

Vegetation-environment relationships in the regenerating shrubland of Remus Hill, Cass, in the eastern South Island high country

Yinpeng Wang¹, Frank Ashwood¹  and Sarah V. Wyse^{1*} 

¹Te Kura Ngahere | School of Forestry, University of Canterbury, Private Bag 4800, Christchurch 8140, New Zealand

*Author for correspondence (Email: sarah.wyse@canterbury.ac.nz)

Published online: 16 September 2025

Abstract: This study investigated the composition and distribution of vegetation on Remus Hill, near Cass, in the eastern South Island, New Zealand. The area was deforested following human activity and converted to pasture, but after the cessation of grazing, shrubland communities are re-establishing. We explored the interactions between vegetation composition and distribution in relation to environmental factors such as soil characteristics and topography. We established 27 5 m × 5 m vegetation plots in a grid pattern across the site and collected soil samples for chemical and physical analyses. The results revealed three distinct vegetation clusters: *Discaria toumatou* and mixed grassland; *Veronica brachysiphon*, *Cytisus scoparius*, and *Leptospermum scoparium* mixed shrubland; and *D. toumatou*, *Corokia cotoneaster* mixed shrubland. Shrub cover was highest in the southeast-facing areas of the site. Exotic grasses such as *Agrostis capillaris* and *Dactylis glomerata* were dominant at the site, while the exotic shrub *Cytisus scoparius* was frequent. To prioritise the future restoration of native vegetation, it is essential to control invasive exotic plant species at this site.

Keywords: aspect; Cass Mountain Research Area (CMRA); environmental relationships; invasive species; soil nutrients; vegetation distribution; vegetation succession

Introduction

Human-induced fires have been a major cause of forest loss and vegetation change in New Zealand. In drier, lower-elevation areas, once closed forests have been converted to grasslands and shrublands, they rarely revert to their original state (McWethy et al. 2010; Perry et al. 2014). Restoring beech (Nothofagaceae) forests in the eastern South Island is challenging due to the dense swards of herbaceous vegetation that prevent seedling establishment and survival through competition (Ledgard & Davis 2004; Stevenson & Smale 2005).

The Cass area in the central South Island, New Zealand, was once extensively covered with *Fuscospora cliffortioides* forests, but after human arrival most of the forest was lost, leaving only a few remaining *F. cliffortioides* stands (Young et al. 2016). From the 1870s, efforts were made to improve the native grasslands and sow exotic pasture for sheep farming. After 1950, agricultural activities in the area became more intensive, with aerial top-dressing and over-sowing (Burrows 1977), although Young et al. (2016) suggest that the Cass Mountain Research Area (CMRA) in which this study occurred was never over-sown or top-dressed.

Within the CMRA lies the 70-hectare site of Remus Hill (Fig. 1). Grazing has now ceased entirely at this site and shrubland and grassland dominate the vegetation (Molloy 1964). Remus Hill is now the site of an active restoration project, initiated in 2022, that aims to restore *F. cliffortioides* forest (Evison & Wyse 2023). At this early stage of the

restoration, we wish to gain a comprehensive understanding of the existing plant ecology of Remus Hill. Specifically, we aim to (1) identify and classify the major vegetation communities of Remus Hill, (2) quantify topographic variables and chemical and physical properties of the soil at the site, and (3) assess the vegetation-environment relationships to reveal how these environmental factors influence the vegetation composition. The findings are expected to enhance ecological understanding of Remus Hill and provide scientific support for conservation and ecological projects within the area.

Methods

Study site

The elevation range of Remus Hill (43°02'S, 171°45'E) is 580 to 669 metres, with glacial activity being the primary factor influencing its landforms (Soons 1977). The parent material is greywacke from the Torlesse group, and the soil, formed from weathered greywacke, primarily consists of yellow-brown earth according to Cutler (1977), or Allophanic Brown soil following the New Zealand Soil Classification (Hewitt 2010). The annual precipitation in 2019 at Remus Hill was 1886 mm, with total rainfall in November and December reaching 799 mm (Etherington et al. 2022). The mean annual temperature was 11.2°C.

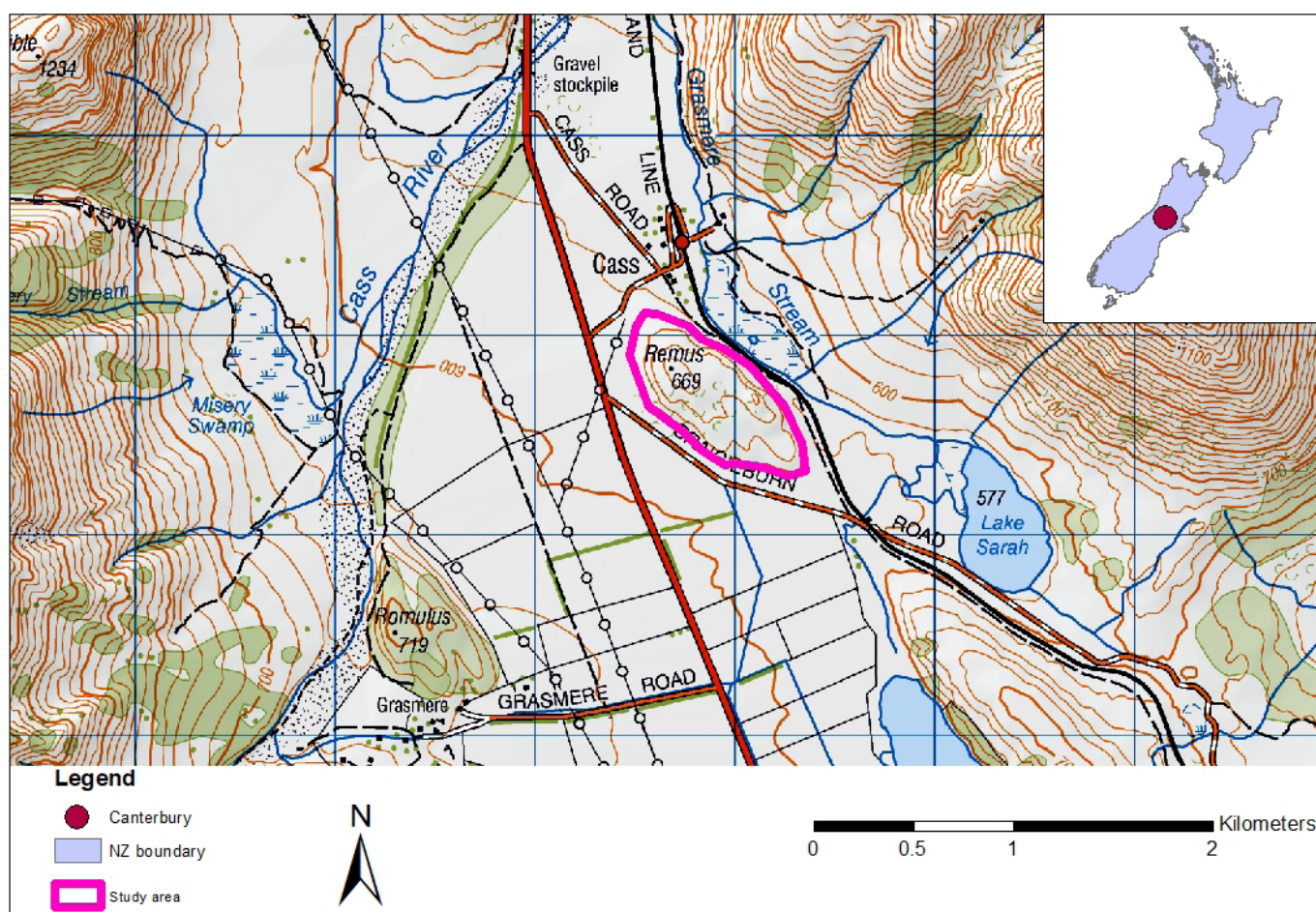


Figure 1: Map of the area surrounding Remus Hill at the Cass Mountain Research Area, and its location in New Zealand (inset).

Data collection

A 120 m × 120 m grid was applied over the area, with the grid intersections serving as plot locations. The 27 plots were 5 m × 5 m in size. The locations of three plots were adjusted due to inaccessibility caused by steep slopes or dense shrub cover, with a maximum displacement of no more than 50 metres (Fig. 2).

The field survey was conducted between April and May 2024, and followed the RECCE method (Hurst & Allen 2007). Within each RECCE plot, all observed plant species were recorded and categorised into six height tiers (5–12m, 2–5m, 1–2m, 0.3–1m, 0.1–0.3m, < 0.1m). For each plant species, cover-abundance was recorded using six cover classes (1 = < 1%, 2 = 1–5%, 3 = 6–25%, 4 = 26–50%, 5 = 51–75%, 6 = 76–100%).

Topographic data from “NZ Contours (Topo, 1:50k)” (LINZ 2024) were analysed using ArcMap 10.8.1 to obtain each plot’s elevation, slope, and aspect, cross-verifying the topographic data collected in the field survey. The recorded aspect was transformed into two variables: northness and eastness.

The methods for soil sampling and calculations for bulk density and moisture followed standard guidelines (Cools & De Vos 2016). In each plot two random points were selected, where a 50 mm diameter cylindrical corer was inserted to a depth of 10 cm to obtain a soil sample. In cases where the corer could not reach to 10 cm depth due to excessively stony

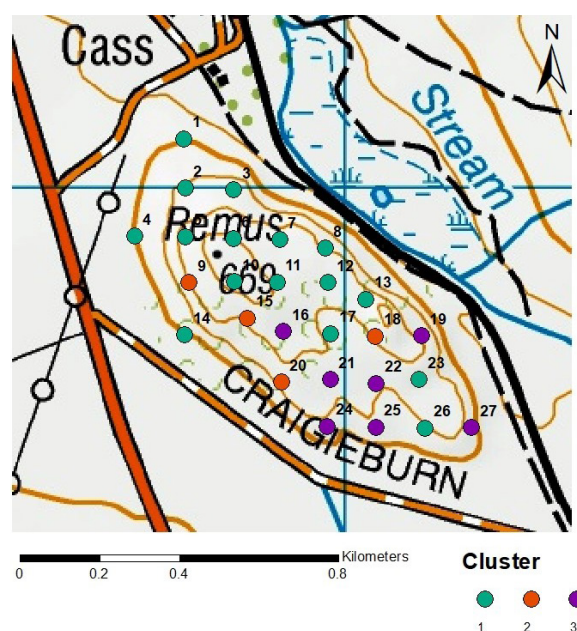


Figure 2: Plot locations at Remus Hill, with points in three different colours representing the three vegetation clusters. Cluster 1 = *Discaria toumatou* and mixed grassland; Cluster 2 = *Veronica brachysiphon*, *Cytisus scoparius*, and *Leptospermum scoparium* mixed shrubland; Cluster 3 = *Discaria toumatou* and *Corokia cotoneaster* mixed shrubland.

soil, the sample was taken to the maximum depth possible. These samples were used for both soil bulk density and soil moisture content analysis ($n = 54$ samples). Where soil bulk density samples had a coarse fragment content greater than 5%, a correction for the volume of coarse fragments in the case of stony soils was applied (Cools & De Vos 2016). Additionally, at each RECCE plot, three random points were selected, where a Dutch auger was inserted to a depth of 10 cm to obtain loose soil samples, which were combined into one sealed bag for subsampling for chemical analysis ($n = 27$ samples analysed in total). All sample bags were stored at a constant 4 °C prior to analysis. Soil chemical analysis was undertaken by Hill Labs (R J Hill Laboratories Limited) in Christchurch for the following parameters: pH, Olsen phosphorus (mg L^{-1}), potentially available nitrogen (%), anaerobically mineralisable nitrogen ($\mu\text{g g}^{-1}$), organic matter (%), total carbon (%), and total nitrogen (%).

Statistical Analysis

We followed previous authors' treatments of RECCE data and calculated vegetation importance values (IV) for each species per plot, which reflect the species' relative biomasses and the volume of the plot they occupy (Hall 1992; Burns & Leathwick 1996; Wiser et al. 2011; Wyse et al. 2014; Young et al. 2016). Importance values were calculated by multiplying the midpoint of each cover class (c_{ij}) by the upper limit of the tier height range (t_j). The values for a species across all tiers within a plot were summed to obtain IV_i (Burns & Leathwick 1996; Equation 1). The importance value was then log-transformed using $\log_{10}(IV_i + 1)$ to adjust the IV for subsequent analysis.

$$IV_i = \sum_{j=1}^7 (t_j \times c_{ij}) \quad (1)$$

Bray-Curtis dissimilarity was used to quantify differences between plots (Bray & Curtis 1957), and a hierarchical cluster analysis was conducted using Ward's minimum variance method (Ward Jr. 1963) to classify and group plots into discrete vegetation communities. Subsequently, the *metaMDS* function from the "vegan" library (Oksanen et al. 2019) was used to process and visualise the data through non-metric multi-dimensional scaling (nMDS). The *envfit* function from the "vegan" library was then used to assess relationships between the environmental vectors and the vegetation ordination.

Analysis of variance was used to evaluate differences in vegetation and environmental factors between clusters. For factors showing significant differences, Tukey's HSD test was applied for multiple comparisons to identify which clusters differed significantly from others.

To explore the relationships among environmental factors, between environmental factors and common plant species, and among plant species, Spearman's rank correlation analysis was used. We adjusted the resulting P-values to reduce the type-1 error rate using the Benjamini-Hochberg method (Benjamini & Hochberg 1995) via the *p.adjust* function in the "stats" package. The correlations were visualised by creating a heatmap with the "corrplot" package (Wei & Simko 2024), and significance testing was conducted. All analyses were conducted using R version 4.3.3 (R Core Team 2024).

Results

Vegetation composition

A total of 43 plant species were identified across the 27 plots (Table 1). Following the definitions of McGlone and Richardson (2023), who defined trees as woody species capable of reaching five metres in height, we recorded one tree (*L. scoparium*), 13 shrub species, four fern species, four vine species, seven grasses, ten herbs, and four mosses. There were 25 native and 18 exotic species, with native plants accounting for 58.1% of the species richness and 55.0% of the total (summed) IVs of all species. Ranked by their summed IV across all plots, the top ten species were *A. capillaris* (29.17), *D. toumatou* (26.61), *D. glomerata* (20.71), *Festuca novae-zelandiae* (19.73), *C. scoparius* (12.68), *L. scoparium* (10.66), *C. cotoneaster* (9.14), *Melicytus alpinus* (7.04), *Ozothamnus leptophyllus* (5.40), and *Veronica brachysiphon* (5.02).

Cluster analysis divided the plots into three clusters (Fig. 3). Cluster one ($n = 16$) can be characterised as "*D. toumatou* and mixed grassland", and represents the primary vegetation type of Remus Hill, predominantly distributed in the central and northern areas. Cluster one had the lowest species diversity. Shrubs were primarily represented by *D. toumatou* with a minor presence of *M. alpinus* (mean IV per plot = 0.25). The herbaceous layer was dominated by *A. capillaris*, *D. glomerata*, and *F. novae-zelandiae*.

Cluster two ($n = 4$) can be characterised as "*V. brachysiphon*, *C. scoparius*, and *L. scoparium* mixed shrubland". This cluster occurred in the steeper areas of Remus Hill and was primarily composed of these three species. A notable feature of cluster two was the absence of the commonly found herbaceous combination of *A. capillaris*, *D. glomerata*, and *F. novae-zelandiae*. In contrast, *V. brachysiphon* appeared in this cluster and was not found in any other plots.

Cluster three ($n = 7$) can be described as "*D. toumatou* and *C. cotoneaster* mixed shrubland", and was primarily distributed on the southern side of Remus Hill. This cluster had the highest species diversity and featured *D. toumatou*, *C. cotoneaster*, and *L. scoparium*, along with herbaceous species. Within this cluster, plot 19 lacked the typical herbaceous combination of *A. capillaris*, *D. glomerata*, and *F. novae-zelandiae*. Instead, the species with the highest importance value was *Coprosma propinqua*, followed by *Rosa rubiginosa*, both of which were rarely found in other plots. *Pteridium esculentum* was also abundant in plot 19.

Environmental factors

There were significant differences among the three clusters in Olsen phosphorus, carbon/nitrogen ratio, slope, northness, and eastness (Table 2). The phosphorus content in cluster two soils was relatively low, only half of that in cluster one, with a significant difference between the two. There were no significant differences in anaerobically mineralisable nitrogen, organic matter, total carbon, or total nitrogen among clusters (Table 2). The carbon/nitrogen ratio of cluster one was significantly lower than that of clusters two and three, with no significant difference between cluster two and cluster three. There was no significant difference in soil bulk density or moisture content among clusters (Table 2).

The slope of cluster one differed significantly from that of cluster two, with cluster two's mean slope being nearly double that of cluster one, exceeding 30° (Table 2). Northness and eastness differed significantly among clusters: cluster

Table 1: List of plant species identified at Remus Hill, with status classified as either exotic or native to New Zealand. Asterisk (*) denotes exotic species that are classified as environmental weeds by McAlpine and Howell (2024).

Scientific name	Species code	Common name	Status
<i>Acaena novae-zelandiae</i>	ACANOV	Biddy-biddy	Native
<i>Achillea millefolium</i>	ACHMIL	Yarrow	Exotic
<i>Aciphylla aurea</i>	ACIAUR	Golden Spaniard	Native
<i>Agrostis capillaris</i>	AGRCAP	Browntop	Exotic*
<i>Anthoxanthum odoratum</i>	ANTODO	Sweet vernal grass	Exotic
<i>Asplenium flabellifolium</i>	ASPFLB	Necklace fern	Native
<i>Blechnum penna-marina</i>	BLEPEN	Little hard fern	Native
<i>Breutelia affinis</i>	BREAFF		Native
<i>Briza media</i>	BRIMED	Quaking-grass	Exotic
<i>Calystegia tuguriorum</i>	CALTUG	New Zealand bindweed	Native
<i>Cerastium fontanum</i>	CERFON	Mouse-ear chickweed	Exotic
<i>Cirsium vulgare</i>	CIRVUL	Scotch thistle	Exotic*
<i>Coprosma intertexta</i>	COPINT		Native
<i>Coprosma propinqua</i>	COPPRO	Mingimingi	Native
<i>Corokia cotoneaster</i>	CORCOT	Korokio	Native
<i>Crataegus monogyna</i>	CRAMON	Hawthorn	Exotic*
<i>Cytisus scoparius</i>	CYTSCO	Broom	Exotic*
<i>Dactylis glomerata</i>	DACGLO	Cock's-foot	Exotic*
<i>Discaria toumatou</i>	DISTOU	Matagouri	Native
<i>Festuca novae-zelandiae</i>	FESNOV	Hard tussock	Native
<i>Festuca rubra</i>	FESRUB	Red fescue	Exotic*
<i>Hypnum cupressiforme</i>	HYPCUP	Cypress-leaved plait-moss	Native
<i>Hypochaeris radicata</i>	HYPRAD	Catsear	Exotic
<i>Ilex aquifolium</i>	ILEAQU	European holly	Exotic*
<i>Leptospermum scoparium</i>	LEPSCO	Mānuka	Native
<i>Melicytus alpinus</i>	MELALP	Porcupine shrub	Native
<i>Muehlenbeckia complexa</i>	MUECOM	Scrambling pohuehue	Native
<i>Mycelis muralis</i>	MYCMUR	Wall lettuce	Exotic
<i>Ozothamnus leptophyllus</i>	OZOLEP	Tauhinu	Native
<i>Pilosella aurantiaca</i>	PILAU	Orange hawkweed	Exotic
<i>Pilosella officinarum</i>	PILOFF	Mouse-eared hawkweed	Exotic*
<i>Pimelea oreophila</i>	PIMORE	Pimelea	Native
<i>Polystichum vestitum</i>	POLVES	Prickly shield fern	Native
<i>Pteridium esculentum</i>	PTEESC	Bracken fern	Native
<i>Racomitrium lanuginosum</i>	RACLAN	Woolly fringe-moss	Native
<i>Rosa rubiginosa</i>	ROSRUB	Sweet briar	Exotic*
<i>Rubus fruticosus</i>	RUBFRU	Blackberry	Exotic
<i>Rubus schmidelioides</i>	RUBSCH	White-leaved lawyer	Native
<i>Schoenus pauciflorus</i>	SCHPAU	Bog rush	Native
<i>Styphelia nesophila</i>	STYNES	Patotara	Native
<i>Thuidiopsis sparsa</i>	THUSPS	Sparse fern moss	Native
<i>Trifolium pratense</i>	TRIPRA	Red clover	Exotic
<i>Veronica brachysiphon</i>	VERBRA	Hooker's hebe	Native

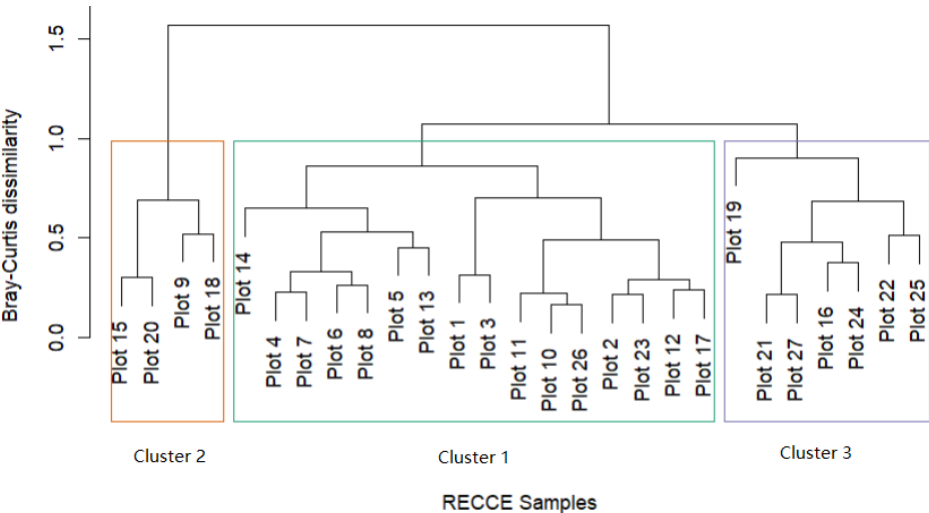


Figure 3: Hierarchical cluster analysis of the 27 plots at Remus Hill, showing three distinct vegetation communities. Cluster 1 = *Discaria toumatou* and mixed grassland; Cluster 2 = *Veronica brachysiphon*, *Cytisus scoparius*, and *Leptospermum scoparium* mixed shrubland; and Cluster 3 = *Discaria toumatou* and *Corokia cotoneaster* mixed shrubland.

Table 2: Summary of environmental factors and importance values across different clusters at Remus Hill. Values are presented in the format of mean (standard error), with letters below each value indicating the results of pairwise comparisons among clusters where different letters signify significant differences ($P < 0.05$). * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

	Cluster 1 <i>Discaria toumatou</i> and mixed grassland	Cluster 2 <i>Veronica brachysiphon</i> , <i>Cytisus scoparius</i> , and <i>Leptospermum scoparium</i> mixed shrubland	Cluster 3 <i>Discaria toumatou</i> and <i>Corokia cotoneaster</i> mixed shrubland
Number of plots	16	4	7
pH	5.6 (0.1)	5.8 (0.1)	5.5 (0.1)
Olsen phosphorus (mg L^{-1}) *	4.9 (0.6) A	2.3 (0.5) B	3.4 (0.2) AB
Anaerobically mineralisable N ($\mu\text{g g}^{-1}$)	120.6 (16.0)	49.8 (18.4)	107.7 (19.5)
Organic matter (%)	10.7 (0.7)	8.4 (1.6)	11.6 (1.2)
Total carbon (%)	6.2 (0.4)	4.8 (0.9)	6.7 (0.7)
Total nitrogen (%)	0.47 (0.03)	0.31 (0.06)	0.46 (0.04)
C/N ratio ***	13.4 (0.2) A	15.6 (0.9) B	14.6 (0.3) B
Bulk density (kg m^{-3})	657.2 (30.5)	669.5 (77.1)	574.0 (59.2)
Moisture (%)	40.7 (3.3)	33.3 (5.6)	32.6 (3.4)
Slope ($^{\circ}$) **	15.3 (1.9) A	31.2 (1.5) B	23.2 (4.5) AB
Elevation (m)	634.1 (5.4)	638.8 (4.4)	624.3 (5.0)
Northness *	0.17 (0.20) A	-0.65 (0.08) B	-0.57 (0.26) C
Eastness **	0.02 (0.16) A	-0.74 (0.07) B	0.43 (0.13) A
Summed vegetation importance value per plot ***	5.6 (0.3)	6.0 (0.7) A	8.8 (0.4) A B

two primarily faced west and south, cluster three faced east and south, and cluster one did not show a specific directional trend in its mean value.

The vegetation composition was significantly correlated with several factors: carbon/nitrogen ratio ($R^2 = 0.37$, $P = 0.004$), eastness ($R^2 = 0.29$, $P = 0.007$), total nitrogen ($R^2 = 0.24$, $P = 0.032$), soil moisture ($R^2 = 0.25$, $P = 0.044$), Olsen phosphorous ($R^2 = 0.26$, $P = 0.045$), and slope ($R^2 = 0.21$, $P = 0.05$) (Fig. 4). The samples in cluster one were associated with higher Olsen phosphorous, total nitrogen, and soil moisture, while the samples in cluster three were correlated with higher eastness and a higher carbon/nitrogen ratio.

Correlation analysis

Soil pH was negatively correlated with Olsen phosphorous and total nitrogen (adjusted $P < 0.05$; Fig. 5a). All soil nutrient factors, except for the carbon/nitrogen ratio, showed significant correlations with each other. Soil nutrient content was lower in steeper areas, significantly so for phosphorous. Higher soil nutrient levels tended to be associated with lower bulk density but higher soil moisture.

The two exotic grass species, *A. capillaris* and *D. glomerata*, showed similar responses to environmental factors, except for soil moisture, where they displayed opposite trends (Fig. 5b). *Dactylis glomerata* had a stronger correlation with soil

nutrients and was more commonly found in wetter locations. The dominant shrub, *D. toumatou*, was more commonly found in lower-pH and east-facing plots. The native grass *F. novae-zelandiae* had a negative correlation with slope, while steeper slopes were associated with the presence of *V. brachysiphon* and *C. propinqua*. *Leptospermum scoparium* was positively correlated with the carbon/nitrogen ratio and negatively correlated with other soil nutrients. However, following P-value correction for multiple tests, these trends were not significant ($P > 0.05$).

Veronica brachysiphon was significantly negatively correlated with *D. toumatou* and *F. novae-zelandiae*, and positively correlated with *O. leptophyllus* (Fig. 5c). The abundant shrub *D. toumatou* was positively correlated with the grass species *A. capillaris*, *D. glomerata*, and *F. novae-zelandiae*, and the shrubs *C. propinqua* and *M. alpinus*, but had either no association or negative associations with the other species. However, these trends were not significant.

Discussion

Despite the cessation of farming, exotic grasses such as *A. capillaris*, *D. glomerata*, *Anthoxanthum odoratum*, and *Festuca rubra* still dominate at Remus Hill. However,

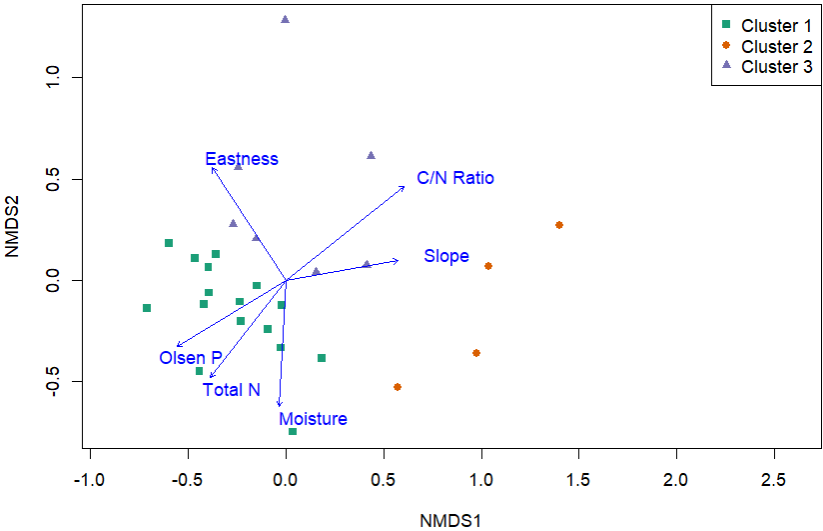


Figure 4: nMDS ordination of the vegetation communities at Remus Hill. Each point represents a plot, classified following cluster analysis. Arrows indicate the fit of environmental variables to the vegetation distribution. Only factors significantly correlated ($P < 0.05$) are shown in the figure. The stress value for the nMDS ordination plot in two dimensions was 0.16. Cluster 1 = *Discaria toumatou* and mixed grassland; Cluster 2 = *Veronica brachysiphon*, *Cytisus scoparius*, and *Leptospermum scoparium* mixed shrubland; and Cluster 3 = *Discaria toumatou* and *Corokia cotoneaster* mixed shrubland.

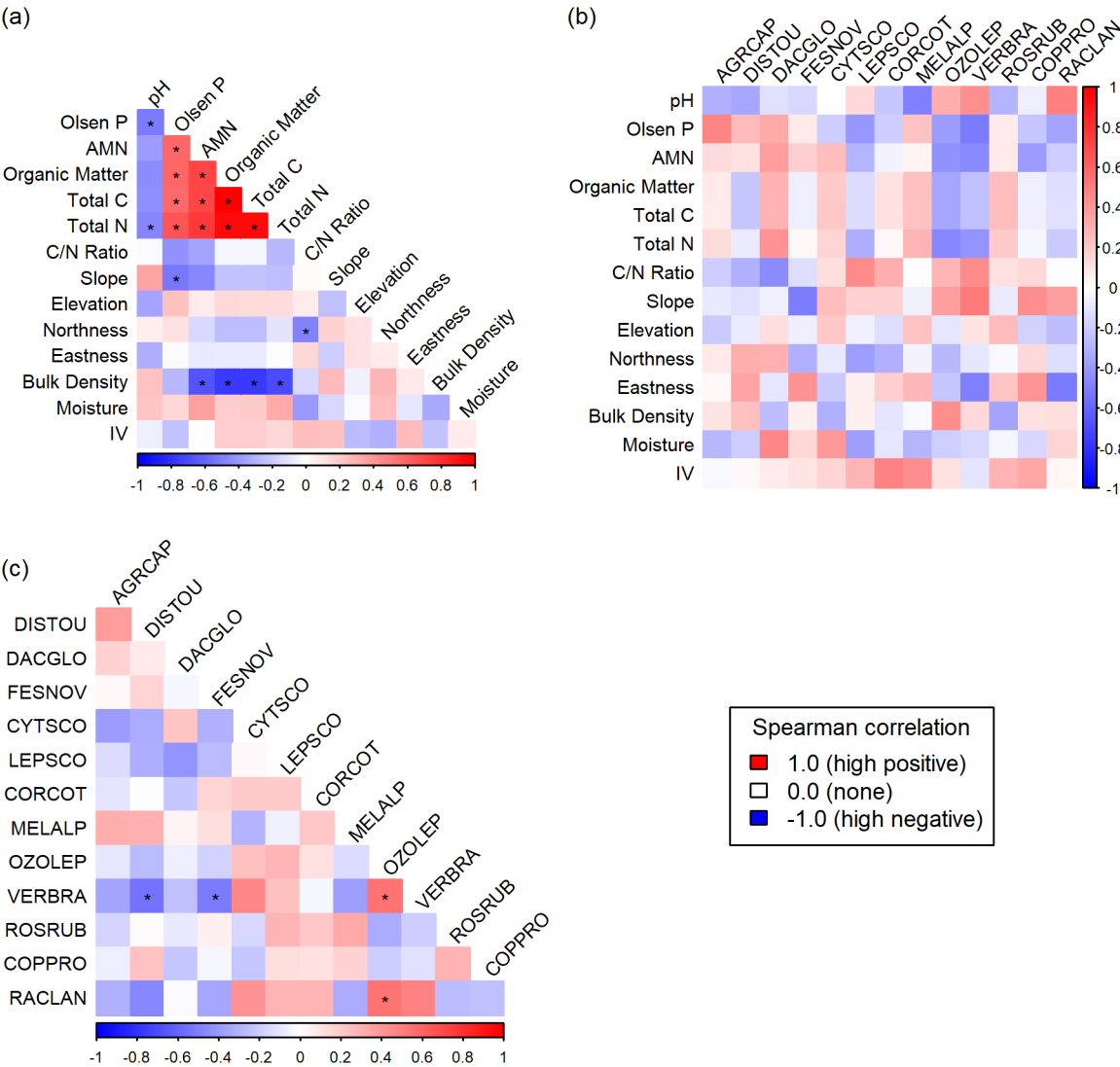


Figure 5: Correlation heatmap of variables: (a) environmental factors vs. environmental factors, (b) environmental factors vs. common plant species, (c) common plant species vs. common plant species. Significantly correlated variable pairs ($P < 0.05$) are indicated by an asterisk (*). Common plant species are the 13 species with the highest summed importance values across all plots. IV represents the total (summed) importance value per plot. AMN represents anaerobically mineralisable nitrogen. Units for all variables are specified in the text. See Table 1 for species codes.

compared with vegetation survey data from 1977 (Burrows 1977) the vegetation composition at Remus Hill has become more diverse, and native shrubs, such as *D. toumatou* and *L. scoparium*, have become more common. However, invasive species such as *C. scoparius* have also begun to appear. A total of 18 exotic species were recorded in the survey, of which nine are environmental weeds (McAlpine & Howell 2024; Table 1). In addition to the pasture grasses mentioned earlier, these include *Cirsium vulgare*, *Crataegus monogyna*, *F. rubra*, and others, collectively accounting for 40.3% of the total IV (i.e. the sum of IVs of all recorded species across all plots). Outside the plots, scattered *Pinus* spp. individuals were also observed.

Discaria toumatou occurrence was negatively correlated with soil pH, while *L. scoparium* was positively correlated with carbon/nitrogen ratio, and *D. glomerata* was correlated with some of the most nitrogen-rich soils. These findings contrast with previous work from dryland communities in central Otago, which found high concentrations of nitrogen associated with woody plants such as *C. propinqua* (Camara 2021). *Discaria toumatou* has previously been described in association with relatively abundant phosphorus (Daly 1969), and while our results were indicative of a positive correlation between *D. toumatou* and Olsen phosphorous, this was not significant.

Leptospermum scoparium, *O. leptophyllus*, and *V. brachysiphon* were more commonly found in nutrient-poor and steeper areas, likely because *L. scoparium* and similar species can better tolerate impoverished conditions and thus thrive in areas with less competition. Additionally, *L. scoparium* may facilitate neighbouring plants, such as *O. leptophyllus* and *V. brachysiphon*, by providing shade and wind protection (Burrows & Lord 1993). Our findings suggest that at Remus Hill non-native pasture grasses may be more competitive where nutrient levels are highest and that native shrubs have been able to re-establish on the lower-nutrient soils. Further, the predominant wind at Cass is from the northwest (Greenland 1977), which will impact the vegetation on the northwest slope of Remus Hill, potentially explaining the dominance of cluster one grassland communities and lower shrub abundances on these slopes.

Since grazing has ceased, Remus Hill is undergoing natural succession, with both native and exotic plant species showing a notable increase in diversity and cover. Vegetation cover is highest on the southern side, particularly on the southeast-facing slopes. However, to prioritise the restoration of native vegetation, it is necessary to control invasive species like *C. scoparius*. This study contributes to a better understanding of vegetation distribution on Remus Hill and its relationship with environmental factors. It provides a foundation for future research and data to support ecological projects in the region, such as biodiversity restoration.

Acknowledgements

We thank Meike Holzenkaempfer, Vicki Wilton, and Jeanette Allen for laboratory, technical, and administrative assistance. We are grateful to Jenny Ladley and the University of Canterbury for authorising the use of the Cass Mountain Research Area for this research. We are grateful to an anonymous reviewer for their helpful comments that have improved this manuscript.

Additional information and declarations

Author contributions: SVW conceived the research idea, YW, SVW, and FA designed the research, YW undertook the data collection and analyses and wrote the manuscript, with editorial contributions from SVW and FA. All authors revised the manuscript.

Funding: This research was supported by the University of Canterbury's School of Forestry discretionary funds allocated to SVW.

Data and code availability: Code used in this paper can be accessed by contacting the corresponding author. All vegetation plot data, and associated soil data, are archived in the National Vegetation Survey Databank (<https://nvs.landcareresearch.co.nz/>).

Ethics: Ethics approval was not required for this research.

Conflicts of interest: The authors declare no conflicts of interest.

References

- Benjamini Y, Hochberg Y 1995. Controlling the false discovery rate: a practical and powerful approach to multiple testing. *Journal of the Royal Statistical Society Series B* 57: 289–300.
- Bray JR, Curtis JT 1957. An ordination of the upland forest communities of southern Wisconsin. *Ecological Monographs* 27(4): 325–349.
- Burns BR, Leathwick JR 1996. Vegetation-environment relationships at Waipoua Forest, Northland, New Zealand. *New Zealand Journal of Botany* 34(1): 79–92.
- Burrows CJ 1977. Cass: history and science in the Cass district, Canterbury, New Zealand. Christchurch, Department of Botany, University of Canterbury. 418 p.
- Burrows CJ, Lord JM 1993. Recent colonisation by *Nothofagus fusca* at Cass, Canterbury. *New Zealand Journal of Botany* 31(2): 139–146.
- Camara AS 2021. Do woody plants create 'fertile islands' in dryland New Zealand? *New Zealand Journal of Ecology* 45(1): 3419.
- Cools N, De Vos B 2016. Part X: Sampling and analysis of soil. In: UNECE ICP Forests Programme Co-ordinating Centre ed. *Manual on methods and criteria for harmonized sampling, assessment, monitoring and analysis of the effects of air pollution on forests*. Eberswalde, Thünen Institute of Forest Ecosystems. 208 pp.
- Cutler EJ 1977. Soils of the Cass district. In: Burrows CJ ed. *History and science in the Cass district, Canterbury, New Zealand*. Christchurch, Department of Botany, University of Canterbury. Pp. 117–141.
- Daly GT 1969. The biology of matagouri. *Proceedings of the New Zealand Weed and Pest Control Conference* 22: 195–200.
- Etherington TR, Perry GLW, Wilmshurst JM 2022. HOTRUNZ: an open-access 1 km resolution monthly 1910–2019 time series of interpolated temperature and rainfall grids with associated uncertainty for New Zealand. *Earth System Science Data* 14(6): 2817–2832.
- Evison D, Wyse SV 2023. Forest restoration at the Cass Mountain Research Area, Canterbury, New Zealand. *New Zealand Journal of Forestry* 68(3): 8–15.

- Greenland DE 1977. Weather and climate at Cass. In: Burrows CJ ed. Cass: History and Science in the Cass District, Canterbury, New Zealand. Christchurch, Department of Botany, University of Canterbury. Pp. 93–113.
- Hall GMJ 1992. PC- RECCE: vegetation inventory data analysis. FRI Bulletin No. 182. Rotorua, Forest Research Institute. 108 p.
- Hewitt AE 2010. New Zealand soil classification. 3rd edn. Landcare Research science series No. 1. Lincoln, Manaaki Whenua Press. 136 p.
- Hurst JM, Allen RB 2007. The RECCE method for describing New Zealand vegetation - field protocols. Lincoln, Manaaki Whenua Landcare Research. 39 p.
- Ledgard N, Davis M 2004. Restoration of mountain beech (*Nothofagus solandri* var. *cliffortioides*) forest after fire. New Zealand Journal of Ecology 28(1): 125–135.
- LINZ 2024. NZ Contours (Topo, 1:50k) Land Information New Zealand. <https://data.linz.govt.nz/layer/50768-nz-contours-topo-150k/> (accessed 13/10/2024).
- McAlpine KG, Howell CJ 2024. List of environmental weeds in New Zealand 2024. Science for Conservation No. 340. Wellington, Department of Conservation. 37 p.
- McGlone MS, Richardson SJ 2023. Sexual systems in the New Zealand angiosperm flora. New Zealand Journal of Botany 61(4): 201–231.
- McWethy DB, Whitlock C, Wilmshurst JM, McGlone MS, Fromont M, Li Z, Dieffenbacher-Krall A, Hobbs WO, Fritz SC, Cook ER 2010. Rapid landscape transformation in South Island, New Zealand, following initial Polynesian settlement. Proceedings of the National Academy of Sciences 107(50): 21343–21348.
- Molloy BPJ 1964. Soil genesis and plant succession in the subalpine and alpine zones of Torlesse Range, Canterbury, New Zealand: part 2. Distribution, characteristics, and genesis of soils. New Zealand Journal of Botany 2(2): 143–176.
- Oksanen J, Blanchet FG, Friendly M, Kindt R, Legendre P, McGlenn D, Minchin PR, O'Hara RB, Simpson GL, Solymos P, Henry M, Stevens H, Szoecs E, Wagner H 2019. vegan: community ecology package. R package version 2.5-5. <https://CRAN.R-project.org/package=vegan>.
- 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.
- R Core Team 2024. R: A language and environment for statistical computing. Version 4.3.3. Vienna, Austria, R Foundation for Statistical Computing. <https://www.R-project.org/>.
- Soons JM 1977. The geomorphology of the Cass district. In: Burrows CJ ed. Cass: history and science in the Cass district, Canterbury, New Zealand. Christchurch, Department of Botany, University of Canterbury. Pp. 79–91.
- Stevenson BA, Smale MC 2005. Seed bed treatment effects on vegetation and seedling establishment in a New Zealand pasture one year after seeding with native woody species. Ecological Management and Restoration 6(2): 124–131.
- Ward Jr. JH 1963. Hierarchical grouping to optimise an objective function. Journal of the American Statistical Association 58(301): 236–244.
- Wei T, Simko V 2024. R package 'corrplot': visualization of a correlation matrix (Version 0.95). <https://github.com/taiyun/corrplot>.
- Wiser SK, Hurst JM, Wright EF, Allen RB 2011. New Zealand's forest and shrubland communities: a quantitative classification based on a nationally representative plot network. Applied Vegetation Science 14: 506–523.
- Wyse SV, Burns BR, Wright SD 2014. Distinctive vegetation communities are associated with the long-lived conifer *Agathis australis* (New Zealand kauri, Araucariaceae) in New Zealand rainforests. Austral Ecology 39: 388–400.
- Young LM, Norton DA, Lambert MT 2016. One hundred years of vegetation change at Cass, eastern South Island high country. New Zealand Journal of Ecology 40(3): 289–301.

Received: 5 January 2025; accepted: 5 August 2025

Editorial board member: Matt McGlone