of fertiliser, and fire regimes all influence current composition and potential future trajectories, and all of these are probable reasons why the variance in estimates of change in these ecosystems in our study are greater than those for naturally unforested ecosystems.

Novel features of invasive plants and animals also make predictions of rate of change and future composition difficult. Fire was the reason that most deforested ecosystems came into being in the first place, after human settlement (McGlone 2001). However, increasingly from the 19th century many invasive plants in these ecosystems – not just northern hemisphere conifers, but also Mediterranean plants such as thyme, Scotch broom (*Cytisus scoparius*) and gorse (*Ulex europeaus*) – are not only fire-adapted but fire-promoting, so that interactions between drought, invasion, and ignition are likely to further deplete most native species that are poorly adapted to fire, and thus further enhance invasions. For managers of public conservation land this is bad enough, but when fires that begin on invaded public conservation land also interact with the invaded land of neighbours, there can be risks to the public and property as a result of plant invasions.

It is perhaps even more important to understand landscape-level processes across deforested ecosystems and the ecosystems that adjoin them if we are to determine the interrelationships that drive ecological integrity than it is in naturally unforested ecosystems. A study in Central Otago underscores why: there, pastural ecosystems (which were periodically fertilised, etc.) adjacent to deforested ecosystems dominated by tussock grasses were critical in driving populations of rabbits, which, in turn, affected native vegetation structure in the deforested ecosystems on public conservation land, in turn affecting the behaviour and efficiency of introduced predatory mammals, all to the detriment of the survival of populations of endangered native lizard species (Norbury et al. 2013).

Tier 1 plots are only now affording insight into widespread temporal change across New Zealand's historically deforested ecosystems. Because successional trajectories across deforested ecosystems are unclear, it is unfortunate that, in contrast to the forested plots in the Tier 1 network, the investment in historical local plot networks in deforested ecosystems (as well as in naturally unforested ecosystems) was not incorporated in the design.

The missed opportunity to integrate multi-decadal history in interpreting change across the Tier 1 network can best be remedied now by also reinstating and remeasuring Tier 2 plot networks, which can give an insight into change, especially in the highly variable deforested ecosystems. Moreover, the total sample sizes of Tier 1 plots in both non-forested ecosystems are small compared with those available from Tier 1 for forested ecosystems (n = 190 deforested, n = 200 unforested; Table 1, both across a wide range of environments, compared with n = 748 in forested ecosystems, Hawcroft et al. 2024).

It is a good time to appraise Tier 2 networks to determine how they can help resolve issues of change in unforested and deforested ecosystems (as has been done recently for forests; Richardson et al. 2024). A critical appraisal could also lead to partnerships to get priority plot networks measured, including those that straddle deforested public conservation land and either private or public leasehold land (Day & Buckley 2011, 2013). Over most of New Zealand's deforested ecosystems, research and monitoring that featured strongly during the 20th century across government agencies, including DOC (and its predecessors), Crown Research Institutes, and universities, has languished in the early 21st century.

9.3 General features

New Zealand's unforested alpine ecosystems are characterised by high local endemism in the vascular plant flora, large radiations in many genera (e.g. Meudt et al. 2015; Venter 2021) that reflect biogeographical patterns (e.g. Wagstaff & Garnock-Jones 1998; Heenan et al. 2021), and differences in geology and climate (Mark et al. 2000; Wilson & Meurk 2011; Heenan & McGlone 2013). The deforested ecosystems combine both local alpine floras that colonised below the treeline once original cover was removed and local flora that colonised from open habitats such as bluffs (McGlone 2001; Heenan & McGlone 2013).

The high vascular species turnover makes it difficult to draw generalisations across regions, and to determine general patterns in response to pressures such as changing climate, fire, and herbivory by introduced mammals. In an evaluation of the effects of tahr on the vegetation of alpine ecosystems, the high species turnover throughout the range of tahr and a lack of information about their dietary preferences hampered understanding of their impacts at other than local scales (Bellingham et al. 2018).

In this report we placed little emphasis on species richness for vascular plants (other than weed species richness) or changes in richness, and a recent study of change in naturally unforested alpine ecosystems in Australia supports this (Tierney 2024). In that study, evaluation of community-level composition (using NMDS, as we used to assess non-vascular plant communities) was better able to detect change in these ecosystems than species richness.

Some of the issues that attend reporting changes in ecological integrity in unforested and deforested ecosystems can be overcome if plant communities are evaluated in terms of plant functional traits, especially those linked to responses to pressures from changing climate, fire, and herbivory. For some of the genera that dominate New Zealand's naturally unforested and deforested ecosystems, such as *Chionochloa*, functional traits have been well quantified (Williams et al. 1978; Mills et al. 1989), but these are a minority. An important study quantified the traits of common species along elevational gradients in deforested ecosystems (Craine & Lee 2003), but much more data are needed since most of the species it quantified are widespread.

The value of traits for interpreting change is clear from an experimental study that evaluated change over 27 years in deforested ecosystems in New Zealand in response to fertilising and grazing (Laliberté et al. 2012), and other disturbances (Laliberté et al. 2013). For example, greater grazing intensity shifted the plant communities to those characterised by shorter plant height, thicker leaves, and lower leaf nitrogen concentrations, with potential flow-on consequences for invertebrate herbivore and pollinator communities, and rates of decomposition and nutrient cycling. A wider evaluation of the traits of plants across New Zealand's unforested and deforested ecosystems would allow us to evaluate state and trend in them in response to pressures in the same way that we can for New Zealand's forests (e.g. Hawcroft et al. 2024).

The lack of knowledge of the traits of the large, diverse non-vascular flora of New Zealand hampers understanding across all ecosystems. Without knowledge of their traits, we do not know enough to interpret what the compositional differences between unforested and deforested ecosystems signify. Since some mosses and lichens occur at elevations higher than any vascular plant, we can expect that some of those in unforested ecosystems have traits linked to cold tolerance. Other species that are common in deforested ecosystems, such as *Sphagnum cristatum*, have traits associated with tolerance of high moisture levels and disturbance.

Knowledge of traits would also improve the resolution of differences between unforested and deforested ecosystems. For example, the lack of difference in lichen or bryophyte cover between these ecosystems might be interpreted differently if we were able to interpret them in terms of traits that differed according to environmental conditions and to pressures, such as trampling by herbivores, altered soil moisture, and other features that are likely to be linked to climate change. Without this information we are not yet in a position to determine whether the non-vascular flora in Tier 1 plots affords novel insights into ecological integrity and the effects of pressures that add value above that obtained from vascular plants.

Until we can interpret major differences among plots and among ecosystem types in their non-vascular plant communities, there is limited value in measuring compositional change in those communities on a 5-year or even 10-year cycle. Detecting change in non-vascular plant communities is likely to be challenging because we do not know the extent to which measurement error related to observer-level effects accompanies each estimate of the non-vascular plant community. This is known for the vascular plant community (Mason et al. 2018; Morrison et al. 2024), which enables us to tease apart true, compositional change over time from the artefacts of measurement error. If there was a case for requiring data on compositional change in non-vascular plant communities, a first step would be to quantify measurement error before embarking on a full remeasurement of all plots.

10 Recommendations

1. Appraise and prioritise Tier 2 networks in unforested and deforested ecosystems for their remeasurement. This would enhance understanding of state and trends in Tier 1 plots by providing fine-scale spatial resolution and temporal resolution that extends over several decades. Include in this assessment Tier 2 networks of plots in ecosystems adjacent to unforested and deforested ecosystems.
2. Build effective partnerships with key stakeholders and neighbours adjoining public conservation land to evaluate changes in deforested ecosystems and the pressures on them, such as LINZ and the New Zealand Defence Force, and mana whenua (e.g. Ngāi Tahu, Ngāti Tūwharetoa).
3. Build partnerships with researchers who maintain and measure change in unforested and deforested ecosystems, especially in universities.
4. Design a programme to quantify the traits linked with pressures from climate change and herbivory in the vascular flora across deforested and unforested ecosystems. This would include a prioritisation process based on species' relative abundance and biomass contribution, information about sensitivity to pressure, and, for some genera with a high species diversity in architecture and leaf size (e.g. *Aciphylla*, *Brachyglottis*, *Dracophyllum*, *Myosotis*, *Ranunculus*, *Veronica*), a representative range. Linking these traits to quantitative studies of the dietary preferences of a range of mammalian herbivores would add further value.
5. Do not remeasure the non-vascular plant communities until we have adequate information on their ecology and function, and confidence in our capacity to quantify change, so that repeat-measures data from these plants can be interpreted to report on state and change in ecological integrity. A caveat to this recommendation is that there is merit in establishing new Tier 1 plots in areas that have become deglaciated or are no longer in permanent snow or ice since the network was established in 2011, and, in these new plots, record cover and the identity of non-vascular plants, which we could expect to be the first colonists.

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12 References

Abrahim BN, Cullen NJ, Conway JP, Sirguey P 2023. Applying a distributed mass-balance model to identify uncertainties in glaciological mass balance on Brewster Glacier, New Zealand. Journal of Glaciology 69(276): 1030–1046.

Allan Herbarium 2023. Checklist of the New Zealand flora – hornworts, liverworts and mosses. https://datastore.landcareresearch.co.nz/lv/dataset/checklist-of-the-new-zealand-flora-hornworts-liverworts-and-mosses-2023.

Allen K, Bellingham PJ, Richardson SJ, Allen RB, Burrows LE, Carswell FE, et al. 2023. Long-term exclusion of invasive ungulates alters tree recruitment and functional traits but not total forest carbon. Ecological Applications 33(4): e2836.

Allen RB 1993. A permanent plot method for monitoring changes in indigenous forests: a field manual. Lincoln, New Zealand, Landcare Research.

Allen RB, Bellingham PJ, Holdaway RJ, Wiser SK 2013. New Zealand's indigenous forests and shrublands. In: Dymond JR ed. Ecosystem services in New Zealand: conditions and trends. Pp. 34–48.

Aspinall R, Pearson D 2000. Integrated geographical assessment of environmental condition in water catchments: linking landscape ecology, environmental modelling and GIS. Journal of Environmental Management 59(4): 299–319.

Averill C, Dietze MC, Bhatnagar JM 2018. Continental-scale nitrogen pollution is shifting forest mycorrhizal associations and soil carbon stocks. Global Change Biology 24(10): 4544–4553.

Barton K 2022. MuMIn: Multi-Model Inference. R package version 1.46.0.

Bates JW 1998. Is 'life-form' a useful concept in bryophyte ecology? Oikos 82(2): 223–237.

Bellingham PJ, Richardson SJ, Gormley AM, Allen RB, Cook A, Crisp PN, et al. 2020. Implementing integrated measurements of essential biodiversity variables at a national scale. Ecological Solutions and Evidence 1(2): e12025.

Bellingham PJ, Wiser SK, Burge OR, Easdale TA, Richardson SJ 2018. Potential of Tier 1 and alternative monitoring networks to assess the ecological integrity of alpine vegetation exposed to tahr grazing. Manaaki Whenua – Landcare Research contract report: LC3328 for Department of Conservation.

Belnap J, Phillips SL, Troxler T 2006. Soil lichen and moss cover and species richness can be highly dynamic: the effects of invasion by the annual exotic grass *Bromus tectorum*, precipitation, and temperature on biological soil crusts in SE Utah. Applied Soil Ecology 32(1): 63–76.

Bernes C, Macura B, Jonsson BG, Junninen K, Müller J, Sandström J, et al. 2018. Manipulating ungulate herbivory in temperate and boreal forests: effects on vegetation and invertebrates: a systematic review. Environmental Evidence 7(1): 13.

Boudreau S, Payette S 2004. Caribou-induced changes in species dominance of lichen woodlands: an analysis of plant remains. American Journal of Botany 91(3): 422–429.

Brandt AJ, Bellingham PJ, Duncan RP, Etherington TR, Fridley JD, Howell CJ, et al. 2021. Naturalised plants transform the composition and function of the New Zealand flora. Biological Invasions 23(2): 351–366.

Brandt AJ, Maule H, Fridley JD, Gatehouse HAW 2020b. NZ non-native flora growth forms 2020. https://datastore.landcareresearch.co.nz/en_AU/dataset/nz-non-native-flora-growth-forms-2020

Brandt AJ, McGlone MS, Richardson SJ 2020a. NZ native flora growth forms 2019. https://datastore.landcareresearch.co.nz/dataset/nz-native-flora-growth-forms-2019

Brooks ME, Kristensen K, van Benthem KJ, Magnusson A, Berg CW, Nielsen A, et al. 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. The R journal 9(2): 378–400.

Burge OR, Bellingham PJ, Arnst EA, Bonner KI, Burrows LE, Richardson SJ, et al. 2020. Integrating permanent plot and palaeoecological data to determine subalpine post-fire succession, recovery and convergence over 128 years. Journal of Vegetation Science 31(5): 755–767.

Capmourteres V, Rooney N, Anand M 2018. Assessing the causal relationships of ecological integrity: a re-evaluation of Karr's iconic Index of Biotic Integrity. Ecosphere 9(3): e02168.

Carlson CJ 2020. embarcadero: species distribution modelling with Bayesian additive regression trees in R. Methods in Ecology and Evolution 11(7): 850–858.

Chollet S, Baltzinger C, Le Saout S, Martin J-L 2013. A better world for bryophytes? A rare and overlooked case of positive community-wide effects of browsing by overabundant deer. Écoscience 20(4): 352–360.

Cieraad E, McGlone MS, Huntley B 2014. Southern Hemisphere temperate tree lines are not climatically depressed. Journal of Biogeography 41(8): 1456–1466.

Clark DA 2007. Detecting tropical forests' responses to global climatic and atmospheric change: current challenges and a way forward. Biotropica 39(1): 4–19.

Cornelissen JHC, Callaghan TV, Alatalo JM, Michelsen A, Graglia E, Hartley AE, et al. 2001. Global change and arctic ecosystems: is lichen decline a function of increases in vascular plant biomass? Journal of Ecology 89(6): 984–994.

Craine JM, Lee WG 2003. Covariation in leaf and root traits for native and non-native grasses along an altitudinal gradient in New Zealand. Oecologia 134(4): 471–478.

Cruz J, Thomson C, Parkes JP, Gruner I, Forsyth DM 2017. Long-term impacts of an introduced ungulate in native grasslands: Himalayan tahr (*Hemitragus jemlahicus*) in New Zealand's Southern Alps. Biological Invasions 19(1): 339–349.

Damgaard CF, Irvine KM 2019. Using the beta distribution to analyse plant cover data. Journal of Ecology 107(6): 2747–2759.

Day NJ, Buckley HI 2011. Invasion patterns across multiple scales by *Hieracium* species over 25 years in tussock grasslands of New Zealand's South Island. Austral Ecology 36(5): 559–570.

Day NJ, Buckley HL 2013. Twenty-five years of plant community dynamics and invasion in New Zealand tussock grasslands. Austral Ecology 38(6): 688–699.

DeLucia EH, Turnbull MH, Walcroft AS, Griffin KL, Tissue DT, Glenny D, et al. 2003. The contribution of bryophytes to the carbon exchange for a temperate rainforest. Global Change Biology 9(8): 1158–1170.

Denelle P, Weigelt P, Kreft H 2023. GIFT: an R package to access the Global Inventory of Floras and Traits. Methods in Ecology and Evolution 14(11): 2738–2748.

Department of Conservation 2019. Field protocols for DOC Tier 1 Inventory & Monitoring and LUCAS plots. Wellington, Department of Conservation.

Department of Conservation 2020. Field protocols for Tier 1 monitoring – invasive mammal, bird, bat, RECCE surveys. Wellington, Department of Conservation.

Dickie IA, Cooper JA, Bufford JL, Hulme PE, Bates ST 2017. Loss of functional diversity and network modularity in introduced plant–fungal symbioses. AoB Plants 9(1): plw084.

Duncan RP, Webster RJ, Jensen CA 2001. Declining plant species richness in the tussock grasslands of Canterbury and Otago, South Island, New Zealand. New Zealand Journal of Ecology 25(2): 35–47.

Dykes RC, Brook MS, Robertson CM, Fuller IC 2011. Twenty-first century calving retreat of Tasman Glacier, Southern Alps, New Zealand. Arctic, Antarctic, and Alpine Research 43(1): 1–10.

Ewers RM, Kliskey AD, Walker S, Rutledge D, Harding JS, Didham RK 2006. Past and future trajectories of forest loss in New Zealand. Biological Conservation 133(3): 312–325.

Fahey B, Payne J 2017. The Glendhu experimental catchment study, upland east Otago, New Zealand: 34 years of hydrological observations on the afforestation of tussock grasslands. Hydrological Processes 31(16): 2921–2934.

Fenner M, Lee WG, Duncan SJ 1993. Chemical features of *Chionochloa* species in relation to grazing by ruminants in South Island, New Zealand. New Zealand Journal of Ecology 17(1): 35–40.

Ferguson AV, Pharo EJ, Kirkpatrick JB, Marsden-Smedley JB 2009. The early effects of fire and grazing on bryophytes and lichens in tussock grassland and hummock sedgeland in north-eastern Tasmania. Australian Journal of Botany 57(7): 556–561.

Fife AJ 2020. Flora of New Zealand: mosses. Fascicle 47, Mielichhoferiaceae. Lincoln, Manaaki Whenua Press.

Fischer HS 2015. On the combination of species cover values from different vegetation layers. Applied Vegetation Science 18(1): 169–170.

Fox J, Weisberg S 2019. An R companion to applied regression (3rd edn). Sage.

Galloway DJ, Ledingham J 2006. Additional lichen records from New Zealand 48. *Umbilicaria deusta*. Australasian Lichenology 70: 14–16.

González AL, Kominoski JS, Danger M, Ishida S, Iwai N, Rubach A 2010. Can ecological stoichiometry help explain patterns of biological invasions? Oikos 119(5): 779–790.

Gross N, Boerger L, Duncan RP, Hulme PE 2013. Functional differences between alien and native species: do biotic interactions determine the functional structure of highly invaded grasslands? Functional Ecology 27(5): 1262–1272.

Gross N, Liancourt P, Butters R, Duncan RP, Hulme PE 2015. Functional equivalence, competitive hierarchy and facilitation determine species coexistence in highly invaded grasslands. New Phytologist 206(1): 175–186.

Harrell FE 2021. Hmisc: Harrell Miscellaneous. R package version 4.6-0.

Hawcroft A, Bellingham PJ, Jo I, Richardson SJ, Wright EF 2024. Are populations of trees threatened by non-native herbivorous mammals more secure in New Zealand's national parks? Biological Conservation 295: 110637.

Heenan PB, McCarthy JK, Richardson SJ, McGlone MS 2021. Phylogenetic diversity and clustering in modern vegetation communities reflects habitat formation and age during the late Cenozoic in New Zealand. Botanical Journal of the Linnean Society 198(3): 241–258.

Heenan PB, McGlone MS 2013. Evolution of New Zealand alpine and open-habitat plant species during the late Cenozoic. New Zealand Journal of Ecology 37(1): 105–113.

Holdaway RJ, Easdale TA, Carswell FE, Richardson SJ, Peltzer DA, Mason NWH, et al. 2017. Nationally representative plot network reveals contrasting drivers of net biomass change in secondary and old-growth forests. Ecosystems 20(5): 944–959.

Hurst JM, Allen RB, Fergus AJ 2022. The Recce method for describing New Zealand vegetation: field manual. Lincoln, NZ, Manaaki Whenua – Landcare Research.

Husheer SW, Moore SH 2024. The shifting floristic complexion of Molesworth. New Zealand Journal of Ecology 48(1): 3565.

Jo I, Bellingham PJ, Mason NWH, McCarthy JK, Peltzer DA, Richardson SJ, et al. 2024. Disturbance-mediated community characteristics and anthropogenic pressure intensify understorey plant invasions in natural forests. Journal of Ecology, 1–16, https://doi.org/10.1111/1365-2745.14367.

Kandziora M, Burkhard B, Müller F 2013. Interactions of ecosystem properties, ecosystem integrity and ecosystem service indicators: a theoretical matrix exercise. Ecological Indicators 28: 54–78.

Kaufmann MR, Weatherred JD 1982. Determination of potential direct beam solar irradiance. Fort Collins, Colorado, USA, Forest Service, US Dept. of Agriculture.

Keegan LJ, White RS, Macinnis-Ng C 2022. Current knowledge and potential impacts of climate change on New Zealand’s biological heritage. New Zealand Journal of Ecology 46(1): 1–24.

Kentjens W, Glenny D, Curran TJ, Sullivan JJ 2023. Bryophyte community composition is influenced by microhabitat and cover of vascular plants and lichens in New Zealand montane forest. New Zealand Journal of Botany: 1-24, https://doi.org/10.1080/0028825X.2023.2284205.

Keser LH, Visser EJW, Dawson W, Song Y-B, Yu F-H, Fischer M, et al. 2015. Herbaceous plant species invading natural areas tend to have stronger adaptive root foraging than other naturalized species. Frontiers in Plant Science 6: 273.

Knight A 2014. Lichens of New Zealand: an introductory illustrated guide. Dunedin, NZ, Botanical Society of Otago.

Koenker R 2023. quantreg: quantile regression. R package version 5.97.

Laliberté E, Norton DA, Scott D 2013. Contrasting effects of productivity and disturbance on plant functional diversity at local and metacommunity scales. Journal of Vegetation Science 24(5): 834–834.

Laliberté E, Shipley B, Norton DA, Scott D 2012. Which plant traits determine abundance under long-term shifts in soil resource availability and grazing intensity? Journal of Ecology 100(3): 662–677.

Land Information New Zealand 2024. New Zealand road, river and track centrelines (Topo, 1:50k). https://data.linz.govt.nz/layer/50327-nz-river-centrelines-topo-150k/

Leathwick JR 1995. Climatic relationships of some New Zealand forest tree species. Journal of Vegetation Science 6(2): 237–248.

Ledgard N 2001. The spread of lodgepole pine (*Pinus contorta*, Dougl.) in New Zealand. Forest Ecology and Management 141(1): 43–57.

Levine J, Adler P, Yelenik S 2004. A meta analysis of biotic resistance to exotic plant invasions. Ecology Letters 7(10): 975–989.

Lindenmayer DB, Likens GE, Andersen A, Bowman D, Bull CM, Burns E, et al. 2012. Value of long-term ecological studies. Austral Ecology 37(7): 745–757.

Lloyd KM, Pollock ML, Mason NWH, Lee WG 2010. Leaf trait-palatability relationships differ between ungulate species: evidence from cafeteria experiments using naive tussock grasses. New Zealand Journal of Ecology 34(2): 219–226.

LRIS Portal 2020. Potential vegetation of New Zealand. https://lris.scinfo.org.nz/layer/48289-potential-vegetation-of-new-zealand/.

Manaaki Whenua – Landcare Research 2020. LCDB v5.0 – Land Cover Database version 5.0, Mainland New Zealand. https://lris.scinfo.org.nz/layer/104400-lcdb-v50-land-cover-database-version-50-mainland-new-zealand/ (accessed 30 January 2020).

Manaaki Whenua — Landcare Research 2024. Biota of New Zealand. https://biotaNZ.landcareresearch.co.nz (accessed February 2024).

Marburg AE, Allen RB 2010. Background to the Department of Conservation’s business case for implementing an Inventory and Monitoring programme. Manaaki Whenua – Landcare Research Contract Report: LC1732.

Mark AF 2012. Above the treeline: a nature guide to alpine New Zealand. Nelson, NZ, Craig Potton Publishing.

Mark AF, Dickinson KJM 2003. Temporal responses over 30 years to removal of grazing from a mid-altitude snow tussock grassland reserve, Lammerlaw Ecological Region, New Zealand. New Zealand Journal of Botany 41(4): 655–667.

Mark AF, Dickinson KJM, Hofstede RGM 2000. Alpine vegetation, plant distribution, life forms, and environments in a perhumid New Zealand region: oceanic and tropical high mountain affinities. Arctic, Antarctic, and Alpine Research 32(3): 240–254.

Mark AF, McLennan B 2005. The conservation status of New Zealand's indigenous grasslands. New Zealand Journal of Botany 43(1): 245–270.

Mason NWH, Holdaway RJ, Richardson SJ 2018. Incorporating measurement error in testing for changes in biodiversity. Methods in Ecology and Evolution 9(5): 1296–1307.

McCarthy JK, Leathwick JR, Roudier P, Barringer JRF, Etherington TR, Morgan FJ, et al. 2021. New Zealand Environmental Data Stack (NZEnvDS): a standardised collection of environmental spatial layers for biodiversity modelling and site characterisation. New Zealand Journal of Ecology 45(2): 3440.

McGlone M 1989. The Polynesian settlement of New Zealand in relation to environmental and biotic changes. New Zealand Journal of Ecology 12 (Supplement): 115–129.

McGlone MS 2001. The origin of the indigenous grasslands of southeastern South Island in relation to pre-human woody ecosystems. New Zealand Journal of Botany 25(1): 1–15.

McGlone MS, McNutt K, Richardson SJ, Bellingham PJ, Wright EF 2020. Biodiversity monitoring, ecological integrity, and the design of the New Zealand Biodiversity Assessment Framework. New Zealand Journal of Ecology 44(2): 3411.

McGlone MS, Richardson SJ 2023. Sexual systems in the New Zealand angiosperm flora. New Zealand Journal of Botany 61(4): 201–231.

McGlone MS, Richardson SJ, Jordan GJ 2010. Comparative biogeography of New Zealand trees: species richness, height, leaf traits and range sizes. New Zealand Journal of Ecology 34(1): 137–151.

McGlone MS, Wilmshurst JM 1999. A Holocene record of climate, vegetation change and peat bog development, east Otago, South Island, New Zealand. Journal of Quaternary Science 14(3): 239–254.

McNab WH 1993. A topographic index to quantify the effect of mesoscale landform on site productivity. Canadian Journal of Forest Research 23(6): 1100–1107.

Meudt HM, Prebble JM, Lehnebach CA 2015. Native New Zealand forget-me-nots (*Myosotis*, Boraginaceae) comprise a Pleistocene species radiation with very low genetic divergence. Plant Systematics and Evolution 301: 1455–1471.

MfE Data Service 2012. Environmental limiting factors. https://data.mfe.govt.nz/layer/52374-environmental-limiting-factors-2012/.

Michel P, Overton JM, Mason NWH, Hurst JM, Lee WG 2011. Species–environment relationships of mosses in New Zealand indigenous forest and shrubland ecosystems. Plant Ecology 212(3): 353–367.

Michel P, Payton IJ, Lee WG, During HJ 2013. Impact of disturbance on above-ground water storage capacity of bryophytes in New Zealand indigenous tussock grassland ecosystems. New Zealand Journal of Ecology 37(1): 114–126.

Mills JA, Lee WG, Lavers RB 1989. Experimental Investigations of the effects of takahe and deer grazing on *Chionochloa pallens* grassland, Fiordland, New Zealand. Journal of Applied Ecology 26(2): 397–417.

Moloney PD, Forsyth DM, Ramsey DSL, Perry M, McKay M, Gormley AM, et al. 2021. Occupancy and relative abundances of introduced ungulates on New Zealand's public conservation land 2012–2018. New Zealand Journal of Ecology 45(1): 3437.

Morrison LW, Leis SA, Short MF, DeBacker MD 2024. A spatiotemporal comparison of interobserver error in vegetation sampling. Journal of Vegetation Science 35(4): e13286.

Newsome P, Shepherd J, Meurk C, Smale M, Sutherland A, Heke H, et al. 2011. Environmental limiting factors and tree line. Wellington, Ministry for the Environment.

Nielsen JA, Whigham PA, Frew RD, Callaway R, Dickinson KJM 2015. Thyme and space invasion: *Thymus vulgaris* decreases exotic plant species diversity in Central Otago, New Zealand. Biological Invasions 17(8): 2261–2274.

Norbury G, Byrom A, Pech R, Smith J, Clarke D, Anderson D, et al. 2013. Invasive mammals and habitat modification interact to generate unforeseen outcomes for indigenous fauna. Ecological Applications 23(7): 1707–1721.

NZPCN 2024. New Zealand Plant Conservation Network. https://www.nzpcn.org.nz/ (accessed February 2024).

O'Donnell CF, Weston KA, Monks JM 2017. Impacts of introduced mammalian predators on New Zealand's alpine fauna. New Zealand Journal of Ecology 41(1): 1–22.

Oksanen J, Blanchet FG, Friendly M, Kindt R, Legendre P, McGlinn D, et al. 2019. vegan: community ecology package. R package version 2.5-6. https://CRAN.R-project.org/package=vegan.

Orwin J 1970. Lichen succession on recently deposited rock surfaces. New Zealand Journal of Botany 8(4): 452–477.

Payton IJ, Newell CL, Beets PN 2004. New Zealand Carbon Monitoring System: indigenous forest and shrubland data collection manual. Christchurch, NZ, Caxton Press.

Pecl GT, Araújo MB, Bell JD, Blanchard J, Bonebrake TC, Chen I-C, et al. 2017. Biodiversity redistribution under climate change: impacts on ecosystems and human well-being. Science 355(6332): eaai9214.

Peltzer DA 2018. Ecology and consequences of invasion by non-native (wilding) conifers in New Zealand. Journal of New Zealand Grasslands 80: 39–46.

Perry GLW, Wilmshurst JM, McGlone MS 2014. Ecology and long-term history of fire in New Zealand. New Zealand Journal of Ecology 38(2): 157–176.

Perry GLW, Wilmshurst JM, McGlone MS, McWethy DB, Whitlock C 2012b. Explaining fire-driven landscape transformation during the Initial Burning Period of New Zealand's prehistory. Global Change Biology 18(5): 1609–1621.

Perry GLW, Wilmshurst JM, McGlone MS, Napier A 2012a. Reconstructing spatial vulnerability to forest loss by fire in pre-historic New Zealand. Global Ecology and Biogeography 21(10): 1029–1041.

Pharo EJ, Beattie AJ 1997. Bryophyte and lichen diversity: a comparative study. Australian Journal of Ecology 22(2): 151–162.

Pharo EJ, Kirkpatrick JB, Gilfedder L, Mendel L, Turner PAM 2005. Predicting bryophyte diversity in grassland and eucalypt-dominated remnants in subhumid Tasmania. Journal of Biogeography 32(11): 2015–2024.

Plummer M 2003. JAGS: a program for analysis of Bayesian graphical models using Gibbs sampling. In: Hornik K, Leisch F, Zeileis A eds. Proceedings of the 3rd international workshop on distributed statistical computing. Vienna, Austria. http://www.R-project.org/conferences/DSC-2003/.

R Development Core Team 2023. R: s language and environment for statistical computing, v. 4.3.2. Vienna, Austria, R Foundation for Statistical Computing. http://www.r-project.org.

Richardson SJ, Hayman E, Rossignaud L, Jo I, Peltzer DA, Bellingham PJ 2024. Prioritising regional-scale permanent forest plot networks. Manaaki Whenua – Landcare Research Contract Report LC4459.

Rolfe JR, Fife AJ, Beever J, Brownsey PJ, Hitchmough R 2016. Conservation status of New Zealand mosses, 2014. Wellington, Department of Conservation.

Rose A, Basher L, Wiser S, Platt K, Lynn I 1998. Factors predisposing short-tussock grasslands to *Hieracium* invasion in Marlborough, New Zealand. New Zealand Journal of Ecology 22(2): 121–140.

Rose A, Platt K, Frampton C 1995. Vegetation change over 25 years in a New Zealand short-tussock grassland: effects of sheep grazing and exotic invasions. New Zealand Journal of Ecology 19(2): 163–174.

Rose AB, Allen R 1990. Impact of Himalayan thar on vegetation of the North Branch, Godley Valley, Canterbury. Forest Research Institute contract report FWE 90/32.

Rose AB, Frampton CM 2007. Rapid short-tussock grassland decline with and without grazing, Marlborough, New Zealand. New Zealand Journal of Ecology 31(2): 232–244.

Rossignaud L, Kimberley MO, Kelly D, Fei S, Brockerhoff EG 2022. Effects of competition and habitat heterogeneity on native-exotic plant richness relationships across spatial scales. Diversity and Distributions 28(5): 1093–1104.

Santi C, Bogusz D, Franche C 2013. Biological nitrogen fixation in non-legume plants. Annals of Botany 111(5): 743–767.

Scott NA, Saggar S, McIntosh PD 2001. Biogeochemical impact of Hieracium invasion in New Zealand's grazed tussock grasslands: sustainability implications. Ecological Applications 11(5): 1311–1322.

Smithson M, Verkuilen J 2006. A better lemon squeezer? Maximum-likelihood regression with beta-distributed dependent variables. Psychological Methods 11(1): 54–71.

Speed JDM, Austrheim G, Bendiksby M, Kolstad AL, Vuorinen KEM 2020. Increasing Cervidae populations have variable impacts on habitat suitability for threatened forest plant and lichen species. Forest Ecology and Management 473: 118286.

Street LE, Subke J-A, Sommerkorn M, Sloan V, Ducrotoy H, Phoenix GK, et al. 2013. The role of mosses in carbon uptake and partitioning in arctic vegetation. New Phytologist 199(1): 163–175.

Su Y-S, Yajima M 2021. R2jags: using R to run 'JAGS', R package version 0.7-1. https://cran.r-project.org/web/packages/R2jags.

Swets JA 1988. Measuring the accuracy of diagnostic systems. Science 240(4857): 1285–1293.

Tamme R, Götzenberger L, Zobel M, Bullock JM, Hooftman DAP, Kaasik A, et al. 2014. Predicting species' maximum dispersal distances from simple plant traits. Ecology 95(2): 505–513.

Tanentzap AJ, Burrows LE, Lee WG, Nugent G, Maxwell JM, Coomes DA 2009. Landscape-level vegetation recovery from herbivory: progress after four decades of invasive red deer control. Journal of Applied Ecology 46(5): 1064–1072.

Tierney D 2024. Tracking ecosystem decline in an uncertain and changing alpine landscape. Austral Ecology 49(7): e13528.

Turner MG 1989. Landscape ecology: the effect of pattern on process. Annual Review of Ecology and Systematics 20(1): 171–197.

Vavra M, Parks CG, Wisdom MJ 2007. Biodiversity, exotic plant species, and herbivory: the good, the bad, and the ungulate. Forest Ecology and Management 246(1): 66–72.

Venter S 2021. A taxonomic revision of the Australasian genera *Dracophyllum* and *Richea* (Richeeae: Styphelioideae: Ericaceae). Australian Systematic Botany 34(2): 1–205.

Vilà M, Espinar JL, Hejda M, Hulme PE, Jarošík V, Maron JL, et al. P 2011. Ecological impacts of invasive alien plants: a meta analysis of their effects on species, communities and ecosystems. Ecology Letters 14: 702–708.

Wagstaff SJ, Garnock-Jones PJ 1998. Evolution and biogeography of the *Hebe* complex (Scrophulariaceae) inferred from ITS sequences. New Zealand Journal of Botany 36(3): 425–437.

Walker S, Lee WG 2002. Alluvial grasslands of Canterbury and Marlborough, eastern South Island, New Zealand: vegetation patterns and long-term change. Journal of the Royal Society of New Zealand 32(1): 113–147.

Wardle J, Hayward J 1970. The forests and scrublands of the Taramakau and the effects of browsing by deer and chamois. Proceedings New Zealand Ecological Society(17): 80–91.

Wardle P 1991. Vegetation of New Zealand. Cambridge, Cambridge University Press.

Wardle P 2008. New Zealand forest to alpine transitions in global context. Arctic, Antarctic, and Alpine Research 40(1): 240–249.

Watkins RL, Cocklin C, Laituri M 1997. The use of Geographic Information Systems for resource evaluation: a New Zealand example. Journal of Environmental Planning and Management 40(1): 37–58.

Watt AS 1960. The effect of excluding rabbits from acidiphilous grassland in breckland. Journal of Ecology 48(3): 601–604.

Weigelt P, König C, Kreft H 2020. GIFT: a global inventory of floras and traits for macroecology and biogeography. Journal of Biogeography 47(1): 16–43.

Whinam J, Hope GS, Clarkson BR, Buxton RP, Alspach PA, Adam P 2003. *Sphagnum* in peatlands of Australasia: their distribution, utilisation and management. Wetlands Ecology and Management 11(1-2): 37–49.

Williams P, Mugambe S, Nes P, O'Connor K 1978. Macro-element composition of tall-tussocks (*Chionochloa*) in the South Island, New Zealand, and their relationship with soil chemical properties. New Zealand Journal of Botany 16(4): 479–498.

Wilson HD 1976. Vegetation of the Mount Cook National Park, New Zealand. National Parks Authority Scientific Series No. 1. Department of Lands and Survey, Wellington.

Wilson JB, Gitay H 1999. Alternative classifications in the intrinsic guild structure of a New Zealand tussock grassland. Oikos 86(3): 566–572.

Wilson JB, Meurk CD 2011. The control of community composition by distance, environment and history: a regional-scale study of the mountain grasslands of southern New Zealand. Journal of Biogeography 38(12): 2384–2396.

Wright EF, Bellingham PJ, Richardson SJ, McKay M, MacLeod CJ, McGlone MS 2020. How to get a national biodiversity monitoring programme off the ground: lessons from New Zealand. Parks 26(2): 67–78.

Wurtzebach Z, Schultz C 2016. Measuring ecological integrity: history, practical applications, and research opportunities. BioScience 66(6): 446–457.

Xie Y, Hirabayashi S, Hashimoto S, Shibata S, Kang J 2023. Exploring the spatial pattern of urban forest ecosystem services based on i-Tree Eco and spatial interpolation: a case study of Kyoto City, Japan. Environmental Management 72(5): 991–1005.

Yoccoz NG, Delestrade A, Loison A 2010. Impact of climatic change on alpine ecosystems: inference and prediction. Journal of Alpine Research 98(4): 1293.

Zhang J, Guo W, Wang Y, Tang Z, Qi L 2024. Identifying the regional spatial management of ecosystem services from a supply and demand perspective: a case study of Danjiangkou reservoir area, China. Ecological Indicators 158: 111421.

Appendix 1 – Summary of how the 33 land-cover classes from the Land Cover Data Base version 5 (LCDB v.5) were aggregated into six vegetation cover classes

LCDB v.5 cover class	Aggregated vegetation cover class	Abbreviation
Built-up Area (settlement)	Disturbed land	Dist
Surface Mine or Dump		
Transport Infrastructure		
Depleted Grassland	Non-native grassland	NnG
High Producing Exotic Grassland		
Low Producing Grassland		
Orchard, Vineyard or other Perennial Crop		
Short-rotation Cropland		
Urban Parkland/Open Space		
Deciduous Hardwoods	Non-native woody vegetation	NnW
Exotic Forest		
Forest – Harvested		
Gorse and/or Broom		
Mixed Exotic Shrubland		
Alpine Grass/Herbfield	Native grassland	NG
Fernland		
Flaxland		
Herbaceous Freshwater Vegetation		
Herbaceous Saline Vegetation		
Tall Tussock Grassland		
Estuarine Open Water	Non-vegetated land	Nnveg
Gravel or Rock		
Lake or Pond		
Landslide		
Permanent Snow and Ice		
River		
Sand or Gravel		
Broadleaved Indigenous Hardwoods	Native woody vegetation	NW
Indigenous Forest		
Mangrove		
Mānuka and/or Kānuka		
Matagouri or Grey Scrub		
Sub Alpine Shrubland		

Source: Rossignaud et al. 2022.

Appendix 2 – Statistical outputs from the analyses of non-vascular plant communities

Table A1. Correlation table including a first subset of the variables considered for the analysis predicting bryophyte or lichen richness and cover (*n* = 116 plots)

	Bryophyte richness	Lichen richness	Bryophyte cover	Lichen cover	Elevation	Mean top height	Easting (NZTM)	Northing (NZTM)	MAP	MAT
Bryophyte richness	-	0.46	0.56	0.27	–0.16	0.13	–0.43	–0.33	0.35	–0.02
Lichen richness	0.000	-	0.16	**0.70**	–0.10	0.06	–0.20	–0.25	–0.05	–0.02
Bryophyte cover	0.000	0.081	-	0.25	–0.12	–0.02	–0.23	–0.17	0.16	0.00
Lichen cover	0.003	0.000	0.007	-	0.11	–0.06	–0.10	–0.17	–0.09	–0.18
Elevation	0.090	0.308	0.210	0.231	-	–0.24	–0.04	–0.19	0.20	**–0.94**
Mean top height	0.171	0.545	0.799	0.558	0.010	-	0.23	0.25	–0.01	0.29
Easting	0.000	0.030	0.013	0.268	0.651	0.013	-	**0.90**	–0.25	0.32
Northing	0.000	0.006	0.068	0.068	0.044	0.006	0.000	-	–0.09	0.48
MAP	0.000	0.611	0.080	0.348	0.035	0.936	0.006	0.316	-	–0.21
MAT	0.832	0.835	0.972	0.061	0.000	0.001	0.000	0.000	0.026	-
Rocky cover	0.016	0.065	0.011	0.570	0.000	0.336	0.730	0.228	0.125	0.000
Landform index	0.000	0.550	0.134	0.782	0.007	0.905	0.021	0.009	0.000	0.001
Solar radiation	0.224	0.671	0.329	0.743	0.985	0.692	0.577	0.760	0.514	0.974
Hare FPI	0.008	0.813	0.135	0.148	0.776	0.311	0.458	0.713	0.000	0.949
Rabbit FPI	0.430	0.599	0.368	0.933	0.495	0.867	0.387	0.250	0.072	0.613
Ungulate FPI	0.559	0.552	0.564	0.487	0.304	0.518	0.781	0.908	0.093	0.301
Total vascular richness	0.000	0.000	0.000	0.000	0.044	0.891	0.001	0.001	0.126	0.605
Total vascular cover	0.000	0.000	0.008	0.023	0.000	0.065	0.797	0.706	0.158	0.000
Weed cover	0.043	0.789	0.042	0.079	0.000	0.018	0.018	0.123	0.001	0.000
Native cover	0.000	0.000	0.000	0.002	0.000	0.136	0.224	0.796	0.878	0.001

Notes: MAP = mean annual precipitation; MAT = mean annual temperature; FPI = faecal pellet indices. Correlation values can be found above the diagonal delimiter (-) and associated *P* values below the diagonal delimiter (-). In bold, correlation values ≥0.7 or <–0.7.

Table A2. Correlation table including the second subset of variables considered for the analysis predicting bryophyte or lichen richness and cover (*n* = 116 plots).

	Rocky Cover	Landform Index	Solar radiation	Hare FPI	Rabbit FPI	Ungulate FPI	Vascular Richness	Vascular Cover	Weed cover	Native cover
Bryophyte richness	–0.22	0.34	0.11	–0.24	–0.07	–0.06	0.61	0.36	–0.19	0.46
Lichen richness	–0.17	0.06	–0.04	0.02	0.05	0.06	0.45	0.33	–0.03	0.35
Bryophyte cover	–0.24	0.14	0.09	–0.14	–0.08	–0.05	0.37	0.25	–0.19	0.34
Lichen cover	–0.05	0.03	0.03	0.14	–0.01	0.07	0.35	0.21	–0.16	0.29
Elevation	0.59	0.25	0.00	0.03	–0.06	–0.10	–0.19	–0.56	–0.50	–0.37
Mean top height	–0.09	–0.01	0.04	–0.10	–0.02	–0.06	–0.01	0.17	0.22	0.14
Easting (NZTM)	–0.03	–0.22	–0.05	0.07	–0.08	0.03	–0.31	–0.02	0.22	–0.11
Northing (NZTM)	–0.11	–0.24	–0.03	–0.03	–0.11	–0.01	–0.30	0.04	0.14	–0.02
MAP	0.14	0.40	0.06	–0.44	–0.17	–0.16	0.14	–0.13	–0.32	–0.01
MAT	–0.54	–0.30	0.00	0.01	0.05	0.10	0.05	0.51	0.51	0.31
Rocky cover	-	0.21	–0.01	–0.10	–0.07	–0.05	–0.38	**–0.80**	–0.33	**–0.70**
Landform index	0.027	-	0.03	–0.13	0.00	–0.08	0.22	–0.09	–0.24	0.00
Solar radiation	0.875	0.722	-	–0.03	–0.14	0.05	–0.10	0.04	–0.12	0.10
Hare FPI	0.268	0.177	0.728	-	0.13	0.39	0.13	0.16	0.25	0.06
Rabbit FPI	0.479	0.976	0.124	0.152	-	0.04	0.02	0.10	0.24	0.04
Ungulate FPI	0.604	0.418	0.574	0.000	0.676	-	0.09	0.13	0.29	–0.05
Total vascular richness	0.000	0.021	0.296	0.180	0.868	0.341	-	0.61	0.04	0.61
Total vascular cover	0.000	0.318	0.664	0.085	0.270	0.152	0.000	-	0.35	**0.88**
Weed cover	0.000	0.011	0.206	0.007	0.009	0.002	0.679	0.000	-	–0.10
Native cover	0.000	0.976	0.281	0.513	0.639	0.579	0.000	0.000	0.312	-

Notes: MAP = mean annual precipitation; MAT = mean annual temperature; FPI = faecal pellet indices. Correlation values can be found above (-) and associated *P* values bellow (-). In bold, correlation values ≥0.7 or ≤-0.7.

Table A3. The 37 non-vascular species significantly driving differences of community across plots included in the non-metric multi-dimensional scaling (NMDS), with taxon and major group classification, coordinates of the projection of each non-vascular species (dimension 1: NMDS1, dimension 2: NMDS2), their goodness of fit (R2), and P values

NVS Code	Species name	Taxon group	Major group	NMDS1	NMDS2	R^2	*P*
SPHCRI	*Sphagnum cristatum*	Bryophyte	Moss	–0.976	0.220	0.26	0.001
HETCIL	*Heteroscyphus ciliatus*	Bryophyte	Liverwort	–0.955	0.297	0.10	0.003
LEITEN	*Leifidium tenerum*	Lichen	Fruticose	–0.946	0.324	0.06	0.042
DICBIL	*Dicranoloma billardierei*	Bryophyte	Moss	–0.929	0.369	0.06	0.042
BREPEN	*Breutelia pendula*	Bryophyte	Moss	–0.894	–0.448	0.07	0.011
DICROB	*Dicranoloma robustum*	Bryophyte	Moss	–0.893	0.451	0.14	0.001
CAMINT	*Campylopus introflexus*	Bryophyte	Moss	–0.888	0.459	0.10	0.003
SIPDEC	*Siphula decumbens*	Lichen	Foliose	–0.845	0.534	0.06	0.025
DISPUL	*Distichophyllum pulchellum*	Bryophyte	Moss	–0.840	0.543	0.06	0.04
RICCRA	*Riccardia crassa*	Bryophyte	Liverwort	–0.826	0.563	0.18	0.001
KURHIP	*Kurzia hippuroides*	Bryophyte	Liverwort	–0.767	0.641	0.13	0.003
SIPFAS	*Siphula fastigiata*	Lichen	Unknown	–0.747	0.665	0.09	0.01
RADSAI	*Radula sainsburiana*	Bryophyte	Liverwort	–0.739	0.674	0.06	0.037
RHAPUR	*Rhacocarpus purpurascens*	Bryophyte	Moss	–0.706	0.708	0.17	0.001
SYZSON	*Syzygiella sonderi*	Bryophyte	Liverwort	–0.649	0.761	0.09	0.005
LEPOBT	*Lepidozia obtusiloba*	Bryophyte	Liverwort	–0.626	0.780	0.06	0.021
ISOMON	*Isotachis montana*	Bryophyte	Liverwort	–0.554	0.833	0.06	0.043
CHISEM	*Chiloscyphus semiteres*	Bryophyte	Liverwort	–0.473	–0.881	0.16	0.001
THUFUF	*Thuidiopsis furfurosa*	Bryophyte	Moss	–0.427	–0.904	0.17	0.001
RACSTR	*Racomitrium striatipilum*	Bryophyte	Moss	–0.292	0.956	0.06	0.033
HYPCUP	*Hypnum cupressiforme*	Bryophyte	Moss	–0.221	–0.975	0.09	0.01
HYPLUG	*Hypogymnia lugubris*	Lichen	Foliose	–0.195	0.981	0.11	0.002
EURPRA	*Eurhynchium praelongum*	Bryophyte	Moss	–0.086	–0.996	0.13	0.006
ANDACU	*Andreaea acutifolia*	Bryophyte	Moss	–0.058	0.998	0.14	0.001
RACCRI	*Racomitrium crispulum*	Bryophyte	Moss	–0.017	1.000	0.21	0.001
BLIROB	*Blindia robusta*	Bryophyte	Moss	0.057	0.998	0.06	0.041
BRAPAR	*Brachythecium paradoxum*	Bryophyte	Moss	0.249	–0.968	0.05	0.047
ANDAUS	*Andreaea australis*	Bryophyte	Moss	0.421	0.907	0.08	0.021
NOTAST	*Notoligotrichum australe*	Bryophyte	Moss	0.441	0.897	0.15	0.001
DICANT	*Dicranoweisia antarctica*	Bryophyte	Moss	0.450	0.893	0.12	0.001
TELVEL	*Teloschistes velifer*	Lichen	Fruticose	0.459	–0.888	0.07	0.044
POLJUN	*Polytrichum juniperinum*	Bryophyte	Moss	0.582	–0.813	0.13	0.001
CERPUR	*Ceratodon purpureus*	Bryophyte	Moss	0.619	–0.786	0.08	0.013
PSECRO	*Pseudocyphellaria crocata*	Lichen	Foliose	0.630	–0.776	0.06	0.043
BARPAP	*Bartramia papillata*	Bryophyte	Moss	0.749	0.663	0.28	0.001
RACPTY	*Racomitrium ptychophyllum*	Bryophyte	Moss	0.789	0.615	0.06	0.041
XANTHO	*Xanthoparmelia* species	Lichen	Foliose	0.868	–0.496	0.07	0.033

Notes: The NMDS was based on non-vascular species present in at least 4 plots (no. species = 149, no. plots = 116, stress = 0.14).

Table A4. Model selection process showing the 10 models with the lowest AICc from a combination of biotic and environmental variables: mean annual precipitation (MAP in mm), mean annual temperature (MAT in ˚C), elevation (m), ecosystem (deforested vs unforested), lichen or bryophyte richness (Lichen_Rich or Bryo_Rich) or cover (Lichen_Cov or Bryo_Cov, in proportion), weed cover (proportion), vascular plant cover (Vascular_Cov, in proportion), landform index, rocky cover (in %), solar radiation (solrad), Mean top height (in m), faecal pellet index (FPI), and interaction terms are denoted by ×.

Formula	Df	AICc	Delta
a) Bryophyte richness			
Ecosystem x Lichen_Rich + MAP + Elevation + Weed_cover + Vascular_Cov + Landform_Index	10	771.32	0
MAP + Elevation + Ecosystem + Lichen_Rich + Weed_cover + Vascular_Cov + Landform_Index	9	775.54	4.22
Ecosystem x Weed_cover + MAP + Elevation + Lichen_Rich + Vascular_Cov + Landform_Index	10	776.53	5.21
MAP + Elevation + Ecosystem + Lichen_Rich + Weed_cover + Vascular_Cov + Landform_Index + MeanTopHeight	10	776.56	5.24
Ecosystem x MAP + Elevation + Lichen_Rich + Weed_cover + Vascular_Cov + Landform_Index	10	777.19	5.87
MAP + Elevation + Ecosystem + Lichen_Rich + Weed_cover + Vascular_Cov + Landform_Index + (1| Year)	10	777.77	6.45
MAP + Elevation + Ecosystem + Lichen_Rich + Weed_cover + Vascular_Cov + Landform_Index + UngulateFPI	10	777.78	6.46
MAP + Elevation + Ecosystem + Lichen_Rich + Weed_cover + Vascular_Cov + Landform_Index + solrad + MeanTopHeight	11	779.01	7.69
MAP + Elevation + Ecosystem + Lichen_Rich + Weed_cover + Vascular_Cov + Landform_Index + HareFPI + UngulateFPI	11	779.81	8.49
MAP + Elevation + Ecosystem + Lichen_Rich + Weed_cover + Vascular_Cov	8	784.56	13.24
b) Bryophyte cover			
MAP + Lichen_Cov + Weed_cover + Vascular_Cov + Landform_Index	7	–243.37	0
MAP + Lichen_Cov + Weed_cover + Vascular_Cov	6	–243.09	0.28
MAP + Elevation + Lichen_Cov + Weed_cover + Vascular_Cov + Landform_Index	8	–242.98	0.39
MAP + Lichen_Cov + Weed_cover + Vascular_Cov + Rocky_Cover	7	–241.48	1.89
MAP + Elevation + Ecosystem + Lichen_Cov + Weed_cover + Vascular_Cov + Landform_Index	9	–240.64	2.73
MAP + Lichen_Cov + Weed_cover + Rocky_Cover	6	–240.59	2.78
MAP + Ecosystem + Lichen_Cov + Weed_cover + Rocky_Cover	7	–240.16	3.22
Ecosystem × Lichen_Cov + MAP + Weed_cover + Vascular_Cov + Landform_Index	9	–240.01	3.36
MAP + Ecosystem + Lichen_Cov + Weed_cover + Rocky_Cover + Vascular_Cov	8	–239.86	3.51
MAP + MAT + Ecosystem + Lichen_Cov + Weed_cover + Rocky_Cover	8	–239.67	3.7

Formula	**Df**	**AICc**	**Delta**
c) Lichen richness			
MAP + Bryo_Rich + Rocky_Cover + Vascular_Cov	6	664.7	0
MAP + Bryo_Rich + Vascular_Cov	5	665.01	0.31
Ecosystem x Rocky_Cover + MAP + Bryo_Rich + Vascular_Cov	8	666.18	1.48
MAP + Bryo_Rich + Weed_cover + Rocky_Cover + Vascular_Cov	7	666.55	1.85
Ecosystem × Bryo_Rich + MAP + Rocky_Cover + Vascular_Cov	8	667.62	2.92
Ecosystem × MAP + Bryo_Rich + Rocky_Cover + Vascular_Cov	8	667.86	3.15
MAP + Ecosystem + Bryo_Rich + Weed_cover + Rocky_Cover + Vascular_Cov	8	668.04	3.33
MAP + Ecosystem + Bryo_Rich + Weed_cover + Vascular_Cov	7	668.27	3.57
MAP + Elevation + Ecosystem + Bryo_Rich + Weed_cover + Vascular_Cov	8	669	4.29
MAP + Elevation + Ecosystem + Bryo_Rich + Weed_cover + Vascular_Cov + Landform_Index	9	670.81	6.11
d) Lichen cover			
MAP + MAT + Bryo_Cov + Weed_cover + Rocky_Cover + Vascular_Cov	8	–520.75	0
MAP + MAT + Ecosystem + Bryo_Cov + Weed_cover + Rocky_Cover + Vascular_Cov	9	–518.44	2.31
Ecosystem × Rocky_Cover + Bryo_Cov + MAP + MAT + Weed_cover + Vascular_Cov	10	–517.64	3.12
Ecosystem × Bryo_Cov + MAP + MAT + Weed_cover + Rocky_Cover + Vascular_Cov	10	–517.55	3.2
Ecosystem × MAP + MAT + Bryo_Cov + Weed_cover + Rocky_Cover + Vascular_Cov	10	–517.49	3.26
Ecosystem × Weed_cover + MAP + MAT + Bryo_Cov + Rocky_Cover + Vascular_Cov	10	–516.52	4.24
MAP + MAT + Ecosystem + Bryo_Cov + Weed_cover + Rocky_Cover + Vascular_Cov + MeanTopHeight	10	–516.04	4.71
MAP + Elevation + Bryo_Cov + Weed_cover + Rocky_Cover + Vascular_Cov	8	–515.75	5
MAP + MAT + Ecosystem + Bryo_Cov + Weed_cover + Rocky_Cover + Vascular_Cov + solrad + MeanTopHeight	11	–513.64	7.12
MAP + Elevation + Ecosystem + Bryo_Cov + Weed_cover + Vascular_Cov	8	–511.45	9.31

Table A5. Raw output from generalised linear models with the lowest AICc with bryophyte or lichen richness and cover predicted from mean annual precipitation (MAP in mm), mean annual temperature (MAT in ˚C), elevation (m), ecosystem (deforested vs unforested), lichen or bryophyte richness or cover (%), weed cover (%), vascular plant cover (vascular cover, in %), landform index, rocky cover (%), and interaction terms are denoted by ×.

Formula	**Estimate**	**Std. error**	**z value**	***P***
a) Bryophyte richness				
(Intercept)	0.99	0.36	2.74	0.01
MAP	<0.001	<0.001	1.69	0.09
Elevation	<0.001	<0.001	−2.80	0.01
Unforested	0.88	0.22	4.05	<0.001
Lichen richness	0.04	0.01	4.48	<0.001
Weed cover	−0.77	0.30	−2.60	0.01
Vascular cover	1.24	0.23	5.48	<0.001
Landform Index	0.03	0.01	2.56	0.01
Unforested × Lichen richness	−0.04	0.02	−2.60	0.01
*b) Bryophyte cover**				
(Intercept)	−3.08	0.29	−10.79	<0.001
MAP	<0.001	<0.001	2.60	0.009
Lichen cover	5.83	1.96	2.97	0.003
Weed cover	−0.77	0.38	−2.03	0.042
Vascular cover	1.10	0.28	3.91	<0.001
c) Lichen richness				
(Intercept)	0.86	0.40	2.16	0.031
MAP	<0.001	<0.001	−3.37	0.001
Bryophyte richness	0.03	0.01	4.51	<0.001
Rocky cover	0.004	0.003	1.58	0.113
Vascular cover	1.14	0.42	2.71	0.007
d) Lichen cover				
(Intercept)	−3.66	0.35	−10.35	<0.001
MAP	<0.001	<0.001	−2.29	0.022
MAT	−0.09	0.03	−3.10	0.002
Bryophyte cover	0.67	0.35	1.93	0.053
Weed cover	−0.61	0.30	−2.06	0.039
Rocky cover	0.005	0.003	1.99	0.047
Vascular cover	1.63	0.31	5.20	<0.001

Table A6. Model selection process showing the models predicting liverwort richness with the lowest AICc from a combination of biotic and environmental variables: mean annual precipitation (MAP in mm), elevation (m), ecosystem (deforested vs unforested), distance to the nearest river (DIST_River, km), weed cover (%), vascular plant cover (Vascular_Cov, %), landform index, rocky cover (%), ungulate or rabbit faecal pellet index (FPI) and interaction terms are denoted by ×.

Formula	Df	AICc	Delta
Ecosystem × DIST_River + MAP + Elevation + Exotic_cover + Vascular_Cov	9	552.97	0
Ecosystem × DIST_River + MAP + Elevation + Exotic_cover + Vascular_Cov + Landform_Index	10	555.13	2.16
Ecosystem × DIST_River + MAP + Elevation + Exotic_cover + Vascular_Cov + UngulateFPI + RabbitFPI	11	556.72	3.75
Ecosystem + MAP + Elevation + Exotic_cover + Vascular_Cov + Landform_Index + DIST_River	9	558.97	6.01
Ecosystem + MAP + Elevation + Exotic_cover + Vascular_Cov + Landform_Index	8	560.68	7.71
Ecosystem × Exotic_cover + MAP + Elevation + Exotic_cover + Vascular_Cov + Landform_Index	9	561.52	8.55
Ecosystem × MAP + Elevation + Exotic_cover + Vascular_Cov + Landform_Index	9	561.83	8.86

Table A7. Raw output from generalised linear models with the lowest AICc with liverwort richness predicted from mean annual precipitation (MAP in mm), elevation (m), ecosystem (deforested vs unforested), distance to the nearest river (Dist_River, km), weed cover (%), vascular plant cover (Vascular Cover, %) with (a) deforested ecosystem as a reference (or called intercept) and (b) unforested ecosystem as a reference and interaction terms are denoted by ×.

Formula	**Estimate**	**Std. error**	**z value**	***P***
a) Intercept: Unforested	1.38	0.88	1.56	0.12
Vascular cover	2.98	0.49	6.12	<0.001
MAP	<0.001	<0.001	3.17	0.002
Dist_River	1.09	0.91	1.19	0.23
Unforested	–0.34	0.35	–0.97	0.33
Unforested x Dist_River	–2.66	1.00	–2.65	0.01
Elevation	–0.002	<0.001	–4.29	<0.001
Weed cover	–3.09	0.63	–4.89	<0.001
b) Intercept: Deforested	1.03	0.78	1.33	0.18
Vascular cover	2.98	0.49	6.12	<0.001
MAP	<0.001	<0.001	3.17	0.002
Unforested x Dist_River	2.66	1.00	2.65	0.01
Unforested	0.34	0.35	0.97	0.33
Dist_River	–1.57	0.45	–3.48	<0.001
Elevation	–0.002	<0.001	–4.29	<0.001
Weed cover	–3.09	0.63	–4.89	<0.001