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Timing of snowmelt affects species composition via plant strategy filtering

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Abstract

Plant strategy schemes aim to classify plants according to measurable traits and group species according to their shared evolutionary responses to selective pressures. In this way, it becomes possible to make meaningful comparisons among ecosystems and communities and to predict how plant communities might respond to changes in their environment. Here, we classified common alpine plants which occur in snowpatches (Early and Late snowmelt sites) and in adjacent vegetation (Snow-free sites which melt early in the growing season) using Grime's CSR plant strategy scheme. Alpine plant communities are largely driven by environmental filters associated with a relatively constant gradient of snowmelt timing. Since snow persistence influences the abiotic environment and plant assemblages alike, we hypothesised that these patterns would be reflected in community CSR scores. Weighted community CSR scores were clustered towards the stress-tolerator (S) corner of the triangular CSR space, and Snow-free communities were significantly more stress-tolerant than Early and Late snowmelt communities. This suggests that snowpatch communities are functionally distinct from surrounding vegetation when considering the major axes of plant variation identified by CSR theory. These results lend further support to the importance of the timing of snowmelt as a key filter, influencing how species and plant strategy types distribute themselves across the alpine landscape.

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Keywords: Alpine; CSR; Environmental filtering; Local species distributions

Introduction

Plant strategy schemes attempt to develop a universal approach to ecology whereby species can be grouped according to their shared responses to selective pressures (Grime, 1974, 1977, 2001; Westoby, 1998). The competitor (C), stress tolerator (S) and ruderal (R) strategy scheme of Grime (1974, 2001) proposes that plant species have evolved under three key selective pressures: stress, disturbance and competition. The basis for these three primary strategies is that a species' investment into growth and life-history traits is finite and can signal which dominant selective pressures have shaped

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its evolution. Thus, the primary strategy of a plant species can be inferred through the measurement of physical functional traits that represent the trade-off between resource acquisition and conservation. Grime (2001) predicted that stressful (unproductive but stable) environments will support a higher proportion of plant species with stress-tolerator (S) traits. Typically, such plants have traits that promote resource conservation, have slow growth and long life-span. In frequently-disturbed environments, Grime predicted that ruderal (R) species (those adapted to disturbance, typically with short life-spans and high reproductive output) would dominate. In highly productive environments (with infrequent disturbance), competitors (C) or species with traits that allow them to outcompete other species are expected to dominate.

Grime (2001) claim that the CSR approach can be used to predict responses of plant communities and populations to changes in land use, climate, resources and disturbance regimes. Indeed, there is increasing support for the scheme (Cerabolini et al., 2010) in both the northern (Moog, Kahmen, & Poschlod, 2005; Caccianiga, Luzzaro, Pierce, Ceriani, & Cerabolini, 2006; Frenette-Dussault, Shipley, Léger, Meziane, & Hingrat, 2012) and southern (Cross, Green, & Morgan, 2015) hemispheres, and at broad spatial scales (Schmidtlein, Feilhauer, & Bruelheide, 2012). Recent advances in the classification of species in the CSR scheme (Pierce, Brusa, Vagge, & Cerabolini, 2013; Pierce et al., 2017) allow for species classification using only a few, easily measured leaf traits.

While the CSR scheme can be used to reveal which of the three primary strategies are present in a suite of plant species, it can also be useful for investigating the role of environmental filters in community assembly. Environmental filters are the abiotic conditions that exclude species with unsuitable functional traits from entering or persisting in a community and hence, can shape community assembly (McGill, Enquist, Weiher, & Westoby, 2006; Cornwell & Ackerly, 2009; Kraft et al., 2015). For example, a species with a competitive strategy (tall species with large leaves) cannot persist in environmental conditions with limited resources; instead, species with conservative leaf economics are selected for. Where resources are restricted, environmental filters can limit the species pool in the absence of other assembly processes (Cornwell & Ackerly, 2009). Ruderal species (R) which are able to persist under variable conditions may be less affected by environmental filters, or simply 'anticipate' and benefit from changing conditions as a result of disturbances; thus it is possible for R species to coexist with S species in harsh environments (Chesson et al., 2004; Pierce et al., 2017). The effect of changes in environmental filters depends on the range of plant strategies that are present in a community (Diaz & Cabido, 2001). This makes existing environmental gradients a useful tool to examine natural variation in vegetation community responses to environmental variation (McGill et al., 2006; Venn, Green, Pickering, & Morgan, 2011).
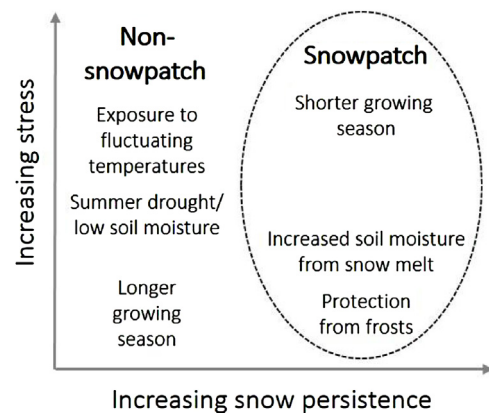

Fig. 1. Diagrammatic representation of the relative levels of potential stresses associated with snow persistence in the alpine landscape. Positions on the diagram are relative estimations of the effects of each "stress" on plant communities based on literature (Billings & Bliss, 1959; Atkin & Collier, 1992; Kudo & Ito, 1992; Wipf et al., 2006).

Mountainous regions provide an ideal setting for applying the CSR strategy scheme across environmental gradients. Over relatively small spatial scales, rapid changes in elevation interact with local topography to create steep gradients in temperature and precipitation (Stanton, Rejmanek, & Galen, 1994; Körner, 1999). One such example is the snowpatch (or snowbank) plant communities which occur in alpine areas where snow accumulates and persists on lee slopes for several months after adjacent areas have thawed, even well into summer or autumn (Wahren, Williams, & Papst, 2001; Venn & Morgan, 2007; Edmonds, Lunt, Roshier, & Louis, 2006; Green & Pickering, 2009a, 2009b). Snowmelt timing across snowpatches follows a relatively constant annual pattern, resulting in a mosaic of plant communities which are closely associated with the timing of snowmelt (Billings & Bliss, 1959; Kudo & Ito, 1992; Galen & Stanton, 1995; Venn & Morgan, 2007).

In the CSR framework, it is tempting to regard late-lying snow as an environmental stress since it substantially reduces the length of the growing season, which in turn directly affects rates of soil formation, litter decomposition and microbial activity (Buckeridge & Grogan, 2008; Buckeridge, Zufelt, Chu, & Grogan, 2010). Timing of snowmelt also directly affects alpine plants through phenological timing, with late snow melt resulting in an overall reduction in carbon assimilation, nutrient reabsorption, reproduction and fitness (Wipf & Rixen, 2010; Gehrmann, Hänninen, Liu, & Saarinen, 2017). On the other hand, the more prolonged snowmelt associated with late lying snow may provide some protection against seasonal drought and frost (Billings & Bliss, 1959) with advanced snowmelt exposing plants to stressful temperature fluctuations in early spring (Wipf, Rixen, & Mulder, 2006). Early snowmelt also increases the probability that plants will be damaged by frost events (Venn, Morgan, & Green, 2009, Fig. 1).

Here, we aim to test the utility of the CSR scheme across a fine-scale gradient of snow persistence within alpine communities in south-eastern Australia. We compare species and life-form composition as well as community CSR scores across a gradient of snow-persistence in order to investigate three alternative hypotheses:

H_0. There is no difference in the community CSR scores between snowpatches and snow-free sites, despite differences in snow persistence;

H_1. Snowpatch communities are floristically distinct from snow-free zones and have higher community S scores due to lower productivity associated with late snow melt;

H_2. Snow-free communities have higher community S scores than snowpatches due to the extreme environmental conditions associated with early snowmelt.

Materials and methods

Study region

The study was conducted in the Australian Alps, near the summits of Mount Hotham (1861 m) and Mount Loch (1800 m) (36° 58′44.6″S, 147° 07′58.3″E). Mean annual precipitation is ~1500 mm (Australian Bureau of Meterology, 2017). Monthly temperatures vary seasonally ranging from 5 to 16 °C in summer (December to February) and −4 to 0 °C in winter (June to August; Australian Bureau of Meterology 2017). Frequent frosts occur throughout the year (Williams, 1987), particularly in early spring and late autumn (i.e. in the Snow-free period). The entire area is covered by snow for 4–5 months of the year (generally between July and October), with snowpatch communities being under snow for up to 7 months (Wahren et al., 2001; Venn & Morgan, 2007). The vegetation of the study sites is short alpine herbfield, consisting of forbs, tussock grasses and scattered low shrubs. Snowpatches are typically dominated by short forb and graminoid species (~5–15 cm high), whereas low scattered shrubs (<1 m) are present outside of snowpatches. The study was conducted over the 2006 snow season, and most of the snow in the landscape had melted by mid-September, with only snowpatches remaining after this.

Study design

We selected 21 sampling sites for this study throughout an alpine area between the summit of Mount Hotham and
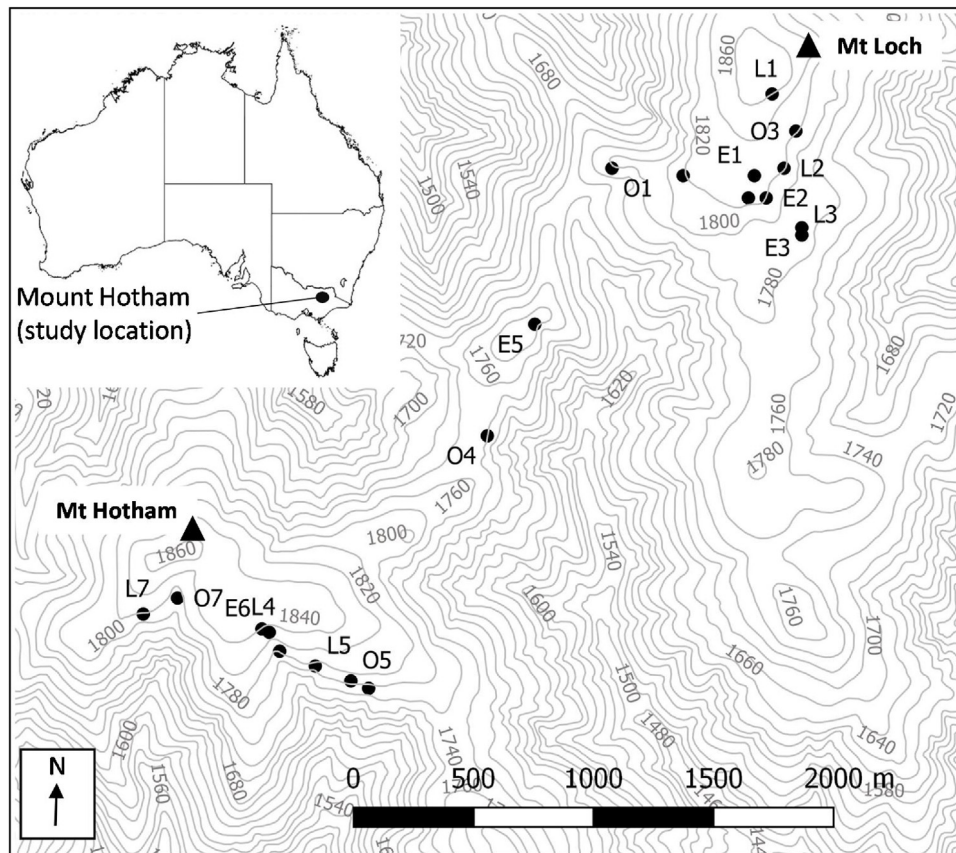

Fig. 2. Location of the study area within Australia (inset), with individual site locations (black circles) and contours of elevation in grey. The summits of Mount Hotham and Mount Loch are labelled and marked with black triangles. The relative snow persistence classes for each site and their locations are labelled (O = Snow-free, E = Early snowmelt, and L = Late snowmelt) and numbered 1–7.

the summit of Mount Loch (Fig. 2). There were seven replicates of each of three snow persistence classes; 'Snow-free', 'Early snowmelt' and 'Late snowmelt' (thaw date measured as Julian day; Fig. 2). 'Snow-free' sites were non-snowpatch areas that had melted prior to day 268. 'Early snowmelt' sites melted out prior to day 288, while 'Late snowmelt' sites retained snow cover until at least day 325. Although we aimed to choose sites with consistent elevation, slope and aspect, there was some variability in these factors among sites. A likely explanation for the differences in snow-melt timing among the three snow persistence classes is the tendency for Snow-free sites to have a more westerly aspect and a slightly less steep incline (Fig. 2). The boundaries of all snowpatches were marked, and Early and Late snowmelt sites were judged to have melted when less than 10% of snow cover remained. The study was conducted following the 2006 snow season which was a below-average snow year, with snow depth recorded as less than half of the 26 year average at the peak of the snow season (www.hotham.com.au). Despite the poor snow year, the snowpatches we observed in 2006 represent the typical long-term patterns of snowmelt at the study sites. Edmonds et al. (2006) demonstrated that snowmelt patterns in the Australian Alps are fairly consistent over time and that snowmelt corresponds well with vegetation composition (Wahren et al., 2001; Venn & Morgan, 2007; Venn et al., 2011).

Vegetation surveys were conducted in the middle of the austral summer (January 2007) over the peak flowering season. At each site, we used a 1 m² grid containing 100 points and placed the grid haphazardly at 5 locations within each site (500 points per site). At each point, a steel pin (diameter = 2 mm) was placed at a ∼90° angle to the ground and all plant species touching the pin were recorded (each species received a maximum of one touch per point). Abundance was calculated for each species as the proportion of touches for the species to the total number of touches for each site. Dominant species were identified for each of the snow persistence classes and were defined as those that contributed more than 10% cover to the total cover for each snow persistence class.

Allocation of CSR scores

CSR classification, based on measurable traits, makes it possible to ordinate species according to which selective pressures (competition, stress or disturbance) they are most adapted to, such that all species occur on a continuum between the three extreme strategy types: competitor (C), stress tolerator (S), ruderal (R). The methodology for CSR classification has been developed and refined over several years (Grime et al., 1997; Hodgson, Wilson, Hunt, Grime, & Thompson, 1999; Pierce et al., 2013, 2017). The most recent studies (Pierce et al., 2013, 2017) have demonstrated the effectiveness of just three easily measured leaf traits—Leaf Area (LA), Leaf Dry Matter Content (LDMC), and Specific Leaf Area (SLA)—for species classification across a range of

species and life-forms on a global scale. Pierce et al. (2017) demonstrated that the trade-off between these three leaf traits represent the three primary strategies in the CSR scheme. Specifically, species with small, soft leaves (high SLA) are R strategists, species with small, dense, tough leaves (high LDMC) are S strategists and species with the largest leaves can only occur in conditions where it is possible to have intermediate leaf economics (C strategists).

A similar CSR classification system, developed by Hodgson et al. (1999), involved several additional traits including canopy height, lateral spread, flowering period, and month of flowering start. This method has been used successfully but was limited to herbaceous species (Moog et al., 2005; Caccianiga et al., 2006; Frenette-Dussault et al., 2012; Cross et al., 2015). The updated method of Pierce et al. (2017) allows the classification of woody species, making it ideal for our study which includes a variety of life forms including shrubs.

A total of 43 species were allocated C, S and R scores based on the Pierce et al. (2017) method (see Appendix A in Supplementary material). For each species, ten individual plants were collected to measure the following traits: leaf area (mm²), leaf dry matter content (%), specific leaf area (mm² mg^{-1}). All specimens were allowed to re-hydrate overnight before measurements were made to ensure full leaf turgidity. Leaves were weighed after re-hydration using a balance (1×10^{-5} g sensitivity) and again after drying at $80\,°C$ for 48 h to determine dry matter content and leaf dry weight. Leaf area was measured after re-hydration using a standard flatbed scanner (600 dpi) and leaf area program following Hodgson et al. (1999). Means of these traits were calculated for each species and entered into the CSR calculator tool ('Stratefy') developed by Pierce et al. (2017) which calculates CSR ternary coordinates (%) for plotting onto the CSR triangle. We then used these C, S and R ternary coordinates for each species to create a triangular CSR plot.

The CSR percentages for each species were weighted for species abundance by multiplying CSR percentages by the proportional abundance for each species. Community CSR scores were calculated as the sum of the weighted scores of species within each site. By weighting the C, S and R scores this way, rare species effectively contribute little to the aggregate scores for a site. We excluded rare species that contributed less than 1% of total touches for each site type from the CSR classification, unless they had already been assessed elsewhere (P. Green and J.W. Morgan *unpublished data*). We then used these weighted community C, S and R ternary coordinates for each site to create a triangular CSR plot to visualise any differences among the three snow persistence classes (Snow-free, Early snowmelt and Late snowmelt).

Statistical analyses

To visualize differences in species composition among sites, an NMDS ordination was created, based on a

Table 1. Mean species richness and life form proportions per square meter (±SE) in the three snow persistence classes (Snow-free, Early snowmelt and Late snowmelt). Snow persistence classes with the same letter are not significantly different (1-way ANOVA; $P < 0.05$).

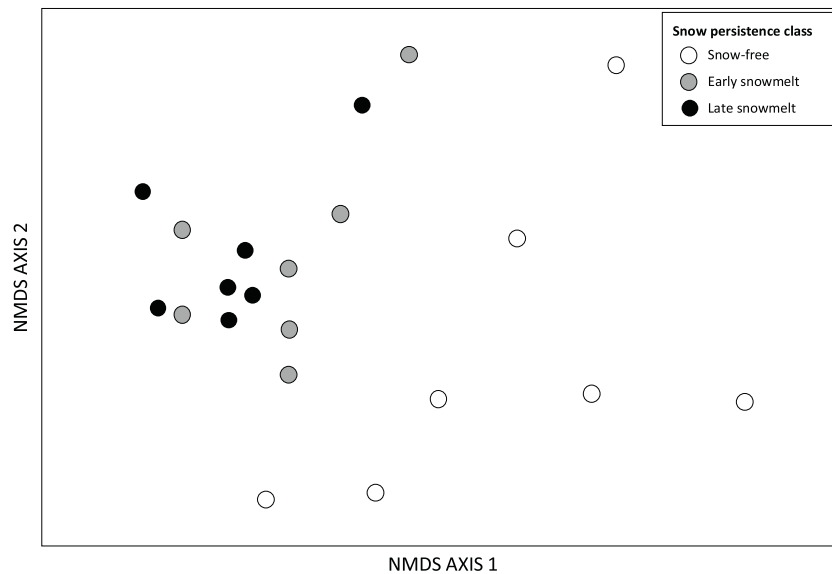| Snow persistence class	Mean species richness per m^2 (±SE)	Mean proportion (±SE)		
		Shrub	Forb	Graminoid
Snow free	15 (±1)[ab]	0.10 (±0.20)[a]	0.34 (±0.05)[a]	0.56 (±0.05)[a]
Early snowmelt	17 (±2)[a]	0.05 (±0.02)[ab]	0.25 (±0.05)[ab]	0.70 (±0.05)[ab]
Late snowmelt	11 (±1)[b]	0.01 (±0.01)[b]	0.15 (±0.03)[b]	0.83 (±0.04)[b]

Fig. 3. Non-metric multidimensional scaling ordination based on Bray–Curtis resemblance of square-root transformed species abundance in Snow-free, and Early snowmelt and Late snowmelt sites. Stress = 0.13.

Bray–Curtis similarity matrix of log-transformed abundance data. Floristic composition of sites was analysed using an Analysis of Similarity (ANOSIM) to determine the level of dissimilarity between the three site types in terms of species composition and abundance. Community CSR scores, species richness, and life-form abundances were compared using one-way ANOVA, and Tukey's multiple range test was used to determine significant differences among means. We used Primer Statistical Package version 6.1.16 (Clarke & Gorley, 2006) for multivariate analyses and R for univariate analyses and CSR ternary plots (R Core Team, 2017).

Results

Floristic composition

Mean species richness (per m^2) varied significantly among snow persistence classes (Table 1). Early snowmelt sites had significantly higher average species richness than Late snowmelt sites ($P = 0.032$), but not Snow-free sites ($P > 0.05$).

Graminoids dominated all sites. There were, however, significant differences in the proportion of shrubs, graminoids and forbs that contributed to each site. Shrubs and forbs contributed significantly more to the vegetation cover in Snow-free sites than they did in Late snowmelt sites ($P = 0.05$ and $P = 0.02$ respectively; Table 1). Conversely, Late snowmelt sites contained a significantly higher proportion of graminoid cover than Snow-free sites ($P = 0.02$).

Species contributing more than 10% cover in Snow-free sites included three graminoids (*Poa hiemata* (26%), *P. costiniana* (23%) and *P. fawcettiae* (21%)) and two forbs (*Celmisia* spp. (22%) *Stylidium* sp. (15%)). In Early snowmelt sites, the graminoid species *P. fawcettiae* and *Luzula acutifolia* and the prostrate shrub *Kunzea muelleri* contributed >10% cover. Late snowmelt sites were sparsely vegetated and only the graminoids *P. fawcettiae* and *L. acutifolia* contributed >10% cover.

Floristic composition varied significantly among snow persistence classes (1-way-ANOSIM, Global R = 0.317, P = 0.001). Snow-free sites were more floristically variable than Early and Late snowmelt sites, and differed significantly from them in composition (Fig. 3; R = 0.408, P = 0.003 and R = 0.544, P = 0.003 respectively). Early and Late snowmelt sites were clustered and not compositionally dissimilar (P > 0.05).
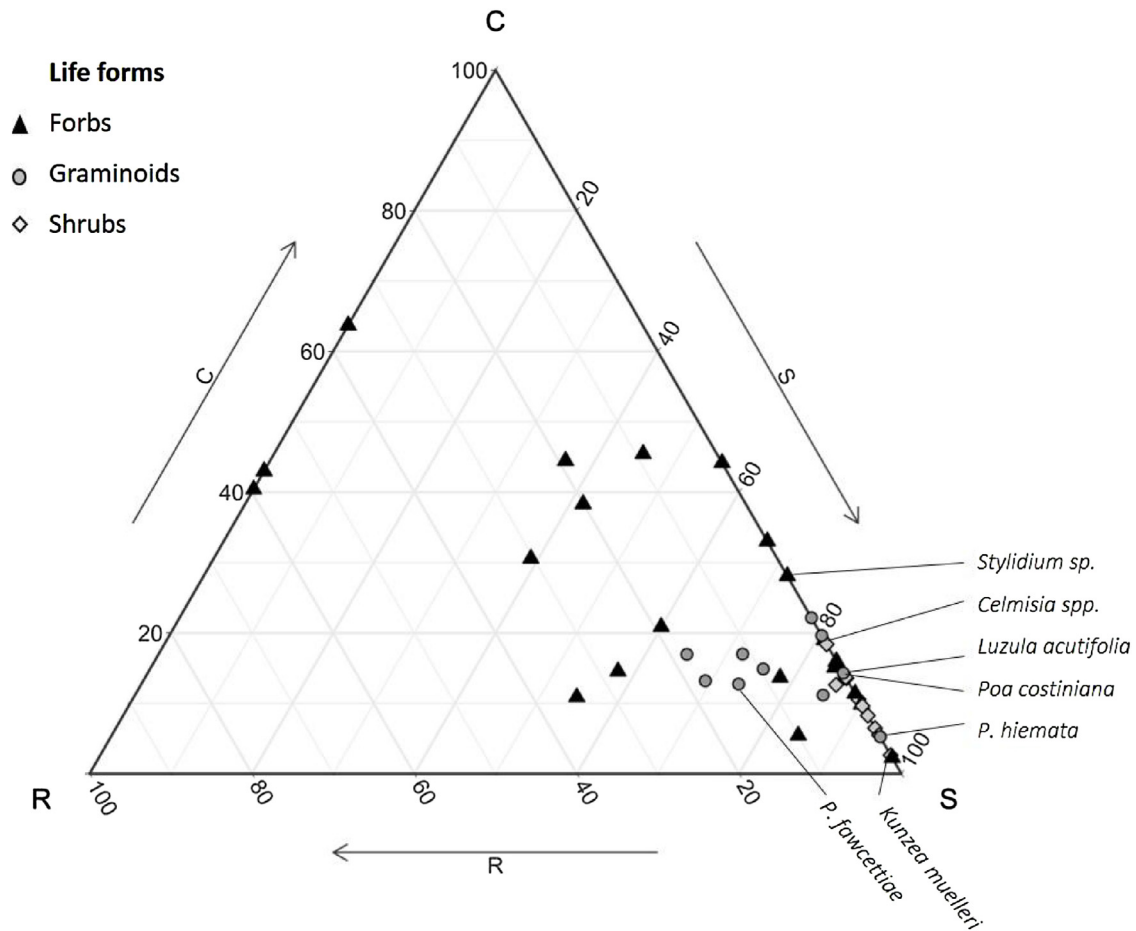
Fig. 4. All of the 43 species that were classified in this study, plotted onto CSR space and separated into forbs (black triangles), graminoids (grey circles) and shrubs (grey diamonds). Species contributing to >10% cover in any of the snow persistence classes are labelled.

Comparison of CSR strategies

Species were distributed across a large proportion of CSR space (Fig. 4). Graminoids and shrub species were clustered towards the S corner of the ternary plot, with mean S percentages (±SE) of 78.6 (±2.6) and 89.7 (±1.5) respectively. Forb species ranged from highly stress-tolerant to moderately ruderal, with many species occupying the centre region of the triangle (Mean S = 59.2 ± 6.4; Fig. 4). The most abundant species across the snow persistence classes (*P. hiemata, P. fawcettiae, P. costiniana, Celmisia* spp*., Stylidium* sp*., L. acutifolia, K. muelleri*) were clustered around the S corner (Fig. 4). This indicates that the spread of species across the triangle was probably a reflection of the less abundant species (that contributed 1–10% cover).

Weighted community scores were clustered towards the S corner of the CSR triangle; S scores ranged between 60–85% (Fig. 5A). Weighted community S scores were significantly higher in Snow-free sites than in Early and Late snowmelt sites (Fig. 5B). Conversely, weighted community R scores were significantly higher for Late snowmelt sites than Snow-free sites. Weighted community C scores did not vary significantly among site types (Fig. 5B).

Discussion

This study demonstrated the utility of the CSR plant strategy scheme for distinguishing patterns among plant communities along a fine-scale snow persistence gradient in an alpine environment. Our results supported Hypothesis 3, that Snow-free communities were more stress-tolerant than Early and Late snowmelt communities, and not the alternative hypothesis that Late snowmelt communities would have the highest community stress-tolerator scores. This result is consistent with studies investigating the effects of earlier snowmelt on species interactions in alpine plant communities whereby early snowmelt increases the importance of positive plant interactions due to the harsher conditions experienced by species early in the growing season (Wipf et al., 2006; Venn et al., 2009). Based on the most literal interpretation of Grime's CSR theory (2001), we might have expected the less productive (Late snowmelt) communities to have higher community S scores. However, Snow-free sites—where snowmelt occurs very early in the growing season—are exposed to extreme climatic conditions such as frosts and large fluctuations in diurnal temperatures. Protection from these stressors must outweigh any loss
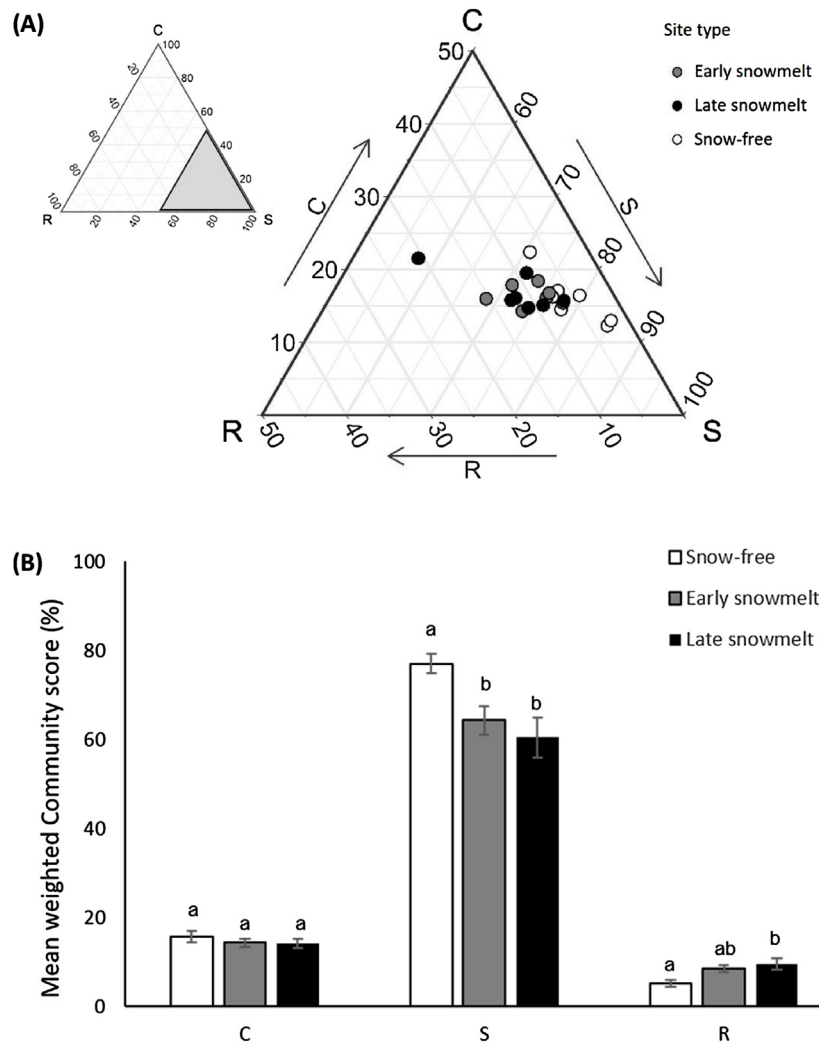
Fig. 5. CSR scores weighted by species abundance in the three snow persistence classes (Snow-free, Early snowmelt and Late snowmelt). (A) Weighted scores for each site plotted onto CSR space, with each dot representing a site (n = 7), and (B) weighted mean C, S, and R scores for each snow persistence class (Snow-free, Early snowmelt and Late snowmelt). Mean scores with the same letter are not significantly different.

of productivity experienced by late snow-melt vegetation. Therefore, productivity and soil nutrients may not always be an appropriate proxy for measuring stress gradients.

Mean species richness was significantly lower in the late-melting zones of snowpatches compared to the early-melting zones, as it is elsewhere in the Australian Alps (Venn et al., 2011). Environmental filtering likely limits the number of species that can persist under late-lying snow as growing degree days are few (Venn & Morgan, 2007) and opportunities for regeneration are negligible. Interestingly, non-snowpatch sites had similar species richness to the late snowpatch sites. These patterns could be driven by competitive effects of the generally taller-statured, non-snowpatch vegetation, or it could also be due to a different suite of environmental filters associated with earlier snowmelt in non-snowpatch zones (Venn & Morgan, 2007; Venn et al., 2011).

We found a clear difference in life-form composition among snow persistence classes, with shrub and graminoid species tending to cluster together in CSR space. Shrub species had consistently high (>80%) S scores, and shrubs were mostly absent from Early and Late snow-melt sites. This was unsurprising since Australian snowpatch communities are generally dominated by graminoid and forb species; shrubs are generally excluded from deep snow areas but are common outside of late-lying snowpatches (Venn et al., 2011). Australian alpine shrub species generally exhibit typical stress-tolerator traits such as being evergreen and having small, sclerophyllous and densely-packed leaves, making them well suited to the harshest alpine conditions (Lim, Pollock, & Vesk, 2017). Earlier and more variable snowmelt is predicted for the coming decades (Hennessy et al., 2003) and expected to promote shrub encroachment into previously herbaceous-dominated snowpatch communities, likely due to their superior stress-tolerating traits (Pickering, Green, Barros, & Venn, 2014). Indeed, Pickering et al. (2014) have documented significant compositional shifts within the latest-

lying snowpatches of the Australian Snowy Mountains over a relatively short period.

Although R scores were universally quite low, those species with higher R scores were most abundant in Late snowmelt sites. Here, the ruderal strategy may be advantageous because the short growing season requires plants to develop and grow quickly. Indeed, snowmelt provides a pulse of moisture during the warmest part of the growing season, potentially allowing plants to grow faster at this time than those growing outside of snowpatches where soil moisture stress may be more significant (Griffin & Hoffmann, 2012). Physical destruction of plant material may also occur more frequently within snowpatches; heavy ice pack can creep and tear off above-ground plant parts (Höller, Fromm, & Leitinger, 2009) and may be one key reason that shrubs are absent from snowpatches.

Conclusion

Our study adds further weight to the recognition that the timing of snowmelt has fundamental implications in the assembly of alpine plant communities. Here, we demonstrated that a gradient of snowmelt has implications for the functional composition of alpine plant communities, with earlier snowmelt associated with higher S scores. Changes in the timing of snowmelt with a changing climate will undoubtedly result in a shift in the functional composition of alpine communities with those at the extreme end of the snowmelt gradient (snowpatches) experiencing the most fundamental change.

Acknowledgements

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.baae.2019.01.004.

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