A resurvey of late-lying snowpatches reveals changes in both species and functional composition across snowmelt zones

Catherine Pickering · Ken Green · Ana Agustina Barros · Susanna Venn

Abstract Alpine snowpatches are areas that, due to topographical and climatic factors, retain snow long after the thaw in the surrounding landscape. Within snowpatches there are often reliable patterns of snowmelt resulting in differences in plant composition, with snowpatch specialists limited to areas of late snowmelt. In 2013, we resurveyed vegetation in early, mid and late snowmelt zones across seven alpine snowpatches in the Snowy Mountains, Australia, 6 years after the initial 2007 survey. In both surveys, there were differences in vegetation cover and species composition among snowmelt zones; in particular, the cover of graminoids was higher in areas of earlier thaw. Differences in functional composition between survey periods were determined using functional traits (plant height, percent leaf dry matter content and specific leaf area) to calculate community trait-weighted means. In both surveys, early and mid snowmelt zones were dominated by taller species with larger leaves, mostly graminoids. Notably, by 2013 there was an increase in species richness in the late snowmelt zone and an increase in the cover of the tall tussock grass *Poa costiniana* across all snowmelt zones, driving changes in the community trait-weighted means for plant height and specific leaf area in the late snowmelt zone. The results highlight that snowpatch vegetation can change within relatively short time periods and that snowpatch plant communities may not remain as discrete units in the near future due to the encroachment of more competitive and productive species from the surrounding landscape.

Keywords Snowbeds · Climate change · Alpine · Short alpine herbfield · Snowy Mountains · Australia · Kosciuszko National Park

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Introduction

Predicted increasing temperatures and declining precipitation with climate change will lead to reductions in snow cover in many alpine areas (IPCC 2014). Because snow cover directly and indirectly affects the distribution and functioning of ecological assemblages in alpine areas, climate change is a major threat to many alpine ecosystems (Körner 2003; IPCC 2014). Decreases in snow cover have already been documented in many alpine areas (Beniston 2003; IPCC 2014) including in the Australian Alps, where average temperatures have increased and snow cover has declined by 30 % over the past 60 years (Green and Pickering 2009a; Davis 2013). As a consequence of decreasing snow cover and associated changes, the vegetation composition and ecosystem function is already changing in many alpine areas, including mountain summits (Gottfried et al.

2012; Pauli et al. 2012), nival zones (Grabherr et al. 1994; Pauli et al. 2007) and snowpatch communities (Green and Pickering 2009b).

Snowpatches (synonymous with snowbeds), occur in alpine and tundra landscapes where interactions with weather and topography favour the accumulation of snow, usually on the lee-side of ridgelines and peaks, and result in deeper winter snow than in the adjacent areas (Kudo and Ito 1992; Björk and Molau 2007). As such, the thaw is often delayed until well into summer or autumn. Strong and predictable gradients in snowmelt within snowpatches also occur, often leading to distinct snowmelt zones with differences in vegetation cover, species richness, plant composition across these snowmelt gradients (Kudo and Ito 1992; Stanton et al. 1994; Galen and Stanton 1995; Björk and Molau 2007; Venn and Morgan 2007; Green and Pickering 2009b; Schöb et al. 2009; Carbognani et al. 2012).

Areas with longer growing seasons around the edges of snowpatches are favoured by taller more competitive and productive species (Venn et al. 2011). In contrast, areas nearer to the centre of the snowpatch often have shorter growing seasons, and vegetation can be dominated by more specialized, shorter, smaller-leaved species (Björk and Molau 2007; Venn et al. 2011). As such, areas near the centre of snowpatches usually support fewer species and less vegetation cover than the surrounding earlier thaw areas, which support higher species richness and a greater vegetation cover (Carbognani et al. 2012). Therefore, these rare ecosystems often contain rare and specialized plant species that are excluded from the surrounding alpine areas, contributing to the high conservation value of many snowpatches worldwide (Costin et al. 2000; Björk and Molau 2007; Schöb et al. 2009; Carbognani et al. 2012).

Across snowpatches, snowmelt date is undoubtedly the most important environmental filter (Green and Pickering 2009a) exerting a strong influence on small-scale vegetation patterns, as well as on plant growth, phenology (Venn and Morgan 2007; Kameyama and Kudo 2009; Carbognani et al. 2012; Rumpf et al. 2014) and ecosystem functioning (Venn et al. 2011; Carbognani et al. 2012). The predicted decreases in snow cover may reduce the strength of this environmental filter allowing snowpatch communities to be colonized by more competitive species which require longer growing seasons in adjacent areas (Björk and Molau 2007; Green and Pickering 2009b; Schöb et al. 2009; Venn et al. 2011). Analysing changes in plant composition and functional composition across spatial and temporal scales within snowpatch communities can help us understand how snowpatch vegetation will respond to future changes in this important environmental filter (Venn et al. 2011).

In this study, we use a repeat vegetation survey, combined with an assessment of plant functional traits, to assess short-term change in species and functional composition over snowmelt gradients in snowpatches in the Snowy Mountains of south-eastern Australia. This study is part of a longer term monitoring programme of the duration, size and number of snowpatches, which are decreasing in line with the overall snow cover in this region (Green and Pickering 2009a, b). The snowpatches provide habitat for rare plant communities and species with high conservation value, including species endemic to this, the highest alpine region in Australia (Costin et al. 2000). Among the latest-lying snowpatches in the region, snowmelt date is the major determinant of the small-scale patterns in plant cover, composition and species richness (Green and Pickering 2009b). In addition, plant functional trait analyses revealed that late snowmelt zones within snowpatches are characterized by relatively shorter, smaller-leaved species, whereas earlier snowmelt zones are characterized by taller and bigger, potentially more competitive and productive species (Venn et al. 2011). Together, these results indicate that the composition of these specialized plant communities has great potential for change, especially around the snowpatch edges where the likelihood of colonization by taller, more competitive and productive species is the greatest (Venn et al. 2011).

We resurveyed seven snowpatches in 2013 to assess spatial and temporal changes in species and functional composition across the snowmelt gradients since the initial survey in 2007. Given the decreasing snowpack in the region we ask: (1) is the gradient in snowmelt date as strong as it was during the initial survey in 2007? (2) Have species richness, vegetation cover and composition changed in the 6 years between surveys across the snowmelt zones? (3) Are any changes in plant composition mirrored by changes in functional composition across the snowmelt zones, which may then infer changes in ecological processes across snowmelt zones?

Materials and methods

Study site

This study was conducted across seven snowpatches of the Main Range in the alpine area of Kosciuszko National Park, the Snowy Mountains, south-eastern Australia. The alpine area is characterized by snow cover for approximately 4–5 months of the year, with the first snow contributing to the winter snowpack usually occurring between May and June. Snow cover becomes discontinuous in October, although large drifts along the highest ridgelines may persist until March or later. Cumulative snow depth and thaw date for the past 60 years from the nearby weekly monitored snow course at Spencers Creek (1,830 m, 5 km from the study sites), show high inter-annual variability, with the integrated snow profile ranging from 63 to 439 metre-days,

and the date of thaw ranging from day 278 to 348 of year (Fig. 1). However, there is an overall trend of declining snow cover and earlier thaws over the past 60 years (Fig. 1). In addition, the 2007 survey occurred during the longest drought period on record in Australia with higher than average temperatures, lower precipitation (BOM 2013), shallow snow cover and earlier snow thaw (Green and Pickering 2009b). In contrast, conditions before the 2013 survey were wetter with more snow and a later thaw (BOM 2013). Hence, the vegetation would have experienced a shorter, but wetter growing period before the resurvey in 2013 compared to 2007.

Snowpatches in this region are considered to be discrete habitats within the alpine area, which reflect differences in abiotic conditions including soil depth, nutrients and temperatures, duration of the growing season and amount of rock cover (Costin 1954; Green and Pickering 2009b). For example, although highly organic alpine humus soils dominate all bedrock types and under most physiographic conditions within this alpine area (Costin 1954), soils were
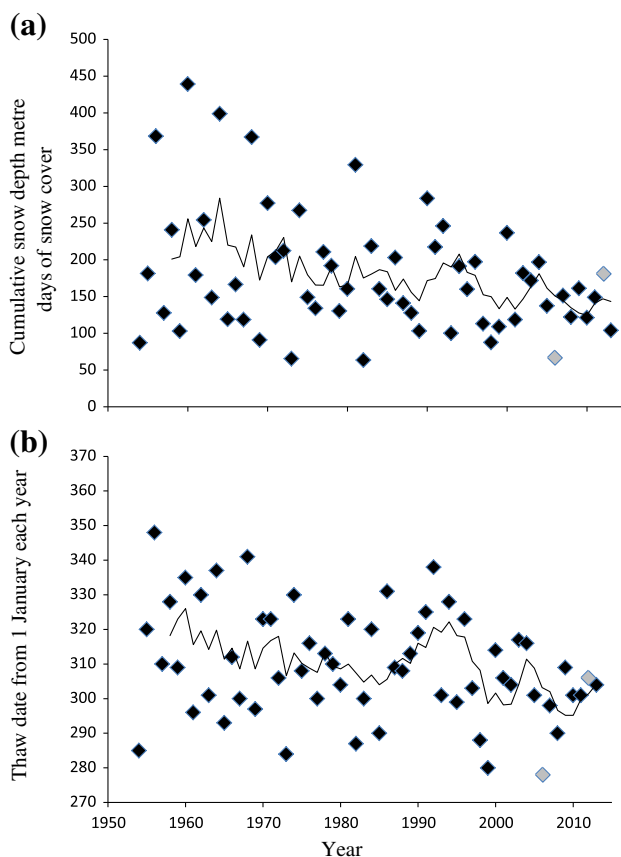

Fig. 1 Variation in **a** cumulative snow depth metre-days of snow cover and **b** thaw date from 1 January each year from 1954 to 2013 for the Spencers Creek snow course, 1,830 m a.s.l. Values in *grey* indicate the winter/spring before the 2007 and 2013 vegetation sampling. The *line* represents the running 5-year average value

shallower and there was more exposed loose rock on the surface in the centre of the snowpatches than in areas immediately down slope where soils were deeper and there was less exposed loose rock (Green and Pickering 2009b).

Vegetation within the snowpatches reflects these differences in abiotic factors, with a generally distinct pattern of plant communities. In the centre of the snowpatch where snow lasts the longest there may be little or no vegetation. Higher up the slope where snow duration is shorter but there is still exposed loose rock on the surface, the limited vegetation cover consists of Snowbank Feldmark. In contrast, down slope of the centre of the snowpatch there is often greater vegetation cover consisting of Short Alpine Herbfield on the deeper snowpatch meadow soils and poor fen peats that are often much wetter from snow melting in spring and summer (Costin 1954; Costin et al. 2000; Green and Pickering 2009b). As these two communities are restricted to snowpatches, their total distribution is very limited with only 156 ha of Snowbank Feldmark and 82.2 ha of Short Alpine Herbfield recorded in the Kosciuszko alpine area (Costin 1954). Further down slope from the centre of the snowpatch, where the growing season is even longer, the vegetation consists of Tall Alpine Herbfield on deep alpine humus. This community is the most common in the Kosciuszko alpine area (5,340 ha) accounting for 55 % of the total Kosciuszko alpine area (Costin 1954; Costin et al. 2000). Since the removal of cattle grazing in the 1950s, few grazing mammals have been found in Kosciuszko alpine area: mainly the native vole-like broad-toothed rat (*Mastacomys fuscus*) and introduced European hares (*Lepus europaeus*) (Green and Osborne 1994).

Vegetation sampling

The seven snowpatches sampled are among the latest lying in Australia, and are well defined and localized within an area of 20 km^2 (Supplementary Material 1). Plant composition was recorded in the seven snowpatches using permanently marked 1 m^2 quadrats in March 2007 and March 2013, following the protocols outlined in Green and Pickering (2009a). Quadrats were allocated to the centre of the snowpatches where snow lies the latest and is frequently bare ground and rock with occasional plants, some characteristic of Snowbank Feldmark. Down slope from the centre of the snowpatch in Short Alpine Herbfield, where it is less rocky and there is wet snowpatch meadow soils and poor fen peats resulting even though snowmelt is still relatively late and in Tall Alpine Herbfield further down slope from the snowpatch centre where snowmelt is even earlier and soils deeper. Between these three zones defined by plant communities, narrow transition zones were recognized.

Three 1 m^2 quadrats were randomly located at the same elevation across the slope in all the plant communities and
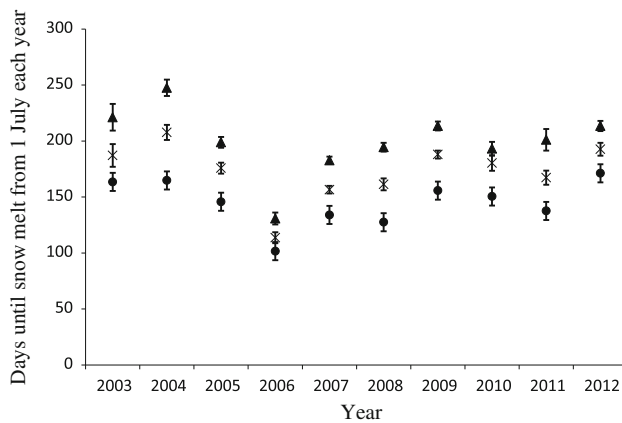
Fig. 2 Mean (±1 SE) number of days until snowmelt from 1 July in each year, for the three snowmelt zones across the seven snowpatches used in this study from 2003 to 2013. *Circles* denote early, *crosses* denote mid, and *triangles* denote late snowmelt zones

transition zones present in each of the seven snowpatches. The set of three replicate quadrats were at least 4 m apart with an average distance of 4.5 ± 1.1 m apart. As not all plant communities and hence transitions zones were present in all snowpatches, this resulted in a total of 83 quadrats sampled across the seven snowpatches, with one quadrat not relocated in 2013. Details of which plant communities and transition zones were present in each snowpatch are included in Green and Pickering (2009a).

Although the plant communities roughly correspond with snowmelt date, we more accurately determined zones of snowmelt across the seven snowpatches using detailed data on snow thaw dates, obtained from 29 soil temperature loggers (Gemini Data Loggers, Chichester, England). The soil temperature loggers were located among the three quadrats in each plant community and transition zone. As previous observations of snowmelt patterns had found close similarities in patterns among the three quadrats across slope within a snowpatch, the same snowmelt date was given to each of the three quadrats. The temperature loggers were buried at 7.5 cm depth in every community and transition zone in the seven snowpatches with soil temperature recorded every 2 h from 2003. This provided a 10-year average of snowmelt date across the snowpatches, based on when the soil temperature first rose above 3.2 °C at noon, or within 2 h either side of noon, which has been found a reliable estimate of snowmelt date and the commencement of the growing season in a wide range of alpine regions (Körner and Paulsen 2004). These temperature data were then used to assign quadrats in each plant community and transition zone to a snowmelt zone, based on the range and mean number of days since 1 July until the thaw for each year between 2003 and 2013 (Fig. 2): early snowmelt zone (74–210 days, mean 143 days since 1 July, $n = 26$

quadrats), mid snowmelt zone (85–223 days, mean 172 days since 1 July, $n = 30$ quadrats) and late snowmelt zone (114–288, mean 203 days since 1 July, $n = 27$ quadrats). Although the date of snow melt changed among years, the relative separation and sequence of snowmelt among snowmelt zones remained consistent (Fig. 2).

In each 1 m^2 quadrat during March 2007 and March 2013, the percent cover of all vascular plant species, bare ground, rock and litter was visually assessed to 0.5 % accuracy using a 20×20 cm grid. Cover values for individual species were summed to obtain overlapping cover for herbs and graminoids for each quadrat, while total vegetation top cover was calculated as 100 % less the sum of cover values for rock, litter and bare ground. Species names follow Costin et al. (2000).

Selection and measurement of functional traits

Morphological functional traits including canopy height, leaf size and specific leaf area, can reflect the overall competitive ability of a species, its capacity to tolerate stress and acquire resources, and its potential growth rate (Cornelissen et al. 2003) (Supplementary Material 2). By combining these types of traits for individual species with measures of species relative abundance, it is possible to generate indices of community functioning such as the community trait-weighted mean (CTWM) across environmental gradients (Díaz and Cabido 2001; McGill et al. 2006). By comparing changes in the CTWM over time, it should be possible to assess snowpatch community responses to changing environmental filters, such as snowmelt date (Díaz and Cabido 2001; McGill et al. 2006).

We chose these functional traits [plant height, leaf area, percent dry matter content of leaves and specific leaf area (SLA)] based on the individual plant and ecosystem functions in which they are involved (Westoby 1998; Cornelissen et al. 2003; Lepš et al. 2006; Petchey and Gaston 2006) (Supplementary Material 2). Trait data for each species of flowering plant found in the snowpatches were obtained from ten adult individuals outside the quadrats to avoid destructively sampling within the quadrats, using the standardized protocols of Cornelissen et al. (2003).

We calculated the CTWM for the assemblages of plants recorded in the three snowmelt zones, for each of the four traits. 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 us to calculate the relative cover of individual trait responses to the different zones of snowmelt over time, weighted by the absolute individual species covers, rather than provide an aggregate index based on multi-trait space (Villeger et al. 2008). We utilized the software of Lepš and de Bello (2008) to assist in scaling our trait and cover values for the quadrat

data from the three snowmelt zones to calculate the CTWM values. Trait data were not available for four uncommon species (*Colobanthus affinis*, *Isolepis subtilissima*, *Luzula atrata* and *Poa hiemata*) that had a combined cover value of less than 1.5 % and so the cover values for these species were excluded, as were the traits for one fern and two bryophytes with low cover and frequency values (Supplementary Material 3). For two *Carex* species with moderate cover values where trait data were not available, we substituted trait data for the two most morphologically similar species (e.g. for *Carex cephalotes* we used trait data for *Carex hebes,* for *Carex hypandra* we used trait data for *Carex canescens*).

Data analysis

Changes in vegetation and functional traits among snowmelt zones and between the two surveys were analysed using general linear mixed models (MIXED) in SPSS (Version 22.0). Quadrats were nested within snowmelt zones which were then nested within snowpatches. Snowmelt zones, snowpatches, year and their interaction were included as fixed factors, and quadrats as random factors. Separate general linear mixed models were performed for the following dependent variables: species richness, vegetation cover, overlapping cover of graminoids and herbs, and the CTWMs for canopy height, leaf area, percent leaf dry weight and specific leaf area. Before analysis, vegetation cover and the cover of graminoids and herbs were arsine square root transformed. The normality of the data was assessed by using quantile–quantile plots of the residuals. When appropriate, post hoc comparisons were conducted using Fisher's least significant difference (LSD) for multiple comparisons ($P > 0.05$).

To compare the variation in species composition in each quadrat between sample years, we used the Jaccard's similarity coefficient on species presence/absence data, where a value of 1 indicates composition is identical in the two quadrats being compared and a value of 0 indicates there are no species in common between the two quadrats. Changes in the Jaccard's similarity coefficient across snowmelt zones were also analysed with the MIXED procedure, with snowmelt zones and snowpatches used as fixed factors and quadrats used as a random factor.

Species composition changes over time across the snowmelt zones were assessed using non-metric multidimensional scaling (NMDS) ordination performed in the multivariate statistical package PRIMER (Version 6.1.12). Cover data for all vascular plant species and other surface categories (bare ground, rock and litter cover) were used to calculate dissimilarity matrices using the Bray–Curtis dissimilarity measures. Non-metric multidimensional scaling was then used to describe the maximum variation among quadrats in two dimensions (NMDS axes 1 and 2) with the closeness of fit of the NMDS axes to the dissimilarity matrix expressed in terms of stress. To determine if there were significant differences in vegetation among the six combinations of snowmelt zones and years, a one-way analysis of similarity (ANOSIM) was used for the dissimilarity matrices. ANOSIM is a non-parametric permutation procedure applied to a rank dissimilarity matrix that is analogous to analysis of variance but is distribution-free (Clarke 1993). The SIMPER function was used on the NMDS dissimilarity matrices for plant composition to identify which factor, i.e. plant species, rock, bare ground or litter, contributed to the separation of the snowmelt zones in each year.

In addition, overall temporal changes in functional composition across the snowmelt zones were assessed using NMDS ordinations with Euclidian dissimilarity matrices of normalized values of CTWMs in the multivariate statistical package PRIMER. Significant differences among years/melt zones were also tested using ANOSIM for the CTWM per quadrat. The contribution of important traits to explaining significant variation (r^2) in the ordinations was calculated using a Pearson's correlation coefficient with vectors of significant traits displayed on the ordination.

Results

The timing of snowmelt within snowpatches

Despite inter-annual variation in snow cover, there were relatively consistent differences in snowmelt dates between the three zones between 2003 and 2012 (Fig. 2). Therefore, plants in quadrats in early snowmelt zones consistently experienced shorter snow seasons and hence longer growing seasons compared to those in mid and late snowmelt zones. In the early snowmelt zone, the average thaw date in the early snowmelt zone was 143 days since 1 July, snow in the mid snowmelt zone melted an average of 29 days later, while in the late snowmelt zone it was an average of 60 days after quadrats in the early snowmelt zone.

Plant composition including species richness

A total of 51 species of plants were recorded from the 83 plots during the two sampling periods. These included 36 species of herbs, 18 graminoids, one species of fern and two mosses (Supplementary Material 3). Of these, 31 species were recorded in both surveys, 11 were only recorded in 2007 and 13 were only recorded in 2013. Of the species lost by 2013, three were graminoids and eight were herbs, including the endemic herbs *Ranunculus acrophilus* and *R. dissectifolius*. Of the species gained since 2007, there were four graminoids, eight herbs and one fern, all of which are

common in the local species pool and characteristic of the surrounding Tall Alpine Herbfield community.

Species richness in the late snowmelt zone increased from 19 to 27 species between surveys, with most of the new species of herbs considered to be more characteristic of the surrounding Tall Alpine Herbfield rather than Short Alpine Herbfield plant communities (Supplementary Material 3). In contrast, there were similar numbers of species for both surveys in the early and mid snowmelt zones (32 species vs. 29 for the early snowmelt zone, 29 vs. 32 for the mid snowmelt zone in 2007 and 2013, respectively).

The species richness of flowering plants per quadrat varied from 1 to 11 species (mean 4.4 species). Although there was no change in the average species richness per quadrat between surveys, there was a slight decrease in richness per quadrat from 2007 to 2013 in the early snowmelt zone and a slight increase in richness in the late snowmelt zone (Table 1; Fig. 3a). As a result, species richness was significantly different between these two zones in 2013 in several snowbanks when compared using post hoc texts (least significant differences).

There was considerable species turnover within individual quadrats between the two surveys. Overall similarity values based on presence/absence data for quadrats ranged from no species in common (values of 0) to all species in common (values of 1), with an average Jaccard's similarity of 0.42 between quadrats sampled in 2007 and those sampled in 2013 (Fig. 3b). The degree of change in composition significantly differed among snowmelt zones (Table 1), with less similarity in composition between surveys for the late snow melt zone as reflected in a low Jaccard's value. This is likely to reflect the new species recorded in this snowmelt zone in 2013.

There were no consistent changes in overall vegetation cover between surveys, with similar differences among snowmelt zones in both years (Table 1; Fig. 4a). Quadrats in the late snowmelt zone had less vegetation cover (33 %) compared to those in the early snowmelt zone (90 %) in both years (Table 1; Fig. 4a). However, there were significant increases in overall graminoid cover between years (44 % in 2007 vs. 53 % in 2013), and differences in cover among snowmelt zones, with quadrats in the late snowmelt zone having less graminoid cover (11 %) than those in the early snowmelt zone (82 %). Herb cover also changed between surveys, but this was mostly limited to the mid snowmelt zone where herb cover declined from 18 to 7 % between the surveys (Table 1; Fig. 4c). Although these overall patterns were apparent, the extent of the changes varied among snowpatches resulting in significant three-way (year by snowmelt zone by snowpatch) interactions in the general linear mixed models for each of these dependent variables (Table 1).

Table 1 Results of general linear mixed models examining changes in vegetation parameters and functional traits (community trait-weighted means) between 2007 and 2013 for the three snowmelt zones across the seven snowpatches

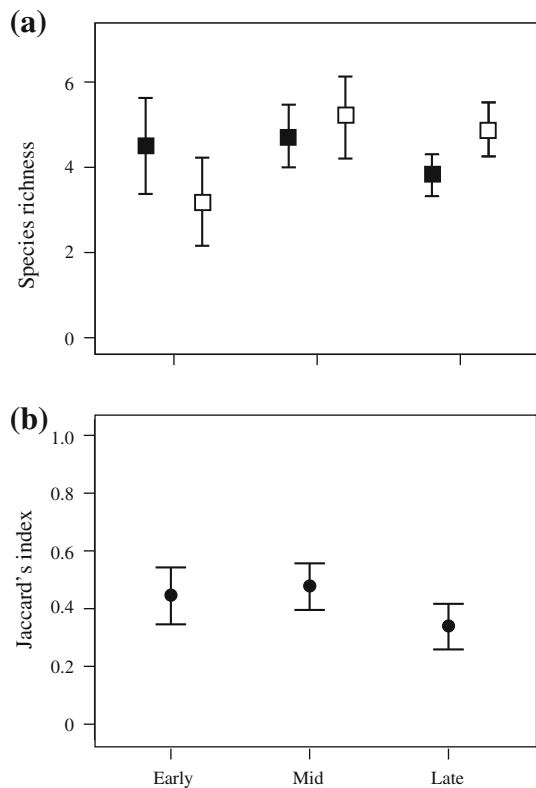|	Snowmelt zone df = 2		Snowpatch df = 6		Snowmelt zone × Snowpatch df = 9		Year df = 1		Year × Snowmelt zone df = 2		Year × Snowpatch df = 6		Year × Snowmelt zone × Snowpatch df = 9	
	F	P	F	P	F	P	F	P	F	P	F	P	F	P
Species richness	5.281	0.007	5.410	<0.001	3.270	0.002	0.468	0.496	14.903	<0.001	2.154	0.059	5.778	0.001
Jaccard coefficient	11.000	<0.001	4.050	0.002	1.494	0.169								
Vegetation cover	83.966	<0.001	8.543	<0.001	2.892	0.006	3.342	0.072	2.974	0.058	1.554	0.175	2.149	0.037
Graminoid cover	100.219	<0.001	9.588	<0.001	6.183	<0.001	23.183	<0.001	1.560	0.218	2.286	0.046	2.393	0.021
Herb cover	4.103	0.021	21.110	<0.001	9.457	<0.001	5.883	0.018	3.514	0.036	1.258	0.289	3.351	0.002
Plant height	37.300	<0.001	5.090	<0.001	5.206	<0.001	75.474	<0.001	7.096	0.002	0.704	0.647	3.048	0.004
Leaf area	11.180	<0.001	4.167	0.001	2.560	0.014	12.616	0.001	3.537	0.035	1.444	0.212	2.219	0.032
% leaf dry weight	6.311	0.003	8.003	<0.001	2.140	0.038	39.902	<0.001	1.030	0.363	4.972	<0.001	2.019	0.051
SLA	2.434	0.096	8.090	<0.001	2.836	0.007	8.456	0.005	9.664	<0.001	7.422	<0.001	3.426	0.002

(a)

(b)

Fig. 3 Mean percent **a** species richness and **b** Jaccard's ±95 % confidence intervals for the three snowmelt zones in 2007 (*closed squares*) and 2013 (*open squares*) across seven snowpatches. $N = 26$, 30 and 27 quadrats in the early, mid and late snowmelt zones, respectively

The combined effect of changes in vegetation cover, rock and bare ground and species composition between years and changes in species abundance among snowmelt zones, resulted in significant differences in overall plant composition between all year/zone combinations (ANOSIM, $\rho = 0.414$, $P = 0.001$ overall, $P < 0.05$ for all pairwise combinations between snowmelt and year). The late snowmelt zone was characterized by loose rock (66 %), with the limited vegetation growing in this zone dominated by the herb *Neopaxia australasica* (11.6 %), unknown moss (11.4 %), and the grass *Poa fawcettiae* (2.1 %) (Supplementary Material 3). In contrast, the late snowmelt zone had limited areas of loose rock (4 %) with most of the area covered by the grasses *Poa costiniana* (65.8 %) and *Rytidosperma nudiflorum* (10.4 %), and the herb *Celmisia costiniana* (6.1 %). The main differences between years were due to increases in the cover of the taller tussock grasses *P. costiniana* (24 % in 2007, 40 % in 2013) and *P. fawcettiae* (4.7–6.5 %). The area of bare loose rock decreased slightly as it was covered by vegetation (33–30 %). The cover of the unknown moss (8.5–7.7 %), the small herb *N. australasica* (10–4 %), and the short grass
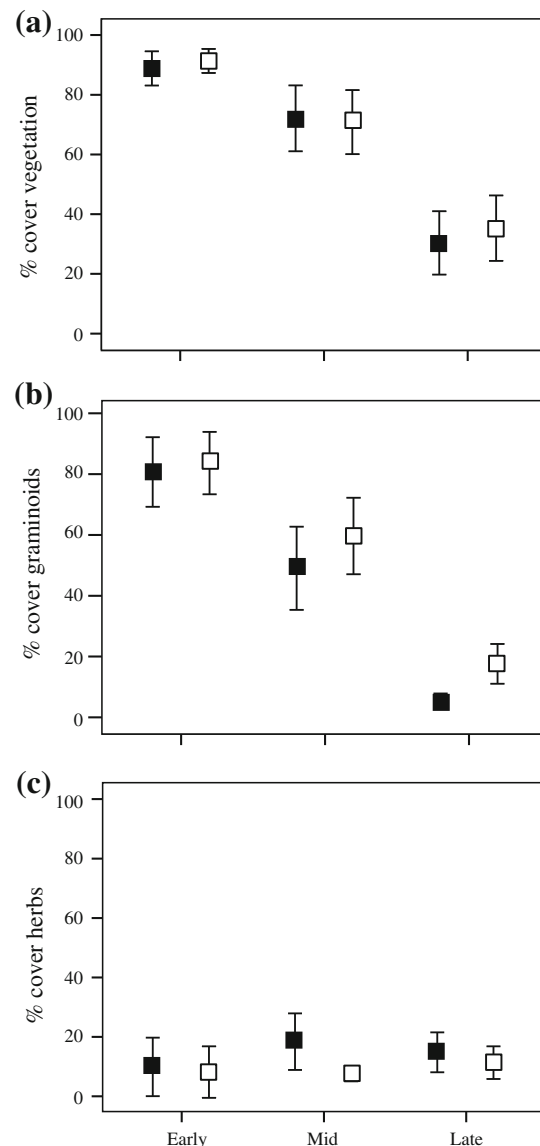

(a)

(b)

(c)

Fig. 4 Mean percent **a** vegetation cover (*top cover*), overlapping cover of **b** graminoids and **c** herbs ±95 % confidence intervals for the three snowmelt zones in 2007 (*closed squares*) and 2013 (*open squares*) across seven snowpatches. $N = 26$, 30 and 27 quadrats in the early, mid and late snowmelt zones, respectively

R. nudiflorum (7.8–0.7 %) all decreased between surveys. The SIMPER function revealed that these changes collectively explained 81 % of the dissimilarity between the two surveys. Similar changes in species frequency and percent cover were found for individual species (Supplementary Material 3).

Functional composition

Overall, there were significant changes between 2007 and 2013 in functional composition as determined by CTWMs
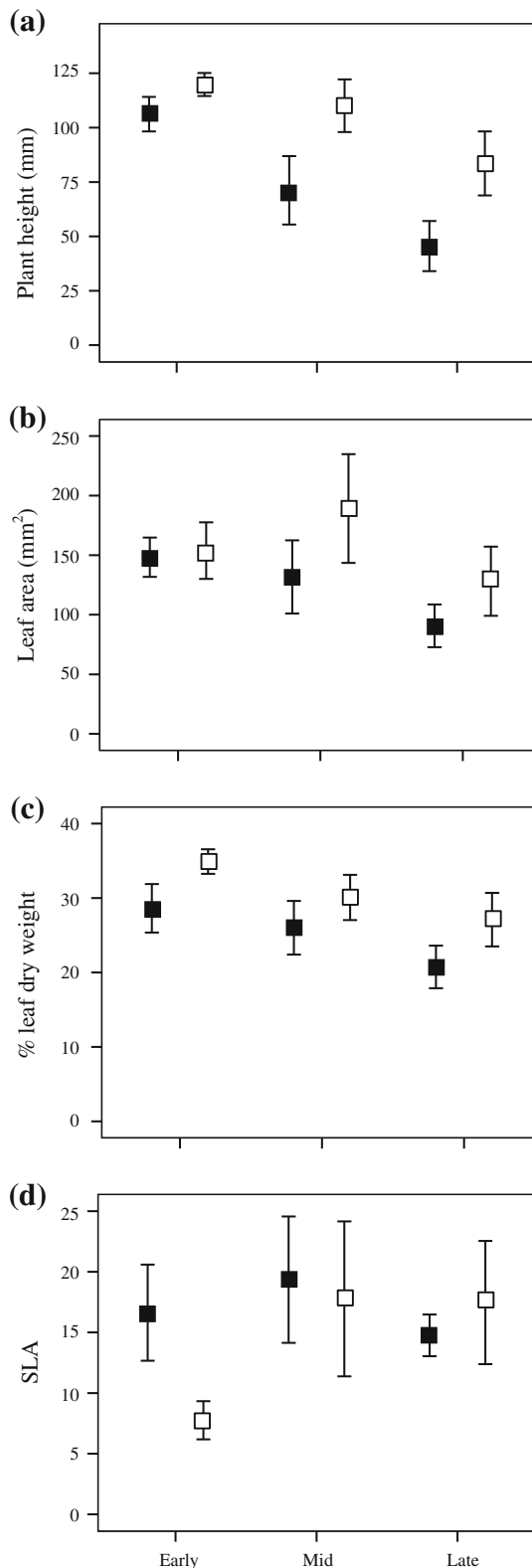
(a)

(b)

(c)

(d)

Fig. 5 The community trait-weighted mean (CTWM) of the four functional traits: **a** plant height, **b** leaf area, **c** percent dry weight of leaves and **d** specific leaf area (SLA), ±95 % confidence intervals for the three snowmelt zones (early, mid and late) in 2007 (*closed squares*) and 2013 (*open squares*) across seven snowpatches. $N = 26$, 30 and 27 quadrats in the early, mid and late snowmelt zones, respectively

for plant height (Fig. 5a), leaf area (b), percent dry weight of leaves (c), and SLA (d). For plant height, leaf area and SLA, however, these changes were not consistent across all snowmelt zones and snowpatches (Table 1). In 2013 a large proportion of the vegetation was taller with large leaves compared to 2007, particularly in the mid and late snow melt zones. There was a higher proportion of plants with relatively tough leaves (higher percent leaf dry weight) in 2013, in all snowmelt zones. As such, the proportion of plants with low SLA was high, but only in the early melt zone in 2013. Despite these overall patterns, the extent of the changes varied among snowpatches resulting in significant three-way (year by snowmelt zone by snowpatch) interactions in the general linear mixed models for plant height, leaf area and SLA (Table 1).

When considering the four measured traits and the CTWMs together in each quadrat, there were significant differences among all combinations of zones and year (ANOSIM, $\rho = 0.231$, $P = 0.001$ overall, $P < 0.05$ for all pairs of year/zones) except for the mid snowmelt zone in 2007 and the late snowmelt zone in 2013 (Fig. 6). In effect, by 2013 the late snowmelt zone functionally resembled what had been found in the mid snowmelt zone in 2007. The NMDS ordination of the CTWMs revealed an overall pattern of early and late snowmelt zones being somewhat discrete, with mid snowmelt zone quadrats appearing functionally similar in ordination space to both the other zones (Fig. 6). By 2013, many of the late snowmelt zone quadrats appear very similar to the mid snowmelt zone quadrats in their functional composition, whereas there is little functional change in quadrats from the early snowmelt zones between 2007 and 2013 (Fig. 6). The vectors overlaid on the ordination confirm the patterns of CTWM with snowmelt zones; notably plant height is driving the separation in functional composition between the early and late snowmelt zones (Fig. 6).

Discussion

Vegetation changes

There was a strong within-snowpatch gradient in snowmelt across the seven snowpatches, despite some years experiencing earlier snowmelt than others. There were also clear differences in vegetation cover and composition among the early, mid and late snowmelt zones in both surveys, with a decreasing dominance of graminoids, and less vegetation cover overall in the late snowmelt zone compared to the earlier snowmelt zones. In addition to these differences, there were changes in vegetation cover and plant composition between the surveys. Specifically, new species had started to colonize the late snowmelt zone and there was an
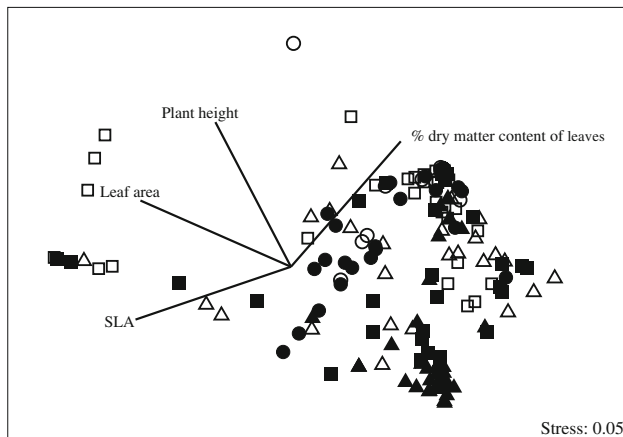
Fig. 6 Non-metric multidimensional scaling ordinations representing the clustering of the 83 1 m² quadrats surveyed in 2007 and in 2013 based on Euclidian dissimilarity values matrices of normalized functional composition as determined by the community trait-weighted mean (CTWM) across early (*circles*), mid (*squares*) and late (*triangle*) snowmelt zones in 2007 (*closed/filled shapes*) and 2013 (*open shapes*). *SLA* specific leaf area

overall increase in the cover of graminoids particularly in the late snowmelt zone in 2013.

The initial 2007 survey of these snowpatches revealed clear within-snowpatch snowmelt zonation, with the early snowmelt zones containing a high proportion of potentially competitive and productive species (Green and Pickering 2009b; Venn et al. 2011). Even at this stage, it appeared that the composition of the snowpatch communities had started to change from the original descriptions of these communities, as discrete communities dominated by low growing herbs ∼50 years earlier (Costin 1954; Wimbush and Costin 1973).

The changes in snowpatch species between the two surveys, particularly in the late snowmelt zone, appear to be driven by the loss of some specialized endemic species, and the gain of more generalist species. The spread of generalist species within snowpatches has been predicted in many other alpine regions with declines in snow cover (Kudo and Ito 1992; Björk and Molau 2007; Schöb et al. 2009). In the Snowy Mountains, snowpatches had an average of 4.4 species per m² compared to a more common range of 5–10 vascular plants per m² (Björk and Molau 2007). The lack of significant changes in species richness in the quadrats between surveys may reflect the dominance of long-lived perennial species at these sites, and most other alpine floras (Costin et al. 2000, Körner 2003), which may slow the rate of change in alpha diversity in these floras.

The CTWMs for the four measured traits partially reflected the patterns in species composition. For example, the increasing proportion of taller species between 2007 and 2013 is likely an effect of increasing dominance of the tall

tussock grass, *P. costiniana*, which almost doubled in percent cover between 2007 and 2013 in all snowmelt zones. In addition, increases in the proportion of species with larger leaves also reflects the dramatic changes in *P. costiniana* overgrowing areas of exposed rock and bare ground, as well as increases in the abundance of other relatively large and productive grass species such as *P. hiemata* and *P. fawcettiae*. In general, *P. costiniana* has not been considered characteristic of snowpatches, although it is common throughout the Kosciuszko alpine region and dominates the Tall Alpine Herbfield community that surrounds snowpatches (Costin et al. 2000).

The dramatic increases in *P. costiniana* within snowpatches may be indicative of changes in the relative length of the growing season and/or resulting changes in soil nutrients. Although we did not resample soil nutrients in 2013, in 2007 the deeper soils in the late snowmelt zones in the snowpatches tended to have a higher carbon and nitrogen content than the mid snowmelt zone (Green and Pickering 2009b). Variation in soil and microbial activity has been found across many snowpatches, with gradients in soil temperatures having flow on effects in terms of nutrient cycling (Bjork and Molau 2007; Carbognani et al. 2014).

The dramatic increase in *P. costiniana*, however, was not limited to snowpatches, with similar increases in the frequency and cover of this grass in other plant communities in the same alpine region over the same period (Green and Pickering 2009b; Venn et al. 2012, 2014). It is therefore equally likely that *P. costiniana* benefited from the generally wetter conditions in 2013 compared to the original survey. In addition, sampling in 2007 was towards the end of a severe *El Niño* event where, due to changes in the relative water temperatures of the southern Pacific, the climate of eastern Australia was much drier than average (BOM 2013). In contrast, sampling in March 2013, occurred during the opposite pattern, where the relative water temperatures of the southern Pacific reverse, resulting in higher than average rainfall in eastern Australia (e.g. a *La Niña* event) (BOM 2013).

Functional changes

The vegetation recorded in the early snowmelt zones in 2007 consisted of a significantly higher proportion of taller and larger leaved species compared to mid and late snowmelt zones, which complements the patterns in species composition. The resurvey in 2013 revealed that the proportion of taller, therefore potentially more competitive species, increased significantly across snowmelt zones, particularly in the mid and late snowmelt zones.

The CTWMs for plant height was strongly affected by changes in the dominant grasses, especially the large increase in *P. costiniana*. As CTWMs specifically

incorporate species abundance, and hence proportions of particular traits in each quadrat, large increases in any one species will drive changes in the CTWM. *Poa costiniana* is relatively tall compared to other snowpatch vegetation and has long leaf blades. As such, we expect this species to be more competitive and productive relative to other snowpatch species and potentially out-compete many of the shorter, slower growing species especially in the early snowmelt zone given its height, longevity and establishment success rate (Venn and Morgan 2009; Venn et al. 2011).

Shorter grasses and other herbaceous species which were present in the early and mid snowmelt zones in low abundance, also contributed to the variation observed in the CTWMs for plant height in the mid and early snowmelt zones. The patterns in the CTWMs for leaf area, percent leaf dry matter content and SLA do not appear to relate to specific patterns in vegetation composition. The sharp decrease observed in 2013 in the CTWM for SLA in the early snowmelt zones may be a combination of decreasing cover of *R. nudiflorum*, *L. acutifolia* and *C. costiniana* and the large increase in *P. costiniana* cover (+26 %). The first three species have mean SLA values of 45, 13 and 10, respectively; while *P. costiniana* has a relatively low mean SLA value of around 5 and therefore may have driven the low CTWM for SLA in the early snowmelt zone.

Given that the timing of snowmelt provides the most critical environmental filter across snowpatches (Canaday and Fonda 1974; Galen and Stanton 1995; Green and Pickering 2009b; Schöb et al. 2009; Venn et al. 2011), we expect the functioning of snowpatch communities to change dramatically as this filter weakens in coming decades with reductions in snowpack, leading to changes in the distribution of species with competitive and productive traits, and those which can tolerate various ambient conditions. As documented in this study, the potential for functional change may be driven by only a few, but abundant species and changes can occur relatively rapidly, even in an alpine landscape dominated by long-lived perennial species.

Conclusions

Comparing the results of the 2007 survey, with the resurvey in 2013 confirms that snowpatch vegetation is changing. Over the 6 years between the two surveys tall, potentially competitive species increased across all snowmelt zones. With even greater reductions in winter snowfall and rising temperatures predicted for the Australian alpine region (Hennessey et al. 2008), growing seasons are likely to continue to lengthen in and around snowpatches. Hence, the present characteristic snowpatch communities may re-assemble dramatically over the next few decades.

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