

SHORT COMMUNICATION

Effects of sheep grazing exclusion on alpine tall tussock grasslands

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Published online: 8 September 2015

Abstract: Substantial areas of alpine tall tussock grasslands are being retired from grazing as part of Crown pastoral lease tenure review because of the perceived negative impact of grazing livestock. However, relatively little is known about the effect of sheep exclusion on these grasslands. We analysed data from five grazing exclosure plots over a 6-year period to examine the effect merino sheep have relative to hares and rabbits in alpine tall tussock grasslands used for summer grazing. Unfortunately, because of snow damage to fences, we were unable to detect any significant hare and rabbit effects. Over the time of this study, there was no evidence for significant vegetation recovery after exclusion of sheep grazing. This may be because of other grazing animals in the system, or the low stocking rates and non-random grazing behaviour of merino ewes. There was, however, a significant increase in the cover of exotic herbs *Pilosella officinarum* and *P. praealta* and a significant decrease in the cover of native tussocks *Festuca novae-zelandiae* and *Poa colensoi* regardless of grazing exclusion. While this pattern has been previously documented in studies at lower elevations and usually with a history of burning, our results demonstrate that alpine grasslands with no burning history can also be invaded by *Pilosella* spp. over relatively short time frames. Replicated grazing exclosure trials such as the one described in this paper are important for providing objective information on both long-term trends in vegetation composition and the impacts of grazing animals in alpine grasslands as a basis for making informed decisions on their future management.

Keywords: *Chionochloa*; exclosure plots; *Festuca*; grazing effects; hare; Himalayan tahr; merino sheep; New Zealand; *Pilosella*

Introduction

Mammalian herbivores represent a novel form of disturbance in New Zealand's native grasslands, which evolved in the presence of avian herbivores (Caughley 1989; Antonelli et al. 2011). New Zealand's natural grasslands (referred to here as alpine grasslands) are dominated by tall tussocks from the genus *Chionochloa* and were largely restricted to above the natural alpine treeline, with short tussocks (*Festuca* and *Poa* spp.) a relatively minor component (Wardle 1991). However, with human colonisation some 800 years ago, widespread anthropogenic fire resulted in substantial forest loss and the expansion of both tall and short tussocks to lower elevations, especially in eastern areas of the South Island (McGlone 2001; Perry et al. 2014). With European settlement from the mid-19th century, both induced and natural grasslands were rapidly occupied and exploited for livestock grazing (O'Connor 1982), especially by sheep (*Ovis aries*), which has continued in many areas to the present day. A range of other introduced mammals have also invaded alpine grasslands including red deer (*Cervus elaphus scoticus*), Himalayan tahr (*Hemitragus jemlahicus*), chamois (*Rupicapra rupicapra*), hares (*Lepus europaeus occidentalis*), and rabbits (*Oryctolagus cuniculus*).

Because of their high elevation, alpine grasslands are usually grazed for only a few months each year, mainly by merino ewes. Typically, farmers will run their ewes at low stocking rates (<1 stock unit ha⁻¹) in alpine grasslands for 2–4 months in late summer and autumn after lambs have been weaned. Alpine grassland grazing is usually used to allow

lower-elevation country to recover from grazing through the lambing period. Sheep are brought down off the alpine grasslands in autumn before the first winter snows arrive and these areas are then left ungrazed until the next season. The majority of alpine grasslands that continue to be grazed in this manner are included within Crown pastoral leases (Swaffield & Hughey 2001; O'Connor 2003). When a pastoral lease comes up for tenure review, alpine grasslands are usually retired from grazing and the land is transferred to the public conservation estate. One reason for this is the perceived negative impact of grazing livestock on these grasslands (Mark & McLennan 2005).

The effect of grazing removal on the composition and structure of induced tall tussock grasslands below the natural alpine treeline has been investigated in several studies (Rose & Platt 1992; Meurk et al. 2002; Mark & Dickinson 2003). There is less information for alpine grasslands above the natural treeline. In general, tall tussock cover appears to increase with grazing cessation in the few alpine grasslands that have been studied, with greatest recovery at lower elevations (Jensen et al. 1997; Grove et al. 2002), although some of this recovery is also related to cessation of burning (Gitay et al. 1992). However, decreases in the abundance and diversity of inter-tussock species occurs as tall tussock cover increases with the cessation of grazing (Grove et al. 2002). Lee et al. (1993) showed that tall tussock regeneration was higher with low or no grazing in alpine grasslands. The relationship between grazing and invasive plant species in alpine grasslands is less clear, with the expansion of *Pilosella* and *Hieracium* species since the

middle of the 20th century appearing to occur irrespective of grazing management (Treskonova 1991; Day & Buckley 2013; Steer & Norton 2013). The relative impact of different grazing animals (sheep versus lagomorphs) has only been considered in two studies, in the Mackenzie Basin (Meurk et al. 2002) and Rakaia catchment (Rose & Platt 1992; Holdaway et al. 2014), but both were conducted in induced tussock grasslands below the natural treeline. A third study (Scroggie et al. 2012) assessed the relative effect of sheep and lagomorphs at three lower elevation (500–700 m), semi-arid Otago sites, but focused on measuring pasture productivity on sheep grazing land. Our objectives in this study were to examine the effect of merino sheep exclusion relative to lagomorph exclusion in alpine tall tussock grasslands with no recent burning history but with a long history (>100 years) of summer grazing.

Methods

Study area and site description

The study was undertaken at five sites within the Cass Valley, Godley Ecological District, Canterbury (43.68°S, 170.37°E). All sites were similar in elevation (1132–1448 m a.s.l.) and topography (gently sloping faces or fans). The underlying rocks are weakly indurated Triassic/Jurassic-aged greywacke sandstones and argillite (Torlesse supergroup), while soils are Allophanic Brown Soils. Estimated average annual rainfall is likely to be c. 2000 mm based on data from adjacent climate stations. The study area is part of the Glenmore Station Pastoral Lease and is used for summer grazing by merino ewes for around 8 weeks between mid-February and mid-April each year. The effective stocking rate is about 0.1 stock unit ha⁻¹ yr⁻¹ (excluding areas unavailable for grazing such as riverbed, scree slopes and mountain peaks), which is comparable to summer grazing stocking rates on other high country pastoral leases. Hares and tahr are consistently present and graze in the area year-round, although grazing pressure is unknown. Rabbits are present, but most likely less common than hares, because the study sites are high elevation, but we refer to hares and rabbits collectively as lagomorphs in this paper as relative densities and impacts of hares and rabbits at our study sites are unknown.

The vegetation at the study sites was characterised by the tall tussock *Chionochloa*, the mountain daisy *Celmisia lyalli*, and the short tussocks *Festuca novae-zelandiae* and *Poa colensoi*. The two *Chionochloa* species were segregated spatially by site (*C. macra* at two sites and *C. rigida* at three sites). Woody species made up a minor component of the total vegetation cover and comprised low-growing *Dracophyllum* species (*D. pronum* and *D. uniflorum*), *Acrothamnus colensoi* and, rarely, *Ozothamnus leptophyllus*. The major components of the inter-tussock flora included two exotic hawkweed species (*Pilosella officinarum* and *Pilosella praealta*), *Rytidosperma pumila*, mats of *Raoulia subsericia* and non-vascular plants; other herbaceous species formed a minor component. Exotic grasses, mainly *Anthoxanthum odoratum* and *Agrostis capillaris*, were present at very low cover and not widely distributed through the study sites.

Study design and data collection

One grazing enclosure plot was established at each site in January 2009. A 20 × 20 m area was fenced off from sheep and half of this (20 × 10 m) was enclosed with rabbit netting to

exclude lagomorphs. Fences were checked after winter snows in 2010 and 2012 and were found to be still functional and excluding sheep and lagomorphs. Two 20 × 5 m strips located either side of the fenced enclosure (to minimise environmental variation) were then used for the control. This gave three 20 × 10 m grazing treatments: (a) open to all grazing, (b) sheep excluded (but allowing access to lagomorphs), and (c) all (sheep, hares and rabbits) excluded. There was no evidence of sheep camping adjacent to the fences at any of our sites. It was not possible to exclude tahr, which had access to all treatments due to their ability to jump fences. Five 2 × 2 m permanently marked quadrats were randomly established within each of the treatment areas. Within each of these quadrats, the cover abundance of all vascular plants, lichen, moss, bare ground, litter, rock, and stone was visually estimated. For cover abundances ≥10%, cover was estimated to the nearest 5% and for cover abundances <10% cover was estimated to the nearest 1%. Cover was independently estimated in January 2009 by two observers and consensus values recorded. Cover was again estimated in January 2015, independently by two observers, one of whom also did the initial cover measurements. Additionally in 2015, the presence/absence of faecal pellets of mammalian herbivores was recorded and browse of three common palatable species (*Chionochloa* spp., *C. lyalli* and *Aciphylla aurea*) was scored using a four-point intensity score (0 = none, 1 = low, 2 = medium, 3 = high). Low browse involved minor damage to only a few leaves on one or a few plants. Medium browse involved consistent damage across several plants, but plants were not heavily browsed. High browse involved consistently heavy browse to >50% of plants.

Data analysis

Due to heavy winter snowfall in this alpine environment, and snow-creep at the enclosure plot sites, the rabbit netting acted as a trap for snow, resulting in damage to the fences. This allowed lagomorphs to access some of the grazing exclusion treatments, for at least the last 2 years of the study period. However, annual inspection and occasional maintenance of fences by the farmer ensured that all fences remained sheep-proof throughout the study. Notwithstanding this limitation, we undertook the data analysis comparing the three treatment effects because we are confident that damage to the rabbit-netting only occurred during the last 2 years of the study, so for most of the study period lagomorphs were effectively excluded.

We ran an ordination on vegetation cover data using non-metric multi-dimensional scaling (nMDS, Manhattan distance) to display the vegetation compositional structure in two dimensions. We used permutational multivariate analysis of variance (PerMANOVA, 1000 permutations, Manhattan distance) to test for overall differences in group means of the compositional data between the experimental treatments in 2009 and 2015, analysing the effects of grazing treatment, year and the interaction between them. We tested whether there was any effect of grazing treatment (three factor levels), year (two factor levels), or their interaction on percent cover of plant species in our study system using repeated measures analysis of variance (ANOVA) models. Individual species responses were tested against the above predictor variables using arcsine (square-root) transformed percent cover data. The five individual quadrats within plots were included in the model as a random effect. To test the effect of grazing treatment on both the presence of mammal pellets and on browse intensity, we used generalised linear models (GLM) with a binomial error distribution for the pellet data and Poisson

error distribution for the browse data.

We present results for mean species richness per quadrat and for all dominant (>5% cover) and widespread (>75% occupancy) species, known palatable species (*A. aurea*, *F. novae-zelandiae*), woody erect shrubs (*Dracophyllum* species and *O. leptophyllus*), and other species for which significant effects are shown in the models. Exotic grasses were defined as *A. odoratum* and *A. capillaris* with their covers pooled. We also pooled the two *Chionochloa* species for analysis because each species on its own was not widespread enough to analyse separately. The two *Chionochloa* species showed the same responses when examined separately, therefore pooling the two species was legitimate and allowed for a more powerful statistical analysis. Results are presented as means ± 1 SE. Statistical analyses were performed in the statistical package R version 3.2.0 (R Development Core Team 2011) and the ‘vegan’ package was used for the nMDS and PerMANOVA analyses (Oksanen et al. 2013).

Results

Overall 70 vascular plant species were recorded from the study sites, 84% of which were native. The average number of species per 2 × 2 m quadrat was 17.4 ± 0.1. The dominant species in terms of overall mean percent cover per quadrat (and percent of quadrats occupied) were *Celmisia lyallii* 24.0 ± 1.5% (97%), *Pilosella officinarum* 14.0 ± 1.4% (80%), *Chionochloa rigida* 9.1 ± 1.2% (57%), *Poa colensoi* 8.5 ± 0.9% (93%), *Festuca novae-zelandiae* 7.1 ± 1.3%, *Chionochloa macra* 6.7 ± 1.2% (25%), and *Dracophyllum pronum* 5.1 ± 1.9% (51%). Percent cover of the two *Chionochloa* species combined was 15.8% (83%). In addition two species were very widespread but occurred at low abundance; *Rytidosperma pumila* 1.0 ± 0.1% (84%) and *Pilosella praealta* 0.8 ± 0.1% (84%).

There were compositional differences in the vegetation among the five sites (nMDS ordination stress = 0.0812), but community composition of the individual treatments within each site was similar (Fig. 1). While there were subtle, but

non-significant, shifts in community composition between 2009 and 2015 within each grazing treatment at each site, there was no significant effect of any of the grazing treatments on the magnitude of these changes in the PerMANOVA.

There were no statistically significant effects that could be attributed to the imposition of the grazing exclusion treatments (year × grazing treatment interaction). The effect of grazing treatment independent of year was significant only for mean species richness per quadrat ($F_{2,135} = 4.81, P = 0.010$). A strong year effect independent of grazing treatment was evident for several of the species examined. There was a highly significant increase between 2009 and 2015 (Fig. 2) in the cover of *Aciphylla aurea* ($F_{2,135} = 11.54, P < 0.001$), exotic grasses ($F_{2,135} = 16.61, P = 0.008$), *P. officinarum* ($F_{2,135} = 36.64, P < 0.001$), *P. praealta* ($F_{2,135} = 62.39, P < 0.001$), *R. subsericea* ($F_{2,135} = 21.23, P = 0.001$), *R. pumilum* ($F_{2,135} = 47.82, P < 0.001$), lichen ($F_{2,135} = 31.37, P < 0.001$), and moss ($F_{2,135} = 15.74, P < 0.001$). Bare ground ($F_{2,135} = 10.70, P = 0.001$) and the mean species richness per quadrat ($F_{2,135} = 19.72, P < 0.001$) also increased significantly. In contrast, there was a significant decrease between 2009 and 2015 in cover of *Festuca novae-zelandiae* ($F_{2,135} = 20.16, P < 0.001$) and *Poa colensoi* ($F_{2,135} = 8.11, P = 0.005$) (Fig. 2). Of the other dominant, widespread and palatable species and species groups tested (*Chionochloa* species, *C. lyallii*, erect shrubs and native species as a proportion of mean species richness per quadrat) no significant effects of year, grazing treatment or their interaction were found (Fig. 2).

Lagomorph pellets were recorded in all three grazing treatments in 2015, but there was no significant difference in pellet presence between treatments ($P > 0.05$); 76–80% of the 2 × 2 m quadrats contained pellets. In contrast, sheep and tahr pellets were rare, with each type only recorded in 1 of the 75 quadrats. The presence of browse (at any intensity) was observed on *C. lyallii* in 55% of quadrats (where *C. lyallii* was present), with browse scores significantly lower in both sheep-excluded (mean browse score = 0.8 ± 0.2; $P = 0.017$) and all-excluded (0.9 ± 0.2; $P = 0.050$) treatments than in the open treatment (1.5 ± 0.2). Browse was recorded on *A. aurea*

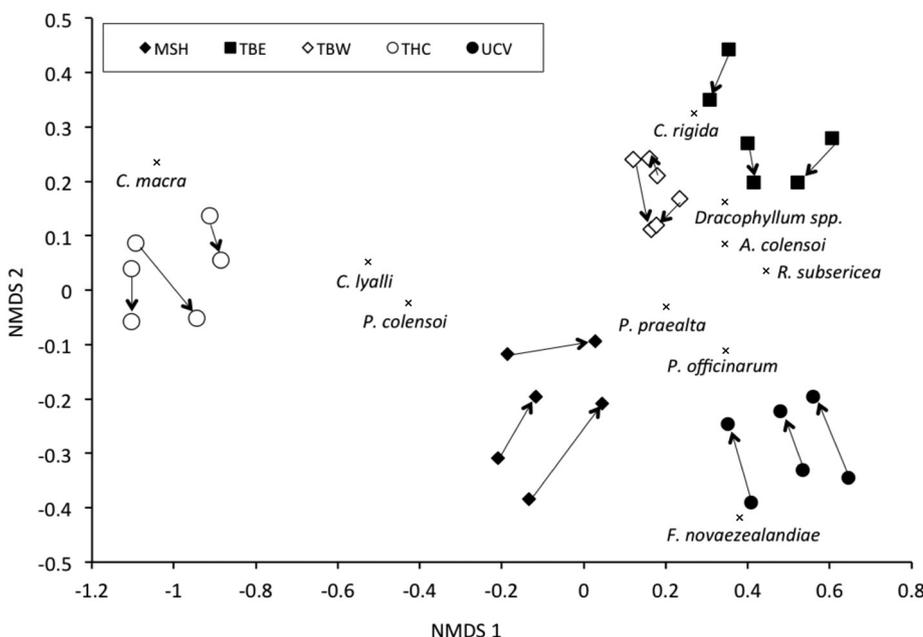


Figure 1. nMDS ordination of vegetation community composition at the five sites (MSH, TBE, TBW, THC, UCV) in the Cass Valley. Arrows show the direction of compositional change for individual grazing treatment plots between 2009 and 2015. The positions of the most abundant plant species (present at >10% total cover) on the ordination space are also presented.

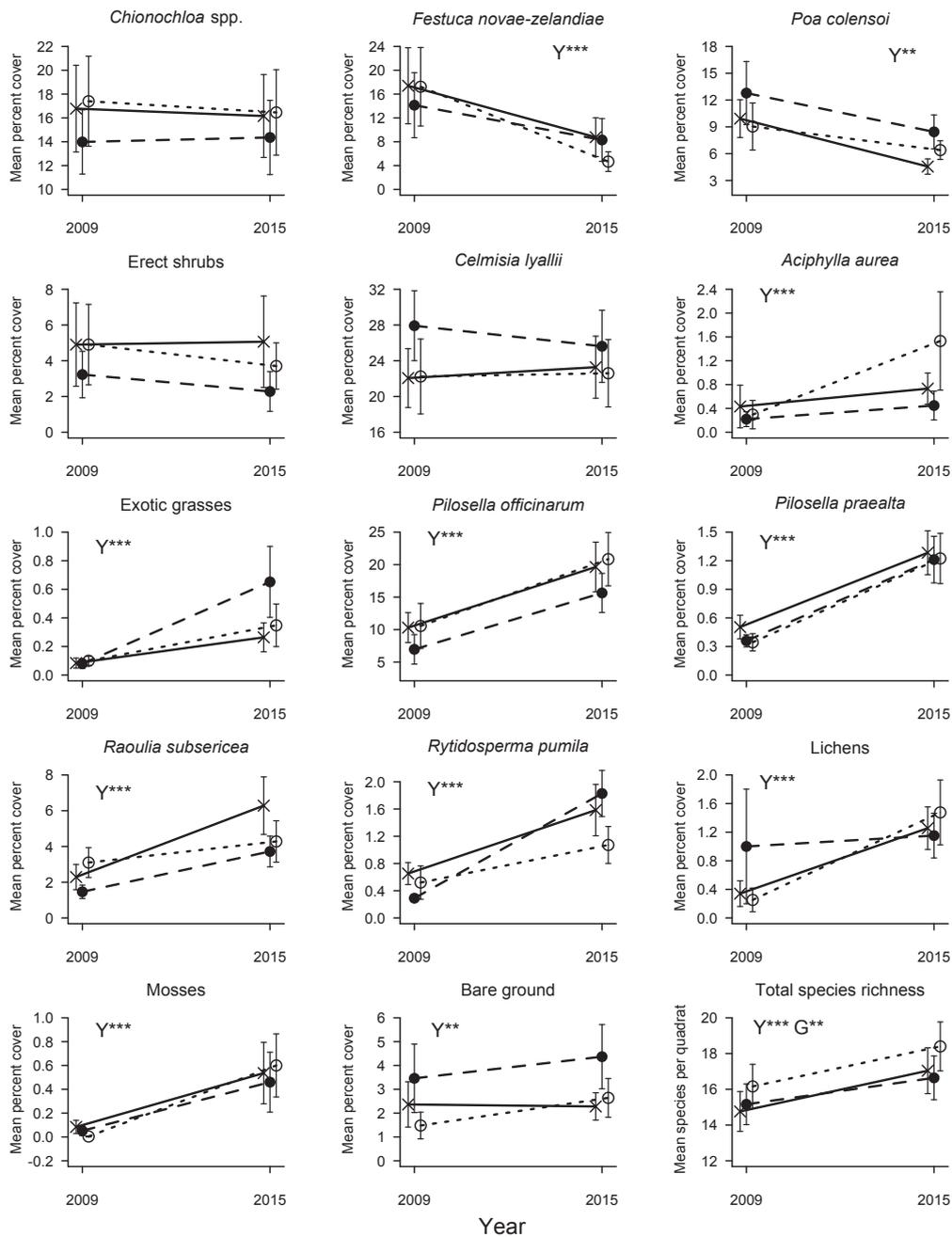


Figure 2. Mean percent cover (± 1 SE) of the dominant, widespread and palatable plant species and species groups, and for vegetation attributes, for the three grazing treatments in 2009 and 2015. Grazing exclusion treatments: - - - - open to all grazing; sheep excluded; ——— all excluded. Only significant effects are indicated (Y = Year, G = Grazing treatment, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$). Note the Y-axis for total species richness is mean number of species per quadrat.

in 30% of the quadrats (where present) and on *Chionochloa* species in 16% of the quadrats (where present), but there were no significant differences in browse scores for these two species between the three grazing treatments; mean browse intensity scores were low for both species (0.4 ± 0.1 and 0.3 ± 0.1 , respectively).

Discussion

We found no evidence for significant change in alpine tussock grassland vegetation relating to the exclusion of sheep or

lagomorph grazing over the 6-year period of this study. This differs from other studies where a strong response to the removal of sheep grazing from tall tussock grasslands has been documented for some species, particularly *Chionochloa*. For example, Mark and Dickinson (2003) observed significant increases in both the cover and height of *C. rigida* after grazing removal at mid-elevations (690–770 m) in Central Otago’s Lammerlaw Range after 16 years and again over the subsequent 14 years. Similarly, at two mid-elevation sites in the Mackenzie Basin (609–944 m), Meurk et al. (2002) observed recovery of degraded *C. rigida* grasslands in some ungrazed sites over a 10-year study period. However, at higher-elevation sites

comparable to those in our study, little or no change in tussock cover has been observed with grazing removal over a 5-year period (Grove et al. 2002). At our sites, overall *Chionochloa* mean percent cover did not change significantly in either of the grazing exclusion treatments between 2009 and 2015.

The lack of vegetation recovery after 6 years of either sheep or sheep and lagomorph grazing exclusion in these alpine tussock grasslands could be the result of three possibly interrelated factors. It may be that the study period was too short to detect any change in vegetation within high-elevation alpine tussock grasslands, as Grove et al. (2002) also noted in their 5-year study. This could be because growth rates are slower and growing seasons are shorter in these high-elevation grasslands, and therefore any response to grazing removal will be slow. Certainly at lower elevations, changes have been detected over longer time periods (10–16 years; Meurk et al. 2002; Mark & Dickinson 2003). Longer periods may be required to see significant changes at higher elevations.

A second possible explanation is that the stocking rate of merinos in these grasslands was too low to have any marked effect on the vegetation. While the estimated stocking rates in our study blocks averaged 0.1 stock unit ha⁻¹ yr⁻¹, the actual stocking rate in the tall tussock grasslands where our enclosure plots were located was possibly lower than this. Steer (2012) monitored the movements of 16 merino ewes with GPS collars during the March–April 2012 summer grazing period in the same grazing blocks in which we worked and observed that their habitat use was not uniform relative to its availability. In particular, merino ewes spent disproportionately large parts of the day in the low-elevation parts of these grazing blocks (river flats and lower hill slopes in short-tussock vegetation), while making little use of the abundant tall tussock grasslands, except for night camps (Steer 2012). Low merino stocking rates coupled with non-random feeding behaviour might also therefore be a factor in the limited response of higher elevation grasslands to grazing exclusion. This is also likely to be the case in other summer grazing blocks, based on anecdotal evidence from farmers about their sheep grazing patterns.

A third factor that is likely to be involved in the limited vegetation response to sheep grazing exclusion is that other mammalian grazers are also likely to be important in these tall tussock grasslands. Hares are widely dispersed through these alpine grasslands, although probably at low densities, and are known to feed on a range of plant genera including *Chionochloa*, *Celmisia* and *Poa*. In alpine grasslands in Cupola Basin, Nelson Lakes National Park, hares mainly grazed *P. colensoi* in summer and species of *Chionochloa* and *Celmisia* in winter (Flux 1967). Although we recorded pellets from only one plot, tahr are major herbivores and are known to occur at high densities in our study area (W. Murray pers. comm.; DAN & LMY pers. obs.). One tahr was observed in one of the enclosure plots in January 2010 (DAN pers. obs.). Parkes and Forsyth (2008) analysed rumen content from 246 tahr shot between 1989 and 1995 from the eastern side of the main divide in similar vegetation communities to those we sampled and observed that tahr diet was dominated by native grasses (56%). *Chionochloa* spp. and *Poa colensoi* were the main grass species consumed, while *Celmisia* and *Aciphylla* species were the most common herbs. Given the presence of hares and especially tahr in the alpine grasslands we studied, it is uncertain whether sheep are actually having a substantial impact over and above that of these other herbivores.

Our ability to compare the effects of different herbivores was limited by the failure of the lagomorph exclusion fencing,

although this probably only occurred within the last 2 years of the study. Maintaining lagomorph exclusion fencing in an alpine environment subject to heavy winter snowfalls is challenging. Snow movement rendered our fencing ineffective against lagomorphs as was evidenced by the presence of pellets in 2015 within the all-excluded treatments. Hare pellets at comparable altitudes (1289–1500 m) in Nelson Lakes National Park had an average decay time of 3 years (Flux 1967), which supports the suggestion that the hare pellets could be 2 years old, matching with our records on the condition of the fencing. While effective at excluding sheep, the exclusion fences were most likely ineffective against tahr due to their ability to jump high obstacles; this was recognised at the outset of the study and therefore this experiment did not quantify the relative impacts of tahr. Furthermore, there was no *Chionochloa* browse recorded in plots open to sheep grazing; all browse occurred inside enclosure plots, suggesting that sheep were not browsing *Chionochloa* in this study, but other herbivores were.

The major vegetation change that occurred over the 6-year period of this study was a significant increase in cover of eight species (or groups of species) and of mean quadrat species richness, and a significant decrease in cover of two species (Fig. 2). Some of these changes involved very small cover values (e.g. mean lichen cover increased from 0.5–1.3%) and may be due to observer differences between the two survey periods, although this is less likely as one observer was the same in both years. However, significant changes that occurred for species that were abundant and/or dominant elements of the vegetation are likely to represent real biological effects. We focus on these changes below.

Mean cover of the exotic *P. officinarum* doubled over the 6-year period from 9.3 to 18.7% (and *P. praealta* cover tripled from 0.4 to 1.2%), while *F. novae-zelandiae* cover decreased to less than half (9.8 to 4.3%) and *P. colensoi* cover to slightly more than half (10.6 to 6.5%). These changes occurred regardless of grazing treatment. Both *Pilosella* species are now widely distributed across the study area, but both are significantly more common at lower elevations (Steer & Norton 2013). The lower abundance of *P. officinarum* at higher elevations might be because it is still expanding its range or because it is less competitive at higher elevations. The fact that we observed a significant increase in *P. officinarum* and *P. praealta* cover over the 6-year study period supports the suggestion that *Pilosella* species are probably still increasing in abundance at higher-elevation sites (Day & Buckley 2011). Interestingly, at one of the enclosure plot sites, *Pilosella* species were still very low in abundance (<0.1% cover). This site is the most isolated from the major seed source (>5 km compared with <1 km for the other four sites), which is the main Cass River valley where both *Pilosella* species are abundant (Dickinson & Norton 2011; Steer & Norton 2013). Re-measurements of *Pilosella* cover at these study sites in the future will provide valuable insight into future population dynamics of *Pilosella* species in alpine grasslands in the area.

It is widely reported that a decrease in *F. novae-zelandiae* abundance is correlated with increasing abundance of *Pilosella* spp., irrespective of grazing (Scott et al. 1988; Rose et al. 1995, 2004; Meurk et al. 2002), although these studies have all taken place in lower-elevation, induced short tussock grasslands. It is interesting to see the same pattern emerging in natural alpine tall tussock grasslands, again irrespective of grazing. However, without more information it is difficult to ascribe a cause and effect relationship. Direct competition with *Pilosella* species may well be a key factor in the decline

of *F. novae-zelandiae* (e.g. Rose et al. 1995, 2004). However, it has also been suggested that this decline could be due to senescence of even-aged cohorts resulting from historic burning (Holdaway et al. 2014), although burning was not a factor in our study. A third factor in the decline of *F. novae-zelandiae* and *P. colensoi* might be preferential browse by tahr (Parkes & Forsyth 2008), which had access to all grazing exclusion treatments. Our results suggest that the increase in *Pilosella* species and the decline in *F. novae-zelandiae* and *P. colensoi* are either occurring independently of sheep grazing or, if this is a factor, then summer grazing by sheep appears to be having little effect over and above that of other grazers in these systems (lagomorphs and tahr).

It is interesting to question whether these alpine grasslands are likely to recover to any pre-European condition if current livestock grazing is removed. It would seem likely that the long history of livestock grazing (O'Connor 1982) coupled with ongoing grazing by the full range of herbivores is likely to have eliminated many palatable plant species. There is evidence that many previously widespread species in alpine ecosystems are now largely confined to herbivore-free refugia (Norton 1995). Even where palatable species may survive in such refugia, seed dispersal limitations (Young 2012), coupled with changing biotic (competition, mutualists, etc.; Moen & Meurk 2001) and abiotic (Payne & Norton 2011) conditions, may still filter what vegetation recovery is possible. Sheep exclusion alone may therefore be unlikely to allow full vegetation recovery, especially in the presence of other grazing mammals.

Conclusions

We found no evidence for vegetation recovery after six summers of excluding sheep grazing from alpine tall tussock grassland. This is perhaps partly because of the short time over which this study was conducted, the low sheep-stocking rates and non-random grazing behaviour of merino ewes, and/or the influence of other grazing animals in the system. Notwithstanding the short time period of this study, the significant increase in abundance of two *Pilosella* species and decrease in *F. novae-zelandiae* and *P. colensoi* shows that alpine grasslands can change over relatively short time frames. This replicated trial provides the opportunity to remeasure future responses to quantify the longer-term trends in *Pilosella* abundance and its potential impact on these alpine grasslands.

The impacts of hares, in particular, on alpine grasslands are poorly understood and, as such, likely to be underestimated. Despite one of the primary objectives of this study being to understand the relative impacts of lagomorphs (particularly hares) on alpine grasslands, our lagomorph exclusion treatment was ineffective due to snow damage to fences during the later part of the study. Thus, there remains a strong need to better understand the relative impacts of sheep, lagomorphs, and tahr in these alpine grasslands. This can be done either through using alternative fencing methods to exclude different types of grazers, or by taking another approach to address this issue, e.g. faecal analysis coupled with feeding behavioural studies (Flux 1967; Young et al. 2012). Such approaches will allow better interpretation of whether summer grazing by merino ewes has any significant impact on alpine tussock grasslands at the stocking rates occurring in this study over and above the impacts of lagomorphs and tahr, allowing for more informed decision making about the future management of these alpine grasslands.

Acknowledgements

We thank the Murray family for permission to undertake this research on Glenmore Station, Will Murray, Josh Harrex and Tony Payne for assistance in building the enclosure fences, and Peter Espie for assisting with initial vegetation measurements. We thank Jason Tylianakis for statistical advice, Nicola Day, Robert Holdaway, and Dave Kelly for commenting on early drafts of the manuscript, and two anonymous reviewers for their constructive comments. This research was supported with funding from the University of Canterbury and the Tindall Foundation.

References

- Antonelli A, Humphreys AM, Lee WG, Linder HP 2011. Absence of mammals and the evolution of New Zealand grasses. *Proceedings of the Royal Society B* 278: 695–701.
- Caughley G 1989. New Zealand plant-herbivore systems: past and present. *New Zealand Journal of Ecology* 12: 3–10.
- Day NJ, Buckley HL 2011. Invasion patterns across multiple scales by *Hieracium* species over 25 years in tussock grasslands of New Zealand's South Island. *Austral Ecology* 36: 559–570.
- Day NJ, Buckley HL 2013. Twenty-five years of plant community dynamics and invasion in New Zealand tussock grasslands. *Austral Ecology* 38: 688–699.
- Dickinson Y, Norton DA 2011. Divergent small-scale spatial patterns in New Zealand's short tussock grasslands. *New Zealand Journal of Ecology* 35: 76–82.
- Flux JEC 1967. Hare numbers and diet in an alpine basin in New Zealand. *Proceedings of the New Zealand Ecological Society* 14: 27–33.
- Gitay H, Lee WG, Allen RB, Wilson JB 1992. Recovery of *Chionochloa rigida* tussocks from fires in South Island, New Zealand. *Journal of Environmental Management* 35: 249–259.
- Grove PB, Mark AF, Dickinson KJM 2002. Vegetation monitoring of recently protected tussock grasslands in the southern South Island, New Zealand. *Journal of the Royal Society of New Zealand* 32: 379–414.
- Holdaway RJ, Rose AB, Newell CL, Carswell FE 2014. Demographic drivers of biomass carbon recovery in degraded perennial tussock grassland, with and without domestic grazing. *New Zealand Journal of Ecology* 38: 221–229.
- Jensen CA, Webster RJ, Carter D, Treskonova M 1997. Succession in tussock grasslands: implications for conservation management. *Science for Conservation* 61. Wellington, Department of Conservation. 30 p.
- Lee WG, Fenner M, Duncan RP 1993. Pattern of natural regeneration of narrow-leaved snow tussock *Chionochloa rigida* ssp. *rigida* in Central Otago, New Zealand. *New Zealand Journal of Botany* 31: 117–125.
- 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: 655–668.
- Mark AF, McLennan B 2005. The conservation status of New Zealand's indigenous grasslands. *New Zealand Journal of Botany* 43: 245–270.
- McGlone MS 2001. The origin of the indigenous grasslands of

- southeastern South Island in relation to pre-human woody ecosystems. *New Zealand Journal of Ecology* 25: 1–15.
- McGlone MS, Webb CJ 1981. Selective forces influencing the evolution of divaricating plants. *New Zealand Journal of Ecology* 4: 20–28.
- Meurk CD, Walker S, Gibson RS, Espie P 2002. Changes in vegetation states in grazed and ungrazed Mackenzie Basin grasslands, New Zealand, 1990–2000. *New Zealand Journal of Ecology* 26: 95–106.
- Moen J, Meurk CD 2001. Competitive abilities of three indigenous New Zealand plant species in relation to the introduced plant *Hieracium pilosella*. *Basic and Applied Ecology* 2: 243–250.
- Norton DA 1995. Vegetation of goat-free islands in a low-alpine lake, Paparoa Range, and implications for monitoring goat control operations. *New Zealand Journal of Ecology* 19: 67–72.
- O'Connor KF 1982. The implications of past exploitation and current developments to the conservation of South Island tussock grasslands. *New Zealand Journal of Ecology* 5: 97–107.
- O'Connor KF 2003. Conflicting innovations: a problem for sustainable development of New Zealand high-country grasslands. *Mountain Research and Development* 23: 104–109.
- Oksanen F, Blanchet G, Kindt R, Legendre P, Minchin PR, O'Hara RB, Simpson GL, Solymos P, Stevens MHH, Wagner H 2013. Vegan: community ecology package, version 1.17-0. R package version 2.0-10. Available from: <http://CRAN.R-project.org/package=vegan/>
- Parkes JP, Forsyth DM 2008. Interspecific and seasonal dietary differences of Himalayan thar, chamois and brushtail possums in the central Southern Alps, New Zealand. *New Zealand Journal of Ecology* 32: 46–56.
- Payne T, Norton DA 2011. Influence of shade on soil and foliage water in a depleted short tussock grassland, Mackenzie Basin. *New Zealand Natural Sciences* 36: 21–31.
- Perry GLW, Wilmshurst JM, McGlone MS 2014. Ecology and long-term history of fire in New Zealand. *New Zealand Journal of Ecology* 38: 157–176.
- R Core Development Team 2011. R: a language and environment for statistical computing. Vienna, Austria, R Foundation for Statistical Computing. <http://www.r-project.org/>
- Rose AB, Platt KH 1992. Snow tussock (*Chionochloa*) population responses to removal of sheep and European hares, Canterbury, New Zealand. *New Zealand Journal of Botany* 30: 373–382.
- Rose AB, Platt KH, Frampton CM 1995. Vegetation change over 25 years in a New Zealand short tussock grassland: effects of sheep grazing and exotic invasion. *New Zealand Journal of Ecology* 19: 163–174.
- Rose AB, Suisted PA, Frampton CM 2004. Recovery, invasion, and decline over 37 years in a Marlborough short-tussock grassland, New Zealand. *New Zealand Journal of Botany* 42: 77–87.
- Scott D, Dick RD, Hunter GG 1988. Changes in the tussock grasslands in the central Waimakariri River basin, Canterbury, New Zealand, 1947–1981. *New Zealand Journal of Botany* 26: 197–222.
- Scroggie MP, Parkes JP, Norbury G, Reddiex B, Heyward R 2012. Lagomorph and sheep effects on vegetation growth in dry and mesic grasslands in Otago, New Zealand. *Wildlife Research* 39: 721–730.
- Steer MA 2012. Merino sheep habitat use in Canterbury high country tall tussock grasslands. MSc thesis, University of Canterbury, Christchurch, New Zealand.
- Steer MA, Norton DA 2013. Factors influencing abundance of invasive hawkweeds, *Hieracium* species, in tall tussock grasslands in the Canterbury High Country. *New Zealand Journal of Botany* 51: 61–70.
- Swaffield S, Hughey K 2001. The South Island high country of New Zealand. *Mountain Research and Development* 21: 320–326.
- Treskonova M 1991. Changes in the structure of tall tussock grasslands and infestation by species of *Hieracium* in the Mackenzie Country, New Zealand. *New Zealand Journal of Ecology* 15: 65–78.
- Wardle P 1991. *Vegetation of New Zealand*. Cambridge, Cambridge University Press. 672 p.
- Young LM 2012. Seed dispersal mutualisms and plant regeneration in New Zealand alpine ecosystems. PhD thesis, University of Canterbury, Christchurch, New Zealand. 165 p. <http://hdl.handle.net/10092/6992> (accessed 27 August 2015).
- Young LM, Kelly D, Nelson XJ 2012. Alpine flora may depend on declining frugivorous parrot for seed dispersal. *Biological Conservation* 147: 133–142.

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Received 1 June 2015; accepted 19 August 2015