Ecological Responses to 52 Years of Experimental Snow Manipulation in High-Alpine Cushionfield, Old Man Range, South-Central New Zealand

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Abstract

Periodic monitoring over 52 years have revealed temporal changes in the vegetation and floristic patterns associated with what has been acclaimed to be the world's oldest known experimental snow fence, which is located on an exposed high-alpine cushionfield on the Old Man Range in south-central New Zealand. The induced pattern of intermittent snow-lie has been increased by the fence from the normal ~140 days to more than 200 days (and up to 140 cm deep), estimated from subsurface soil temperatures, together with periodic observations and measurements of snow depth. Some but not all species associated with natural snowbanks on the range have established in areas of induced snow accumulation. The timing of species establishment was not obviously related to relevant features of the local snowbank species or their distribution on the range, but the abundance of various plant species and their functional traits across zones of snowmelt point to competition and plant productivity being associated with the deepest snow in the lee of the fence. In addition, three of the several measured physical and chemical soil factors (Mg, available PO_4^{3-}, and C:N) have differentiated significantly in relation to the vegetation and snow-lie pattern at year 52, although these seem not to be relevant on the basis of the pattern of the same factors in two nearby natural snowbanks on the range.

Introduction

Snow cover and its duration are among the most important factors controlling microenvironments and habitat conditions in the alpine zone, globally (Bliss, 1963; Gjaerevoll, 1956, 1965; Helm, 1982; Gibson and Kirkpatrick, 1985; Isard, 1986; Kudo and Ito, 1992; Walker et al., 1993; Grabherr, 1997; Körner, 2003; Björk and Molau, 2007). New Zealand studies to date have shown a strong relationship between duration of snow-lie and plant community structure and composition (Mark and Bliss, 1970; Hadley and Rosen, 1974; Burrows, 1977a, 1977b; Talbot et al., 1992; Bannister et al., 2005), as with many studies abroad.

One aspect of research on the effects of climate change concerns the ecological effects of predicted changes in the duration of winter snow cover. Several empirical studies have involved designing fencing systems to experimentally alter snow cover (Walker

et al., 2001). A recent review of such studies by Wipf and Rixen (2010) has ranked an experimental snow fence built in 1959 at 1650 m elevation in exposed high-alpine cushionfield near the crest of the Old Man Range (1682 m), south-central New Zealand, as one of the oldest continuously running snow ecology experiments in Arctic and alpine ecosystems.

The fence was originally built as part of a study to retain additional snow and augment water discharge into its catchment, used downstream for both irrigation and hydroelectric generation. Several seedlings of five subalpine North American tree species (*Pinus contorta*, *P. flexilis*, *P. aristata*, *Picea engelmanni,* and *Abies lasiocarpa*) were planted behind the fence and alongside it to the north in 1961, as well as at four lower elevation sites on the mountain, to assess their potential. Only *P. contorta* established but remained dwarfed and nonreproductive at the snow fence site, and these were removed with minimum disturbance together with all plants from the other sites in March 1974 to assess their performance. Despite its effectiveness, no other fences were built (Harrison, 1986a, 1986b). Located on the upper windward slope of the range, the 12 × 2 m fence is made of 100 × 25 mm wooden slats placed vertically at 50% density and set at 7° off-vertical angle. It is aligned across a gentle (~5°) slope, normal to the prevailing westerly (SW to NW) winds (Fig. 1). A netting fence, built around the site in 1961 (6 m windward and 30 m leeward) to exclude sheep, was removed in 1998 when the area became conservation land and grazing stock were removed.

Since its construction, periodic monitoring of the surrounding vegetation (up to 2011: year 52) has shown that the presence of the snow fence has modified the cushionfield vegetation in its vicinity. In the initial study, Harrison (1986b) reported on both the drift pattern (based on a central transect perpendicular to the fence) and the duration and density of the drifted snow, in addition to initial observations of the snow-lie pattern. He reported the snow drift in October 1976 was 21 m in length with the greatest snow depth (2.1 m) occurring within 12 m of the fence. The snow density was somewhat greater within the pack (500 kg m^{-3}) than at nearby control sites (est. 450 kg m^{-3}) (Harrison, 1986b), although both conform with "old snow" according to Körner (2003, p. 47). Harrison (1986b) was the first to report on changes to the structure and composition of the alpine plant community in the immediate vicinity of the fence (based on point samples in the 1978–1979 season). More specifically, the dominant plant species of the cushionfield, *Dracophyllum muscoides*,[1] was reduced from 49% cover to merely 4%, while the cover of litter (17%) and bare ground (12%) had increased slightly (21% and 15%, respectively) behind the fence. Despite an observed increase in species richness, two lichens (*Thamnolia vermicularis* and *Cetraria islandica* subsp. *antarctica*) had disappeared from behind the fence at this time. Harrison (1986b) also reported that drifts of snow produced by the fence persisted up to five weeks after it had thawed from the surrounding area. However, he did not comment on the short-term drifts that may periodically follow snowstorms that can occur at any time during the snow-free period (Alan Mark, personal observation).

Harrison (1986b) correctly predicted that, because of the slow growth and establishment of plants in the area, the process of adjustment may be continuing. This has been demonstrated with several subsequent studies, the latest in 2011, 52 years after erection of the fence, including an analysis of plant functional traits in order to determine potential mechanisms of plant community change. Here we describe these more detailed studies and the ecological effects of the snow fence up to year 52 (2011), and compare

these results with those from three separate studies of natural snow banks on the range (Mark and Bliss, 1970; Korsten, 2011; Guevara, 2012). Although snow fences are not uncommon in alpine regions abroad, most have been built to manage drifting snow for various purposes, and relatively few have been purpose built for studying the ecological effects of artificially manipulating snow depth and the duration of snow-lie, according to Wipf and Rixen (2010), who credit our study as the longest on record by 15 years.

Methods

STUDY SITE

The snow fence was built at 45°19′31″S, 169°11′50″E and 1650 m elevation, on the upper western slope of the Old Man Range (1682 m) (Fig. 1), which, like the other block-faulted high plateau mountains of Central Otago, is characterized by relatively low summer temperatures, near-freezing mean annual air temperature, frequent freeze-thaw cycles throughout the five-month growing season, very strong westerly winds, and a persistent winter snow cover (see Mark, 1994, and references therein).

SNOW-LIE PATTERNS AND SOIL TEMPERATURES

We used snow depth data as recorded by Smith (Smith, 1991; Smith et al., 1995) with a graduated stake on a 3 × 2 m grid covering the 50 × 30 m study site; he also measured wind speed with a handheld anemometer at 15 cm height at each of his 100 quadrat locations (Smith, 1991). In addition, we photographed the snow pattern periodically (Fig. 1), and measured its depth on 20 October 2004, also on a 3 × 2 m grid, but over the reduced (30 × 20 m) study site (122 grid intersections), using a surveyor's level and graduated staff (Fig. 2). The ground surface profile was similarly measured when the site was snow-free.

The number of days with snow cover was derived from subsurface (–1 cm) and soil (–10 cm) temperatures as measured over two years with two Campbell (Model CR-10) data loggers, installed in April 2003. Sensors were located at 3 m intervals along a transect, bisecting the center of the snow fence from 5 m to its windward to 24 m to leeward (Fig. 3). The criteria of Fosaa et al. (2004) were used to determine presence of snow cover: days with a daily range <0.5 °C and a daily average subsurface (–1 cm) temperature of <1 °C. These records were compared with data collected from soil (–10 cm) using the same criteria. Additional sensors were placed at 5 and 20 cm depths at 2 of the 10 positions, one 4 m to leeward of the fence, associated with maximum snow accumulation, and the second 20 m to leeward where snow was minimal.

SOIL NUTRIENTS AND PH

Relationships between several soil macronutrients and pH, and snow-lie were assessed at year 52 (mid-April 2011) by Guevara (2012). Near-surface (0–10 cm) soil samples of 150 cm^3 were pooled from subsamples taken from the alternate corners of all 120 quadrats from the extended study site (see below). Samples were bagged and stored frozen until defrosted overnight and immediately analyzed at room temperature. Stones and traces of roots were removed with forceps before 20 g were taken for analysis of NO_3-N and NH_4^+-N. The remainder was then dried at 35 °C for 24 h and sieved (2 mm) for analyses of total N, total C, available PO_4^{3-}, Ca, K, Mg, and pH. Spectrophotometry (Carter, 1993) was used to analyze the two N components, as well as available PO_4^{3-} (Olsen et al., 1954; Blakemore et al.,

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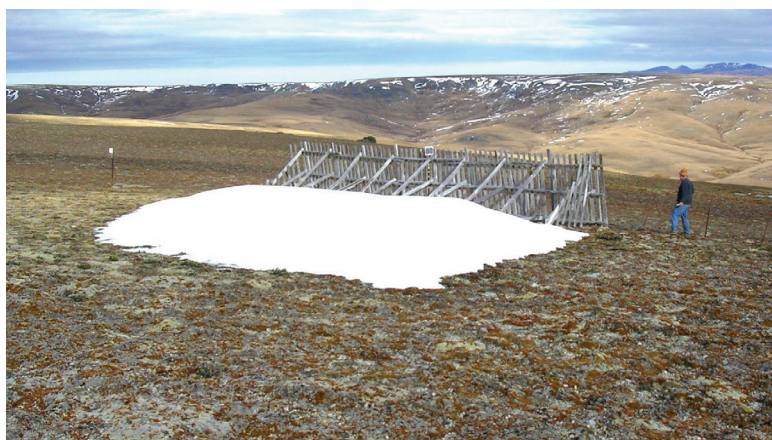[1]Nomenclature follows that of Mark (2012).

FIGURE 1. (Upper) View northeast to the crest of the Old Man Range in midwinter, showing accumulation of snow behind the snow fence, and a generally thin snow cover with a mostly icy surface in the foreground, indicating snow removal by the prevailing westerly wind. 2 July 1962. (Lower) View southwest, showing a late autumn pattern of snow-lie in the lee of the snow fence, typical of the temporary snow-lie during the nonwinter period. Note that snow has also accumulated in natural snowbanks on the leeward slope above the western side of the Fraser basin in the distance. 19 May 2005.

1987), Ca, Mg, and K (Carter, 1993; Varian SpectrAA, 2000). Total N and total C were determined using the Dumas combustion method (Elementar Vario Max CNS, 2004) following Rowell (1994), and pH (in water) was measured using an electronic pH meter (Orion 420A) following Blakemore et al. (1987).

VEGETATION MONITORING

Following the initial observations by Harrison (1986b) in the 1978–1979 season at year 20, monitoring of the temporal changes associated with the snow fence has been based on stratified ran-
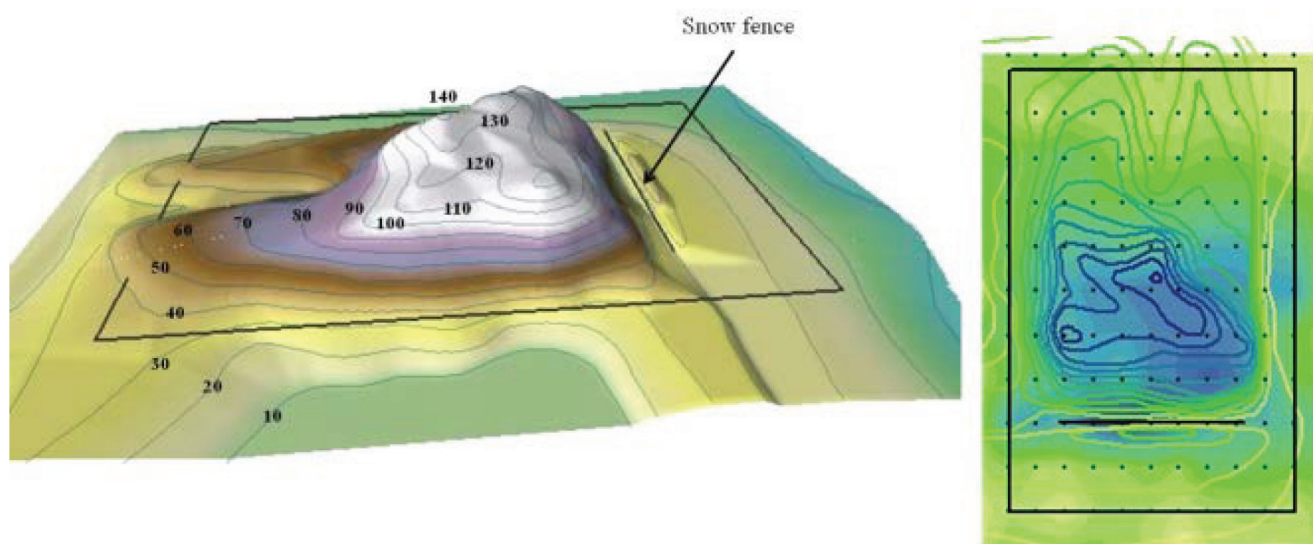

FIGURE 2. Snow depth pattern in relation to the snow fence, as recorded in May 1991 by Smith (1991), shown for the smaller (30 × 20 m) study site, with 10 cm contour lines. The maximum depth is 140 cm; the minimum is <10 cm. The 3 × 2 m grid pattern, together with the contour lines, is shown on the flat image (right).
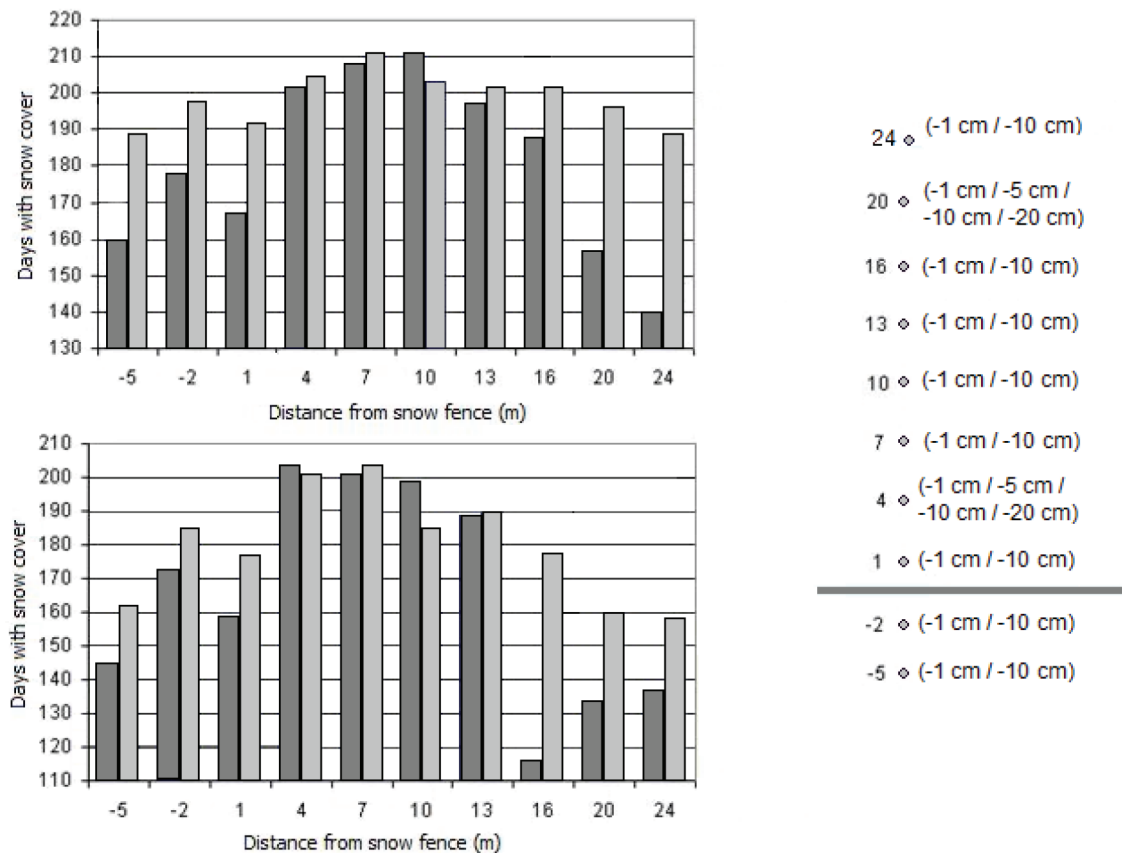
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FIGURE 3. Number of days with snow cover along a transect through the center of the 20 × 30 m study site (see panel on right), based on subsurface (–1 cm) and soil (–10 cm) daily temperatures during the main snow-lie period (May–November) for two years, 2003 (above) and 2004 (below).

dom methods using quadrats. In the summer of 1990–1991, year 32, Smith (Smith, 1991; Smith et al., 1995) used 100 0.25 × 0.25 m quadrats with 25 5 × 5 cm subquadrats to sample local shoot frequency and percent cover (eye estimates, assisted by the 25 subquadrats) of plant species, together with that of four nonplant types—rock, stone pavement, bare soil, and dead plants—in a stratified random design on a 50 × 30 m study site surrounding the snow fence (Fig. 4, part A). The site extended 20 m windward and 30 m leeward of the fence, with a 9 m strip on either side. This sampling pattern was retained but, because the quadrat size was subsequently considered too small for an adequate sample, it was enlarged (0.5 × 0.5 m with 25 10 × 10 cm subquadrats) when next sampled in January 2002 (i.e., southern hemisphere summer), at year 43. Using the larger quadrat increased the sampled area from <0.5% (0.42%) to 1.67% of the 50 × 30 m study site, but inspection of the 2002 results indicated that the density of sampling in the immediate lee of the snow fence was too sparse to adequately record the obvious floristic variation that was then present.

Consequently, the area of the study site was reduced to 30 × 20 m, with the fence located 6 m from the windward edge, 24 m from the leeward edge, and 4 m in from the lateral edges (Fig. 4, part B).

This smaller study site, which contained 44 quadrats of the original 100, appeared to provide an adequate margin unaffected by the snow fence, but the quadrat number was now considered inadequate. Hence, sampling was repeated one year later, using a stratified random sample with 100 2 × 3 m grid cells, each with the

same 0.5 × 0.5 m quadrats as used previously and again randomly located within each of the grid cells (Fig. 4, part B). Both local shoot frequency and percent cover were again recorded, as with the 2002 sampling. This 2003 sample covered 4.2% of the reduced study site and this method was repeated at year 52, using the same quadrat placings, in January 2011. The study site was extended 4 m along the northern margin at this time, in response to results of the previous (2003) sample, which showed the effects of the snow fence had aligned with this boundary.

In order to follow the changing pattern of species colonization and distribution over time, we used percent cover and shoot frequency values of individual plant species, and percent cover of rock, pavement, bare soil, and dead plants in each quadrat, as recorded in 1991 (Smith, 1991; personal communication, 2001), 2002, 2003, and 2011. Lichens and the minor bryophytes were not recorded in 2011 and so are not included in the 2003 versus 2011 comparison. All data were square root transformed and standardized prior to being analyzed in the software package Primer v6 (Clarke, 1993). We defined plant community groups for each monitored year by running a hierarchical clustering analysis on the Bray-Curtis similarity matrix and tested the resulting cluster groupings for significance ($p < 0.05$), using a SIMilarity PROfile (SIMPROF) permutation test (Clarke and Gorley, 2006; Clarke et al., 2008). We then used a SIMilarity PERcentages (SIMPER) analysis to determine discriminating species that contributed most to average similarity within each of the quadrat (community) groups and average dissimilarity between particular quadrat groups.
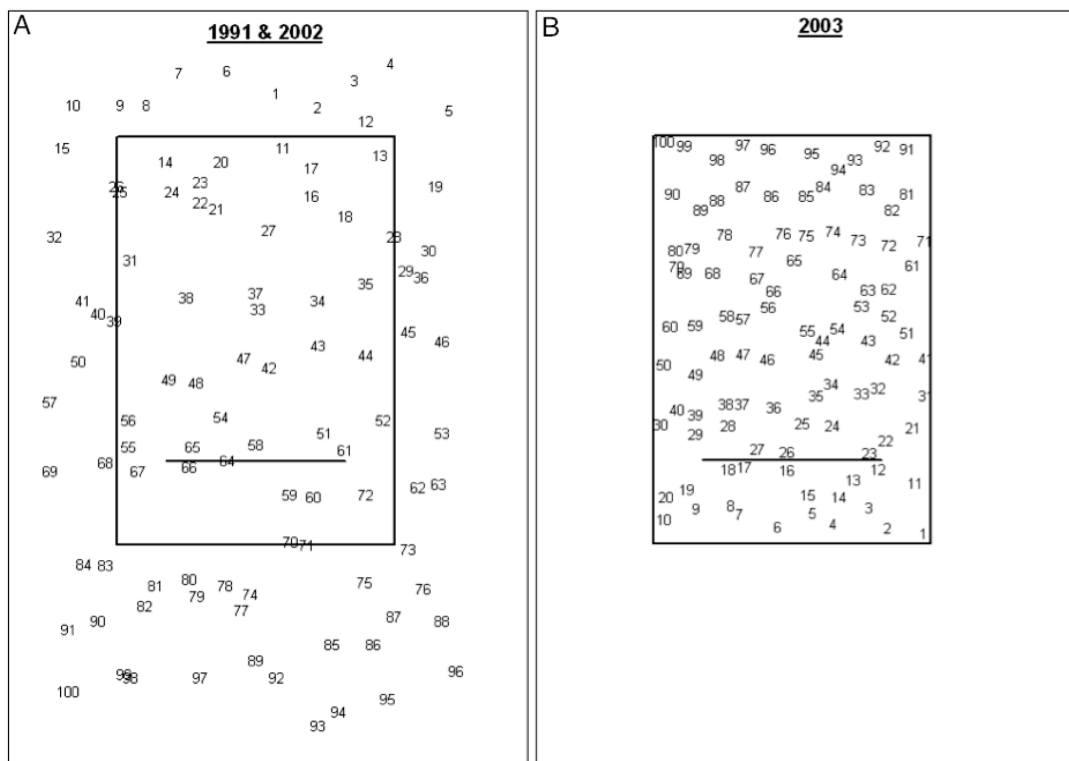
FIGURE 4. Sampling plan for (A) the larger (30 × 50 m) study site with 100 quadrat sites in a stratified random pattern, as used in 1991 and 2002, and (B) the smaller (20 × 30 m) study site with 100 quadrats (B), also distributed in a stratified random pattern, in relation to location of the snow fence (lower center) as used in 2003 and 2011.

To determine species response to variation in snow depth, we tested correlation between frequency values for plant species and the four nonplant categories, recorded in 2003, with snow depth as measured in May 1991 (Smith et al., 1995), using Spearman rank correlation coefficients.

Spatial patterns of changes in frequency between 2003 and 2011, of selected species were illustrated in GIS ARCMap9.0. The central location of each sampling quadrat was entered to generate a shapefile and the vegetation sampling records then added as attribute data.

ASSESSMENT OF PLANT FUNCTIONAL TRAITS

Several morphological functional traits were measured, during the 2010–2011 season, for every species recorded within each of 12 50 × 50 cm quadrats, randomized within the three subsections of the study site recognized at that time (2003 in Fig. 5). We measured leaf dry matter content (LDMC), specific leaf area (SLA), leaf nitrogen content, plant height, and seed mass from at least 10 individuals for each species in order to produce a mean value for each trait for each species. Leaf samples were collected from individuals in the general vicinity of the snow fence, not from the plot. We chose these traits as they are indicative of a range of ecological processes that are important for community functioning and dynamics (McGill et al., 2006; Westoby et al., 2002), and which are likely to have changed given the altered snowmelt regime at this site. Both LDMC and SLA are indicative of a plant's strategy for conserving, capturing, and allocating resources (Cornelissen et al., 2003). Additionally, leaf nitrogen content has been closely linked with mass-based photosynthetic rate and therefore indicates productivity (Cornelissen et al., 2003). Plant

height can indicate a species competitive ability, while seed mass indicates a range of reproductive strategies, including dispersal and successful seedling establishment (Westoby et al., 1996; Cornelissen et al., 2003).

In order to demonstrate functional differences between different snowmelt zones behind the snow fence, and allude to the ecological processes operating at the site, we calculated the community trait-weighted mean (CTWM) separately for each of the four traits for the species recorded in 2011 in an adjacent area, beyond the influence of the snow fence, in the mid-melting zone and in the late-snowmelt zone, as defined in 2003. The CTWMs were calculated by the method proposed by Mason et al. (2003), interpreted by Mason et al. (2005), and modified by Lepš et al. (2006). This method allowed calculation of the relative abundances of individual trait responses to the different snowmelt zones, weighted by the absolute individual species abundances. We utilized the software of Lepš and de Bello (2008) to assist in scaling our trait and abundance values for the data from the three snowmelt zones to calculate the CTWM values. Differences in mean CTWMs between the snowmelt zones were assessed by examining the overlap of the 95% confidence intervals from a normal distribution of the data (Cumming and Finch, 2005)

We then modeled the probability of every species and life form group (graminoid, cushion, forb, shrub) occurring in either the snow accumulation area behind the snow fence or in the adjacent area outside of the influence of the snow fence, using the trait information and the species abundances in either zone, with ordinal regression, logistic regression, and generalized linear models with a logit link function. The models were fitted in R 2.15.1 using the package "Ordinal" (Christensen, 2012; R Core Team, 2012).
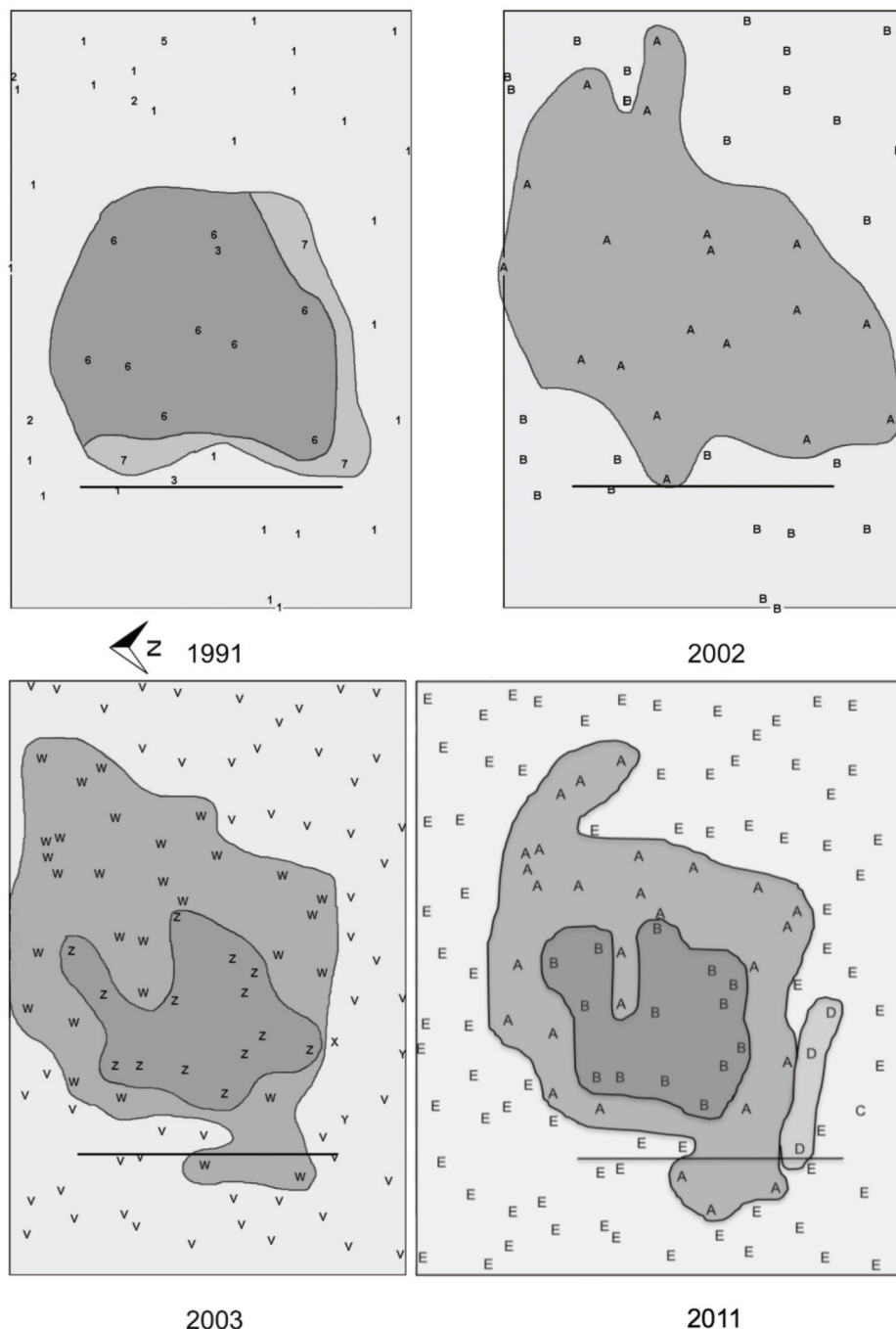
FIGURE 5. Changes in alpine plant community patterns on the 20 × 30 m study site from 1991 to 2011, in relation to the snow fence, with an angle slightly to the north, consistent with the pattern of snow-lie (see Fig. 2). Note that the density of sampling increased between the 2002 and 2003 sampling and the site was extended 4 m along the northern boundary for the 2011 sampling. Letters indicate species grouping derived from the cluster analyses of shoot frequency data. Shading represents the communities recognized (species groups: dark = one or two snowbank communities and light = cushionfield community). See text for further details.

Comparisons were also made using one-way ANOVA, between functional traits of species that had established behind the fence and snow bank species on the range that had not yet established. Data were tested prior to analysis for normality and equality of variance.

WIND-BORNE MATERIAL TRAPPED BY THE SNOW FENCE

Four "coir plain" (coconut fiber) mats, 74 × 45 cm, were pinned down, equi-spaced 2.0–2.5 m behind the fence in mid-autumn (21 March) 2014, with the intention of trapping wind-borne material, including propagules and plant fragments which might include species that had established since its construction.

The mats were emptied 9 and 12 months later (15 December 2014 and 24 March 2015) by inverting them on a plastic sheet and beating ~20 times with a flat steel handle. The extracted material was stored in sealed vials for weighing (air-dried) and then placed in separate petri dishes and moistened with a complete nutrient solution to check for viable seed.

DATA ARCHIVED

All of the vegetation data (percent cover and frequency) for the 2002, 2003, and 2011 sampling, together with results of the 2011 soil analyses, have been stored on a CD, which is appended to the Department of Botany's copy of Guevara (2012).
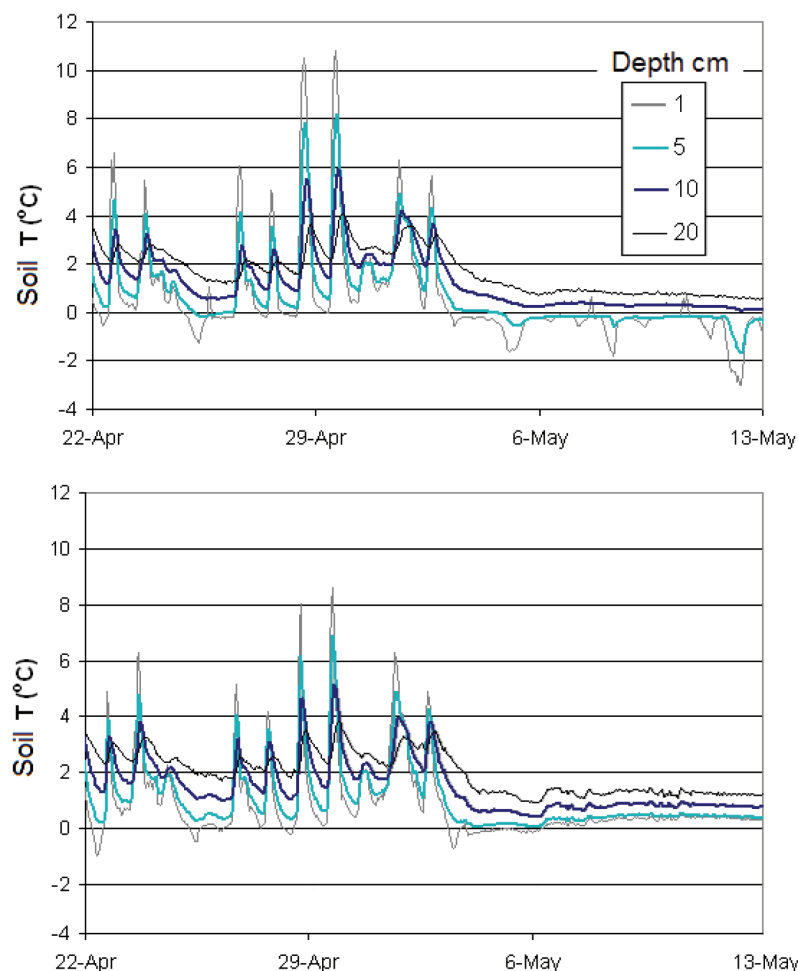
FIGURE 6. Soil temperatures at four depths (–1, –5, –10, and –20 cm) at two sites, one beyond the influence of snow accumulation associated with the snow fence (above), the other near the site of maximum snow accumulation, 4 m to leeward of the fence. Values over this 21-day period in late autumn (22 April–13 May) in 2003, show the contrasting effects between these sites in relation to snow accumulated from a fall on May 4.

Results

SNOW-LIE PATTERNS AND SOIL TEMPERATURES

Snow persisted behind the fence over winter and for shorter periods at other times, and up to ~140 cm deep during most winters (Figs. 1–2). Of the several measurements made, those recorded by Smith (1991) appeared to be typical, with a maximum depth of ~140 cm and decreasing to <10 cm in the surrounding area (Fig. 2), and so these records were used to determine species response to variation in snow depth in all subsequent analyses.

The number of days with snow cover for each of the 2003 and 2004 winters was estimated from the daily course of temperatures from continuous records on both the subsurface (–1 cm depth) and soil (–10 cm) across the transect bisecting the center of the snow fence (Fig. 3). Differences in the estimates between the two methods were further analyzed by viewing the course of temperatures on those days where the results differed between the two assessments. We concluded that the subsurface (–1 cm) temperatures provided a better parameter for snow cover than those at –10 cm, since they responded more rapidly to changes in snow cover. On this basis, we assumed that the annual duration of snow cover exceeded 200 days at 4 to 10 m behind the fence and declined irregularly to about 160 days in the immediate lee, and also further down-wind, to reach values of the surrounding area (~140 days) some 16 to 24 m from the fence (Fig. 3).

Soil temperatures at four depths (1, 5, 10, and 20 cm) at sites with contrasting snow accumulation, 4 m and 20 m behind the snow fence, over a three-week period before and after a snowfall, showed the moderating effect of the fence both before and following snow accumulation (Fig. 6). Without snow cover, daily temperature maxima were up to 2 °C higher in the subsurface (–1 cm) and about 1 °C lower at 20 cm depth behind the fence than away from its influence, while minima were only slightly less variable, but both sites experienced subfreezing temperatures at 1 cm depth. Following a snowfall on 4 May 2003, however, temperatures became less variable close (4 m) behind the fence, particularly the subsurface (–1 cm), where they remained relatively stable at about 0.5 °C, while temperatures fell to –3 °C at this depth well away (20 m) from the fence (Fig. 6).

SOIL NUTRIENTS AND PH

Of the 10 factors analyzed, only three showed significant correlations with snow depth: Mg ($F_{1.48} = 7.0$, $p < 0.01$) and available PO_4^{3-} ($F_{1.48} = 9.8$, $p < 0.01$) were positively correlated while the C:N ($F_{1.48} = 4.4$, $p < 0.05$) was negatively correlated (Guevara, 2012). Values for Mg increased from 0.10 ± 0.02 to 0.16 ± 0.03 me 100 g^{-1} and for PO_4^{-3} from 8.08 ± 0.57 to 9.71 ± 0.40 ppm with increasing snow depth, while the C:N decreased from 17.85 ± 0.06 to 16.28 ± 0.38. The values for NO_3^{-}-N ranged from 9.60 ± 0.79 to 10.69 ± 0.24 ppm,

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those for NH_4^+-N from 14.26 ± 1.92 to 16.51 ± 1.82 ppm, while values for K varied from 0.24 ± 0.02 to 0.27 ± 0.02 me 100 g^{-1}, those for Ca from 0.36 ± 0.08 to 0.40 ± 0.08 me 100 g^{-1}, with total N ranging from $0.14\% \pm 0.01\%$ to $0.15\% \pm 0.01\%$, and total C from $2.32\% \pm 0.15\%$ to $2.51\% \pm 0.20\%$, while pH varied from 4.80 ± 0.05 to 4.87 ± 0.02 (Guevara, 2012). Values for total C, total N, K, Ca, and Mg were all highly correlated with each other (all $r > 0.45$; $p < 0.001$) and less so with NH_4^+-N (all $r < 0.45$; $p < 0.05$, except for Mg). Values for pH were negatively correlated with total C, total N, C:N, K, and Mg ($p < 0.05$), while the C:N was positively correlated with K ($p < 0.01$) and Ca ($p < 0.05$); only NO_3^- and PO_4^{3-} values showed no correlation with those for any other nutrient or pH (Guevara, 2012).

VEGETATION PATTERNS

The 1991 Pattern

Smith's detailed descriptions of the snow-lie and vegetation patterns around the snow fence (Smith, 1991; Smith et al., 1995) were generally similar to those described earlier by Harrison (1986a, 1986b). Both floristic and functional diversity described by Smith increased significantly with increasing snow accumulation behind the fence but wind speed, by contrast, only affected functional diversity. More specifically, *Dracophyllum muscoides* and lichens, which dominate the cushionfields, became more sparse with increasing snow depth, as reported earlier by Harrison (1986b). Several forbs, however—for example, *Argyrotegium* (*Gnaphalium*) *mackayi* and *Craspedia lanata* (both Asteraceae) and *Epilobium tasmanicum*—thrived under increasing snow cover, which was associated with decreased wind speed (Smith et al., 1995).

A cluster analysis of shoot frequency from Smith's (1991) quadrat sampling, discriminated at 45% Bray-Curtis similarity, revealed eight quadrat groups or plant communities, but only two (1 and 6) were numerous. Community 1 comprised 75 of the 100 quadrats, which were distributed around the margin of both the larger (50×30 m) and reduced (30×20 m) study site (Fig. 5). This community embraced the generally unmodified cushionfield where the dominant species included the ericoid *D. muscoides* (25% contribution), a moss *Polytrichum juniperinum* (23.5%), and monocots *Luzula pumila* (10.3%) and *Poa colensoi* (10.2%); these species contributed cumulatively to 69% of the 59% average similarity among these quadrats. By contrast, Community 6, located in the lee of the snowfence, was characterized by *E. tasmanicum* (14% contribution), a native tussock grass *Poa colensoi* (13.5%), *P. juniperinum* (25.4%), and the exotic grass *Agrostis capillaris* (12.6%), species that cumulatively contributed to 65.4% of the 53.4% average similarity between quadrats in this group. Community 7 on its margin (Fig. 5) had *P. colensoi* (52.6%) plus the mat daisy *Raoulia hectorii* (16.8%) and the cushion plant *Phyllachne rubra* (16.2%) as its main contributors. The remaining five communities were all of minor importance, comprising 1–5 quadrats that were reduced to 0–3 within the smaller study site. Communities 1 and 6 showed an average dissimilarity of 64% with *D. muscoides*, *E. tasmanicum*, *A. capillaris*, *R. hectorii*, *L. pumila, P. juniperinum,* and *P. rubra* contributing most (>50% cumulative contribution) to the dissimilarity between communities (Table 1, part A).

The 2002 Pattern

The cluster analysis of shoot frequency at this time discriminated only two quadrat groups or communities (A and B). Community A contained 19 quadrats located in the lee of the fence, while Community B contained the remaining 25 within the smaller (30×20 m) study site (Fig. 5). Community A was characterized by two native grasses *Rytidosperma pumilum* and *Agrostis muelleriana*, as well as *E. tasmanicum* and *P. juniperinum*, while Community B had *D. muscoides, P. juniperinum,* and *P. colensoi* as the major contributors.

These two communities showed 73.2% average dissimilarity, with *D. muscoides*, *R. pumilum*, *E. tasmanicum*, *P. juniperinum, P. colensoi,* and *L. pumila* contributing most to the dissimilarity between them (Table 1, part B).

The 2003 Pattern

The cluster analysis of shoot frequency for the 100 quadrats in 2003 discriminated five quadrat groups or communities (V–Z), with three large (V, W, and Z: 14–53 quadrats) and two minor (X and Y: 1–2 quadrats) groups. Community V was the largest, with 53 quadrats located around the periphery of the study site, and was characterized by dead plants and *D. muscoides*, while Community W, comprising 31 quadrats, was located within a zone that widened away from the fence and even extended locally, immediately upwind of the fence, and was characterized by dead plants, *E. tasmanicum* and *R. pumilum.* Community Z comprised 14 quadrats, which formed a central core in the lee of the fence (Fig. 5), and also featured the *E. tasmanicum* and dead plants but included *R. australe* and *Poa incrassata*, with *A. mackayi* and *C. lanata* also prominent here. The two minor communities (X and Y) were adjacent but within the peripheral Community V (Fig. 5).

Dissimilarity between the most contrasting communities, V and Z, averaged 64.2%, with *D. muscoides, E. tasmanicum, R. australe, A. mackayi, P. incrassata, C. lanata, R. hectorii,* and *L. pumila* among the major contributors (50% cumulative contribution; see Table 1, part C). Dissimilarity between Communities V and W averaged 45.6%, with *E. tasmanicum, D. muscoides, R. pumilum, P. incrassata, P. juniperinum, C. lanata, L. pumila, R. hectorii,* and *P. colensoi* being the major contributors (50% cumulative contribution; see Table 1, part D). Dissimilarity between Communities W and Z averaged 49.5%, with *Rytidosperma* spp. *A. mackayi,* and *R. hectorii* being the main contributors (27% cumulative contribution) (Table 1, part E).

The 2011 Pattern

Eight years later, year 52, three communities (E, A, and B) were again prominent, with a pattern generally similar to that in 2003, but with a somewhat different set of characteristic species. Community E was located around the periphery, and involved 72 quadrats, including all 20 of those added along the northern boundary of the site (Fig. 5). This community comprised 12 species of which *D. muscoides, R. hectorii, L. pumila, P. juniperinum,* and *A. muelleriana* were the most important, with dead plants, pavement, and bare soil also notable. Community A, comprising 28 quadrats and 39 species, formed the outer margin of the area affected by the snow fence and was characterized by *R. pumilum, P. juniperinum, E. tasmanicum, R. hectorii, P. rubra, P. incrassata,* and *C. lanata*, with dead plants, pavement, and bare soil again prominent. Community B quadrats formed the inner core, with 14 quadrats and 33 species, of which *P. juniperinum, E. tasmanicum, C. lanata, P. rubra,* and *R. pumilum* were characteristic, together with the previously unimportant cushion plants *Hectorella caespitosa* and *Colobanthus buchananii* and the small native grass *Deschampsia chapmanii.* Dead plants, pavement, bare soil, and rock were also prominent in Community B quadrats.

TABLE 1

Species abundance and their contributions to dissimilarity between quadrat groups (plant communities) defined from cluster analyses for 1991, 2002, and 2003. The exotic species is indicated with an asterisk.

	Average abundance	Average abundance	Percentage contribution	Cumulative percentage contribution
1991				
(A) Average dissimilarity = 64.0	Group 1	Group 6		
Dracophyllum muscoides	12.16	0.78	13.26	13.26
Epilobium tasmanicum	0.07	8.56	9.52	22.78
Agrostis capillaris	0.01	3.67	7.25	30.02
Raoulia hectorii	3.65	4.22	6.15	36.17
Luzula pumila	2.85	0.33	6.03	42.20
Polytrichum juniperinum	11.93	12.22	5.26	47.46
Phyllachne rubra	1.80	2.44	5.21	52.67
2002				
(B) Average dissimilarity = 73.2%	Group A	Group B		
Dracophyllum muscoides	0.75	16.48	14.13	14.13
Rytidosperma pumilum	7.70	0.56	9.43	23.56
Epilobium tasmanicum	6.20	0.06	8.21	31.77
Polytrichum juniperinum	6.65	4.28	6.72	38.50
Poa colensoi	3.55	3.06	6.58	45.07
Luzula pumila	1.30	2.10	5.47	50.54
2003				
(C) Average dissimilarity = 64.2	Group V	Group Z		
Dracophyllum muscoides	18.23	0.71	8.91	8.91
Epilobium tasmanicum	0.70	18.43	8.61	17.52
Rytidosperma australe	0.00	12.29	7.19	24.71
Argyrotegium mackayi	0.00	9.43	6.18	30.88
Poa incrassata	0.43	8.36	5.54	36.42
Craspedia lanata	0.62	8.57	5.26	41.68
Raoulia hectorii	6.68	1.50	4.21	45.89
Luzula pumila	6.70	0.86	4.11	50.00
(D) Average dissimilarity = 45.6	Group V	Group W		
Epilobium tasmanicum	0.70	13.70	9.64	9.64
Dracophyllum muscoides	18.23	4.80	8.72	18.35
Rytidosperma pumilum	5.91	12.29	6.86	25.22
Poa incrassata	0.43	5.30	5.32	30.53
Polytrichum juniperinum	10.09	10.43	4.99	35.52
Craspedia lanata	0.62	3.60	4.44	39.96
Luzula pumila	6.70	2.30	4.36	44.31
Raoulia hectorii	6.68	7.77	4.04	48.35
Poa colensoi	4.17	2.93	3.76	52.11

TABLE 1
Continued

	Average abundance	Average abundance	Percentage contribution	Cumulative percentage contribution
(E) Average dissimilarity = 49.5	Group W	Group Z		
Rytidosperma australe	2.43	12.29	7.28	7.28
Rytidosperma pumilum	12.20	1.57	7.05	14.33
Argyrotegium mackayi	0.37	9.43	6.99	21.31
Raoulia hectorii	7.77	1.50	5.35	26.67
Polytrichum juniperinum	10.43	9.57	4.35	31.02
Dracophyllum muscoides	4.80	0.71	4.32	35.34
Craspedia lanata	3.60	8.57	4.13	39.46
Poa incrassata	5.30	8.36	3.63	43.09
Agrostis muelleriana	3.73	1.07	3.57	46.66
Celmisia sessiliflora	0.40	3.07	3.50	50.15
2011				
(F) Average dissimilarity = 54.8	Group E	GpB		
Dracophyllum muscoides	4.89	0.33	8.95	8.95
Epilobium tasmanicum	0.16	3.71	8.71	17.66
Deschampsia chapmanii	0.05	3.34	7.82	25.48
Craspedia lanata	0.25	2.64	5.84	31.32
Raoulia hectorii	2.54	0.60	5.11	36.43
Polytrichum juniperinum	1.94	3.75	5.05	41.48
Rytidosperma pumilum	1.84	1.55	4.22	45.70
Agrostis muelleriana	1.68	0.17	3.81	49.50
Luzula pumila	1.89	0.80	3.72	53.24
(G) Average dissimilarity = 44.4	Group E	Group A		
Dracophyllum muscoides	4.89	1.36	8.69	8.69
Epilobium tasmanicum	0.16	2.78	7.82	16.51
Rytidospermum pumilum	1.84	3.92	6.95	23.46
Polytrichum juniperinum	1.94	3.56	6.23	29.69
Poa incrassata	0.19	1.77	4.82	34.51
Craspedia lanata	0.25	1.75	4.81	39.32
Agrostis muelleriana	1.68	0.86	4.25	43.57
Raoulia hectorii	2.54	2.48	4.02	47.59
Luzula pumila	1.89	1.57	3.96	51.55
(H) Average dissimilarity = 42.3	Group A	Group B		
Deschampsia chapmanii	0.44	3.34	8.14	8.14
Rytidosperma pumilum	3.92	1.55	7.16	15.30
Raoulia hectorii	2.48	0.60	5.97	21.27
Craspedia lanata	1.75	2.64	4.51	25.78
Dracophyllum muscoides	1.36	0.33	3.85	29.63
Poa incrassata	1.77	1.28	3.81	33.44
Celmisia sessiliflora	0.21	1.36	3.81	37.25

TABLE 1
Continued

	Average abundance	Average abundance	Percentage contribution	Cumulative percentage contribution
Epilobium tasmanicum	2.78	3.71	3.71	40.96
Luzula pumila	1.57	0.80	3.71	44.67
Phyllachne rubra	1.87	1.43	3.53	48.20
Carex pyrenaica v. *cephalotes*	0.26	1.24	3.50	51.70

Dissimilarity between the most contrasting communities, E and B, averaged 54.8% with *D. muscoides, E. tasmanicum, D. chapmanii, C. lanata, R. hectorii, P. juniperinum, R. pumilum, A. muelleriana,* and *L. pumila* contributing 50%, in decreasing order (Table 1, part F). Dissimilarity between Communities E and A averaged 44.4% with *D. muscoides, E. tasmanicum, R. pumilum, P. incrasata, C. lanata, A. mulleriana, R. hectorii,* and *L. pumila,* again in decreasing order, collectively contributing 50% (Table 1, part G), while

TABLE 2

Mean shoot frequency of all species recorded in 120 quadrats on the study site in 2011, in relation to the five quadrat groups recognized. See Figure 5 for the distribution pattern of the five groups. The status of each species (increaser, decreaser, or neutral) in response to increasing snow-lie, has been indicated. Exotic species are indicated with an asterisk.

Species	Status	Group E	A	B	C	D
Abrotanella inconspicua	Neutral	1.7	11.0	2.6	0.0	0.0
Agrostis capillaris	Increaser	0.0	0.0	3.1	0.0	0.0
Agrostis muelleriana	Decreaser	16.5	7.9	0.9	0.0	9.3
Argyrotegium mackayi	Increaser	0.0	0.6	12.6	0.0	0.0
Anisotome flexuosa	Increaser	0.6	1.1	1.1	0.0	0.0
Anisotome imbricata	Neutral	1.2	2.4	0.3	0.0	0.0
Anisotome lanuginosa	Neutral	1.1	1.1	0.3	12.0	0.0
Brachyscome sinclairii	Neutral	0.0	0.6	0.3	0.0	0.0
Brachyglottis bellidioides	Neutral	0.0	0.1	0.0	0.0	0.0
Carex pyrenaica v. *cephalotes*	Increaser	1.7	1.7	13.7	0.0	0.0
Celmisia argentea	Increaser	0.2	0.3	0.9	0.0	0.0
Celmisia brevifolia	Neutral	2.0	3.7	0.3	0.0	0.0
Celmisia laricifolia	Decreaser	6.6	3.3	0.3	0.0	0.0
Celmisia sessiliflora	Increaser	0.3	1.3	13.4	0.0	0.0
Celmisia viscosa	Neutral	0.0	0.1	0.0	0.0	0.0
Chionohebe thomsonii	Decreaser	0.2	0.0	0.0	0.0	0.0
Colobanthus buchananii	Increaser	6.0	7.0	10.6	68.0	0.0
Coprosma perpusilla	Neutral	0.1	2.3	0.0	0.0	0.0
Craspedia lanata	Increaser	1.6	17.9	34.3	0.0	0.0
Deschampsia chapmanii	Increaser	0.4	2.9	49.7	0.0	1.3
Dracophyllum muscoides	Decreaser	71.8	16.7	2.0	0.0	8.0
Epilobium tasmanicum	Increaser	1.1	34.9	58.3	0.0	0.0
Euphrasia zelandica	Decreaser	0.3	0.0	0.0	0.0	0.0
Gentianella bellidifolia	Increaser	0.2	1.4	4.6	0.0	0.0
Hectorella caespitosa	Neutral	10.0	9.6	15.1	16.0	26.7
Hieracium lepidulum	Neutral	0.0	0.1	0.0	0.0	0.0
Kelleria childii	Neutral	0.2	2.0	0.6	0.0	0.0

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TABLE 2
Continued

Species	Status	Group E	A	B	C	D
Leptinella goyenii	Decreaser	4.6	1.7	2.3	0.0	0.0
Luzula pumila	Decreaser	20.8	14.6	6.3	28.0	26.7
Luzula rufa	Neutral	0.0	1.3	0.6	0.0	0.0
Lycopodium fastigiatum	Decreaser	2.8	0.7	6.0	0.0	0.0
Muehlenbeckia axillaris	Decreaser	0.1	0.0	0.0	0.0	0.0
Myosotis pulvinaris	Neutral	0.4	1.0	0.0	0.0	0.0
Myosotis pygmaea	Neutral	0.2	0.7	0.0	0.0	0.0
Phyllachne colensoi	Neutral	0.0	0.0	0.0	32.0	0.0
Phyllachne rubra	Decreaser	18.1	17.4	13.4	0.0	28.0
Plantago lanigera	Neutral	0.0	0.9	0.0	0.0	0.0
Poa colensoi	Decreaser	4.2	4.3	1.4	0.0	1.3
Poa incrassata	Increaser	1.0	16.6	12.6	0.0	5.3
Polytrichum australe	Decreaser	0.4	0.0	0.0	0.0	0.0
Polytrichum juniperinum	Increaser	24.5	56.0	58.0	68.0	16.0
Psilopilum australe	Neutral	0.0	0.0	0.0	0.0	1.3
Ranunculus enysii	Increaser	0.0	0.3	0.6	0.0	0.0
Raoulia grandiflora	Increaser	1.4	4.7	6.6	0.0	0.0
Raoulia hectorii	Decreaser	31.1	31.1	5.1	0.0	0.0
Rytidosperma pumilum	Neutral	24.3	64.4	18.0	20.0	81.3
Trisetum spicatum	Decreaser	2.0	0.0	0.0	0.0	6.7
Bare soil		27.4	15.6	15.4	84.0	21.3
Dead		98.8	98.1	91.7	96.0	100.0
Pavement		52.0	46.7	56.9	88.0	66.7
Rock		6.3	5.9	7.7	16.0	0.0

the average dissimilarity between Communities A and B was only slightly less, 42.3%, with *D. chapmanii, R. pumilum, R. hectorii, C. lanata, D. muscoides, P. colensoi,* the previously minor cushion daisy *Celmisia sessiliflora, E. tasmanicum, L. pumila, P. rubra,* and the obligate snowbed sedge *Carex pyrenaica* var. *cephalotes* collectively contributing 50%, in decreasing order (Table 1, part H).

The contrasting species response patterns are more precisely revealed with the mean shoot frequency for each of the five communities recognized in analysis of the results for year 52 (2011) sample (Table 2). Here, among the 47 plant species, the number of increasers and decreasers were similar (15 and 14), while the neutral (no-response) species were only slightly more numerous (18).

RELATIONSHIPS TO SNOW PATTERNS

Significant correlation with snow depth was obtained for 22 plant species and 3 nonplant categories (dead plants, bare soil, and rock), based on the 2003 monitoring records (Table 3). Four species (*D. muscoides, L. pumila, A. muelleriana,* and the lichen *Thamnolia vermicularis*) and two categories (bare soil and dead plants) were significantly ($p = <0.001$) negatively correlated ($r < –0.310$) to snow depth (Group A in Table 3), while two grass species and a daisy (*Tri-*

setum spicatum, P. colensoi, and *Celmisia laricifolia*) showed lower ($r = –0.250$) but significant ($p = <0.01$) negative correlations with snow depth (Group B in Table 3). Nine species (*R. pumilum, Myostis pygmaea, Phyllachne colensoi, Plantago lanigera, C. pyrenaica* var. *cephalotes, Anisotome flexuosa, Luzula rufa,* the exotic *A. capillaris,* and *C. sessiliflora*), together with rock, showed a slight ($r = <0.300$) positive correlation with snow depth, while six species (*Gentainella bellidifolia, A. mackayi, C. lanata, P. incrassata, Rytidosperma australe,* and *E. tasmanicum*) showed a strong ($r = >0.480$) and highly significant ($p = <0.001$) positive correlation (Table 3, part D). Another 12 species (including *Abrotanella inconspicua, Anisotome imbricata, Celmisia brevifolia, C. buchananii, H. caespitosa, Leptinella goyenii, Lycopodium fastigiatum, P. rubra, Raoulia grandiflora,* and *R. hectorii*), together with pavement, showed no significant correlation with the depth of snow (Group E in Table 3).

The contrasting responses to the changed patterns of snow-lie are shown in Figure 7, where patterns of frequency in 2003, year 44, of four species that declined with increasing snow cover are compared with four that increased to varying degrees. The most obvious changes were the striking decrease in importance of *D. muscoides* in the immediate lee of the snow fence, similar but less prominent responses shown by *L. pumila* and *A. muelleriana,* contrasting pat-

TABLE 3

Results of a Spearman Rank Order Correlation between 34 plant species plus four non-plant categories, recorded with the 2003 sampling, and snow-lie pattern as recorded at the snow fence study site in 1991. The five groups recognized (A–E) range from those whose mean frequency values are strongly (A) or slightly (B) negatively correlated with snow-lie, those slightly (C) or strongly (D) positively correlated with snow-lie, and those which show no significant correlation with length of snow-lie (E). The exotic species is indicated with an asterisk.

Species	r	p
Group A		
Dracophyllum muscoides	–0.725	<0.001
Luzula pumila	–0.565	<0.001
Bare soil	–0.544	<0.001
Dead plants	–0.535	<0.001
Thamnolia vermicularis	–0.400	<0.001
Agrostis muelleriana	–0.330	<0.001
Group B		
Trisetum spicatum	–0.302	0.002
Poa colensoi	–0.272	0.006
Celmisia laricifolia	–0.259	0.009
Group C		
Rytidosperma pumilum	0.200	0.046
Myosotis pygmaea	0.205	0.040
Phyllachne colensoi	0.219	0.029
Plantago lanigera	0.238	0.017
Rock	0.249	0.013
Carex pyrenaica v. *cephalotes*	0.253	0.011
Anisotome flexuosa	0.282	0.005
Luzula rufa	0.287	0.004
*Agrostis capillaris	0.301	0.002
Celmisia sessiliflora	0.318	0.002
Group D		
Gentianella bellidifolia	0.488	<0.001
Argyrotegium mackayi	0.578	<0.001
Craspedia lanata	0.658	<0.001
Poa incrassata	0.678	<0.001
Rytidosperma australe	0.705	<0.001
Epilobium tasmanicum	0.775	<0.001
Group E		
Raoulia grandiflora	0.108	0.285
Celmisia brevifolia	0.106	0.291
Abrotanella inconspicua	0.099	0.327
Polytrichum juniperinum	0.039	0.701

TABLE 3
Continued

Species	r	p
Hectorella caespitosa	0.017	0.867
Anisotome imbricata	0.001	0.997
Colobanthus buchananii	–0.028	0.779
Leptinella goyenii	–0.032	0.752
Lycopodium fastigiatum	–0.094	0.350
Pavement	–0.123	0.221
Phyllachne rubra	–0.139	0.168
Raoulia hectorii	–0.154	0.125
Anisotome lanuginosa	–0.176	0.080

terns shown by the two species of *Rytidosperma*, with *R. australe* showing a positive response to increasing snow cover, together with *E. tasmanicum*, *A. mackayi*, and *P. incrassata* (Fig. 7).

By 2011, year 52, differentiating patterns for the same eight species were somewhat more accentuated, while another four species, the moss *P. juniperinum*, plus *C. pyrenaica* var. *cephalotes*, *C. sessiliflora*, and *P. rubra* showed less distinct responses (Fig. 8).

VARIATION IN PLANT FUNCTIONAL TRAITS AND LIFE FORM GROUPS

For three of the five functional traits measured, there were clear patterns across the snowmelt zones: outer, middle, and late/center. Based on the community trait-weighted means (CTWMs), the abundance of species with lower leaf dry matter content (LDMC) was higher in the late snow zone in the center of the snowpatch, whereas the abundance of species with relatively higher specific leaf area (SLA) was only marginally higher in the late snowmelt zone (Fig. 9). There was a significantly higher abundance of species that were relatively taller and with relatively heavier seeds in the mid- and late-snowmelt zones compared to the area beyond the influence of the snow fence; however, there were no strong patterns in relation to leaf nitrogen content across the snowmelt zones (Fig. 9).

Models investigating the probability of life form occurrence and the patterns in traits across the snowmelt zones revealed several positive associations between SLA and plant height, with the late- and mid-snowmelt zones. There were large interactions between high SLA and relatively taller plants in the two snow accumulation zones when treated as one snow zone, compared to the outer zone, beyond the influence of the snow fence. Interactions between plant height and life form indicated forbs and graminoids showed the strongest effects, most likely due to the number of taller grasses that were only found behind the fence, but not beyond its influence. Life form was more important in determining species presence or absence behind the fence than species height. In addition, those species behind the snowfence were more likely to be forbs with high SLA, rather than shrubs with high SLA (Fig. 10). When plant height and SLA were in the same model, SLA was more important than height and forbs deviated the most (Fig. 10).

RECRUITMENT OF SNOWBANK SPECIES

The partial replacement of the previously dominant cushion-field species, *Dracophyllum muscoides*, and some others, including
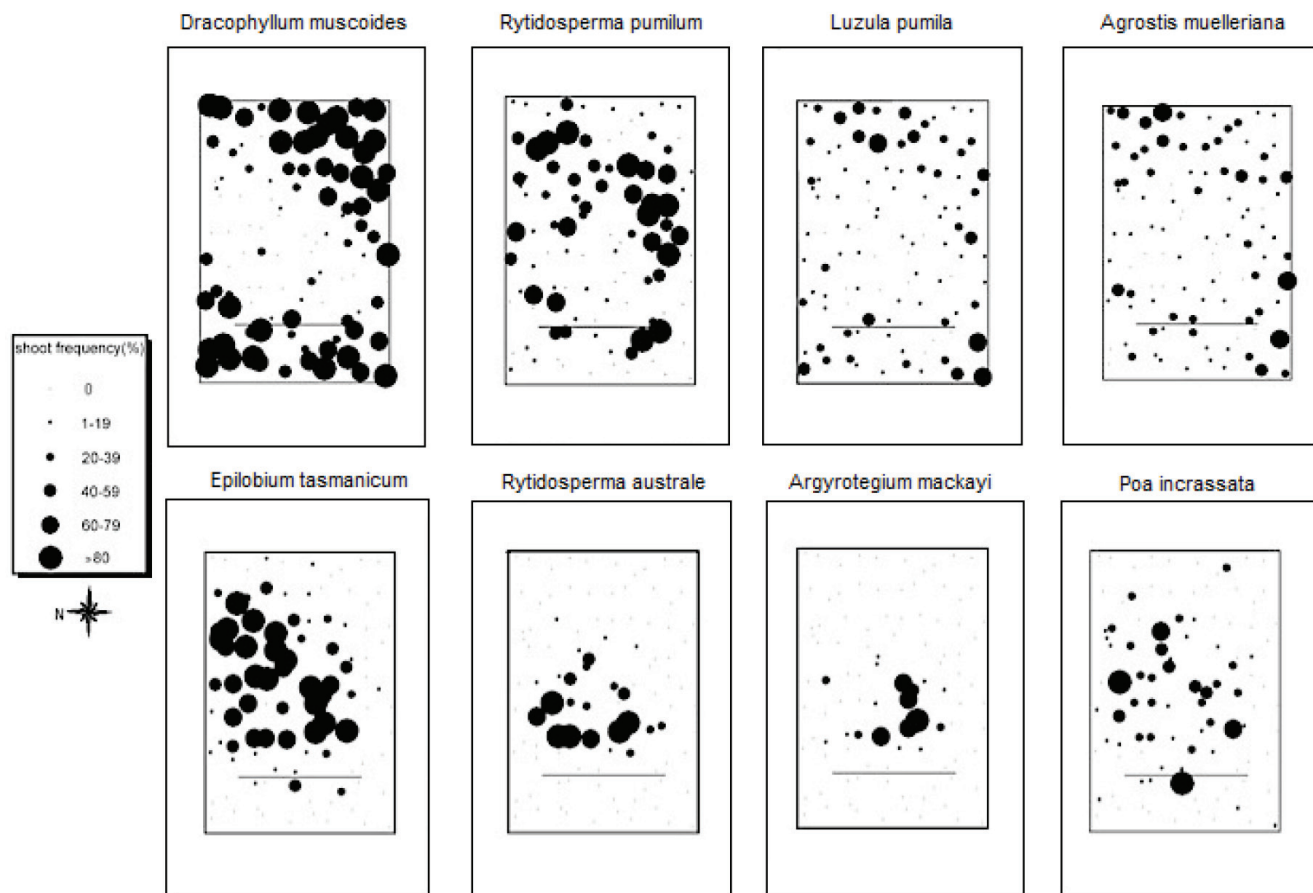
FIGURE 7. Frequency values as sampled in 2003, using 100 quadrats over the 20 × 30 m study site, showing the variation in response of eight species to differential snow-lie associated with the snow fence (also shown). The four species depicted in the top row show a negative response to the accumulation; those in the bottom row show a positive response.

the lichens *Thamnolia vermicularis* and *Cetraria islandica* subsp. *antarctica*, in the lee of the snow fence with species more tolerant of prolonged snow-lie was apparent when sampled at years 20 and 27. This broad shift in site occupancy has continued to be observed during successive sampling, but the rate has generally declined over time. These patterns have been tabulated in relation to several possibly relevant ecological features of the various species (Table 4). Several species found only occasionally in the cushionfield community have increased noticeably over time in the areas of snow accumulation, most notably *Carex pyrenaica* var. *cephalotes*, *Celmisia sessiliflora*, *Epilobium tasmanicum*, *Poa incrassata*, and *Polytrichum juniperinum* (Group A in Table 4). Newly recruiting species first recorded in year 32 were the small rosette herb *Argyrotegium mackayi* and the graminoid *Luzula rufa*, while by year 44 there were an additional six new species, involving several life forms (C in Table 4), and by year 52 there were an additional two species, including the exotic forb *Hieracium lepidulum* (D in Table 4). However, there are several species recorded from natural snowbanks on the Old Man Range that have not yet established in the area of maximum snow-lie (Group E in Table 4). Relevant ecological features of the nine species that have established at various times over the past 52 years are compared with those of 29 local snowbank species that have not (Table 4). A one-way ANOVA detected no significant differences in seed mass, plant height, SLA, and LDMC between species that had established (Groups B, C, and D) and those that had not yet established (Group E) (seed mass:

$F_{1,23} = 1.52$; height $F_{1,21} = 1.82$; SLA: $F_{1,20} = 2.25$; LDMC: $F_{1,17} = 1.47$; all analyses $P > 0.1$).

WIND-BORNE MATERIAL TRAPPED BY THE SNOW FENCE

The first samples collected in December 2014, air-dried, averaged 18.5 ± 4.6 g and comprised a mix of fine mineral material and plant debris; mostly leaves of *Poa colensoi* plus small fragments of several lichens (*Cetraria* sp., *Thamnolia vermicularis*, and *Hypogymnia lugubris*) and the cushion species (*Dracophyllum muscoides* and *Colobanthus* sp.). Even with a binocular microscope, seed were not obvious among the fine mineral debris. However, some 86 seed germinated over the first 60 days, including 55 morphologically similar grass seedlings with small entire ligules, probably of *P colensoi*, and 31 dicots comprising 12 with fine stems and alternate leaves and 24 that had not developed beyond the cotyledon stage, but 13 of which were similar and glabrous while 11 were pilose and similar. All the lichen fragments appeared to be alive, and there was also a fragment of the cushion *Colobanthus canaliculatus*, which resumed growth (Fig. 11).

Discussion and Conclusions

Differing tolerances to snow-lie is a well-known phenomenon among alpine plant species (Walker et al., 1993; Körner, 2003;
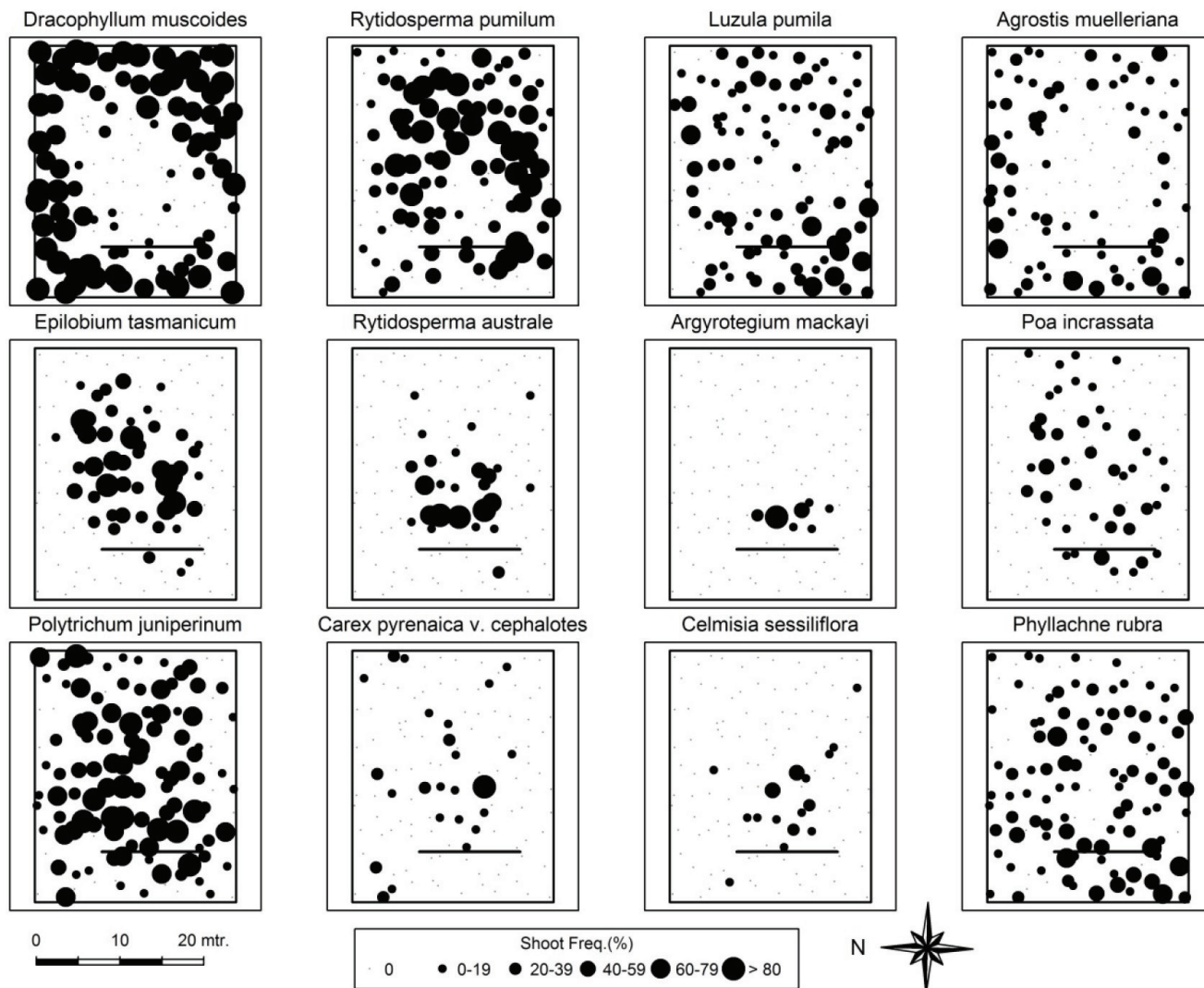
FIGURE 8. Frequency values for 12 species as sampled in 2011, using 120 quadrats over the 24 × 30 m study site (note: a 4 m strip was added on the northern side, post 2003), showing the variation in response of the same eight species as shown for 2003 (Fig. 7) plus four additional species that show a range of responses to differential snow-lie associated with the snow fence.

Björk and Molau, 2007) and has also been demonstrated for the Central Otago mountains of southern New Zealand (Mark and Bliss, 1970; Talbot et al., 1992; Korsten, 2011; Guevara, 2012). For example, exposed sites on the Rock and Pillar Range (1450 m) have been recorded to have about 90 days of snow cover compared with almost 200 days in late snow-melt sites, with the pattern generally consistent from year to year (Talbot et al., 1992). Alpine species on the Rock and Pillar Range have been shown to vary in their frost resistance inversely with their tolerance of snow-lie (Bannister et al., 2005). The present study has found that exposed cushionfield sites on the Old Man Range, being 200 m higher, have somewhat longer but intermittent snow-lie (~140 days). Modification of this snow-lie pattern, explicitly through the erection and maintenance of a wooden-paneled, 12 × 2 m snow fence at 1650 m, across a relatively exposed high-alpine cushionfield habitat on the windward crest of the Old Man Range, has demonstrated temporal changes in the responses of alpine species over five decades. Because the snow fence was constructed primarily as a small experimental exercise to assess the ability to capture and retain snow beyond the period of spring snow melt, combined with assessing the

potential of five North American subalpine conifer species, there was no study of the vegetation response until year 20, by which time the still small plants of the one surviving species had been removed and changes to the original vegetation cover were obvious, and visual assessments of these were documented by Harrison (1986b). Since then, periodic quantitative studies have been made at years 32, 43, 44 (when the procedure was modified to improve the records, but vegetation changes over this one year are assumed to be negligible), and most recently (2011), year 52. Changes in vegetation and species patterns in areas where snow accumulated and persisted were apparent before the initial assessment at year 20, which preceded the first detailed sampling at year 32 (Smith, 1991). Distinction of two, snow-induced plant communities to leeward of the fence became more apparent when the density of quadrat sampling was increased from <0.5% to 1.67% of the study site area at year 44 (2003).

Despite a change in sampling protocol between 2002 and 2003 (denser sampling close to the snow fence where the response was more evident), the temporal changes have been gradual over the 52 years of study to date and appear to be
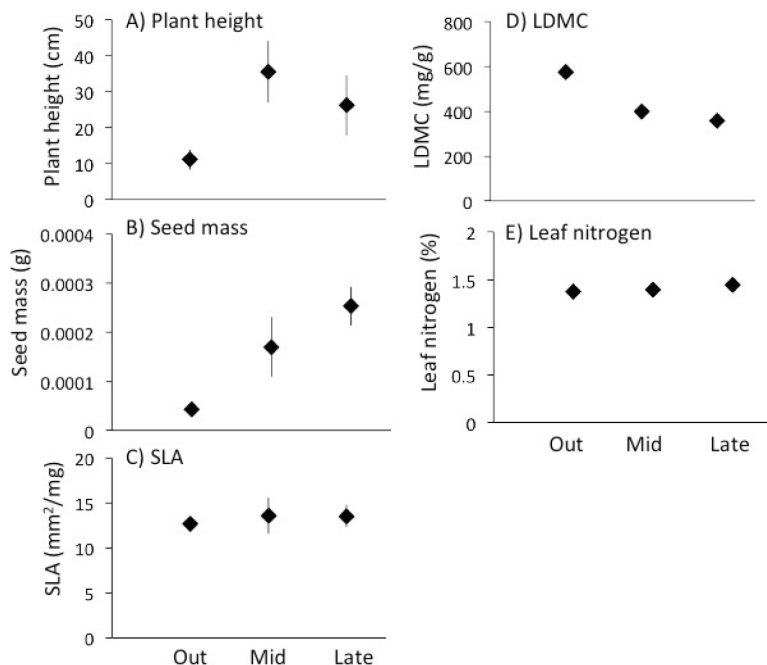
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FIGURE 9. The community trait-weighted means bounded by 95% confidence intervals for each of the measured traits: (A) plant height, (B) seed mass, (C) specific leaf area (SLA), (D) leaf dry matter content (LDMC), and (E) leaf nitrogen, across the three snowmelt zones: Out, adjacent to the snow fence and beyond its influence; mid, within the influence of the snow fence; and late, in the center of the snow patch.

continuing. The dominant cushionfield species, *Dracophyllum muscoides*, showed a rapid negative response to the increased snow-lie, yet a few plants have persisted throughout the period. By contrast, several occasional species from the original cushionfield community have increased noticeably over time in the area of snow accumulation, for example, *Carex pyrenaica* var. *cephalotes*, *Celmisia sessiliflora*, *Epilobium tasmanicum*, *Poa incrassata*, and *Polytrichum juniperinum*, while additional species were recorded when sampled at years 44 and 52, and now total nine. This suggests that increased snow-lie has not only favored previously minor species perhaps at the limits of their tolerance in the cushionfield but also facilitated colonization by new species present in the wider species pool.

Material caught in the four mat traps over the first nine months (autumn–early summer: 68% of total weight) and the following three months (32%) of a full year (March 2014–March 2015) indicated some 20.4 g (61.3 ± 18.4 g m^{-2}) of mostly fine mineral material was deposited close behind the fence. Viable seed from the first collection produced some 55 grasses, assumed to be most-
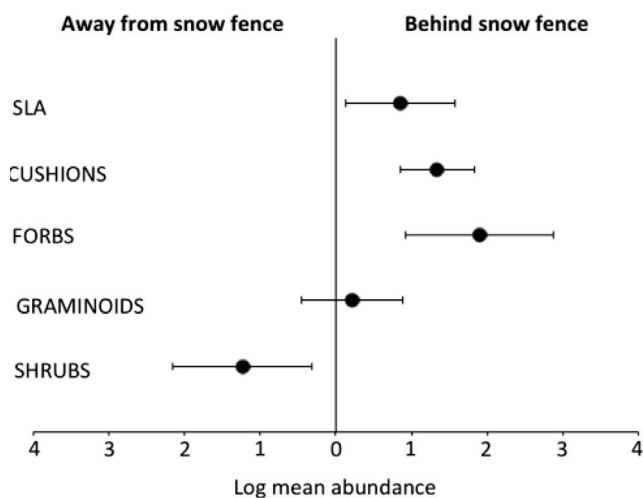
FIGURE 10. The modeled probability of occurrence of species with relatively higher SLA as well as species life form groups, in the area away from the influence of the snow zone (left), or behind the fence (right). Modeled estimates are log-transformed means of abundance; bars represent 95 % confidence intervals.

FIGURE 11. Fragment of the cushion species *Colobanthus canaliculatus*, collected in a trap in the lee of the snow fence. It subsequently sprouted (arrows), as shown, when moistened in a petri dish.

TABLE 4

Species recorded from the snow fence study site, including information about dispersal, position in relation to snow cover, and mean values for functional traits, arranged in the assumed order of their presence at the site. (A) Species listed first are those originally present and recorded on the perimeter of the site, uninfluenced by the increasing snow-lie induced by the snow fence; (B) followed by the additional species first recorded by Harrison (1986b) and Smith (1991); (C) then in 2002–2003 by T. Humar-Maegli (personal communication); and (D) most recently by Guevara (2012). (E) Species previously recorded from natural snowbanks on the Range (Mark and Bliss, 1970; Korsten, 2011; Guevara, 2012; Mark, 2012), but not yet established on the snow fence study site are listed last. Out, Mid, and Center refer to the three zones recorded in 2003 (V, W, and Z in Fig. 5), for which frequency values subsequently recorded by S. Venn in 2011 (personal communication) are presented. Aspects relevant to the ecology of the species are given, where available, including dispersal codes (see footnote); SLA = specific leaf area; LDMC = leaf dry matter content. * = exotic species.

Species	Family	Out	Mid	Center	Day last exposed[†]	Life form	Seed mass (mg)[§]	Height (cm)[§]	SLA (mm² mg⁻¹)	LDMC (mg g⁻¹)	Leaf N (%)	Dispersal unit and adaptation	Dispersal[‡]
(A) Natural cushionfield species													
Abrotanella inconspicua	Asteraceae	0	41.7	41.7		cushion		0.63	11.34	373.79	1.04	Cypsella	Wi
*Agrostis capillaris	Poaceae	0	16.7	33.3		graminoid			16.9	342.13	2.63	Floret	
Agrostis muelleriana	Poaceae	91.7	33.3	25	345	graminoid	0.1	7.83	15.99	350.25	1.92	Floret	Wa Wi
Anaphalioides bellidioides	Asteraceae					pros forb		7.83	20.01			Pappate cypsella	Wi
Anisotome flexuosa	Apiaceae	8.3	8.3	0	358	ros forb	0.56	3.13	6.57	278.26	2.47	Winged mericarp	Wi
Anisotome imbricata	Apiaceae	0	8.3	8.3	345	cushion	1.08	1.31	6.72	337.37	1.77	Winged mericarp	Wi
Anisotome lanuginosa	Apiaceae	8.3	0	0	338	ros forb	0.66	1.98	5.87	314.1		Winged mericarp	Wi
Carex pyrenaica v cephalotes	Cyperaceae	0	25	50	366	graminoid	0.26	2.25	13.26	343.31	1.34	Utricle	Wa Gr Wi
Celmisia argentea	Asteraceae	0	0	8.3		cushion		0.72	12.57	344.18		Pappate cypsella	Wi
Celmisia brevifolia	Asteraceae	16.7	16.7	16.7	352	subshrub		13.5	6.16	406.06	1.4	Pappate cypsella	Wi
Celmisia gracilenta	Asteraceae					graminoid	0.4	5.19	11.15	247.3		Pappate cypsella	Wi
Celmisia laricifolia	Asteraceae	8.3	66.7	8.3	341	graminoid	0.1	1.14	11.13	384.02	1.26	Pappate cypsella	Wi
Celmisia sessiliflora	Asteraceae	8.3	33.3	83.3	296	cushion	0.53	1.12	6.14	456.01	0.87	Pappate cypsella	Wi
Celmisia viscosa	Asteraceae				354	graminoid	1.5	7.17	4.29	431.01		Pappate cypsella	Wi
Chionohebe thomsonii	Plantaginaceae					cushion						Seed	Ba Wi Wa
Chionochloa macra	Poaceae	0	8.3	8.3	327	graminoid		64.3	3.11	480	1.19	Floret	Wi
Colobanthus buchananii	Caryophyllaceae	0	16.7	0	366	cushion	0.04	0.33	34.98	233.11	1.67	Winged seed	Wt ?Wi ?Ba
Coprosma perpusilla	Rubiaceae				355	cushion		2.05	12.02	270.06		Fleshy drupe	Fr
Craspedia lanata	Asteraceae	0	75	91.7		ros forb		30	7.83	333.33	1.22	Pappate cypsella	Wi
Dracophyllum muscoides	Ericaceae	100	75	33.3	345	cushion	0.03	0.57	12.62	641.14	1.32	Minute seed	Wi
Epilobium tasmanicum	Onagraceae	0	100	91.7	355	forb		0.42	17.59	228.11	1.35	Pappate seed	Wi
Gaultheria depressa v. nz	Ericaceae					subshrub	0.02	5.1	7.38	429.29		Fleshy berry	Fr In
Gentianella bellidifolia	Gentianaceae	0	33.3	33.3	363	ros forb	0.32	3.63	13.19	228.11		Censer seed	Ba Wi Wa
Geranium microphyllum	Geraniaceae					ros forb	2.27	4.83	23.6	263.49		Explosive seed	Ba Wi ?At

TABLE 4
Continued

Species	Family	Out	Mid	Center	Day last exposed†	Life form	Seed mass (mg)§	Height (cm)§	SLA (mm² mg⁻¹)	LDMC (mg g⁻¹)	Leaf N (%)	Dispersal unit and adaptation	Dispersal‡
Geum leiospermum	Rosaceae	33.3			354	ros forb	0.38	2.52	14.91	247.89		Hooked achene	At
Hectorella caespitosa	Montiaceae	0	58.3	83.3	352	cushion		0.9	18.34	230.15	2.52	?Capsule	?At
Kelleria childii	Thymeleaceae	0	33.3	8.3	373	cushion		0.29	60.31	201.76	1.27	Achene	?Wi
Leptinella goyenii	Asteraceae	0	0	8.3	355	cushion		1.3	15.6	347.79	1.58	Papery cypsella	Wi ?At
Luzula pumila	Juncaceae	50	83.3	66.7	366	cushion	0.21	1.84	13.49	287.2		Seed	At ?Wi ?Ant
Phyllachne rubra	Stylidiaceae	58.3	91.7	91.7	366	cushion		0.3	7.73	310.17	0.71	?Capsule	Wi ?Cap ?Inv
Poa colensoi	Poaceae	8.3	41.7	50	373	graminoid	0.14	4.38	11.55	315.87	1.54	Floret	Wi ?Wa At
Poa incrassata	Poaceae	0	83.3	100	355	graminoid		2.58	22.99	297.72	1.61	Floret	Wi ?Wa At
Raoulia grandiflora	Asteraceae	0	41.7	83.3	355	cushion	0.56	0.99	14.84	347.01	0.75	Pappate cypsella	Wi
Raoulia hectorii	Asteraceae	83.3	91.7	41.7	355	cushion		1.13	12.87	501.54	1.11	Pappate cypsella	Wi
Rytidosperma pumilum	Poaceae	33.3	100	91.7		graminoid	0.38	50	10.72	428.57	1.49	Floret	Wi ?At
Trisetum spicatum	Poaceae	8.3	0	0		graminoid		15	18.54	119.34	1.62	Caryopsis	Wi ?At
(B) 1991													
Argyrotegium mackayi	Asteraceae	0	33.3	75	355	ros forb	0.03	0.76	25.09	193.5	2.35	Pappate cypsella	Wi
Luzula rufa	Juncaceae				355	graminoid	0.3	3.81	14.16	265.52		Seed	At ?Wi ?Ant
(C) 2003													
Brachyscome sinclairii	Asteraceae	0	8.3	16.7	341	ros forb	0.26	1.63	10.63	237.65	1.83	Pappate cypsella	Wi
Chionohebe densifolia	Plantaginaceae					subshrub						Seed	?Wi ?Wa
Rytidosperma australe+	Poaceae	0	33.3	100		graminoid						Floret	Wi Wa At
Phyllachne colensoi	Stylidiaceae	0			355	cushion	0.17	0.3	16.84	425.52		?Capsule	Wi ?Cap ?Inv
Plantago lanigera	Plantaginaceae	0	8.3	8.3	358	ros forb	0.18	0.99	13.4	139.86		Viscid seed	?Wi ?Wa ?Gr
Ranunculus erysii	Ranunculaceae	0	8.3	8.3		forb	0.68	3.24	12.16	181.15	1.4	Achene	Gr ?At
(D) 2011													
Brachyglottis bellidioides	Asteraceae					ros forb	0.47	0.26	11.56	168.39		Pappate cypsella	Wi
*Hieracium lepidulum	Poaceae	0	0	16.7		forb	0.19	0.18	12.75	208.4	1.47	Pappate cypsella	Wi

TABLE 4
Continued

(E) Snowbank species not yet established

Species	Family	Out	Mid	Center	Day last exposed[†]	Life form	Seed mass (mg)[§]	Height (cm)[§]	SLA (mm² mg⁻¹)	LDMC (mg g⁻¹)	Leaf N (%)	Dispersal unit and adaptation	Dispersal[‡]
Blechnum pennamarina	Blechnaceae					fern		3.57	9.09	257.26		Spore	Wi
†*Caltha obtusa*	Ranunculaceae					pros forb						Seed	Wa
Carex berggrenii	Cyperaceae					graminoid						Utricle	Wa Gr Wi
Celmisia haastii	Asteraceae				373	ros forb	0.35	3.56	7.69	246.95		Pappate cypsella	Wi
Celmisia prorepens	Asteraceae		16.7			ros forb	1.22	4.73	11.06	245.78		Pappate cypsella	Wi
Chaerophyllum colensoi	Apiaceae	0		0		ros forb						Hairy mericarp	Wi ?At
Chionohebe glabra	Plantaginaceae				341	cushion		0.1	22.42	283.25		Seed	Bal Wi Wa
Colobanthus strictus	Caryophyllaceae	0	0	50	355	graminoid	0.03	1.34	19.07	229.6		Winged seed	Wt ?Wi ?Bal
Gaultheria rubicola	Ericaceae				355	subshrub	0.05	0.83	6.88	444.4		Fleshy berry	Fr Inv
Geum pusillum	Rosaceae					ros forb						Achene	At
Hebe imbricata	Plantaginaceae				332	shrub		5.22				Seed	Wi
Hebejeebie trifida	Plantaginaceae					subshrub						Seed	?Wi ?Wa
†*Isolepis aucklandica*	Asteraceae				355	graminoid	0.12	1.86	21.81	338.38		Nut	Wa Gr At
Kelleria villosa	Thymeleaceae				327	subshrub	0.6	1.48	26.35	402.78		Achene	?Wi
Lobelia glaberima	Lobeliaceae					pros forb						Fleshy berry	Fr Inv
Lobelia linnaeoides	Lobeliaceae				355	subshrub	0.01	0.51	24.55	180.27		Fleshy berry	Fr ?Inv
Ourisia glandulosa	Plantaginaceae					pros forb	0.06	0.07	7.62	256.21		Minute seed	Wi
Polystichum cystostegia	Dryopteridaceae					fern						Spore	Wi
Ranunculus pachyrrhizus	Ranunculaceae				373	forb		1.76	14.19	177.35		Achene	Wi ?At
Raoulia subulata	Asteraceae				373	cushion	0.07	0.35	31.11	414.04		Pappate cypsella	Wi
Scleranthus uniflorus	Caryophyllaceae				328	cushion	1.24					Perigynous cup	?Wi ?Cap
Taraxacum magellanicum	Asteraceae				353	ros forb	0.46	3.3	26.35	140		Pappate cypsella	Wi
Viola cunninghamii	Violaceae				332	ros forb	0.79	2.29	28.86	204.91		Arillate seed	Bal?Ant
Wahlenbegia albomarginata	Campanulaceae				341	ros forb	0.02	0.76	16.49	211.27		Censer seed	Bal Wi

† Information from Korsten (2011).
§ Information from S. Venn (personal communication, 2013).
‡ Information from Thorsen et al. (2009): Ant = ant; At = attachment; Ba = ballistic; Cap = capsule; Fr = frugivory; Gr = gravity; Inv = invertebrate; Wa = water; Wi = wind.
+ Also includes *Deschampsia chapmanii*.

ly *Poa colensoi*, and 31 dicots of at least three unidentified species, together with viable fragments of several lichens and at least one cushion species, *Colobanthus canaliculatus*, which resumed growth, a situation apparently not previously recorded.

There remains some 24 species which occupy natural snow banks on the range that have not yet established. Neither has the cushion species, *C. canaliculatus*, although *C. buchananii* is not uncommon. Relevant ecological features of the nine species that have established at various times over the past 52 years when compared with those of the 24 local snowbank species that have not, fail to provide any clear indication as to which ecological features may facilitate or prevent their establishment. Distance could be a factor in relation to the type of propagule and dispersal mechanism involved (Table 4), since the nearest late snowbank habitat is ~1 km up-wind (according to a satellite image) in relation to the prevailing, often strong westerly winds (NW to SW). It was reported by Körner (2003), based on studies in the European Alps, that natural recruitment of alpine species generally reflects their adaptations for dispersal: those with "parachutist" (pappate or papillate) diaspores, well developed in most Asteraceae and generally much less in species of *Epilobium*, predominated as colonizers. Species with winged diaspores were much less common and those without special adaptations, including very small seed, were of minor importance, with few such seed trapped more than 40 cm from the source (Körner, 2003). A detailed dispersal study by Scherff et al. (1994) of the Rocky Mountain snowbed species *Ranunculus adoneus* showed that virtually all its achenes remained within 16 cm of the source plant, and secondary dispersal through snow movement, melt water, or rain could add but 10 cm to the primary distance. The same could apply to *Ranunculus pachyrrhizus*, a species common in late snow-lie sites on the Old Man Range (Mark and Bliss, 1970), but not yet established at the snowfence site. The additional water provided by the melting snow accumulated in the lee of the fence is unlikely to be of ecological importance because of its relatively limited volume, the gentle slope (~5°) to windward, and the generally good drainage through the loess-dominated sandy loam to loam soils on the crest of the range (Mark and Bliss, 1970; Mark, 1994); surface water did not lie as snow melted on the site. Thus the lack of persistent saturated soil may be an additional factor preventing establishment of species characteristic of boggy microsites, for example, *Carex berggrenii* and *Caltha obtusa*, but continued monitoring may reveal further changes.

Analysis of plant functional traits at the study site points to a more productive and competitive plant community behind the fence where the snow lies longest and there is considerable wind protection. In addition, the higher abundance of species with heavier seeds might indicate that well-resourced seedlings may have a better chance of survival in this zone than species with smaller seeds. In addition, the partial protection from wind and frost provided by the additional snow cover and the fence has led to the dominance of high SLA species in its lee, compared with the relatively tougher-leaved, long-lived, low SLA plants that remain around its periphery. Korsten (2011) found similar responses for some of the traits described in natural snowpatches close to the study site. SLA increased and LDMC decreased with longer snow-cover days. However, some of these patterns in plant traits across snowmelt zones are contradictory to those in the natural snowpatch environments on the Old Man Range (Korsten, 2011), where seed mass decreased with longer snow cover. The pattern of functional traits observed in our study also differed from patterns on the Snowy Mountains, Australia, described by Venn et al. (2011), where there was a higher abundance of taller, more productive species (based on leaf area) around the edges of snow patches. Future work

should try to unravel the mechanisms that have led to the new, productive snowpatch community in the lee of the snow fence studied here, and particularly, investigate whether current patterns in species traits represent a transitional state brought about by the ongoing adjustment in relative dominance of existing species and colonization by species in the wider species pool. It may be that in time the vegetation pattern induced by the snow fence will eventually converge on the functional trait pattern seen in natural snowpatch communities elsewhere on the Old Man Range (Korsten, 2011).

Differential snow accumulation is known to be associated with differences in soil physical and chemical properties (Billings and Bliss, 1959; Bowman, 1992; Stanton et al., 1994; Scott and Rouse, 1995; Walker et al., 2001; Körner, 2003; Choler, 2005). However, it was concluded by Billings and Bliss (1959), following their comprehensive study of alpine snowbed ecology, that the distribution of alpine plant species in these habitats is primarily controlled by the rate of snow melt. This is likely also the case on the Old Man Range where Guevara (2012) described different patterns of soil chemical factors in relation to duration of snow cover between two nearby natural snowbanks and the snow fence at year 52, and found little correlation between them: under all depths of snow there were higher levels of all measured soil nutrients, as well as higher pH, associated with two natural snowbanks than with the induced snowbank. Negligible particulate matter appeared to be trapped by snow around the study site or elsewhere on the range and the westerly winds that prevail in this and other mountain regions of the South Island probably carry only a small nutrient load compared with some northern hemisphere regions. The mean annual nitrogen inputs recorded for seven sites in upland Central-eastern Otago (Lammerlaw-Rock and Pillar Ranges: 490–1340 m and ~70 km to the E-SE of Old Man Range), was a mere 0.03 kg ha^{-1} of NO$_3$-N and 0.05 kg ha^{-1} of NH$_4^+$-N (Holdsworth and Mark, 1990). In contrast, on the Colorado Front Range, annual wet deposition of inorganic nitrogen in 1990 was 7.5 kg ha^{-1} (NADP-NTN: http://nadp.sws.uiuc.edu/ntn/). According to W. D. Bowman (personal communication, November 2014) the total nitrogen deposition here (including dry deposition) would be ~150% greater than this (~11.25 kg ha^{-1}), or some 140 times greater than recorded on upland Otago. According to Bowman (1992; 2014, personal communication) the greatest amounts are associated with "the easterly, upslope storm track [which] carries atmospheric moisture across agricultural (livestock and fertilized cropland) and industrial regions of Colorado before reaching Niwot Ridge." Moreover, as he explains, the redistribution of snow due to high winds here, can greatly modify the nitrogen input locally and may partly explain the spatial heterogeneity of primary production, and presumably also floristic differences in the alpine ecosystems.

Given the changes and trends recorded over the first 52 years, continued studies of the snow fence vegetation-soil pattern on the Old Man Range could reveal whether time remains a factor in the vegetation-snow relationships here. Moreover, given the length of the study to date, the site could be a valuable long-term study site for assessing possible impacts of predicted global warming (Halloy and Mark, 2003; Gottfried, et al., 2012; Pauli et al., 2012), additional to those already in place in southern New Zealand (Mark et al., 2006; Dickinson et al., 2007; Lord et al., 2013), and this should not be impeded by the recently achieved protected status for this study site and the uplands of the Old Man Range.

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