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**Vascular plant distribution in relation to topography, soils and micro-climate at five GLORIA sites in the Snowy Mountains, Australia**

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Abridged title: Effect of abiotic variables on alpine plant composition

**Abstract.** As part of the Global Observation Research Initiative in Alpine Environments program the relative contribution of abiotic variables in explaining alpine vegetation was determined for five summits on a spur of Mt Clarke in the Snowy Mountains, Australia. Vascular plant species and life-form composition, topography, soil nutrients and soil temperature were measured on each aspect of each summit by standardised methods. Ordinations were performed on vascular plant species and life-form composition, topography, soil nutrients and soil temperature derived variables. Abiotic variables were tested against the biotic dissimilarity matrices to determine which were best correlated with current plant composition. Summits differed in plant composition with a decrease in the cover of shrubs,

and an increase in herbs and graminoids with increasing altitude. Altitude was the main determinant of species composition, accounting for over 80% of the variation among summits. Soil temperature variables accounted for more than 40% of the variation in composition among summits. Soils were not significantly different among summits, but certain soil variables, principally calcium were important in predicting plant composition. Because temperature is correlated with current vegetation on these five summits, predicted increased temperatures and decreased snow cover are likely to affect future plant composition in this mountain region.

## **Introduction**

Topography, soils, climate, disturbance, herbivory and competition can affect distributions of alpine plant species and hence community composition (Körner 2003). In mountain systems, climate can have a major effect on vegetation, determining the location of tree lines, the boundary between alpine and nival zones and affecting vegetation patterns within the alpine zone (Körner 2003). As a result, alpine communities have been identified as being particularly at risk from predicted changes in climate (Grabherr *et al.* 2000; Walther *et al.* 2005). With increasing temperatures and changes in snow cover regimes predicted for alpine regions around the world (Hennessy *et al.* 2003; Pauli *et al.* 2007; IPCC 2007; Van de Ven *et al.* 2007), it is important to determine the relative importance of environmental factors including climate on current vascular plant composition within and among mountain systems.

Climatic conditions have changed in the past century in many alpine areas, with increased mean air temperatures in the European Alps and an increase in the duration of snow-free periods in the northern and southern hemispheres (Casty *et al.* 2005; IPCC 2007). Changes in plant species distributions associated with increased temperatures have already been recorded in alpine areas in Europe, North American and New Zealand (Wardle and Coleman 1992;

Grabherr *et al.* 1994; Moiseev and Shiyatov 2003; Lesica and McCune 2004; Walther *et al.* 2005; Pauli *et al.* 2007).

Temperatures in the alpine and subalpine areas of mainland Australia are predicted to rise by +2.6°C (high emission scenario) by 2050 (Hennessy *et al.* 2003). This would result in dramatic changes in snow cover. The total area that receives at least 60 days snow cover a year is predicted to decrease by 97% (high emission scenario by 2050, Hennessy *et al.* 2003). There is evidence that the amount of snow cover had already declined significantly between the 1950s and 2008 (Green and Pickering 2002; Green 2008). These changes in temperature and snow cover are likely to result in longer and warmer growing seasons, overall decreases in soil moisture, changes in relative competitive ability of plants, increase in exotic plants and changes to the reproductive ecology of some species (Pickering and Armstrong 2003; Pickering *et al.* 2004).

To measure climate and the impacts of any changes in climate on alpine ecosystems, long term monitoring sites (Global Observation Research Initiative in Alpine Environments) have been established on 160 summits from 41 mountain regions around the world (see [www.gloria.ac.at](http://www.gloria.ac.at)). Variation among summits in species richness and measures of similarity have been recorded for GLORIA summits in Europe (Bertin *et al.* 2001; Coldea and Pop 2004; Kanka *et al.* 2005; Stanisci *et al.* 2005; Erschbamer *et al.* 2006; Kazakis *et al.* 2006) in New Zealand (Mark *et al.* 2006) and in Australia (Pickering *et al.* 2008). Changes in species richness and composition over a decade, paralleling changes in temperature, have also been found for Schrankogel, Tyrol in Austria, a GLORIA site, established in 1994 (Pauli *et al.* 2007). In addition to examining patterns in species richness, it is important to test the relative importance of different environmental variables including climate in predicting current vascular species composition on GLORIA summits, because an implicit assumption in the establishment of the program is that current and future climatic conditions will be correlated

with changes in vascular plant composition. Therefore we tested the relative importance of topography, soil type and soil temperature on species composition for five GLORIA summits sampled along a 385 m altitudinal gradient in the Snowy Mountains close to continental Australia's highest mountain.

The specific aim of this study was to determine the relative contribution of topography, temperature and soils to variation in plant species and life-form composition among the GLORIA summits and aspects, where the composition of the vegetation is predicted to be related to climate. A secondary aim of the study was to characterise the vascular plant composition topography, soil chemistry and soil temperatures of the five GLORIA summits and their principal aspects (North, South, East and West).

## **Methods**

### *Study area*

The total alpine area (area of vegetation above the natural tree line) of the Snowy Mountains in Australia (250 km<sup>2</sup>) is not large, and the altitudinal range is only ~380 m from the tree line at about ~1850 m to the top of the highest mountain (Mt Kosciuszko 2228 m) (Costin *et al.* 2000). The absence of high-altitude refuges or a nival zone in Australia is likely to restrict altitudinal succession in the event of an increase in temperature and decrease in snow cover. The area is characterised by continuous snow cover for at least four months per year with six to eight months having minimum temperatures below freezing. Precipitation is in the range of 1800-3100 mm per year with about 60% of this falling as snow as a result of predominantly westerly winds and associated low pressure systems (Davis 1998; Costin *et al.* 2000). The two main rock types are granite and sedimentary rock with deep, well developed alpine humus soil. Cattle and sheep grazing in the summer in the alpine area from the late 1850s till as late as the 1950s resulted in massive soil erosion. As a result, some areas were actively

rehabilitated (Green *et al.* 2005). Currently there are few grazing mammals, principally introduced hares (*Lepus europaeus*) and the broad toothed rat, *Mastacomys fuscus* (Green and Osborne 1994).

### *GLORIA summits*

In the GLORIA protocol, sampling points are based on summits which are considered either the uppermost peak of a mountain, or a ‘hump’ on a ridge if it projects more than 20 elevation metres above the surrounding land features. Based on the GLORIA definitions, five summits on a spur running roughly east from Mt Clarke on the Main Range, down towards the Snowy River in alpine zone of the Snowy Mountains were selected for long-term monitoring using the GLORIA multi-summit methods (Fig. 1). The summits covered a horizontal distance of 1600 m and an altitudinal range of 385 m, extending from the upper alpine zone where grassland and herbfields were dominant to the lower alpine zone where dwarf-shrubs were dominant. The highest summit sampled is only 114 m lower in altitude than Mt Kosciuszko, the highest mountain in continental Australia, which is located 3.5 km to the south-west.

Each summit was selected using specific criteria specified by the GLORIA procedure (Pauli *et al.* 2004). The top section of each summit was divided into eight summit area sections (SAS) – four covering the area between the summit and 5 m altitudinally below the summit (the -5 m isoline) for each of the four principal compass bearings (here after referred to as the upper SAS), and another four covering the area of mountain between 5 m altitudinally below the summit and 10 m altitudinally below the summit (hereafter referred to as the lower SAS, Pauli *et al.* 2004, Fig 2). At each of the four compass bearings at the -5 m isoline a cluster of nine 1 m<sup>2</sup> quadrats was established in a 3 m by 3 m arrangement. Due to the density of shrubs on the lowest summit, permanent clusters of quadrats could not be established.

### *Vegetation sampling*

In each of the four corner 1-m<sup>2</sup> quadrats in the 3 m by 3 m grid (Fig. 2), the top cover of surface types (vascular plant cover, solid rock, lichens on soil, bryophytes on soil, bare ground, and litter) were estimated visually in January 2004. In addition, overlapping cover (e.g. can add up to more than 100% - henceforth, cover) of all vascular plant species present in each corner quadrat was estimated. In each of the four upper SAS and four lower SAS (Fig. 2) the percentage top cover of surface types and the complete species list and percentage cover of each vascular plant species were estimated using a random step-point method (200 points per area) (Pauli *et al.* 2004). Any species not sampled by the step-point method were visually assessed for cover. Nomenclature of species follows Costin *et al.* (2000), or for exotics, the standard GLORIA European naming protocols. The total area sampled for each SAS ranged from 10876 to 12355 m<sup>2</sup>.

### *Soil temperature data*

Temperature loggers (Tinytag plus -Gemini Data Loggers, Chichester England) were buried 10 cm below the surface on each summit from mid- January 2002 to mid-January 2007 and in the centre square of each of the 3 m by 3 m quadrat clusters from late January 2004 to early January 2007. Temperatures were recorded every 2 hours. Based on these data, the following values for each aspect on each summit were calculated for 2005, absolute minimum, annual daily average, and absolute maximum soil temperature. Temperature data from 2005 were used as it was the first year after vegetation sampling (conducted in 2004) for which there was a complete annual data set. In addition, it was possible from the data for all aspects on all summits to measure the date of thaw for 2004, 2005, and 2006 based on when the temperature began fluctuating after the long period of constant low temperatures associated with snow

cover. Within this period of fluctuation the actual day of thaw was determined as when the temperature first rose above 3.2 °C at noon or within two hours either side of noon, this day was also taken as the commencement of the growing season (Körner and Paulsen 2004). The end of the growing season was calculated in a similar fashion and was the point at which the noon temperature  $\pm$  2 hours fell below 3.2° C and remained below that level. The growing season length was defined as the difference between these two days minus days when soil temperature was  $<3.2^{\circ}$  C at noon  $\pm$  2 hours. Absolute minimum soil temperature, annual daily average soil temperature, absolute maximum soil temperatures and length of the growing season have been used to characterise the thermal regimes of alpine areas in Europe (Korner *et al.* 2003). Also, annual daily average soil temperatures have already been used in analysis of patterns of species richness in this (Pickering *et al.* 2008) and other GLORIA sites (Staniski *et al.* 2005; Kazakis *et al.* 2006).

### *Soil Samples*

In 2003, a single soil sample was collected at each aspect from close to the 3 m by 3 m grids giving four individual soil samples per summit. At each aspect a minimum 500 g was collected in a single sample of soil taking the top 10 cm of soil in a 75 mm core. Samples were air dried and sieved through a 2-mm mesh. Soil was analysed by the CSIRO Division of Soil and Water. Total carbon and nitrogen were determined by high temperature combustion in an atmosphere of oxygen with a Leco CNS-2000 Elemental analyzer. Carbon was converted to CO<sub>2</sub> and determined by infrared detection. Nitrogen was determined as N<sub>2</sub> by thermal conductivity detection (Matejovic 1997). Inorganic nitrogen was determined by segmented flow colorimetry following extraction with 2M KCl. Nitrate was dialysed then reduced to nitrite by Cd reduction and the resultant nitrite reacted with N-1-naphthylethylenediamine dihydrochloride (NEDD) with sulphanilamide (Rayment and



Higginson 1992a).  $\text{NH}_4^+$  was separated from interferences by gas diffusion and determined after reaction with sodium salicylate and dichloro-isocyanurate (DCIC). This procedure is modified from Rayment and Higginson (1992a) according to the International Standard ISO 11732 (1997). Extractable phosphorus was determined by segmented flow colorimetry following Colwell extraction using 1 M  $\text{NaHCO}_3$  at pH 8.5 (Rayment and Higginson 1992b). Total metals were determined by US EPA method 3051A (1998). The finely ground sample was digested in a microwave oven using a mixture of nitric acid and hydrochloric acid. The solution was then analysed for a wide range of elements by inductively coupled plasma optical emission spectrometry (ICPOES).

#### *Data analysis*

Plant species cover data were used to calculate the percentage overlapping cover of lifeforms (graminoids, herbs (equivalent to forbs) and shrubs), total species richness, species richness of herbs, shrubs and graminoids, and the number of species endemic to just this alpine region. This was done at three spatial scales four corner 1-m<sup>2</sup> quadrat (data only available for four summits), upper SAS and lower SAS for each of the four aspects on all five summits. Values were also calculated for the total area of each of the five summits by combining data for the upper and lower SAS for each aspect.

Plant assemblage composition was analysed using ordinations performed in the multivariate statistical package PRIMER (version 5.2.2). First, dissimilarity matrices were calculated by the Bray-Curtis dissimilarity measures. Then, non-metric multidimensional scaling (MDS) was used to describe the maximum variation among quadrats/summit areas graphically in two dimensions (MDS axes 1 and 2) with the closeness of fit of the MDS axes to the dissimilarity matrix expressed in terms of stress. This type of ordination has produced reliable, simple and statistically significant analyses of a wide range of ecological community

data and is commonly used to analyse vegetation composition data including for indirect gradient analysis (Minchin 1987; Clarke 1993; Clarke *et al.* 2006).

Ordinations were performed for percentage cover of all vascular taxa at three spatial scales: (1) the four corner 1-m<sup>2</sup> quadrats in the 3 m x 3 m quadrat cluster combined, (2) the four upper SAS, and (3) the four lower SAS. Ordinations were also performed on cover type categories (cover of herbs, shrubs and graminoids, bare ground, rock and litter) for vegetation at each spatial scale.

Environmental data for each site were also assessed by calculating dissimilarity matrices using normalised Euclidean distance measures (Clarke and Ainsworth 1993). In addition to assessing all environmental variables together, separate dissimilarity matrices were calculated for topographic variables (altitude, area sampled, aspect, slope, surface cover of rocks and bare ground) climate variables (absolute minimum soil temperature, daily average soil temperature, absolute maximum soil temperature for 2005, date of thaw for 2004, 2005, and 2006, and duration of the growing season for 2004-2005 and 2005-2006) and soil chemistry (C, N, NH<sub>4</sub>N, NO<sub>3</sub>N, extractable, P, Al, Ca, Cu, Fe, K, Mg, Mn, Na, Pb, Sr, Zn).

To determine whether there were significant differences among summits and among aspects, a Two-way Analysis of Similarity (ANOSIM) was performed for the plant and abiotic dissimilarity matrixes. ANOSIM is a non-parametric permutation procedure applied to the rank dissimilarity matrix that is analogous to Analysis of Variance but is distribution-free (Clarke 1993). To determine which species were contributing to similarity among summits the SIMPER function was used on the MDS dissimilarity matrixes for plant composition. To identify the combinations of environmental variables best correlated with plant composition the BVSTEP function in PRIMER was used. This is an automated procedure that matches different combinations of environmental variables to the MDS dissimilarity matrix for plant composition using a MANTEL test (Clarke and Ainsworth 1993). To test the significance of

the correlation between combinations of the environmental variables and the plant composition dissimilarity matrix, 1000 permutations were performed to obtain a *P*-value for the highest rank Spearman's correlation coefficients.

## **Results**

### *Vegetation*

All five summits had a nearly complete cover of vegetation, with small areas of bare ground and rock except on summit three, where there was 13% cover of rock (Table 1). There were differences among summits in species composition/abundance at all three sampled spatial scales (Fig. 3, Tables 2 and 3). When percentage cover data for all species were compared using Analysis of Similarity, there were significant differences among summits at the three sampled spatial scales, and high correlation values (Table 2 and 3). There were clearer differences in composition among summits at the upper SAS than at the quadrat scale (Fig. 3*b*). This could reflect the larger area sampled for upper SAS resulting in more consistent estimates of composition among summits (Fig. 3*b*).

There were also significant differences in life-form and surface covers among all summits for the - upper SAS (Fig. 3*b*, Table 2). For the lower SAS there were differences between the two lower altitude summits, but not between the three higher altitude summits in life-forms and surface covers (Fig. 3*c*, Table 2). For the quadrat data there was considerable variation among summits/aspects with no significant differences among summits (Fig. 3*a*, Table 2). The lowest-altitude summits tended to have high cover of shrubs, while the highest summits had high cover of herbs and graminoids (Table 1). There was a greater cover of herbs and graminoids but less cover and diversity of shrubs on the highest summit compared to the lowest (Table 1). There was no consistent pattern in vegetation with aspect (Fig. 3).

### *Environmental variables*

In addition to the obvious differences in altitude, location and aspect among SAS, they also varied in slope, cover of rock and bare ground (Table 1). However, there was no significant difference among summits using Analysis of Similarity on the rank dissimilarity matrix of topographic variables (Table 2, Fig. 4).

The five summits did differ significantly in soil temperature derived variables (Table 2, Fig. 4). However, there was no consistent pattern with altitude as might have been expected. There were differences in mean daily soil temperature, the length of growing season and date of thaw among summits and years (Table 1). Mean soil temperatures were 0.6 °C lower and the growing season ~15 days shorter on the highest summit compared to the lowest (Table 1). The growing season was ~21 days shorter for each summit in 2005-06 than in the previous growing season when it averaged 216 days. The thaw date also varied among summits and years, with later melting of snow in some years at the higher altitude summits. During the snow-free period, temperatures were highly variable even over a few days. However, the absolute maximum temperature at any summit area section was only 17.5 °C. Minimum temperatures were very consistent once snow cover was established with the absolute minimum soil temperature the same for all aspects on the five summits at -0.2 °C. In the full period from 24 January 2004 to ~ 4 January 2007 for which any soil temperature was collected, the minimum temperature at 10 cm depth never fell below -0.7 °C, indicating that extensive ground freezing did not occur on any aspect. However, the summit of CL3 had less consistent snow cover than others, and here soil temperatures fell as low as -5.2 °C.

Soils showed considerable variation among SAS (Fig. 4b), but there was no significant difference among summits (Table 2). This is despite the difference in geology (the highest two summits are on sedimentary rocks and the lowest three on granites) and reflects the fact that soils in the Snowy Mountains are generally independent of rock type and largely

influenced by historically high levels of aeolian inputs from dust originating in the arid interior of Australia (Green *et al.* 2005).

#### *Significant environmental variables*

When the relative importance of environmental variables in explaining the patterns in species composition were assessed (BIOENV), altitude explained 0.849 and 0.817 of the variation in plant composition for the upper and lower SAS ( $P$  values = 0.001, Table 4). For plant composition at a smaller scale (the four 1-m<sup>2</sup> quadrats); however, altitude was not important, whereas season days in 2005/06 and calcium concentrations in the soil accounted for 0.699 of the variation in species composition among summits ( $P = 0.001$ ).

Because soil temperature and potentially some of the other environmental variables were likely to be correlated with altitude, the procedure was repeated excluding altitude (Table 4). Some topographic variables (slope, aspect-north, percentage bare ground) and soil temperature variables (season days 2004-05, date of thaw in 2006) and soil variables (carbon, calcium) were significantly correlated with vegetation composition at the upper and lower SAS (Table 4). To determine which among the climatic variables was significantly correlated with vegetation, the procedure was repeated a final time excluding topography and soil variables. The total amount of variation explained by just soil temperature variables was 0.427, 0.433, and 0.415 respectively for quadrat, upper SAS and lower SAS (Table 5). However, no single soil temperature variable was very effective on its own at explaining variation in plant composition, with minimum and maximum temperatures, length of the growing season and date of thaw all important.

## **Discussion**

There were differences in vascular plant composition among the five summits, with shrub species dominant at the lower altitude summits, and herbs and graminoids having higher cover values at the higher summits. Species richness also differed with a decrease in richness from 53 to 36 species per summit with increasing altitude (Pickering *et al.* 2008). The five summits had near complete vegetation cover (82-97%), with little exposed rock and bare ground. This differs from some other GLORIA sites e.g. in Europe, where lesser vegetation cover can be attributed to different climatic conditions e.g. Sierra Nevada in Spain (2.4-18%, Pauli *et al.* 2003) and Central Apennines (15-32%, Stanisci *et al.* 2005) to a generally more rocky geomorphology e.g. North Eastern Alps (46.6-89.8%, Pauli *et al.* 2003), or to the presence of high elevation zones reaching to the climatic limits of vascular plants, which are absent in Australia. As a result of limited altitudinal range, deep humus soils and few native mammalian herbivores in Australia, most areas excluding the windswept highest ridges and areas of late snowbanks have nearly complete vegetation cover (Costin *et al.* 2000).

Although there were differences among aspects in plant composition, it was not consistent across the five summits in the Snowy Mountains. This contrasts with some other GLORIA target regions, where differences in species richness, vegetation cover and composition as well as soil temperatures occurred among aspects (Bertin *et al.* 2001; Coldea and Pop 2004). This is best explained by the flattened nature of the summits in the Snowy Mountains so that in most cases there are not major differences in exposure to solar radiation among aspects (5.6 to 16.6 ° slope). Nor was there much scope for microtopographic variety leading to increased diversity of niches.

The only significant separation among summits in ordinations occurred for soil temperature variables. When abiotic variables were used to predict patterns in species composition, altitude accounted for most of the variation (>80%) on SAS. Combinations of soil derived temperature variables were also significantly correlated with current variation in

species composition (~ 42%), indicating that soil temperature is likely to be important in determining current vegetation patterns at both the fine (four 1m<sup>2</sup> quadrat) and larger (SAS) scale. Other climatic variables including precipitation and wind speed were not measured although they are also likely to vary among summits and influence current and future vegetation composition.

It is possible that changes in climate including in minimum and maximum soil temperature, length of the growing season and date of thaw are likely to result in changes in the composition of the vegetation in the Snowy Mountains. Based on the differences in vegetation among the five summits, the changes in vegetation could involve an increase in shrub cover and decrease in herb and graminoid cover at the mid altitude summits. For example, the lowest summit currently had an annual average temperature of 5.2 °C, and cover of 75.1% shrubs, 7% herbs and 22% graminoids, while the highest summit averaged 4.6 °C soil temperature and 12.5 % shrubs, 31.5% herbs and 55.3% graminoids. With a predicted change of + 1.0 °C for the region by 2020 (from 1990 values, Hennessey *et al.* 2003), it is possible that shrub cover on the middle summits may increase, with corresponding decreases in herbs and graminoids within one to two decades. However, reduced snow cover due to decreased temperatures and precipitation and possible changes in wind speed/direction could result in vegetation experiencing severe frosts in winter at the lower altitude summits, which may damage shrubs. Winter frost damage to shrubs, particularly on northern aspects (i.e. equator facing), has been observed over the past five years in the Snowy Mountains (Green pers. obs.). Because there was little bare ground on any of the summits, any changes are unlikely to involve changes in total vegetation cover.

The association of vegetation with environmental factors for the five Snowy Mountains summits is consistent with other studies of alpine vegetation in Australia. In a study examining ten different vegetation formations across all the alpine regions in Australia,

climate (mostly air temperatures) was significantly related to differences among formations (Kirkpatrick and Bridle 1999). Other environmental variables that were related to composition among formations were: extractable phosphorus, nitrogen, organic carbon, pH and soil depth, slope, topographic position, bare ground, rock cover and presence of herbivorous wallabies (Kirkpatrick and Bridle 1999).

### *Climate of the Snowy Mountains*

The climatic conditions on the five summits in the Snowy Mountains appear to be relatively favourable for plant growth compared to many alpine summits in Europe. The growing season defined as  $>3.2$  °C soil temperature at 10 cm depth threshold in the Snowy Mountains ranged from 189 to 226 days (average 205) among the summits and years. In a comparative study of 23 alpine sites across Europe at 200-250 m above the climatic treeline growing season (based on first to last incidence of a temperature above  $+2$  °C) ranged from 106 to 261 days, with an average of 164 days (Körner *et al.* 2003). Despite the generally lower latitude (36°S) and hence higher insolation, maximum soil temperatures in the Snowy Mountains were not as high or variable as some in Europe, ranging from 14.2 to 17.5 °C, compared to an average of 18.7 °C (range 13.8-32.1 °C) in Europe. Minimum soil temperatures on summits depend strongly on snow cover. In sites/years with continuous snow cover for winter, minimum temperatures are often  $<-2$  °C (Körner *et al.* 2003). However, where snow cover is intermittent in winter, much lower soil temperatures occurred. For the Snowy Mountains summits, soil temperature data loggers at each aspect on the five summits recorded minimum temperatures of only -0.2 °C. However, for one data logger on the very summit of CL2, temperatures in winter were as low as -5.2 °C due to intermittent snow cover on just the very top of this exposed rocky summit. Similar differences in minimum soil temperatures depending on snow cover were found in Europe, with some summits having consistent low



temperatures when covered by snow and others showing considerable variation, with soil temperatures recorded as low as -14.1°C.

With soil climatic data collected for all GLORIA sites, we suggest the relationship between current plant species composition and climate be examined in many summits. If there is a relationship, it will be interesting to see which climatic variables are best at explaining variation in composition within and among summits. We hypothesise that different soil temperature variables are likely to be important in different alpine regions, with alpine areas showing considerable variation in minimum, maximum and average daily soil temperatures, in duration and predictability in snow cover, in precipitation, predominant wind direction, potential for frosts, in duration of the growing season and in cumulative soil temperatures (Körner 2003; Körner *et al.* 2003; Körner and Paulsen 2004).

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### **References**

Bertin L, Dellavedova R, Gualmini M, Rossi G, Tomaselli M (2001) Monitoring plant diversity in the northern Apennines, Italy. The GLORIA project. *Archivio Geobotanico* **7**, 71-74.

- Casty C, Wanner H, Luterbacher J, Esper J, Böhm R (2005) Temperature and precipitation variability in the European Alps since 1500. *International Journal of Climatology* **25**, 1855-1880.
- Clarke KR (1993) Non-parametric multivariate analyses of changes in community structure. *Australian Journal of Ecology* **18**, 117-143.
- Clarke KR, Ainsworth M (1993) A method of linking multivariate community structure to environmental variables. *Marine Ecology Progress Series* **92**, 205-219.
- Clarke KR, Somerfield PJ, Chapman MG (2006) On resemblance for ecological studies, including taxonomic dissimilarities and a zero-adjusted Bray-Curtis coefficient for denuded assemblages. *Journal of Experimental Marine Biology and Ecology* **330**, 55-80.
- Coldea G, Pop A (2004) Floristic diversity in relation to geomorphological and climatic factors in the subalpine-alpine belt of the Rodna Mountains (The Romanian Carpathians). *Pirineos* **61**, 158-159.
- Costin AB, Gray M, Totterdell CJ, Wimbush DJ (2000) 'Kosciuszko alpine flora.' (Collins: Melbourne)
- Davis CJ (1998) Meteorological aspects of snow. In 'Snow a natural history: an uncertain future.' (Ed. K Green) pp. 1-34. (Australian Alps Liaison Committee: Canberra)
- Erschbamer B, Mallaun M, Unterluggauer P (2006) Plant diversity along altitudinal gradients in the Southern and Central Alps of Southern Tyrol and Trentino (Italy). *Greblariana* **6**, 47-68.
- Grabherr G, Gottfried M, Pauli H (1994) Climate effects on mountain plants. *Nature* **369**, 448-448.
- Grabherr G, Gottfried M, Pauli H (2000) GLORIA: A global observation research initiative in alpine environments. *Mountain Research and Development* **20**, 190-192.

- Green K (2008) Alpine ecosystems. In 'Ten commitments.' (Eds D Lindenmayer, S Morton, S Dovers, M Harriss Olson) pp. 73-78. (CSIRO Publishing: Melbourne)
- Green K, Good RB, Johnston SW, Simpson LA (2005) Alpine grazing in the Snowy Mountains of Australia: degradation and stabilisation of the ecosystem. In 'Land use changes and mountain biodiversity.' (Eds E Spehn M. Liberman, C Körner) pp. 213-225. (CRC Press: Boca Raton)
- Green K, Osborne WS (1994) 'Wildlife of the Australian snow-country.' (Reed: Sydney)
- Green K, Pickering CM (2002) A scenario for mammal and bird diversity in the Snowy Mountains of Australia in relation to climate change. In 'Mountain biodiversity: A global assessment.' (Eds C Körner, EM Spehn) pp. 239-247. (Parthenon Publishing: London)
- Hennessy KJ, Whetton PH, Smith IN, Batholds JM, Hutchinson MF, Sharples JJ (2003) 'Climate change impacts on Snow Conditions in Australia.' (CSIRO: Canberra)
- Intergovernmental Panel on Climate Change [IPCC] (2007) 'Climate change 2007: The physical science basis.' (Intergovernmental Panel on Climate Change: Geneva)
- Kanka R, Kollar J, Barancok P (2005) Monitoring of climate change impacts on alpine vegetation in the Tatry Mts- First Approach. *Ekologia* **24**, 411-418.
- Kazakis G, Ghosn D, Vogiatzakis IN, Papanastasis VP (2006) Vascular plant diversity and climate change in the alpine zone of Lefka Ori, Crete. *Biodiversity and Conservation* **16**, 1603-1615.
- Kirkpatrick JB, Bridle KL (1999) Environmental and floristics of ten Australian alpine vegetation formations. *Australian Journal of Botany* **47**, 1-21.
- Körner C (2003) 'Alpine plant life.' (Springer: Berlin)
- Körner C, Paulsen J (2004) A world-wide study of high altitude treeline temperatures. *Journal of Biogeography* **31**, 713-732.

- Körner C, Paulsen J, Pelaez-Riedl S (2003) A bioclimatic characterisation of Europe's alpine areas. In 'Alpine biodiversity in Europe.' (Eds L Nagy, G Grabherr, C Körner, DBA Thompson) pp. 13-28. (Springer-Verlag: Berlin).
- Lesica P, McCune B (2004) Decline of arctic-alpine plants at the southern margin of their range following a decade of climatic warming. *Journal of Vegetation Science* **15**, 679-690.
- Mark AF, Dickinson KJM, Maegli T, Halloy SRP (2006) Two GLORIA long-term alpine monitoring sites established in New Zealand as part of a global network. *Journal of the Royal Society of New Zealand* **36**, 111-128.
- Matejovic I (1997) Determination of carbon and nitrogen in samples of various soils by the dry combustion. *Communications in Soil Science and Plant Analysis* **28**, 1499-1511.
- Minchin PR (1987) An evaluation of the relative robustness of techniques for ecological ordination. *Vegetatio* **69**, 89-107.
- Moiseev PA, Shiyatov SG (2003) Vegetation dynamics at the treeline ecotone in the Ural highlands, Russia. In 'Alpine biodiversity in Europe.' (Eds L Nagy, G Grabherr, C Körner, DBA Thompson) pp. 423-435. (Springer-Verlag: Berlin)
- Nagy L, Grabherr G, Körner C, Thompson DBA (2003) 'Alpine biodiversity in Europe.' (Springer-Verlag: Berlin)
- Pauli H, Gottfried M, Dirnböck T, Dullinger S, Grabherr G (2003) Assessing the long-term dynamics of endemic plants at summit habitats. In 'Alpine biodiversity in Europe.' (Eds L Nagy, G Grabherr, C Körner, DBA Thompson) pp. 195-207. (Springer-Verlag: Berlin)
- Pauli H, Gottfried M, Hohenwallner D, Reiter K, Casale R, Grabherr G (2004) 'The GLORIA field manual – A multi-summit approach.' (European Commission - DG Research: Luxembourg)

- Pauli H, Gottfried M, Reiter K, Klettner C, Grabherr G (2007) Signals of range expansion and contractions of vascular plants in the high Alps: observations (1994-2004) at the GLORIA master site Schrankogel, Tyrol, Austria. *Global Change Biology* **13**, 147-156.
- Pickering CM, Armstrong T (2003) Potential impact of climate change on plant communities in the Kosciuszko alpine zone. *Victorian Naturalist* **120**, 263-272.
- Pickering CM, Good R, Green K (2004) 'The ecological impacts of global warming: Potential effects of global warming on the biota of the Australian Alps.' (Australian Greenhouse Office: Canberra)
- Pickering, C.M., Hill, W. and Green, K. 2008. Vascular plant diversity and climate change in the alpine zone of the Snowy Mountains, Australia. *Biodiversity and Conservation*. **17**, 1627–1644. 10.1007/s10531-008-9371-y.
- Rayment GE, Higginson FR (1992a) Nitrogen method 7C2. In 'Australian laboratory handbook of soil and water chemical methods.' Inkata Press, Melbourne.
- Rayment GE, Higginson FR (1992b) Phosphorus method 9B2. In 'Australian laboratory handbook of soil and water chemical methods.' Inkata Press, Melbourne.
- Stanisci A, Pelino G, Blasi C (2005) Vascular plant diversity and climate change in the alpine belt of the central Apennines (Italy). *Biodiversity Conservation* **14**, 1301-1318.
- Van de Ven CM, Weiss SB, Ernst WG (2007) Plant species distributions under present conditions and forecasted for warmer climates in an arid mountain range. *Earth Interactions* **11**, 1-33.
- Walther G-R, Beißner S, Burga CA (2005) Trends in upward shift of alpine plants. *Journal of Vegetation Sciences* **16**, 541-548.
- Wardle P, Coleman MC (1992) Evidence for rising upper limits of four native New Zealand forest trees. *New Zealand Journal of Botany* **30**, 303-314.

**Table 1. Location, general vegetation characteristics and average  $\pm$  standard errors of soil temperatures and chemistry variables for each of five summits on Mt Clarke in the Snowy Mountains, Australia.**

(Apart from %C and %N, soil values are in mg/kg). Temp. = temperature. JTD = Julian thaw date. SD = Season days. SAS = summit area sections (see Fig. 2 and methods for details).

**Table 2. Significant differences among summits and aspect in vegetation and environmental variables on Mt Clarke, Snowy Mountains, Australia.** Rho and *P* values are from Analysis of Similarity on multidimensional dissimilarity matrixes for vegetation and environmental variables from the program PRIMER. *P* values in bold are significant. SAS = summit area sections (see Fig. 2 and methods for details).

**Table 3. Plant species that contributed to similarity in vegetation of each summit at three spatial scales (4 x 1-m<sup>2</sup> quadrats at each aspect for four summits, upper and lower SAS for each aspect) from SIMPER function in PRIMER.**

AvCov. = Average cover, Cont% = Percentage contribution to similarity among aspects at that summit. CL = Clarke. \* endemic to just the Kosciuszko alpine region. SAS = summit area sections (see Fig. 2 and methods for details).

**Table 4. Spearman's correlation coefficients for environmental variables that 'best explained' the dissimilarity matrix for plant species cover sampled at three spatial scales on summits on Mt Clarke, Snowy Mountains, Australia.** Values are generated using the BIOENV function in PRIMER where all combinations of environmental variables are tested. JTD = Julian thaw date, %BG = Percentage bare ground, MaxT05 = Absolute maximum temperature in 05, MinT05 = Absolute minimum temperature in 05, SD = Season days. SAS = summit area sections (see Fig 2 and methods for details).

**Fig. 1.** Location of the five GLORIA summits (CL1-CL5) on Mt Clarke in the Snowy Mountains in Australia.

**Fig. 2.** Diagram of the layout of the GLORIA summits (redrawn from Pauli *et al.* 2004 with permission) showing the layout of the eight summit area sections (SAS) and clusters of four 1 m<sup>2</sup> quadrats at the base of the upper zone.

**Fig. 3.** Level of separation in plant species composition among the five GLORIA summits on Mt Clarke in the Snowy Mountains, Australia, based on percentage overlapping cover data for all species on each aspect analysed using normalised MDS ordinations of Bray-Curtis dissimilarity measures. Vegetation was sampled at three spatial scales (a) four 1-m<sup>2</sup> quadrats at each aspect for four summits, (b) upper SAS, (c) lower SAS for each aspect. Summits differ in colour/pattern, with CL5 = black, CL4 = grey, CL3 = stripes, CL2 = dots, and CL1 = white. Aspect is indicated by shape with east an upright triangle, north an inverted triangle, south a square and west a diamond. The stress value gives an estimate of the closeness of fit of the normalised MDS axes to the dissimilarity matrix with the lower the stress value the better the fit.

**Fig. 4.** Level of separation in environmental variables among five GLORIA summits on Mt Clarke in the Snowy Mountains, Australia, based on data for each aspect analysed using normalised Euclidean distances in MDS ordinations. (a) topographic variables (b) soils, (c)

soil temperature variables. Summits differ in colour/pattern, with CL5 = black, CL4 = grey, CL3 = stripes, CL2 = dots, and CL1 = white. Aspect is indicated by shape with east an upright triangle, north an inverted triangle, south a square and west a diamond.

**Table 1. Location, general vegetation characteristics and average  $\pm$  standard errors of soil temperatures and chemistry variables for each of five summits on Mt Clarke in the Snowy Mountains, Australia.**

(Apart from %C and %N, soil values are in mg/kg). Temp. = temperature. JTD = Julian thaw date. SD = Season days. SAS = summit area sections (see Fig. 2 and methods for details).

	CL1	CL2	CL3	CL4	CL5
Altitude (m.a.s.l.)	2114	2079	1992	1948	1729
E	148.2875	148.2911	148.2961	148.3000	148.3078
S	36.4328	36.4328	36.4347	36.4356	36.4356
Average slope	5.9°	7.1°	8.0°	7.4°	10.5°
Area of lower SAS (m <sup>2</sup> )	7581	8196	8551	8920	8664
Area of upper SAS (m <sup>2</sup> )	4722	3373	2860	3435	2212
Total area sampled (m <sup>2</sup> )	12303	11569	11411	12355	10876
% top cover of					
Solid rock	0.9	1.2	13.4	3.8	2.8
Scree	3.2	4.1	0.4	0.9	0
Lichens	0.3	0	0	0.3	0
Bryophytes	0	0.5	0.6	0.2	0
Bare ground	1.9	2.9	3.0	0.8	0.1
Litter	0	0	0	0.1	0
Vascular plants	93.7	91.3	82.6	94.0	97.2
% overlapping cover of lifeforms					
Fern/Fern-like	0	0	0.3	0.1	0
Graminoid	55.3	44.2	46.8	31.4	22.2
Herb	31.5	25.4	30.8	19.3	7.0
Shrub	12.5	29.8	20.8	50.4	75.1
Soil Temperature variables					
Av. temp. 2005	4.57 $\pm$ 0.226	4.67 $\pm$ 0.15	5.27 $\pm$ 0.18	5.27 $\pm$ 0.15	5.24 $\pm$ 0.21
Max. temp. 2005	13.6 $\pm$ 0.68	13.6 $\pm$ 0.24	15.75 $\pm$ 0.66	13.47 $\pm$ 0.45	12.6 $\pm$ 0.59
Min. temp. 2005	-0.19 $\pm$ 0	-0.06 $\pm$ 0.07	-0.12 $\pm$ 0.06	0.002 $\pm$ 0.06	0.07 $\pm$ 0.10
SD 04/05	205.8 $\pm$ 4.4	211.3 $\pm$ 4.1	210.0 $\pm$ 3.4	226.0 $\pm$ 4.9	222.5 $\pm$ 4.9
SD 05/06	186.4 $\pm$ 5.6	194.8 $\pm$ 3.3	189.3 $\pm$ 2.0	204.5 $\pm$ 2.9	199.8 $\pm$ 5.3
JTD 04	321.3 $\pm$ 2.4	318.5 $\pm$ 1.5	320.0 $\pm$ 1.6	314.0 $\pm$ 2.4	321.0 $\pm$ 4.7
JTD 05	311.0 $\pm$ 5.6	301.3 $\pm$ 2.0	315.8 $\pm$ 4.9	298.8 $\pm$ 0.8	312.8 $\pm$ 4.9
JTD 06	210.0 $\pm$ 2.2	309.3 $\pm$ 2.5	308.8 $\pm$ 0.8	306.5 $\pm$ 0.6	302.8 $\pm$ 3.6
Soil chemistry					
%C	5.2 $\pm$ 0.8	7.4 $\pm$ 0.7	8.3 $\pm$ 1.4	11.9 $\pm$ 3.1	12.9 $\pm$ 1.4
%N	0.4 $\pm$ 0.1	0.6 $\pm$ 0.1	0.6 $\pm$ 0.1	0.8 $\pm$ 0.2	0.8 $\pm$ 0.1
NH <sub>4</sub> N	11.1 $\pm$ 3.9	15.1 $\pm$ 6.1	22.9 $\pm$ 7.6	33.4 $\pm$ 19.2	14.7 $\pm$ 3.1
NO <sub>3</sub> N	2.9 $\pm$ 0.9	15.8 $\pm$ 8.8	22.2 $\pm$ 11.9	3.4 $\pm$ 1.4	2.8 $\pm$ 1.5
Ext.P	27.4 $\pm$ 4.0	39.8 $\pm$ 10.2	33.7 $\pm$ 6.7	24.6 $\pm$ 3.6	31.2 $\pm$ 5.8
P	755 $\pm$ 118	982 $\pm$ 152	948 $\pm$ 164	873 $\pm$ 157	1098 $\pm$ 144
Al	25750 $\pm$ 3945	29000 $\pm$ 1291	32250 $\pm$ 3198	36750 $\pm$ 3198	37000 $\pm$ 1291
Ca	400.0 $\pm$ 86.3	265.0 $\pm$ 41.7	415.0 $\pm$ 6.5	972.5 $\pm$ 265.1	482.5 $\pm$ 48.7
Cu	11.2 $\pm$ 2.2	10.0 $\pm$ 1.8	6.5 $\pm$ 1.5	12.5 $\pm$ 0.6	11.3 $\pm$ 0.4
Fe	22750 $\pm$ 3172	19750 $\pm$ 17012	20250 $\pm$ 250	24000 $\pm$ 2381	21750 $\pm$ 2529

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K	6325 ± 1310	5975 ± 477	5450 ± 429	5800 ± 672	5650 ± 29
Mg	4800 ± 1137	3650 ± 921	1900 ± 71	3575 ± 895	3800 ± 204
Mn	392.5 ± 27.8	252.5 ± 58.8	230.0 ± 71.4	330.0 ± 89.7	155.0 ± 17.1
Na	202.5 ± 48.0	217.5 ± 28.1	175.0 ± 11.9	167.5 ± 7.5	180.0 ± 22.7
Pb	7.4 ± 2.4	5.0 ± 0	9.8 ± 1.6	11.4 ± 2.2	14.1 ± 0.8
Sr	35.6 ± 19.9	26.2 ± 7.1	30.7 ± 9.7	31.7 ± 6.7	23.9 ± 2.6
Zn	52.7 ± 10.1	44.8 ± 4.4	47.2 ± 4.4	62.9 ± 5.9	53.4 ± 0.7

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**Table 2. Significant differences among summits and aspect in vegetation and environmental variables on Mt Clarke, Snowy Mountains, Australia.** Rho and *P* values are from Analysis of Similarity on multidimensional dissimilarity matrixes for vegetation and environmental variables from the program PRIMER. *P* values in bold are significant. SAS = summit area sections (see Fig. 2 and methods for details).

	Summit		Aspect	
	Rho	<i>P</i>	Rho	<i>P</i>
Quadrats				
% cover all species	0.764	<b>0.001</b>	-0.16	0.904
Life-forms/surface types	0.029	0.384	-0.2	0.86
Upper SAS				
% cover all species	0.693	<b>0.001</b>	0.04	0.351
Life-forms	0.764	<b>0.001</b>	-0.16	0.902
Lower SAS				
% cover all species	0.859	<b>0.001</b>	-0.211	0.987
Life-forms	0.616	<b>0.001</b>	-0.12	0.809
All environmental variables	0.251	0.058	-0.166	0.905
Topography	0.305	0.063	0.189	0.100
Soil chemistry	0.111	0.244	-0.097	0.686
Soil temperatures	0.285	<b>0.044</b>	-0.063	0.302

**Table 3. Plant species that contributed to similarity in vegetation of each summit at three spatial scales (4 x 1-m<sup>2</sup> quadrats at each aspect for four summits, upper and lower SAS for each aspect) from SIMPER function in PRIMER.**

AvCov. = Average cover, Cont% = Percentage contribution to similarity among aspects at that summit. CL = Clarke. \* endemic to just the Kosciuszko alpine region. SAS = summit area sections (see Fig. 2 and methods for details).

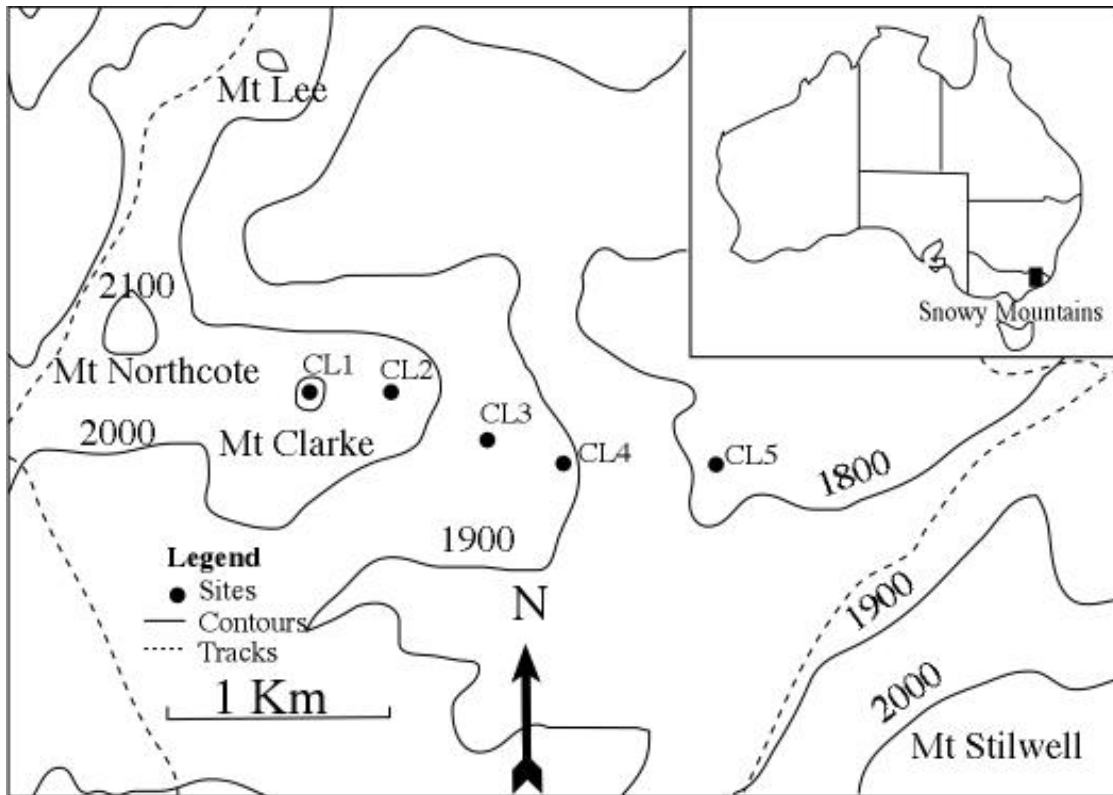
Species	Four 1-m <sup>2</sup> quadrats		Upper SAS		Lower SAS	
	AvCov.	Cont%	AvCov.	Cont%	AvCov.	Cont%
<b>CL1</b>						
<i>Poa</i> sp.	57.6	80.7	41.5	57.1	35.4	49.2
<i>Trisetum spicatum</i>	9.4	7.2	10.3	10.2	7.9	7.0
<i>Craspedia costiniana</i> *	4.4	5.2	3.8	4.7		
<i>Celmisia costiniana</i>			12	6.7	22.1	15.1
<i>Carex hebes</i>			3.3	3.6	2.6	4.0
<i>Microseris lanceolata</i>			8.6	9.7	3.1	3.0
<i>Pentachondra pumila</i>					3.5	3.9
<i>Epacris microphylla</i>					10.9	10.5
<b>CL2</b>						
<i>Poa</i> sp.	46.2	61.6	32.8	44.6	35.6	44.6
<i>Celmisia costiniana</i>	19.4	16.9	7.9	9.0	19.9	21.9
<i>Epacris microphylla</i>	29.2	14.9	24.9	28.8	12.4	15.9
<i>Pentachondra pumila</i>			8.9	5.4	3.8	2.8
<i>Ewartia nubigena</i>			2.1	2.4		
<i>Trisetum spicatum</i>					6	5.1
<b>CL3</b>						
<i>Poa</i> sp.	74.3	89.3	32.9	52.2	34.4	49.0
<i>Carex hebes</i>	5.1	4.6	3.5	3.7	3.5	4.5
<i>Celmisia costiniana</i>			7.8	11.6	14.3	20.4
<i>Prostanthera cuneata</i>			5.6	8.3	2.6	2.9
<i>Trisetum spicatum</i>			3.9	5.1	2.9	2.8
<i>Rumex acetosella</i>			3.9	3.8		
<i>Grevillea australis</i>			2	3.1	3.4	4.0
<i>Phebalium ovatifolium</i> *			1.8	1.6	1.3	1.2
<i>Craspedia</i> sp.B			1.7	1.6		
<i>Empodisma minus</i>					1.3	1.0
<i>Euphrasia collina</i> subsp. <i>diversicolor</i>					1.5	1.0
<i>Epacris microphylla</i>					4.6	3.8
<b>CL4</b>						
<i>Kunzea muelleri</i>	36.3	47.9	22.8	24.1	19.1	12.3
<i>Poa</i> sp.	27.7	26.1	26.1	35.0	26.5	37.3
<i>Epacris microphylla</i>	18.5	19.0	13.8	11.8	7.6	9.0
<i>Grevillea australis</i>			9.0	10.6	12.3	16.9
<i>Celmisia costiniana</i>			7.9	10.2	6.3	10.0
<i>Craspedia</i> sp.B					3.3	3.2
<i>Phebalium ovatifolium</i> *					2.8	2.4
<b>CL5</b>						
<i>Kunzea muelleri</i>			40.9	48.5	30.9	28.6
<i>Phebalium ovatifolium</i> *			16.5	16.9	25.4	35.3
<i>Grevillea australis</i>			5.75	7.4	3.2	2.8
<i>Prostanthera cuneata</i>			6.5	6.7	5.9	3.3
<i>Poa</i> sp.			4.6	5.7	9.4	9.7

<i>Empodisma minus</i>	8.0	5.2	13.3	12.4
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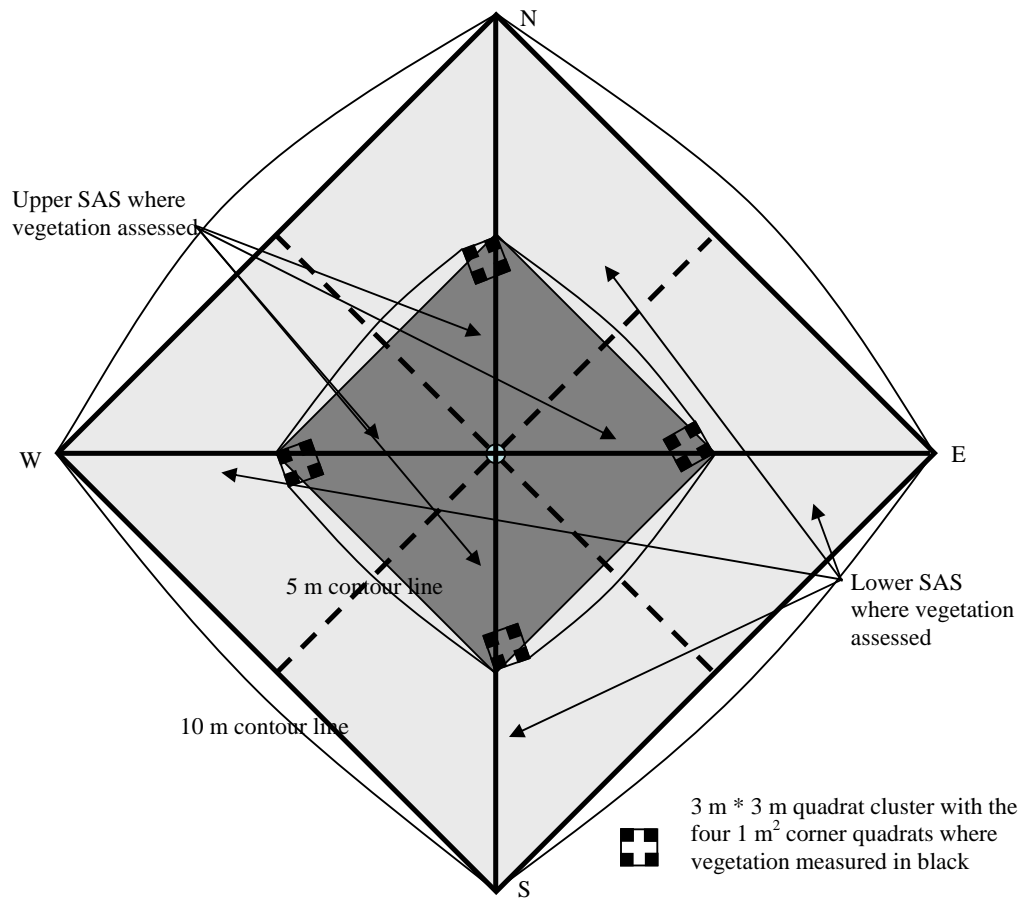
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JTD = Julian thaw date, %BG = Percentage bare ground, MaxT05 = Absolute maximum temperature in 05, MinT05 = Absolute minimum temperature in 05, SD = Season days. SAS = summit area sections (see Fig 2 and methods for details).

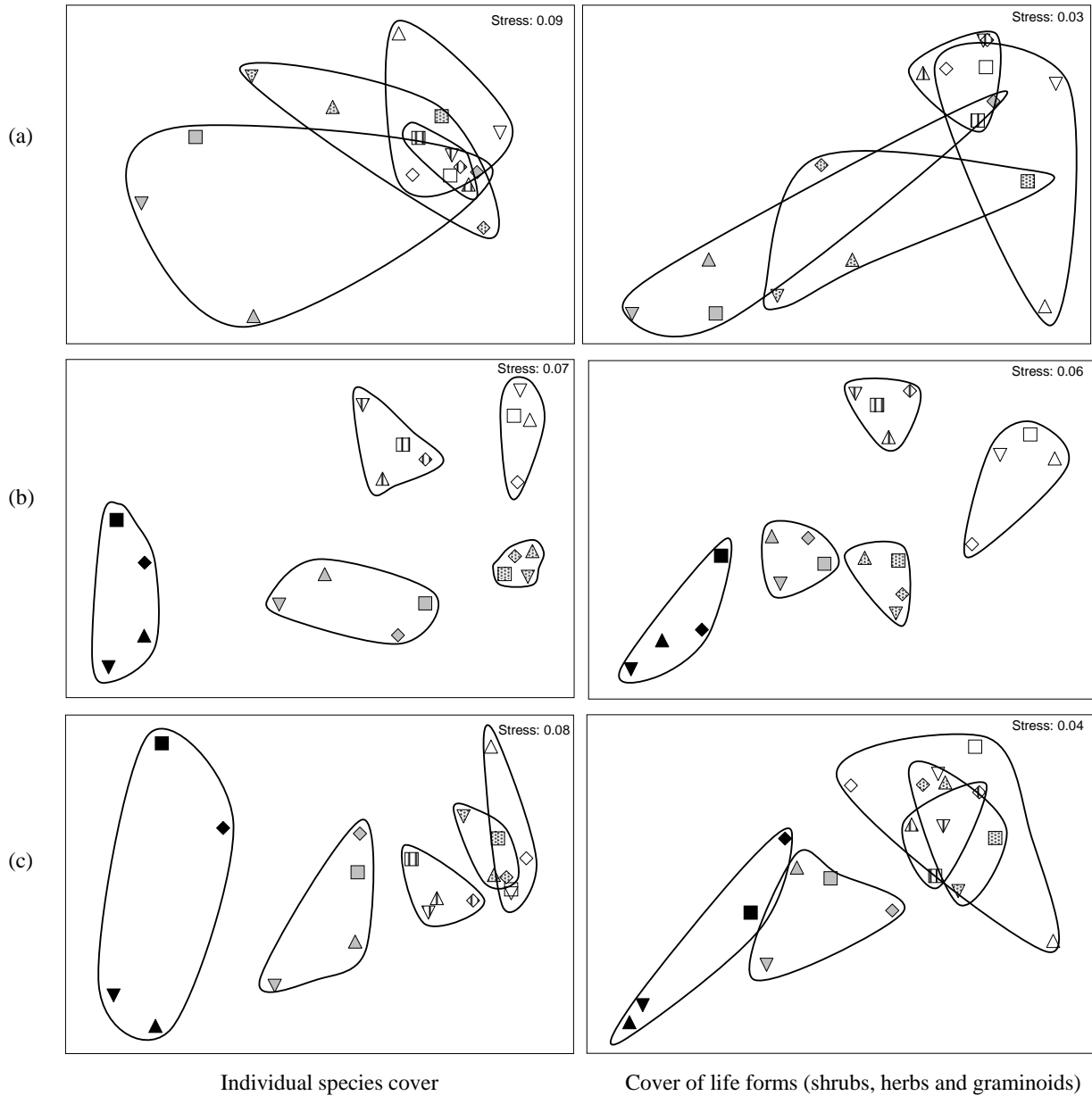
	Combination of variables	R <sup>2</sup>	P
Quadrat data			
All variables	SD05/06, Ca	0.699	<b>0.001</b>
Climatic variables only	MinT05,SD04/05,SD05/06	0.427	0.090
Upper SAS			
All variables	Altitude	0.849	<b>0.001</b>
Excluding altitude	Aspect-N, SD04/05, JTD06, Slope, %BG	0.586	<b>0.001</b>
Climatic variables only	MaxT05, MinT05, SD04/05, SD05/06, JTD06	0.433	<b>0.008</b>
Lower SAS			
All variables	Altitude	0.817	<b>0.001</b>
Excluding altitude	JTD06, Slope, %BG, C, Ca	0.642	<b>0.001</b>
Climatic variables only	MaxT05, MinT05, SD04/05, SD05/06, JTD06	0.415	<b>0.032</b>



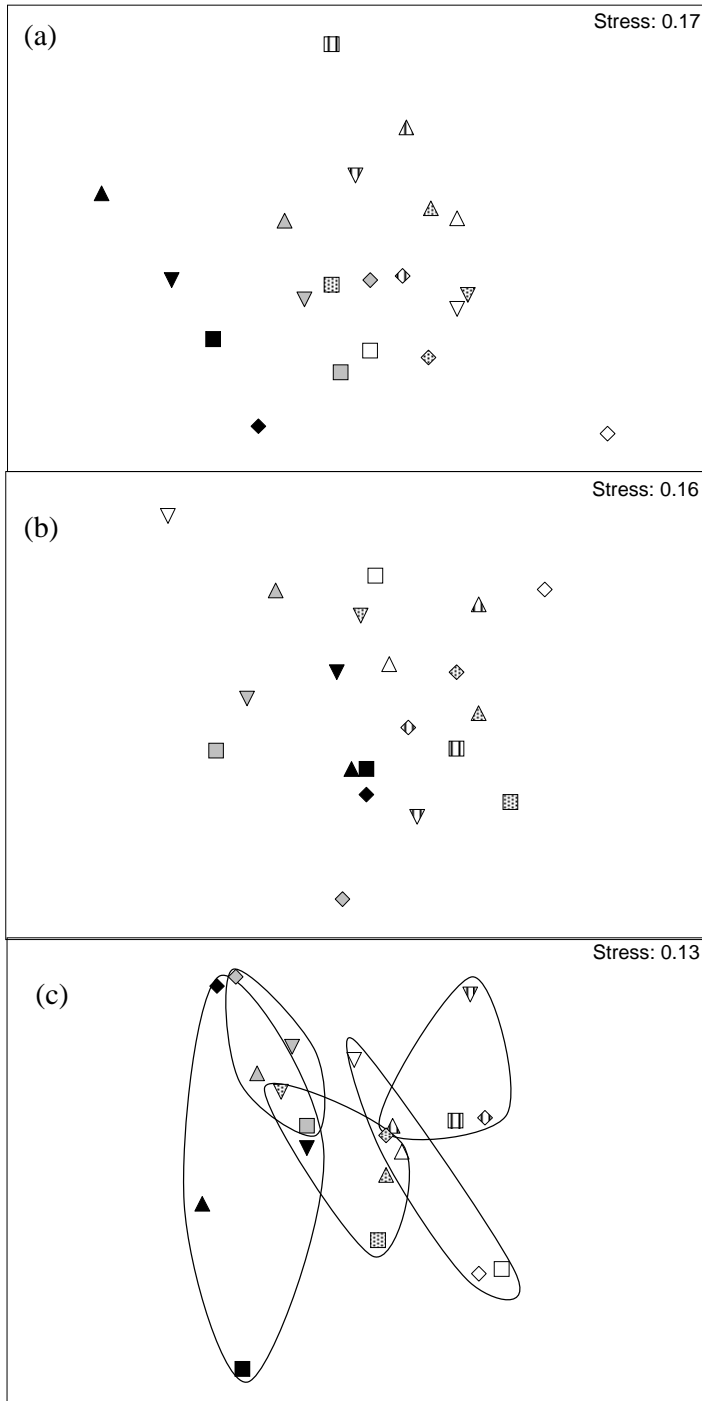
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**Fig. 3.** Level of separation in plant species composition among the five GLORIA summits on Mt Clarke in the Snowy Mountains, Australia, based on percentage overlapping cover data for all species on each aspect analysed using normalised MDS ordinations of Bray-Curtis dissimilarity measures. Vegetation was sampled at three spatial scales (a) four 1-m<sup>2</sup> quadrats at each aspect for four summits, (b) upper SAS, (c) lower SAS for each aspect. Summits differ in colour/pattern, with CL5 = black, CL4 = grey, CL3 = stripes, CL2 = dots, and CL1 = white. Aspect is indicated by shape with east an upright triangle, north an inverted triangle, south a square and west a diamond. The stress value gives an estimate of the closeness of fit of the normalised MDS axes to the dissimilarity matrix with the lower the stress value the better the fit.



**Fig. 4.** Level of separation in environmental variables among five GLORIA summits on Mt Clarke in the Snowy Mountains, Australia, based on data for each aspect analysed using normalised Euclidean distances in MDS ordinations. (a) topographic variables (b) soils, (c) soil temperature variables. Summits differ in colour/pattern, with CL5 = black, CL4 = grey, CL3 = stripes, CL2 = dots, and CL1 = white. Aspect is indicated by shape with east an upright triangle, north an inverted triangle, south a square and west a diamond.