

One hundred years of vegetation change at Cass, eastern South Island high country

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Abstract: Fire, pastoral farming and exotic species have been major drivers of vegetation change in the eastern South Island high country since human arrival. More recently, fire frequency and grazing intensity have declined allowing regeneration of previously suppressed woody elements in some areas, such as our 1775 ha Cass study site. We collected vegetation and abiotic data from 117 Recce plots (10 × 10 m) using an objective grid-based network to classify the vegetation, determine factors influencing vegetation pattern, discuss long-term vegetation changes and assess the role of exotic species. Hierarchical cluster analysis and ordination on compositional data revealed seven broad vegetation types: grassland, mixed shrubland, mānuka shrubland, mountain beech forest, gorse shrubland, wetlands and subalpine vegetation. Within four of these types (mixed shrubland, grassland, subalpine, wetlands) distinct subtypes were also identified. There was evidence for compositional structuring based on altitude and slope. Two vegetation types were characterised by exotic species (gorse shrubland, grassland), with exotic species more common at lower elevations and on gentle slopes. While short tussock grassland dominated the Cass landscape in the early twentieth century, having been induced by burning and grazing, it only dominates 8% of the landscape today. Native woody vegetation (predominantly shrubland) is now the dominant land cover at Cass. As long as fire is excluded, grazing is limited (but not necessarily eliminated) and exotic woody species are controlled, it is likely that these transitional shrublands will be replaced by mountain beech forest in the longer-term. Similar patterns of recovery of native woody elements are likely to occur more widely in similar high country environments in the absence of fire and with careful management of grazing and exotic woody plants.

Keywords: disturbance; exotic invasion; forest loss; grazing; induced grassland; secondary succession; shrubland; woody expansion

Introduction

Natural fires were rare in the predominantly forested New Zealand landscape prior to the arrival of Māori in the 13th century AD (Ogden et al. 1998; McGlone & Wilmshurst 1999; Rogers et al. 2007). With human settlement, fire became one of the dominant drivers of vegetation pattern across much of New Zealand (McGlone 1989; Perry et al. 2012), resulting in an estimated 40% loss of forest cover by 1840 AD (McWethy et al. 2010). Since European arrival, there has been further significant forest loss along with ongoing clearance of regenerating lands (Ewers et al. 2006).

Fire has heavily modified the drier montane zone in the rain shadow east of the Southern Alps, with extensive loss of *Fuscospora* (mountain and black beech) and Podocarpaceae (conifer) forests (Molloy et al. 1963; McWethy et al. 2010). Previously extensive forests have been largely replaced by a mosaic of grassland and shrubland, comprising species otherwise associated with riparian zones, disturbed and/or rocky sites, and colder, higher-elevation areas (Burrows 1960; McGlone 1989). Since European settlement, these extensive areas of shrubland and grassland have been widely used for pastoralism (O'Connor 1982) and are increasingly interspersed with intensified landscapes (e.g. agriculture, forestry). This induced vegetation is characterised by having an historically high fire regime (both deliberate and accidental), with an annual to decadal frequency (Perry et al. 2014), and still experiences novel disturbances including herbivory by introduced mammals and the spreading of fertiliser and seeds. Many non-native plant species introduced for pasture,

cropping, shelter and forestry have become integrated into communities previously dominated by native species. Exotic plants now form a significant component of the vegetation (Rose et al. 1995; Norton et al. 2006; Day & Buckley 2013), perhaps even structuring certain post-disturbance vegetation assemblages (Walker et al. 2009a).

More recently (especially the last c. 50 years), fire frequency and grazing intensity have declined in some areas such as the South Island high country where release from pastoral use following tenure review has allowed regeneration of previously suppressed woody species. Resulting trajectories of vegetation change have been hugely variable, depending on the extent of forest loss, the nature of the surrounding vegetation, ongoing disturbances within the regenerating system, and environmental factors such as rainfall and temperature. Post-fire regeneration has been described in several studies (e.g. Druce 1957; Esler & Astridge 1974; Payton et al. 1984; Wilson 1994; Sullivan et al. 2007; Perry et al. 2010); however, there are fewer descriptions of post-fire regeneration in higher elevation, often moisture-limited sites with short growing seasons that are characteristic of the high country (Wiser et al. 1997; Walker et al. 2009b).

Factors determining post-disturbance vegetation succession and community assembly can be complex and depend on a range of abiotic and biotic conditions e.g. altitude, slope, aspect, drainage, fire frequency and intensity, grazing, seed availability and dispersal, and soil states (Wardle 1991; Standish et al. 2009; Walker et al. 2009b). The limited literature on transitions from non-woody to woody plant communities in eastern South Island high country sites suggests that novel

assemblages of native and exotic species occur (Williams 1983; Bellingham & Coomes 2003; Standish et al. 2009). Knowledge of post-disturbance vegetation patterns and the drivers contributing to present-day vegetation assemblages can assist in better understanding likely future woody assemblages (Standish et al. 2009; Walker et al. 2009a) and aid in land use planning, management and environmental reporting (Allen et al. 2003; Wiser et al. 2011). Few attempts have been made to classify and describe novel post-disturbance assemblages in the eastern South Island high country (Rogers & Leathwick 1994; Walker et al. 1995; Walker et al. 2009b), although the relative importance of the native and exotic components in present-day vegetation assemblages has been quantified more widely (e.g. Rose et al. 1995; Meurk et al. 2002; Day & Buckley 2013).

We studied a 1775 ha area property, the Cass Mountain Research Area (Cass), which is typical of other eastern South Island rain shadow high country areas where fire and grazing disturbances have been reduced and woody species are now re-establishing. Because of one hundred years of detailed information on its ecological and human history (Burrows 1977a; <http://www.ffc.canterbury.ac.nz/cmra/index.shtml>), Cass provides a unique opportunity to better understand long-term vegetation change in these environments. We used an intensive grid-based sampling design to objectively classify post-disturbance successional assemblages and compared these with historical information from Cass. In order to better understand the likely future development of these systems, our aims were to: (a) describe and classify the vegetation present; (b) identify factors that have influenced the vegetation pattern; (c) discuss the long-term changes in the vegetation; and (d) assess the importance of exotic plant species focussing on those species that have influenced, or have the potential to influence, vegetation change in these systems.

Methods

Study site and background

Our research site, Cass, consists of mostly mountainous land in the upper Waimakariri Basin in the eastern rain-shadow of the Southern Alps, 15 km from the main divide of the Southern Alps / Kā Tiritiri o te Moana (Burrows 1977a; Young et al. 2013). The vegetation, soils, climate and disturbance history of Cass is typical of mountain environments and inland basins along the foothills and ranges immediately east of the main axial ranges of Kā Tiritiri o te Moana. Cass comprises the fans, slopes and summits of two prominent peaks, Sugarloaf (1359 m) and Cass Hill (1098 m) as well as adjacent river flats along the Waimakariri and Cass Rivers, with a large (879 m) altitudinal gradient (480–1359 m). The underlying geology is greywacke of the Torlesse Group, which consists of non-schistose quartzofeldspathic sandstones embedded with siltstone and mudstone. Soils are derived from these and include Recent Soils on the young alluvial terraces and Allophanic and Acid Brown Soils (Hewitt 1998) across the fans and hill slopes. While Recent Soils are relatively high in phosphorus (P), Brown Soils typically have low P and have experienced considerable erosion since deforestation (Cutler 1977). Mean annual rainfall at Cass is around 1300 mm (Greenland 1977).

Prior to the arrival of Māori, *Fuscospora cliffortioides* forest cloaked the Cass area and the surrounding intermontane basins of inland Canterbury (Moar 1971; Lintott & Burrows 1973; McGlone et al. 2004). There is an extensive history

of fire since human arrival with most forest disappearing during Māori settlement (Molloy et al. 1963; Molloy 1977). Subsequent European fires have mostly burnt grassland and shrubland areas in an attempt to manage the land for grazing resulting in a predominance of grassland in the early 20th century (Cockayne & Foweraker 1916). Since then, there has been a reduction in overall fire frequency at Cass, allowing development of a secondary shrubland over much of the fire-induced grassland (Dobson & Burrows 1977). While the last major fire affecting Cass occurred in 1947, there have been substantial fires elsewhere in the upper Waimakariri Basin more recently (e.g. Cora Lynn in 1995, Flock Hill in 2015). Today, Cass comprises an extensive range of vegetation types including diverse montane and subalpine tussock grasslands and shrublands with significant exotic components (particularly grasses). Small pockets of *F. cliffortioides* forest remain (Burrows 1977b). Sheep grazing has occurred at Cass for over 100 years and has been at a low stocking rate (0.2 stock units ha⁻¹yr⁻¹) for at least the past fifty years. As far as we are aware, Cass has never been over sown or top-dressed.

Data collection

To obtain a representative sample of the vegetation at Cass we used a grid-based network with a random starting point (Wiser et al. 2011) over the entire 1775 ha area (Fig. 1). The 400 × 400 m grid resulted in 114 non-permanent reconnaissance (Recce) plots 10 × 10 m in size located at every grid intersection. In addition, we established a further three plots where the grid intersection fell on the boundary between two discrete types of vegetation types giving us 117 plots in total. We followed field Recce description protocols (Hurst & Allen 2007) to locate the plots and to record site descriptions and species composition during the 2012/13 summer. We collected compositional data on all vascular plant species within the bounded Recce plots within six height tiers (0–30 cm; >30 cm–2 m; >2 m–5 m; >5 m–12 m; >12 m–25 m) by assigning modified Braun-Blanquet cover abundance scores within six cover classes (1 = <1%, 2 = 1–5%, 3 = 6–25%, 4 = 26–50%, 5 = 51–75%, 6 = 76–100%) to each species. We also assigned a score to the total cover of all bryophytes (not separated by species except for *Racomitrium lanuginosum*, a widespread and abundant moss). Site description and environmental variables collected at each plot included aspect, slope, physiography, altitude, drainage, disturbance history, percent rock, litter, bare ground cover, vegetation cover above 1.35 m, and average vegetation height for the plot (mean top height) (Hurst & Allen 2007). Taxonomic nomenclature follows that of the New Zealand Plant Conservation Network (www.nzpcn.org). Voucher collections for some species are lodged in the Canterbury University Herbarium (CANU) and data are held in the National Vegetation Database (Landcare Research, <http://nvs.landcareresearch.co.nz>).

Data analysis

We used cluster analysis to identify distinct vegetation types, and ordinations of plot and species data to relate these to measured environmental factors. Importance Values (IVs) were used as the basis for all our analyses as they provide a weighted value of abundance (or ecological importance) for each species in each plot. To calculate an IV for each species in each plot, cover scores within each height tier were converted to the mid-point for each percentage cover range within each cover class and summed across all height tiers (Wiser et al.

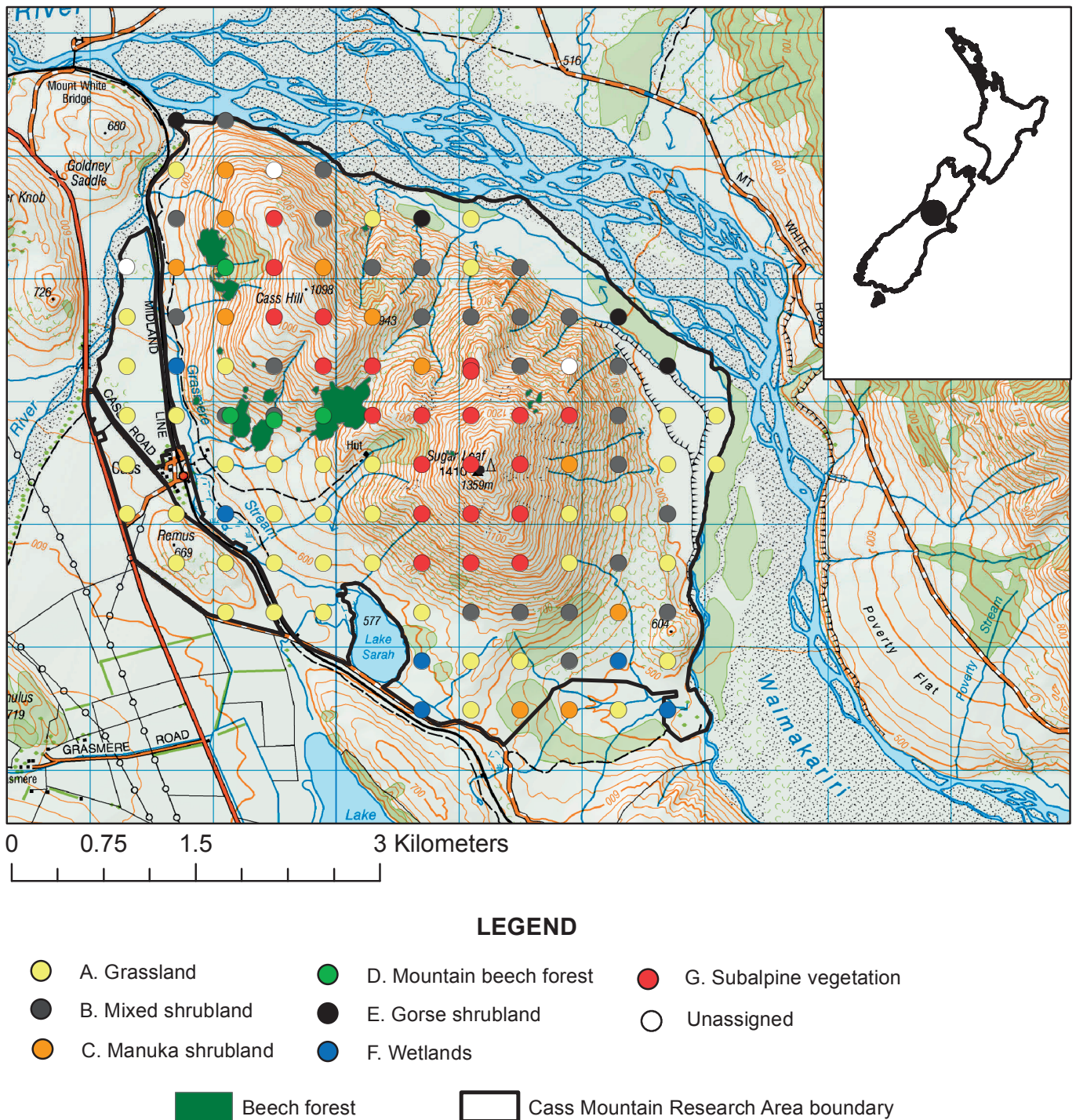


Figure 1. Spatial distribution of the 400 x 400 m network of 177 sample plots at Cass, coloured by the seven broad vegetation types (see online version for coloured map). These include three additional plots established where grid intersections fell on boundary between two discrete vegetation types.

2011). IVs ranged from 0.5 to 171, with higher IVs recorded for large woody species that occurred in several height tiers e.g. *F. cliffortioides*, *Leptospermum scoparium*.

We used hierarchical agglomerative cluster analysis (using Bray-Curtis (BC) dissimilarity metric and Ward’s linkage method) to define the vegetation types on the basis of compositional similarity of the 117 plots. The dissimilarity matrix of distance among plots was created in ‘vegan’ (Oksanen et al. 2013) using the *vegdist* function and data

were normalised to ensure that high IVs did not dominate the distance calculation using the *decostand* function. K-means non-hierarchical clustering yielded similar results, therefore, we present only groups defined through the agglomerative clustering in our results. To describe the components of each cluster (hereafter referred to as vegetation types) we identified the characteristic species within each of them using species presence and relative abundance data (based on IVs). Our criteria for inclusion as a characteristic species included:

(a) species present in every plot within the community regardless of its abundance; (b) species occurring in $\geq 75\%$ of plots with an importance value of ≥ 1 (i.e. the species cover is $\geq 1\%$ in at least one height tier); and (c) species occurring in $\geq 67\%$ of plots with an importance value of ≥ 5 . We use plant common names when referring to broad vegetation types but use full binomial nomenclature for individual species.

We used non-metric multidimensional scaling (nMDS, Bray-Curtis distance) to spatially display the distribution of the 117 plots based on vegetation compositional similarity using the ‘vegan’ package (Oksanen et al. 2013). We ran the ordination twice, first specifying three dimensions and then two dimensions, with stress increasing from 0.15 to 0.21. However, when comparing the ordination plots we found that the third axis did not resolve any more information than was contained in axes 1 and 2 and we therefore present results in two dimensions only. The nMDS plot was centered and rotated so that variance was maximised on Axis 1, with axes scaled to half-change units. Environmental vectors (altitude, aspect, slope, percent rock cover, percent bare ground cover and drainage) were superimposed on the nMDS ordination using the function *envfit* in ‘vegan’ to explore their relationships with the vegetation data. We also superimposed vegetation attribute variables (mean top height, percent canopy cover at 1.3 m, species richness, percent native and exotic richness, total IV and percent native and exotic IV) on the nMDS ordination and *envfit* provided R^2 values as a measure of the goodness of fit of these variables.

Although there are no permanent vegetation monitoring sites at Cass to draw on for an historical perspective, we assessed long-term (100-year) vegetation change utilising a variety of historical information sources from different times during this period. These included general descriptions (Cockayne & Foweraker 1916; Malcom 1925; Burrows 1960, 1977a; Primack 1978), photographs (Chilton 1915) and the limited published quantitative data available on vegetation composition (Malcolm 1925; Burrows 1977a; White 1991).

Results

Vegetation classification

We recorded 370 unique vascular plant species from 117 plots in the 1775 ha area sampled. Native species formed 73% of

the total species richness (270 species) while 98 exotic species were present (two species were unable to be identified). Native species were recorded from all but two of the plots (both dominated by *Ulex europaeus*), while exotic species were present in all but one of the plots (a mountain beech forest plot). The most species-rich growth forms were forbs (174 species), followed by graminoids (82 species), shrubs (51 species), sub-shrubs (21 species), ferns (20 species), trees (17 species) and vines (5 species). Overall, native species dominated in terms of relative abundance, comprising 76.4% of total IV across all plots.

The ten most abundant species (defined by average IV per plot) across all 117 plots were *Agrostis capillaris* (18.7), *Discaria toumatou* (12.5), *Anthoxanthum odoratum* (9.0), *Coprosma propinqua* (7.9), *Hebe brachysiphon* (6.2), *Leptospermum scoparium* (6.1), *Corokia cotoneaster* (4.7), *F. cliffortioides* (4.6), *U. europaeus* (3.5) and *Pteridium esculentum* (3.1). The ten most widespread species (percent of the 117 plots in which present) were *A. odoratum* (92%), *A. capillaris* (88%), *Hypochoeris radicata* (76%), *D. toumatou* (71%), *Cerastium fontanum* (70%), *Festuca novae-zelandiae* (67%), *Poa colensoi* (65%), *C. propinqua* (64%), *Leucopogon fraseri* (62%) and *Pilosella officinarum* (61%).

Six broad vegetation types were apparent from the classification (defined by the dendrogram cut at a BC dissimilarity of 0.28). Four of these types could be further subdivided into distinct subtypes (defined by the dendrogram cut at a BC dissimilarity of 0.14). Three plots were not included in any of the broad vegetation types as they were grouped into a cluster that was not ecologically interpretable, each representing a unique vegetation type. We therefore re-ran the cluster analysis excluding these plots; this did not affect the dendrogram or the groupings. The first broad type comprised grassland plots (n=41) and the other types was considerably greater than the dissimilarity between any of the other types (Fig. 2). The second, third, fourth and fifth broad types then separated out the major distinct groups of woody vegetation; mixed shrublands (n=26 plots), mānuka shrubland (n=11), mountain beech forest (n=4), and gorse shrubland (n=4). The final broad type (n=28) comprised a diverse mix of higher-elevation shrubland, grassland and herbfield vegetation (hereafter subalpine), and low-elevation wetland vegetation. For descriptive purposes, we separated the low-elevation (560 ± 14 m) wetland plots

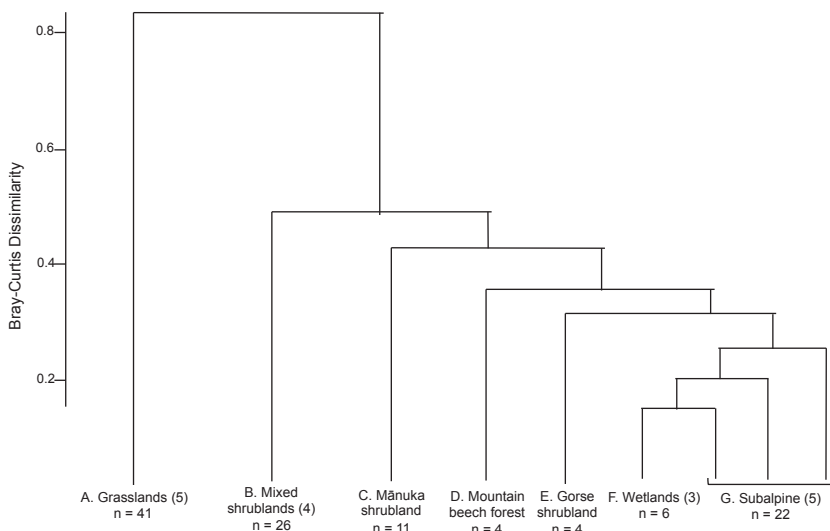


Figure 2. Dendrogram showing the relationship amongst the seven broad vegetation types identified at Cass, defined by hierarchical agglomerative cluster analysis on 117 plots and 370 species. For four of these types, the number of subtypes recognised is indicated in brackets with number of plots (n) within each broad type given below.

($n=6$) from the higher-elevation (1032 ± 27 m) subalpine plots ($n=22$), resulting in a total of seven broad vegetation types (Fig. 2) which we use as a basis for further discussion. Environmental and vegetation attributes of these seven broad vegetation types are summarised in Table 1 and the main species characteristic of each type in Table 2. Descriptions are given in Appendix S1 in Supplementary Material for all seven broad vegetation types and for the subtypes within the four broad types, within which they could be identified. A map showing the spatial distribution of the broad vegetation types at Cass is shown in Fig. 1.

Vegetation gradients

The nMDS ordination showed a clear separation (in the first two dimensions of ordination space) of two vegetation types (mountain beech forest and gorse shrubland; Fig 3). Mixed

shrublands, grasslands and subalpine types also separated out from each other but with some overlap, while mānuka shrubland overlapped these three broad types (Fig. 3). If the wetland plots are grouped as one distinct broad type, they show a wide spread in ordination space, overlapping mixed shrubland, grassland and mānuka shrubland types. However, when broken into finer-level groupings (F1–F3), the individual plots within each of the three wetland subtypes are similar but each subtype is distinct from each other (Fig. 3).

The distribution of characteristic species (Table 2) in ordination space highlights that while they were most common and abundant within a particular vegetation type, some were present across multiple vegetation types. For example, *A. capillaris* (and *A. odoratum* which had a similar distribution) was most abundant in the grassland plots, but also occurred widely through mixed shrubland and subalpine types (Fig.

Table 1. Environmental and vegetation attributes for the seven broad vegetation types identified at Cass. Number of plots within each broad type are given along with plot means (\pm se) for each attribute.

Broad type	n plots	Species richness	% native species richness	Importance Value (IV)	% native IV	% canopy cover ≥ 1.35 m	Mean top height (m)	Altitude (m)	Slope (deg)
A. Grasslands	41	30.7 (1.8)	56 (3)	124 (7)	37 (3)	9.6 (3.8)	0.38 (0.08)	611 (14)	12.5 (2.5)
B. Mixed shrublands	26	40.0 (2.4)	61 (3)	157 (14)	79 (2)	43.1 (6.1)	1.16 (0.09)	665 (24)	28.7 (2.6)
C. Mānuka shrubland	11	38.5 (1.6)	76 (2)	123 (14)	83 (3)	40.5 (8.5)	1.45 (0.31)	747 (49)	22.5 (3.7)
D. Beech forest	4	18.8 (4.6)	91 (4)	158 (26)	96 (2)	70.8 (18.9)	16.3 (3.75)	726 (29)	25.8 (10.6)
E. Gorse shrubland	4	14.5 (2.2)	25 (13)	137 (33)	9 (8)	55.0 (18.5)	1.03 (0.39)	512 (12)	0.0 (0.0)
F. Wetlands	6	39.5 (8)	61 (12)	137 (13)	71 (7)	3.0 (18.3)	0.2 (0.46)	560 (14)	3.0 (7.0)
G. Subalpine	22	38.0 (2.3)	83 (1)	98 (10)	90 (1)	12.7 (5.7)	0.53 (0.09)	1032 (27)	32.8 (2.5)

Table 2. Characteristic species within the seven broad vegetation types at Cass. Criteria for species inclusion were: (a) present in all plots within a type; (b) present in $\geq 75\%$ of plots and with an IV ≥ 1 within a type; and (c) present in $\geq 67\%$ of plots and with an IV ≥ 5 within a type. + Species present in a type but below the cut-off criteria (given above) for a characteristic species. * Exotic species.

Species	A. Grassland	B. Mixed shrubland	C. Mānuka shrubland	D. Mountain beech forest	E. Gorse shrubland	F. Wetlands	G. Subalpine
<i>Agrostis capillaris</i> *	48.0 (100)	6.6 (96)	5.1 (100)	+	+	9.9 (100)	+
<i>Anthoxanthum odoratum</i> *	15.3 (100)	9.8 (96)	6.3 (91)	+	+	3.8 (100)	3.2 (91)
<i>Festuca novae-zelandiae</i>	6.4 (83)	+	2.0 (100)			+	+
<i>Pilosella officinarum</i> *	3.5 (76)	+	5.8 (91)			+	+
<i>Discaria toumatou</i>	11.1 (83)	34.1 (92)	8.3 (91)		+	+	+
<i>Coprosma propinqua</i>	+	27.0 (92)	3.1 (100)	+	+	+	+
<i>Corokia cotoneaster</i>	+	15.0 (88)	3.9 (91)	+	+		+
<i>Leptospermum scoparium</i>	+	+	57.1 (100)			+	+
<i>Fuscospora cliffortioides</i>				137 (100)			
<i>Hebe brachysiphon</i>	+	+	+	+			20.6 (77)
<i>Celmisia spectabilis</i>	+	+	+	+			5.6 (100)
<i>Ozothamnus leptophyllus</i>	+	+	4.1 (82)			+	3.5 (77)
<i>Gaultheria depressa</i>	+	+	+			+	3.4 (81)
<i>Poa colensoi</i>	+	+	1.4 (91)			+	2.8 (91)
<i>Blechnum penna-marina</i>	+	+	+	+	+	+	1.2 (81)
<i>Carex coriacea</i>	+	+	+			33.9 (67)	
<i>Schoenus pauciflorus</i>	+	+	+			28.0 (83)	
<i>Lotus pedunculatus</i> *	+	+	+			7.8 (67)	+
<i>Ulex europaeus</i> *	+				99.4 (100)		
<i>Cytisus scoparius</i> *	+	+			16.4 (75)		

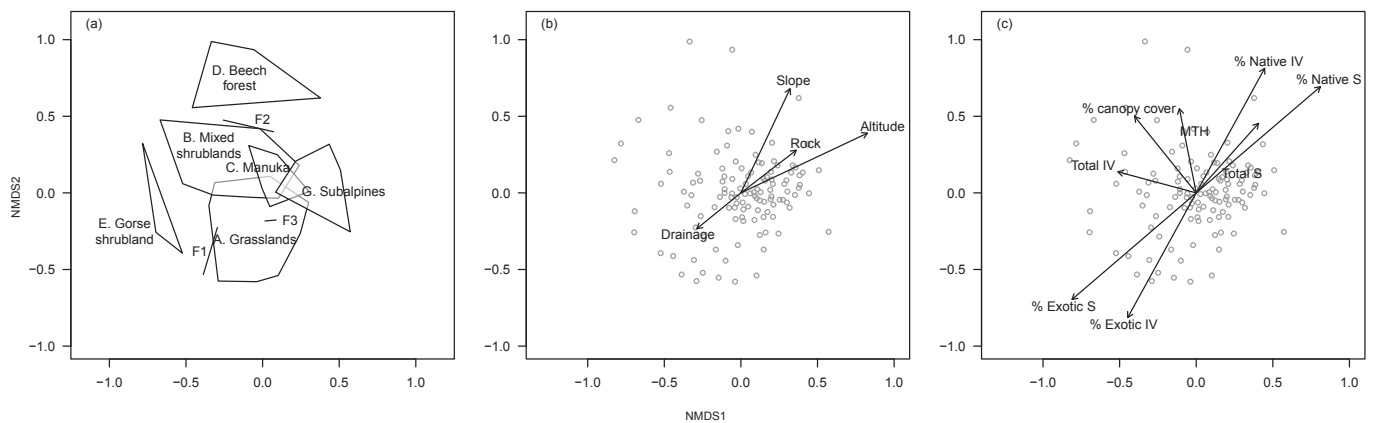


Figure 3. Ordination plots from non-metric multidimensional scaling (nMDS) analysis highlighting the distribution of plots within the seven broad vegetation types at Cass. (a) Polygons show the distribution of plots within each broad vegetation type (but plot scores have been omitted to aid interpretation). F1-3 represent the three separate wetland subtypes (see Appendix S1 for full descriptions). Arrows indicate vector fits for (b) environmental variables and (c) vegetation attributes superimposed over plot scores (grey circles). Stress for the nMDS ordination in two dimensions was 0.21. S = species richness; IV = Importance Value; MTH = mean top height (m).

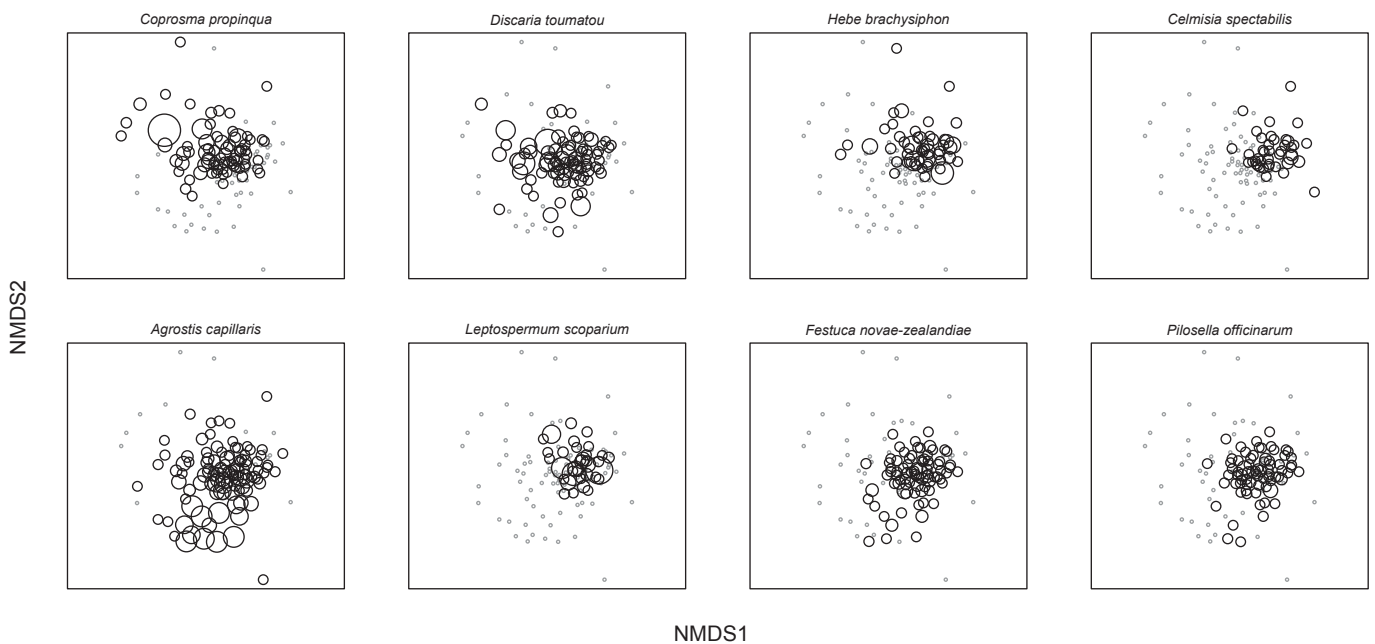


Figure 4. Non-metric multidimensional scaling ordination diagrams (from Fig. 3) highlighting the occurrence and abundance of selected characteristic species. The size of the circles is proportional to species weighted scores (based on IVs). Grey circles show where the species was absent from the plot. Stress for the nMDS ordination plot in two dimensions was 0.21.

4). *F. novae-zealandiae* occurred in a more restricted set of grassland plots, and was found widely through mānuka, subalpine, and some mixed shrubland plots, although not usually in high abundance. *D. toumatou* was most abundant in mixed shrubland plots but was also present across many grassland, mānuka and subalpine plots. *C. propinqua* and *H. brachysiphon* had more restricted distributions but occurred in mixed shrubland, mānuka shrubland and subalpine plots. In contrast, *L. scoparium* occurred predominantly in mānuka shrubland but also occurred in some subalpine plots, while *C. spectabilis* was largely restricted to subalpine plots. *P. officinarum* had a similar distribution to *F. novae-zealandiae* and occurred across a wide range of vegetation types (Fig. 4).

Environmental vector fits superimposed on the nMDS plot showed that the significant ($P < 0.05$) environmental

gradients relating to community composition were altitude ($R^2 = 0.49$), slope ($R^2 = 0.33$), percent rock cover ($R^2 = 0.12$) and drainage ($R^2 = 0.08$) (Fig. 3b). Because the R^2 values for percent rock cover and drainage were low (< 0.30) they were considered less biologically meaningful. Grassland plots typically occurred at lower elevations on more gently sloping sites. Mixed shrublands and mānuka shrubland tended to occur on more steeply sloping sites. Unsurprisingly the subalpine vegetation type occurred at higher elevations.

Several attributes of the vegetation were strongly correlated with the distribution of plots in the nMDS ordination. The strongest relationships were with the percentage of native species in the plots in terms of both the number of species present ($R^2 = 0.79$) and the IVs for native species ($R^2 = 0.60$) (Fig. 3c). Gorse and some grassland plots had the lowest

percentage of native species and native IV, while mountain beech forest and subalpine plots had the highest percentage of native species and native IV. Although mean top height, percent canopy cover, total species richness and total IV were significant ($P < 0.05$), R^2 values were all < 0.30 and were considered less biologically meaningful.

Exotic species comprised a significant component of the total vegetation at Cass both in terms of species richness (27% of all species) and abundance (35% of total IV), although there was considerable variation among the seven broad vegetation types (Table 1). Exotic species were most dominant in gorse shrubland (75% of species and 93% of IV) and grassland (44%, 63%). Although exotic species were an important component of wetlands and mixed shrubland in terms of species richness (both 39%), they were less important in these two broad vegetation types in terms of their contribution to overall abundance (29% and 21% respectively). Exotic species were least important in the subalpine and beech forest vegetation types (17% and 9% species richness and 10% and 4% IV respectively). Exotic species as a percent of total IV had a significantly ($P < 0.05$) negative correlation with altitude ($R^2 = 0.28$) and slope ($R^2 = 0.30$) while exotic species as a percent of total species richness had a significant ($P < 0.05$) negative correlation with altitude only ($R^2 = 0.30$) (Fig. 5).

Discussion

Using a quantitative, objective sampling design we identified seven distinct broad vegetation types at Cass, representing a complex mosaic of regenerating, degrading and remnant vegetation. These vegetation types are characterised by a combination of native and exotic species, which have responded to a complex mixture of environmental drivers, both reflecting the current environment (e.g. elevation, slope) and the history of the site (e.g. time since last fire, localised grazing intensity and propagule availability).

The comprehensive grid-based sampling system used in this study enabled us to objectively describe and classify the vegetation and its relative abundance in the landscape. Such an approach allows for an unbiased assessment of what drives vegetation patterns without being constrained by preconceptions of the major underlying environmental gradients (Allen et al. 2003; Wiser et al. 2011, 2016). Despite the objectivity of our sampling approach, the ability to sample

all of the floristic variation present will always be compromised by the scale of sampling. Our 400 x 400 m grid network (Fig. 1) was a compromise between our desire to obtain as high a sampling density as possible and the logistical constraints of undertaking sampling over one field season. Because of this trade-off, our plot network failed to recognise the presence and extent of some rarer vegetation types, particularly those confined to very limited areas. Distinctive vegetation types present at Cass that were not sampled by the plot grid included: raupo (*Typha orientalis*) swamp, kettlehole sphagnum bog, scree slopes, rock bluffs and ephemeral tarns (see Burrows (1977a) for more information on these types). However, given that we established 117 plots over 1775 ha (15 ha per plot), the unsampled vegetation types are likely to be small (< 15 ha) in area and/or diffusely distributed through the landscape. Notwithstanding the under-sampling of rarer vegetation types, our grid-based sample still detected 80% of the vascular plant flora known from Cass (see Appendix S2 in Supplementary Material).

Wiser et al. (2011, 2016) used an objective, grid-based plot network to classify forest and shrubland communities, and non-forest communities based on vegetation compositional data. While these were national scale classifications, relevant comparisons can still be made with our classification because of the similarity in the sampling approach. Several of the vegetation types identified in our Cass classification are similar to those identified by Wiser et al. (2011, 2016), which they term ‘alliances’. Our mountain beech forest type and mānuka shrubland type align well with Wiser et al. (2011) Alliance 5 and 8 respectively. Our grassland vegetation type aligns well with one of the cool-temperate-low alpine short tussock alliances of Wiser et al. (2016); *Festuca novae-zelandiae*–*Anthoxanthum odoratum*–*Poa colensoi*/*Leucopogon fraseri* tussockland (T8). However, our shrubland subtypes represent more variable assemblages than those identified in Wiser et al. (2011) due to the smaller scale of our sampling; but can still be broadly aligned with their Alliance 2 (*Discaria toumatou* - *Coprosma propinqua* / *Anthoxanthum odoratum* - *Dactylis glomerata* shrubland) and Alliance 3 (*Ozothamnus leptophyllus* (*Dracophyllum uniflorum*) montane shrubland). Alliance 4 (*Pteridium esculentum* – *Ulex europeus*) / *A. odoratum* – *D. glomerata* successional shrubland) also has some similarities with both our gorse shrubland type and our shrubland subtype B3 (sparse grey shrubland with bracken understory).

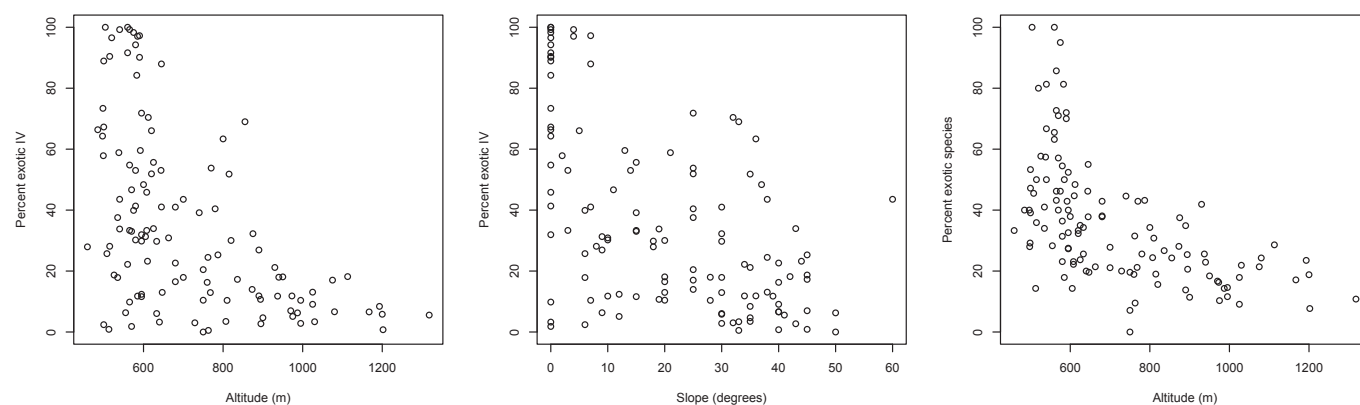


Figure 5. Percent exotic IV as a function of (a) altitude and (b) slope and (c) percent exotic species richness as a function of altitude for the 117 plots at Cass.

Overall, the approach that we used was a robust, comprehensive and unbiased sampling strategy that enabled us to both quantify the major vegetation patterns present at Cass and to comment on the likely environmental drivers of this pattern. The broad vegetation types identified here are typical of those found widely in the higher rainfall parts of the eastern South Island high country.

Drivers of long-term vegetation change at Cass: the role of fire and grazing

The vegetation present at Cass today is much more diverse than what would have likely been present prior to human-induced deforestation or that present at the start of the twentieth century when Cockayne and Foweraker (1916) first described the Cass vegetation. Based on pollen records from Kettlehole Bog (McGlone et al. 2004; located in the southern corner of Cass, south-east of Lake Sarah, Fig. 2), the distribution of soil types and the presence of mountain beech forest remnants (Burrows 1960), the vegetation at the time of Māori arrival would have been dominated by species-poor *Fuscospora cliffortioides* forest. Other pre-human vegetation types would have occupied only limited areas (Burrows 1960), restricted to the Recent Soils close to the Cass and Waimakariri Rivers (supporting short tussock grassland), wetlands associated with Lake Sarah and Grasmere Stream, and the summit of Sugarloaf (supporting tall tussock grassland).

With Māori settlement, as was the case over much of the eastern South Island (Molloy et al. 1963; McWethy et al. 2010),

the previously extensive *F. cliffortioides* forest was burnt and replaced by predominantly grassland vegetation (Lintott & Burrows 1973). It is unclear what types of changes occurred in this grassland prior to European settlement (1850s), but when Cockayne and Foweraker (1916) described the vegetation at Cass they noted that 'low tussock grassland is far and away the most important association in the vicinity of Cass'. The vegetation they described had clearly been strongly modified by at least sixty years of burning and grazing and photographic evidence from that time shows extensive, uniform short tussock grassland across large expanses of Cass (Fig. 6). The earliest known European fire was in 1857, with several more fires in the Cass area up until 1914 when the first ecological descriptions were made (Molloy 1977). Fire continued to play an important role in structuring vegetation at Cass through until at least 1947 (Molloy 1977). The September 1947 fire, which was probably typical of fires up until this time, is the best documented (Percival 1958): 'The fire started by a red hot cinder from a train, about a mile northwards. It burnt scrub on the rocky knob in front of the cottage, swept up the hill-side, singed the marginal beech, went up between the two larger patches of bush and some distance up the hill, finally finishing in the shelter of Sugarloaf to the south.' Fires since then appear to have been smaller and of more limited extent.

Another factor that likely contributed to a relatively uniform vegetation cover in the early twentieth century was the extensive grazing practice that occurred across the South Island high country up until this time. Stocking rates were



Figure 6. Photographs comparing southwest-facing slopes of Cass Hill and Sugarloaf in 1914 (top photos by C. Foweraker) and 2015 (bottom photos by D. Norton).

initially very high (O'Connor 1982), but have decreased since then. Cass was grazed as part of the Grasmere-Cora Lyn run (c. 22,000 ha) with stocking rates of c. 0.7–0.8 sheep ha⁻¹ in the 1880s decreasing to c. 0.5–0.6 sheep ha⁻¹ from 1900–1950 (McLeod & McLeod 1977). The current stocking rate at Cass is c. 0.2 sheep ha⁻¹. It is likely that the higher stocking rate and fires during the early phase of European pastoralism slowed shrubland expansion and helped maintain the relatively uniform and widespread grassland communities that Cockayne and Foweraker described in 1916. Since then, both domestic and wild grazers (hares and rabbits in particular) will have exerted an influence on successional patterns. We have not quantified this although certain species are preferentially grazed (e.g. *Melicetus alpinus*, *Coprosma* spp.) and may be less common than if grazers were absent from Cass.

Shrub invasion and forest reestablishment

One of the key features of the vegetation at Cass today is the emergence of shrubland, which has occurred with the relaxation of the fire regime and lower stocking rate. Cockayne and Foweraker (1916) described short tussock grassland as dominant at that time, at least at lower elevations (Fig. 6), and this appears to have been the case through until the 1950s (Burrows 1960). However, short tussock grassland is only a minor component of the Cass vegetation today, with *Festuca novae-zelandiae* a dominant component of only 8% of the plots. In contrast, native shrubland now dominates with 43% of plots classified as mānuka and mixed shrublands, and 53% of all plots have a woody cover (≥ 1.35 m height) of $>10\%$. While the grassland type comprises 37% of the contemporary landscape, native woody species (especially *Corokia cotoneaster*, *C. propinqua*, *D. toumatou*, *O. leptophyllus*, *L. scoparium*) are also invading the majority of grassland plots. Only six of 41 grassland plots lack native woody species (see below) while only 24% of all plots have no woody cover ≥ 1.35 m. The expansion of shrubland is clearly evident in the modern photos of the previously short tussock covered fans and lower hill slopes at Cass (Fig. 6), as has been observed elsewhere in the Waimakariri Basin (Whitehouse 1982).

The expansion of woody vegetation at Cass appears largely to have been a continuous process, rather than occurring in discrete episodes. Evidence from photos (see Appendix S3 in Supplementary Material) and the current population structure of woody species (LY & DN unpubl. data) does not show any evidence for discrete pulses of woody vegetation expansion after individual fire events. This process appears to be ongoing with woody plants such as *Leptospermum scoparium* having increased in stature and becoming more abundant in grassland vegetation over the last 10–20 years.

In the longer-term (over centuries), it is probable that most of the shrubland types will eventually converge towards *F. cliffortioides* dominated forest, as is the case elsewhere in the eastern South Island (e.g. Wiser et al. 1997). The expansion of *F. cliffortioides* at Cass is currently constrained by dispersal from isolated, gully-centred refuges and spread is likely to be slow, particularly in the early stages of expansion (Burrows 1977b; Wardle 1984), although rare long distance dispersal events are likely to contribute to the re-establishment of this species in the longer term. This is the case already for *Fuscospora fusca* at Cass, where c. ten individuals up to 8 m tall are present as a result of long-distance dispersal from seed sources in Arthurs Pass National Park 5 km to the north (LY & DN unpubl. data; cf. Burrows & Lord 1993). When a seed source is available, *F. cliffortioides* can begin to overtop

Leptospermum scoparium shrubland by 20 years (Ledgard & Davis 2004) and it would seem likely that while initially very slow, once sufficient seed sources have established and a woody cover is present, eventual transition from shrubland to *F. cliffortioides* dominated forest might be quite rapid.

Snow tussock decline

Another major change to the Cass vegetation, which is also the case in many grazed areas of the eastern South Island, is the decline in abundance and distribution of subalpine snow tussock grassland dominated by *Chionochloa* (Rose & Platt 1992; Meurk et al. 2002). In the 1950s there was a large, continuous area of snow tussock grassland on Sugarloaf 'covering some acres' (Burrows 1960). Today, continuous snow tussock grassland is of very limited extent at Cass being confined to a small area of the ridge northwest of Sugarloaf, although none of our sample plots fell in this area. In contrast to Burrows (1960), most of the snow tussock grassland at Cass is now highly degraded with *Chionochloa macra* forming only a minor component. In the five plots that contained snow tussocks, the tussocks themselves are stunted due to grazing, but in some cases occur as regenerating small individuals which occupy little space in terms of cover abundance. While livestock grazing densities have never been high (<1 sheep ha⁻¹) at Cass, the propensity of merino wethers (the main sheep type grazed at Cass at least over the last 10–20 years) to spend considerable periods on the higher parts of Sugarloaf and Cass Hill coupled with low but ongoing deer and chamois grazing (LY & DN pers. obs.) appears to have had a substantial impact on snow tussock communities, especially as much of this loss appears to have occurred over the last 60 years at Cass. Notwithstanding this, even the degraded snow tussock grasslands remaining at Cass still retain many of the other herbaceous and woody species typical of this vegetation type (Day & Buckley 2013). The presence of young *Chionochloa* plants at some higher-elevation sites at Cass does suggest that if grazing pressure is reduced these grasslands may re-establish as has been suggested for other areas (Rose & Platt 1992).

The role of exotic species

Another major influence on the modern vegetation has been the emergence of exotics as a strong element of some vegetation types at Cass. The three most widespread species across all plots at Cass are exotic, the grasses *A. odoratum* and *Agrostis capillaris* and the herb *Hypochoeris radicata* (present in 92%, 88% and 76% of plots respectively). Exotic species are more common at lower elevations and relatively uncommon both in terms of abundance and species richness at higher elevations and in beech forest. Exotic species dominance (in terms of abundance) is largely restricted to grasslands, which occur at lower elevations and on more gently sloping sites, where *A. odoratum* and *A. capillaris* often dominate the grass sward. While many of these exotic species have been present at Cass since at least 1916, they were a relatively minor component at that time. Cockayne and Foweraker (1916) commented that introduced species in short tussock grassland 'play comparatively little part as yet in the economy of the association'. At this time, they did not anticipate that exotic species would become dominant speculating: 'Nor is it to be expected that they [exotics] will greatly increase either in number or aggressiveness under the present condition of affairs'. At Cass today, exotic species are present in all but one of the 117 plots measured.

Agrostis capillaris in particular had become the dominant component of the Cass grasslands by the 1970s (Dobson 1977) and was associated with a decrease in the native herbaceous component (White 1991). In the adjacent Harper-Avoa catchment, Rose et al. (1995) observed a similar increase in the dominance of *A. capillaris* over a similar time period. A dense sward of *A. capillaris* is known to limit the establishment of some native woody species including *F. cliffortioides* (Sessions & Kelly 2000; Ledgard & Davis 2004). However, in our study most plots with a thick sward of exotic grasses (*A. capillaris*, *A. odoratum*, *F. rubra*) still have a low cover of native woody plants suggesting that longer-term woody succession is still possible even through a dense exotic grass sward. The only exception to this might be dense grass swards that have established into the more highly modified wetlands and have a strong *Schoenus pauciflorus* component, but even these are starting to be invaded by *L. scoparium*. Although exotic grasses are having a negative impact on the native herbaceous element (White 1991), it appears that they are not limiting the establishment of native woody species such as *D. toumatou*, *O. leptophyllus*, *L. scoparium*, *H. brachysiphon*, *C. propinqua* at Cass.

Pilosella officinarum is present in nearly two-thirds of the plots sampled at Cass, but is almost always present at very low cover, unlike sites elsewhere (e.g. Rose et al. 1995; Norton et al. 2006; Day & Buckley 2011). The exception to this are a few open sites with a low cover of sward-forming grasses and shrubs, often underlain by thin stony soils where *P. officinarum* can be locally abundant. These sites are typically north-facing spurs and heavily grazed flats where sheep often spend time in high densities (Young & Norton 2015). However, because of the number of plots sampled, these localised high-cover *P. officinarum* sites were only encountered twice (the two adjacent eastern-terrace sites). The situation at Cass is different from other comparable short tussock grasslands that have a higher and perhaps less spatially variable cover of *P. officinarum* (e.g. Rose et al. 1995; Norton et al. 2006; Day & Buckley 2011). However, in these other areas, sward-forming grasses are less dominant and shrub cover lower than at Cass, and this may be an important factor in the differences between those sites and Cass.

Exotic species are not structurally important in the woody vegetation types we describe here because the dominant exotic species have an herbaceous growth form and do not compete directly with the woody canopy. However, there are some notable exceptions to this with the recent increase in several exotic woody species in the Cass area (LY & DN pers. obs.). The exotic legumes *Ulex europaeus* and *Cytisus scoparius* were rare in the Cass area in the 1970s, being largely restricted to localised sites associated with human settlement and *U. europaeus* also occurred in riverbeds (Dobson 1977; Dobson & Burrows 1977). Today however, both of these species are locally common on alluvial flats and lower hill slopes. While *U. europaeus* forms monospecific stands, spreading outwards from initial invasion sites, *C. scoparius* is actively invading native shrubland communities in some areas, as predicted by Dobson (1977). Exotic conifers, especially *Pseudotsuga menziesii* and *Pinus contorta*, are also now widely distributed across parts of Cass (although only recorded in one plot each). Exotic conifers were not present as wild individuals in the 1970s (Burrows 1977a) but have spread rapidly since, especially over the last 10–15 years. While both woody legumes and conifers have the potential to significantly alter successional pathways (Ledgard 2001), ongoing control has

limited their spread at Cass (Young et al. 2013). Ground and aerially applied herbicide has been used to control *U. europaeus* and *C. scoparius* for c. 15 years, while manual felling and more recently aerial spraying has been carried out on wilding conifers over the same period. *Crataegus monogyna* is also spreading into some Cass shrubland communities (although not recorded in any of our plots), but is largely restricted to local sites on Remus and the lower parts of fans on the western side of Sugarloaf (see Fig. 1). Several other exotic species are locally abundant and associated with settlements and the railway, but are not (yet) widespread at Cass: *Ilex aquifolium*, *Ribes uva-crispa*, *Rubus fruticosus*, *Lupinus arboreus* (and herbaceous *L. polyphyllus*) and *Salix fragilis*. Some or all of these species have the potential to spread more widely and could impact vegetation structure. If not controlled, exotic woody species do have the potential to structurally dominate regenerating vegetation and alter successional trajectories at Cass in the future, as is seen at nearby sites (e.g. Craigieburn) and elsewhere in the high country.

Conclusions

The overall trend at Cass is towards a dominance of native woody species. Given the climate and soils present (Burrows 1960), it is likely that as long as fire is excluded, grazing is limited and exotic woody species controlled, *F. cliffortioides* forest will eventually dominate this site again. Even under a low grazing regime, shrubland is actively invading the Cass grasslands. However, grazing may be having a significant impact on the potential recovery of other vegetation types, especially snow tussock grasslands. Fire continues to remain a significant threat to the landscape because of accidental ignitions associated with a major adjacent highway and railway (Molloy 1977; Perry et al. 1999). There is considerable overlap in species composition amongst the different vegetation types reflecting the complex histories of this area and perhaps the strong role of chance in the restructuring of the vegetation. The current diverse shrubland and grassland is probably transitional between the fire- and grazing-induced grasslands described by Cockayne and Foweraker (1916) and *F. cliffortioides* forest similar to that which dominated Cass prior to Māori burning (McGlone et al. 2004).

Cass is an excellent site for studying long-term vegetation change in response to past disturbances because of the one hundred years of detailed information on the ecological and human history (Cockayne & Foweraker 1916; Burrows 1977a; Young et al. 2013; <http://www.ffc.canterbury.ac.nz/cmra/index.shtml>) and has the potential to be critical for understanding future woody vegetation development in the South Island high country more generally. Our results provide an important baseline for future research to better understand the specific mechanisms involved, for example, the processes by which *Fuscospora* species invade and establish into different types of woody vegetation that are now developing over Cass. The extensive knowledge of ecological patterns at Cass collected over the last one hundred years coupled with our more recent initiatives (establishing permanent vegetation monitoring plots and photo-monitoring points; Young et al. 2013) is likely to make Cass a key site for long term ecological research.

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Supplementary Material

Additional supporting information may be found in the online version of this article:

- Appendix S1.** Vegetation types at Cass.
- Appendix S2.** Species richness in the Cass flora.
- Appendix S3.** Woody vegetation explanation.

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