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ORIGINAL PAPER

Short-term variation in species richness across an altitudinal gradient of alpine summits

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Abstract In response to climate warming, high altitude alpine vegetation may be replaced by typically lower altitude species, as species re-assemble and migrate to new areas. However, empirical evidence showing vegetation change in response to climate warming is largely unavailable for Australian alpine areas. Here, we examine changes in species richness with respect to climate and altitude over a 7 year period at a range of spatial scales in a re-survey of five alpine summits that are part of the Global Observation Research Initiative in Alpine Environments monitoring network. Eighty species were recorded in 2011 across all summits, an increase of 6 species since 2004. Mean species richness increased at the whole-of-summit scale from 45 to 50 species (about 12 %). At this scale, the rate of species richness increase was almost one new species per year, with 15 new species recorded at one summit. Here, shrub and graminoid species showed the largest increases. At the smaller spatial scales, changes in species richness were less pronounced. Turnover at the species and community level was typically moderate at all spatial scales and on all summits. The strength and direction of species richness change (the difference in species richness between the two sample periods, +/−) was not related to altitude nor variation in climate. Future re-surveys of the summits will confirm whether these short-term variations in species richness, particularly increases in shrubs, are indeed signals of longer-term trends and interactions with a changing climate.

Keywords Re-visitation study · Flora survey · Species migration · Climate change · GLORIA · Snowy Mountains · Australia

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Introduction

The distribution of alpine plants is strongly controlled by low temperatures and steep gradients in the local climate (Körner and Larcher 1988; Körner 2003). In particular, mountain top vegetation is expected to be highly sensitive to changes in climate (Lesica and Steele 1996), where species may be at their upper altitudinal range limits and topographically featureless summits provide little relief from ambient conditions (Grabherr et al. 1994; Theurillat and Guisan 2001). The general expectation worldwide is for the migration and subsequent replacement of species from the lower altitude alpine areas into the higher alpine and nival areas as species respond to climatic changes, rising temperatures and longer growing seasons (Grabherr et al. 1995; Guisan and Theurillat 2000; Theurillat and Guisan 2001). Indeed, re-surveys of mountain summits from the European Alps, using data from as far back as 1835, have revealed upward shifts of alpine plants and an associated increase in species richness primarily related to recent (late twentieth century) climate warming (Grabherr et al. 1994; Böhm et al. 2001; Holzinger et al. 2008). There are many other examples of shifting species' ranges in the alpine zone across the European mountains (Kullman 2002; Bahn and Körner 2003; Klanderud and Birks 2003; Walther et al. 2005; Holzinger et al. 2008; Lenoir et al. 2008) and in the upper forest belt (Moiseev and Shiyatov 2003). Recent data from high altitudes showed a consistent temporal increase in species richness in the European Alps (Pauli et al. 2003a; Erschbamer et al. 2011; Pauli et al. 2012). However, continual and rapid climate warming over long periods is eventually expected to reduce species richness and diversity through generalist species out-competing specialised, cold-adapted species in (previously) marginal habitats (Grabherr et al. 1995; Theurillat and Guisan 2001; Lesica and McCune 2004; Venn et al. 2011). These processes therefore threaten rare and endemic high altitude species with narrow distribution ranges via range expansion by lower altitude alpine species (Grabherr et al. 1995; Pauli et al. 2003b; Pauli et al. 2007; Engler et al. 2011; Dullinger et al. 2012).

Australian alpine and high mountain areas are considered to be highly vulnerable to climate change (Hughes 2003; Laurance et al. 2011). However, empirical evidence of vegetation shifts in response to recent climate change is largely unavailable, with many studies instead reporting the indirect links of climate change and climate variability with vegetation change; such as investigating the inter-annual variability of snow cover on vegetation patterns (Edmonds et al. 2006) and encroaching sub-alpine treelines into grassy plains (Wearne and Morgan 2001), using space-for-time studies over altitudinal gradients to infer future vegetation change (Venn and Morgan 2005) and using artificial warming experiments in sub-alpine areas to predict climate change effects (Hoffmann et al. 2010). Here, we present the recent results from a comprehensive, on-going, empirical study that has the specific aim of detecting alpine vegetation change on summits in relation to climate change. The study is in its infancy, having been established in 2004, but it is part of a global attempt to detect long-term alpine vegetation change, particularly changes in species richness with respect to local temperatures and altitude, on high mountain summits. An important theoretical basis of this study and the Global Observation Research Initiative in Alpine Environments (GLORIA) monitoring program more generally, is the assumption that patterns in species richness are related to climate. Evidence for this includes patterns of decreasing species richness with increasing altitude at the scale of whole floras and at smaller spatial scales (Körner 1992), as well as the association between vegetation composition and climatic variables (Pickering and Green 2009). Because minimum and maximum temperatures in high mountain areas in Australia have risen (Nicholls 2005) and snow cover has declined over past decades (Green and Pickering 2009), long term monitoring using the GLORIA protocol is therefore timely and essential for detecting and predicting Australian alpine species' responses to local climate change. The climate predictions for the Australian alpine areas include increases in temperature, particularly minima, and further reductions in snowpack; potentially down from the present mean of 183 days with least 1 cm of snow cover at the highest summit in the region, Mt Kosciuszko 2,228 m, to 87 days by 2050 (Hennessey et al. 2003).

Here, we focus our attention on the level of species, species richness and turnover measures to detect change across five summits in the Snowy Mountains first surveyed using the GLORIA protocol in 2004 and re-surveyed in 2011. At this level, changes in species, particularly those endemic to the region, could highlight more general vegetation changes occurring within the alpine area. Specifically we ask, has the overall species richness across the summits changed since 2004? Are changes in species richness related to the scale of sampling? Are changes in species richness related to altitude? Do different life forms or endemic species show strong changes over time? Is there any evidence of migration of species from lower altitudes into these summits?

Methods

Study sites

In January 2011 we re-surveyed the five 'summits' that were originally surveyed in January 2004 along a continuous ridge from close to the valley floor to the summit of Mt Clarke (Pickering et al. 2008; Pickering and Green 2009) (Fig. 1). The summits cover an altitudinal range of 301 m from the lowest at 1,813 m (Clarke 5) through to the highest at 2,114 m (Clarke 1) (Table 1) and cover a horizontal distance of 1,600 m. The sites were selected for long-term monitoring under the GLORIA sampling protocols (Pauli et al. 2004) (Fig. 2), as they experience similar effects of exposure and differences in climate are most likely due to the altitudinal gradient. They are all relatively flat, rather than cone-shaped peaks, and the vegetation is characteristic of nearby summits in the vicinity. The soils are around 350 ± 110 mm in depth (K. Green, unpublished

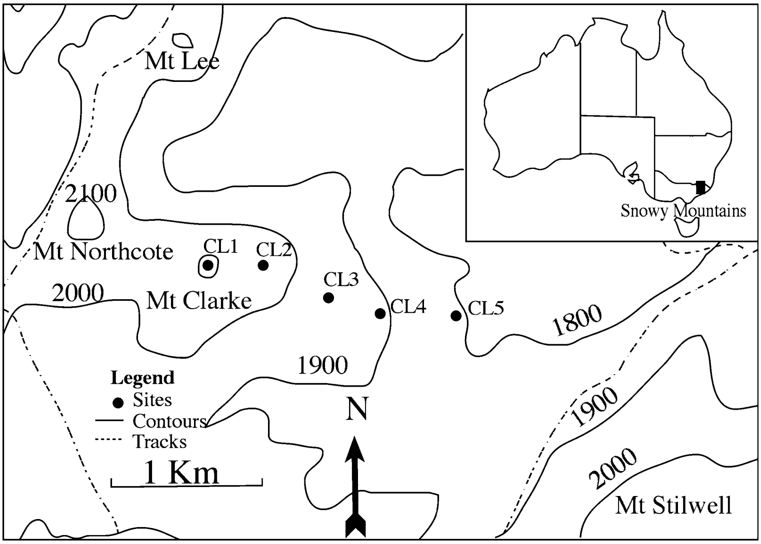

Fig. 1 Location of the Snowy Mountains in Australia and study site locations at Mt Clarke 1–5 (CL1, CL2, CL3, CL4, and CL5) representing the five summits

Table 1 Summary information for the five summits including location, altitude and size of the different SAS, mean species richness in 2011 and the mean difference in species richness (change +/−) between 2004 and 2011 for each summit at the different spatial scales

	Clarke 1		Clarke 2		Clarke 3		Clarke 4		Clarke 5	
Location	E 148.2875, S 36.4328		E 148.2911, S 36.4328		E 148.2961, S 36.4347		E 148.3000, S 36.4356		E 148.3078, S 36.4356	
Altitude (m a.s.l.)	2,114		2,079		1,992		1,948		1,813	
5 m SAS area (m^2)	4,722		3,373		2,860		3,435		2,212	
10 m SAS area (m^2)	7,581		8,196		8,551		8,920		8,664	
5 + 10 m SAS area (m^2)	12,303		11,569		11,411		11,554		10,876	
Mean species richness per area	2011	Change +/−	2011	Change +/−	2011	Change +/−	2011	Change +/−	2011	Change +/−
1 m^2 quadrats mean ± 1 SE	6.6 ± 0.4	+0.4	8.7 ± 0.9	−0.2	8.4 ± 0.8	−1.1	9.1 ± 0.5	+0.6	N/A	N/A
5 m SAS (mean of aspects)	21.2	−0.5	23	+0.3	31.8	+0.5	31	+2.3	30.3	−1.3
10 m SAS (mean of aspects)	25	+4	28.5	+2.8	34.5	+4	34.7	+11.5	32.3	+4.5
5 + 10 m SAS (mean of aspects)	23.125	+1.7	25.7	+1.5	33.1	+2.3	32.8	+6.8	31.3	+1.3

1 m^2 quadrats were not sampled at Clarke 5

N/A not applicable

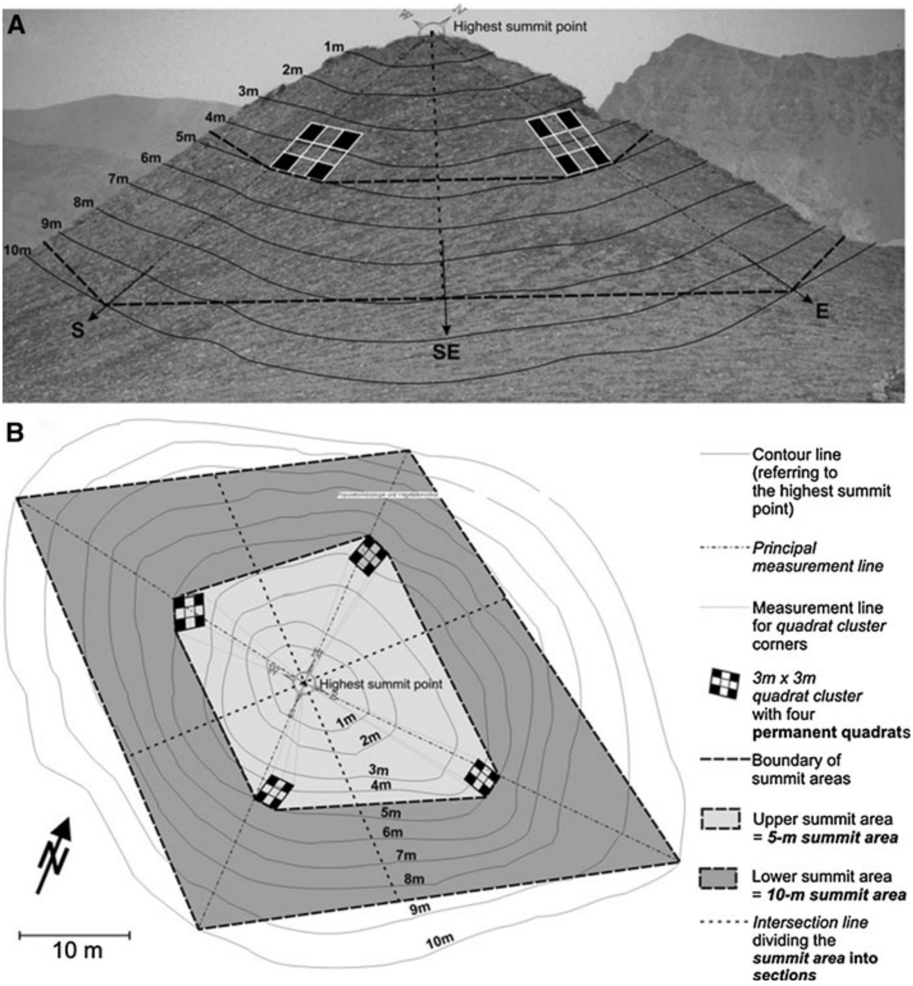

Fig. 2 The layout of sampling methodology of the GLORIA summits showing **a** the positioning of the upper and lower SASs and clusters of 1 m^2 quadrats, and **b** as viewed from above on a hypothetical summit. *Source* Pauli et al. (2004)

data), well-formed alpine humus soils (Costin 1954). The highest summits are dominated by tall alpine herbfield, whereas the lower summits are dominated by shrubs. As a result of the continuous, mostly perennial vegetation cover, biomass is high compared to some other alpine regions (Costin 1954). There are some rock outcrops, but these are not a defining feature of the summits. Disturbance is minimal as cattle grazing ceased >60 years ago, the historical stock travelling route avoided these summits and there are few native and no exotic burrowing mammals at these altitudes. No walking tracks cross the summits resulting in low visitation rates.

Vegetation sampling

The top section of each summit was divided into eight summit area sections (SAS), four covering the area down to 5 m below the summit, the 5 m isoline, for each of the four cardinal compass bearings (hereafter referred to as the upper or 5 m SAS), and another four covering the four compass bearings down to the 10 m isoline (hereafter referred to as the lower or 10 m SAS) (Pauli et al. 2004) (Fig. 2). Where the summit was exceptionally flat, the upper area extended 50 m from the summit and lower extended 100 m. At each of the four cardinal bearings at the 5 m isoline, a cluster of four 1 m^2 quadrats was established (Fig. 2). Due to the density of tall (>1 m) shrubs on Clarke 5, permanent 1 m^2 quadrats were not established. For the other four summits, species composition was recorded in each of the four corner 1 m^2 quadrats. In each of the eight SAS a complete species list was compiled of all vascular plant species (Pauli et al. 2004). Species richness data were therefore compiled at four spatial scales: the 1 m^2 quadrats, on each aspect of the SAS at the 5 and 10 m contour line and through combining the data from the 5 and 10 m SAS to produce a 'whole of summit' species list (5 + 10 m SAS) (Table 1).

Sampling in 2011 was conducted 'blind' without referring to the 2004 data. Sampling in each of the SAS and quadrats was performed by the same people to ensure consistency in the data (Vittoz et al. 2010). Post sampling, a rigorous species identification checking procedure was used to ensure changes in species between 2004 and 2011 were not pseudo-changes, arising from difficulties in species identification. All species names follow Costin et al. (2000) to be consistent with the initial 2004 survey.

Climatic variation

Temperature loggers (Tinytag Plus—Gemini Data Loggers, Chichester England) were buried 10 cm below the ground surface from January 2004 through to January 2011, in the centre of the cluster of four quadrats on each aspect of each summit. Temperatures were recorded every 2 h. Temperature data from across this time period were used to calculate annual values of absolute minimum soil temperature, annual daily mean soil temperature, absolute maximum soil temperature, temperature sums (>5 °C), growing degree days and the length of the growing season across the years sampled. Several climate parameters were derived from these data and used in the subsequent analyses. Precipitation data were collected between 2003 and 2011 from an automated weather station about 8 km to the south at Thredbo (1,957 m) (Bureau of Meteorology), and from Pengilley Bog 13 km to the north-east (1,730 m), during the growing season only.

Data analysis

Variations with climate

Climate parameters derived from the temperature data included mean, minimum and maximum temperatures for each year, mean season days and mean thaw date for each site. We used ANCOVA to determine separately whether these climate parameters explained change in species richness (the difference between the 2004 and the 2011 samples) for both the 5 and 10 m SAS (dependent variables), using altitude as a covariate (see Appendix Table 5). Data from each aspect from each SAS were used in these analyses. To determine the strength of relationships between species richness and climatic parameters, simple linear regression was used with species richness values from the 5 and 10 m SAS from each aspect of each site. In addition, linear regression was used to investigate any relationships between the change (+/−) in species richness, using data from each aspect of each summit as separate data points, with the climatic parameters in both the 5 and the 10 m SAS (see Appendix Table 5).

Changes in species richness

Significant differences in total species richness between 2004 and 2011 were determined within summits and in the 5 and 10 m SAS and the 1 m^2 quadrats using *t* tests and data from each aspect (see Appendix Table 5). The change in species richness, interpreted as the difference (+/−) between the 2004 and 2011 sample times, was analysed with simple linear regression against altitude for all species and for four groups of species: Kosciuszko alpine area endemic species (KNP endemics, Costin et al. 2000), forbs, graminoids and shrubs, in both the 5 and the 5 + 10 m SAS.

Species and vegetation turnover

Frequency data (presence/absence) from 2004 and 2011 were used to calculate turnover of individual species and the vegetation overall. We calculated the individual species turnover (T_{sp}) from the quadrat data (presence/absence in 1 m^2 quadrats) at Clarke 1–4 according to the equation:

$$T_{sp} = (A + D)/(A + D + U) \quad (1)$$

where A is the frequency of quadrats where the species appeared in 2011; D is the frequency of quadrats where the species disappeared; U is the frequency of quadrats where the species' frequency was unchanged (Milberg and Hansson 1993). In addition, a vegetation turnover index (T_{veg}) was calculated for overall changes in species richness at different spatial scales (SAS), life forms and groups according to the equation:

$$T_{veg} = (A + D)/(A + D + B) \quad (2)$$

where A is the number of new species in 2011; D is the number of disappearing species; B is the number of species present in both years of comparison. For both indices, low turnover values are close to 0.01 and complete turnover is 1.0.

The ANCOVA procedure was performed with SPSS version 18. All other statistical analyses were performed with SYSTAT version 10.

Results

General patterns

There was a change in species richness across all spatial scales, with an overall pattern of increasing richness. Across all summits at the whole-of-summit scale (5 + 10 m SAS), 80 species were recorded compared to 74 in 2004 (Table 2). Overall, mean species richness increased at the scale of whole summits (5 + 10 m SAS) from 45 to 50 species (about 12 %) between 2004 and 2011. At the level of individual summits, changes in richness ranged from −1 at Clarke 3, to +15 at Clarke 4. The largest changes in species richness occurred at Clarke 4 (1,948 m) where 17 new species were recorded in the 5 + 10 m SAS (a total increase of +15 species). Mean species richness within the SAS (using the data from each aspect as four replicates) revealed changes between −1.3 and +11.5 mean species (Tables 1, 3), with the largest increases in mean species richness occurring at Clarke 4. The range in mean species richness in 2011 at the quadrat level across sites was less pronounced (between 6.6 and 9.1 species), and the change in mean species richness between 2004 and 2011 resulted in either a gain or loss of ~1 species (Table 1). Among

Table 2 List of species present across the study sites Clarke 1–5 during the 2004 and 2011 surveys, their families, life-form, distribution throughout the Austral region (also present in *A* the Australian Capital Territory, *V* Victoria, *T* Tasmania, *N* New Zealand) and their endemism to the alpine areas of Kosciuszko National Park (Endemic)

Species	Family	Life form	Distribution	Clarke 1		Clarke 2		Clarke 3		Clarke 4		Clarke 5	
				2004	2011	2004	2011	2004	2011	2004	2011	2004	2011
Acaena sp.	Rosaceae	Forb	AVTN								✓		✓
Acetosella vulgaris	Polygonaceae	Forb	I	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
Aciphylla glacialis	Apiaceae	Forb	V	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
Aciphylla simplicifolia	Apiaceae	Forb	AV			✓						✓	✓
Agrostis sp.	Poaceae	Graminoid	AVT	✓	✓		✓		✓		✓		✓
Asperula gunnii	Rubiaceae	Forb	AVT	✓			✓	✓	✓	✓	✓	✓	✓
Astelia psychrocharis	Liliaceae	Forb	Endemic										✓
Australopyrum velutinum	Poaceae	Graminoid	AVT		✓		✓		✓		✓		
Baeckea gunniana	Myrtaceae	Shrub	AVT					✓	✓			✓	✓
Brackyscome obovata	Asteraceae	Forb	AV									✓	
Brachyscome spathulata subsp. *spathulata*	Asteraceae	Forb	AV	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
Cardamine lilacina	Brassicaceae	Forb	AVT				✓				✓	✓	
Carex breviculmis	Cyperaceae	Graminoid	AVTN		✓		✓	✓	✓		✓		✓
Carex hebes	Cyperaceae	Graminoid	AV	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
Celmisia costiniana	Asteraceae	Forb	V	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
Chionogentias muelleriana subsp. *alpestris*	Gentianaceae	Forb	Endemic	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
Chionohebe densifolia	Scrophulariaceae	Shrub	N	✓	✓		✓						
Colobanthus affinis	Caryophyllaceae	Forb	VTN			✓	✓		✓			✓	✓
Colobanthus nivicola	Caryophyllaceae	Forb	Endemic	✓			✓						
Colobanthus pulvinatus	Caryophyllaceae	Forb	T	✓	✓	✓	✓						
Cotula alpina	Asteraceae	Forb	AVT									✓	
Craspedia costiniana	Asteraceae	Forb	Endemic	✓	✓	✓	✓		✓		✓	✓	✓
Craspedia lamicola	Asteraceae	Forb	V									✓	
Craspedia maxgrayi	Asteraceae	Forb	V	✓	✓	✓	✓	✓	✓	✓	✓	✓	

Table 2 continued

Species	Family	Life form	Distribution	Clarke 1		Clarke 2		Clarke 3		Clarke 4		Clarke 5	
				2004	2011	2004	2011	2004	2011	2004	2011	2004	2011
Craspedia sp. B	Asteraceae	Forb	Endemic	✓				✓		✓		✓	
Deyeuxia crassilisica	Poaceae	Graminoid	AVT		✓				✓		✓		✓
Empodisma minus	Restionaceae	Graminoid	AVTN			✓	✓	✓	✓	✓	✓	✓	✓
Epacris microphylla	Epacridaceae	Shrub	Endemic	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
Epacris paludosa	Epacridaceae	Shrub	VA										✓
Epacris petraphila	Epacridaceae	Shrub	VT				✓				✓		
Epacris petrophila	Epacridaceae	Shrub	AVT			✓	✓				✓	✓	✓
Epilobium tasmannicum	Onagraceae	Forb	TNV		✓		✓						
Epilobuim gunnianum	Onagraceae	Forb	VTAN								✓		
Erigeron bellidioides	Asteraceae	Forb	AVT				✓	✓	✓	✓	✓	✓	
Erigeron nitidus	Asteraceae	Forb	AV	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
Euchiton fordianus	Asteraceae	Forb	VT								✓		✓
Euchiton nitidulus	Asteraceae	Forb	VN					✓	✓		✓		
Euphrasia aha	Scrophulariaceae	Forb	Endemic			✓	✓						
Euphrasia collina subsp. *diversicolor*	Scrophulariaceae	Forb	V	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
Euphrasia collina subsp. *lapidosa*	Scrophulariaceae	Forb	Endemic	✓									
Ewartia nubigena	Asteraceae	Shrub	V	✓	✓	✓	✓	✓	✓	✓	✓		
Geranium potentilloides	Geraniaceae	Forb	V								✓		
Grevillea australis	Proteaceae	Shrub	AVT			✓	✓	✓	✓	✓	✓	✓	✓
Helichrysum scorpioides	Asteraceae	Forb	VT										✓
Hypochoeris radicata	Asteraceae	Forb	I		✓		✓	✓	✓	✓	✓		
Kunzea muelleri	Myrtaceae	Shrub	AV					✓	✓	✓	✓	✓	✓
Leptorhynchos squamatus	Asteraceae	Forb	AVT			✓				✓	✓		
Leucochrysum albicans subsp. *alpinum*	Asteraceae	Forb	AV	✓	✓	✓	✓	✓		✓	✓		

Table 2 continued

Species	Family	Life form	Distribution	Clarke 1		Clarke 2		Clarke 3		Clarke 4		Clarke 5	
				2004	2011	2004	2011	2004	2011	2004	2011	2004	2011
Leucopogon montanus	Epacridaceae	Shrub	VT			✓	✓	✓	✓	✓	✓	✓	✓
Luzula acutifolia subsp. *nana*	Juncaceae	Graminoid	Endemic							✓			
Luzula alpestris	Juncaceae	Graminoid	V	✓	✓		✓		✓		✓		✓
Luzula australasica subsp. *dura*	Juncaceae	Graminoid	Endemic	✓	✓	✓	✓	✓				✓	
Luzula novae-cambriae	Juncaceae	Graminoid	TV					✓	✓		✓	✓	✓
Luzula sp.	Juncaceae	Graminoid	AV	✓		✓		✓		✓		✓	
Lycopodium fastigiatum	Lycopodiaceae	Fern-like	AVTN							✓			
Melicytus sp.	Violaceae	Shrub	AV	✓	✓			✓	✓		✓	✓	✓
Microseris lanceolata	Asteraceae	Forb	AV	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
Myosotis sp.	Boraginaceae	Forb	V						✓				
Neopaxia australasica	Portulaceae	Forb	VTN				✓		✓				
Olearia algida	Asteraceae	Shrub	VAT								✓		
Olearia phlogopappa	Asteraceae	Shrub	V					✓	✓	✓	✓	✓	✓
Oreomyrrhis eriopoda	Apiaceae	Forb	AVT	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
Orites lancifolia	Proteaceae	Shrub	AV										✓
Pentachondra pumila	Epacridaceae	Shrub	VTN	✓	✓	✓	✓	✓	✓		✓	✓	✓
Phebalium ovatifolium	Rutaceae	Shrub	Endemic					✓	✓	✓	✓	✓	✓
Pimelea alpina	Thymelaeaceae	Shrub	V		✓	✓	✓	✓	✓	✓	✓	✓	✓
Plantago euryphylla	Plantaginaceae	Forb	AV					✓	✓	✓	✓	✓	✓
Poa sp.	Poaceae	Graminoid	AVT	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
Podocarpus lawrenci	Podocarpaceae	Shrub	AVT						✓				✓
Podolepis robusta	Asteraceae	Forb	AV							✓		✓	
Polystichum proliferum	Blechnaceae	Fern	VT					✓					
Prasophyllum alpestre	Orchidaceae	Forb	AVT	✓	✓		✓	✓	✓		✓	✓	✓

Table 2 continued

Species	Family	Life form	Distribution	Clarke 1		Clarke 2		Clarke 3		Clarke 4		Clarke 5	
				2004	2011	2004	2011	2004	2011	2004	2011	2004	2011
Prasophyllum sp.	Orchidaceae	Forb	AVT			✓					✓		
Prasophyllum tadgellianum	Orchidaceae	Forb	AVT	✓	✓	✓	✓	✓	✓	✓	✓	✓	
Pratia surrepens	Lobeliaceae	Forb	AVT									✓	
Prostanthera cuneata	Lamiaceae	Shrub	AV					✓	✓	✓	✓	✓	✓
Ranunculus acrophilus	Ranunculaceae	Forb	Endemic	✓		✓		✓					
Ranunculus graniticola	Ranunculaceae	Forb	AV					✓	✓	✓	✓	✓	✓
Ranunculus gunnianus	Ranunculaceae	Forb	VT					✓	✓		✓		✓
Ranunculus muelleri	Ranunculaceae	Forb	V	✓	✓	✓	✓					✓	
Richea continentis	Epacridaceae	Shrub	AV									✓	✓
Rytidosperma nudiflorum	Poaceae	Graminoid	AVT	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
Rytidosperma pumilum	Poaceae	Graminoid	N	✓		✓							
Scleranthus biflorus	Caryophyllaceae	Forb	AVTN	✓		✓	✓	✓		✓	✓		✓
Scleranthus singuliflorus	Caryophyllaceae	Forb	V	✓	✓	✓	✓	✓	✓		✓	✓	✓
Senecio gunnii	Asteraceae	Forb	AVT					✓		✓	✓	✓	✓
Senecio pectinatus var. *major*	Asteraceae	Forb	AV					✓					✓
Senecio pinnatifolius var. *pyocephalus*	Asteraceae	Forb	AVT		✓	✓	✓	✓	✓	✓	✓	✓	✓
Stackhousia pulvinaris	Stackhousiaceae	Forb	VT				✓						
Stylidium sp. aff. *graminifolium*	Stylidiaceae	Forb	VT										✓
Trisetum spicatum subsp. *australiense*	Poaceae	Graminoid	AVT	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
Uncinia sp.	Cyperaceae	Graminoid	AVTN	✓	✓	✓							
Viola betonicifolia subsp. *betonicifolia*	Violaceae	Forb	AVT		✓	✓	✓	✓	✓	✓	✓	✓	✓
Wahlenbergia ceracea	Campanulaceae	Forb	VAT										✓

I introduced species

the life forms considered (forbs, graminoids and shrubs), there was variation in species richness between the two time periods with a tendency for increases in shrub and graminoid richness and a decrease in herb richness.

Variation with climate

There were no consistent trends (increases or decreases) in climatic variables between 2004 and 2011 (Fig. 3), although relationships between site altitude and climate between 2004 and 2011 remained consistent; minimum temperatures ($R^2 = 0.28$, $P = 0.016$), mean temperatures ($R^2 = 0.44$, $P = 0.005$) and number of growing season days (snow free days) ($R^2 = 0.23$, $P = 0.032$) all significantly decreased with increasing altitude but not maximum temperatures (using the data from four loggers at each site as replicates).

The climate parameters appeared to have little influence on the changes in species richness between 2004 and 2011, in any of the SAS tested, as the ANCOVA analyses revealed no significant effects (see Appendix Table 6). Linear regressions between climate parameters and the mean species richness from the 5 and 10 m SAS across the altitudinal gradient of sites revealed few significant, strengthened, weakened or predictive relationships (see Appendix Table 6). Only relationships between species richness and the mean soil temperatures from each aspect at each site were significant with any reasonable predictive power (5 m SAS: 2004 $R^2 = 0.26, P = 0.02$, 2011 $R^2 = 0.25, P = 0.03$. 10 m SAS: 2004 $R^2 = 0.06, P = 0.26$, 2011 $R^2 = 0.41$, $P = 0.002$). Linear regressions between the change (+/−) in species richness at each altitude and the climatic parameters revealed no significant relationships with any predictive power for either the 5 or the 10 m SAS (see Appendix Table 6).

Precipitation data from the nearby rain gauges revealed substantial increases in annual and growing season precipitation over the 2010/2011 growing season (start of October to the end of April) in comparison with previous years in which the region experienced low rainfall conditions for almost a decade. At Thredbo, there was a 30 % increase in annual precipitation in 2011 compared with 2004 (mean precipitation between 2004 and 2009 (2010 data missing) was 1,136 mm, whereas in 2011 it was 1,647 mm). Growing season precipitation (October to the end of April) at Pengilley Bog was about 50 % higher in 2011 compared with previous years (mean growing season precipitation between 2003/2004 and 2009/2010 was 575 mm, whereas in 2010/2011 it was 1,182 mm).

Changes in species richness

The *t* tests comparing the total species richness between 2004 and 2011 revealed no significant differences in the 5 m SAS at any sites. In the 10 m SAS, however, there were significant differences between 2004 and 2011 at the two lowest summits, Clarke 4 and Clarke 5 ($P = 0.03$ and $P = 0.04$ respectively) (see Appendix Table 6). The overall total species richness across all sites in the 10 m SAS was higher in 2011 than in 2004 ($n = 20$, mean ± 1 SE: 2004 = 25.8 ± 1.1, 2011 = 31 ± 1.2, $P < 0.001$). There were no overall significant differences in the 5 m SAS between years (see Appendix Table 6).

The change in species richness between the two sample times for particular groups of species (life forms etc.) in both the 5 and the 5 + 10 m SAS showed no significant trends with altitude. The species richness of KNP endemics however, showed weak non-significant trends with altitude for both the 5 and the 5 + 10 m SAS ($R^2 = 0.68$, $P = 0.061$, $R^2 = 0.74$, $P = 0.08$ respectively), with the higher altitude sites losing one or two species and the lower sites gaining one or two species between sample times. Overall, most sites experienced an increase in species richness between the 2004 and the 2011 sample times, with several new records of graminoid

Table 3 The total species richness in 2011 and change (+/−) since 2004, the number of new species and number of those not found in 2011 and also the number of species whose frequency of occurrence remained the same in 2011; used in calculating T_{veg} = the vegetation turnover between 2004 and 2011 for species in the upper, lower and whole summits area sections (5, 10 and 5 + 10 m SAS) and for different groups of species and life forms

Summit, sample area (life form)	Species richness in 2011	Change (+/−) since 2004	No. new species	No. species not found in 2011	No. species same frequency	T_{veg}
Clarke 1, 5 m SAS	34	+1	7	6	3	0.33
Clarke 2, 5 m SAS	34	+4	10	6	2	0.40
Clarke 3, 5 m SAS	42	−2	7	9	2	0.31
Clarke 4, 5 m SAS	44	+5	12	7	2	0.37
Clarke 5, 5 m SAS	44	−1	9	10	0	0.35
Clarke 1, 10 m SAS	34	+1	8	7	0	0.37
Clarke 2, 10 m SAS	44	+4	10	6	0	0.32
Clarke 3, 10 m SAS	49	+8	14	6	0	0.36
Clarke 4, 10 m SAS	53	+20	22	2	1	0.44
Clarke 5, 10 m SAS	51	+9	18	9	0	0.45
Clarke 1, 5 + 10 m SAS	38	0	8	8	0	0.35
Clarke 2, 5 + 10 m SAS	49	+9	15	6	1	0.38
Clarke 3, 5 + 10 m SAS	50	0	8	7	1	0.27
Clarke 4, 5 + 10 m SAS	57	+15	17	5	2	0.37
Clarke 5, 5 + 10 m SAS	55	+3	16	13	0	0.43
Clarke 1, 1 m^2 quadrats	15	−2	3	5	0	0.40
Clarke 2, 1 m^2 quadrats	25	+1	4	3	0	0.25
Clarke 3, 1 m^2 quadrats	26	−4	4	8	1	0.35
Clarke 4, 1 m^2 quadrats	27	−4	7	11	0	0.47
Clarke 1, 5 m SAS (endemics)	3	−2	0	2	0	0.40
Clarke 2, 5 m SAS (endemics)	3	−1	0	1	0	0.25
Clarke 3, 5 m SAS (endemics)	3	+1	1	0	0	0.33
Clarke 4, 5 m SAS (endemics)	3	0	1	1	0	0.50
Clarke 5, 5 m SAS (endemics)	4	+1	1	0	0	0.25
Clarke 1, 5 + 10 m SAS (endemics)	3	−2	0	2	0	0.40
Clarke 2, 5 + 10 m SAS (endemics)	4	−1	0	1	0	0.20

Table 3 continued

Summit, sample area (life form)	Species richness in 2011	Change (+/−) since 2004	No. new species	No. species not found in 2011	No. species same frequency	T_{veg}
Clarke 3, 5 + 10 m SAS (endemics)	3	−1	1	2	0	0.60
Clarke 4, 5 + 10 m SAS (endemics)	3	0	1	1	0	0.50
Clarke 5, 5 + 10 m SAS (endemics)	4	0	1	1	0	0.40
Clarke 1, 5 m SAS (forbs)	17	−2	2	4	2	0.29
Clarke 2, 5 m SAS (forbs)	18	0	3	3	1	0.29
Clarke 3, 5 m SAS (forbs)	22	−4	2	6	2	0.29
Clarke 4, 5 m SAS (forbs)	24	+1	5	4	2	0.32
Clarke 5, 5 m SAS (forbs)	24	−6	3	9	0	0.36
Clarke 1, 5 + 10 m SAS (forbs)	21	−2	4	6	0	0.37
Clarke 2, 5 + 10 m SAS (forbs)	30	+6	9	3	1	0.36
Clarke 3, 5 + 10 m SAS (forbs)	26	−2	3	5	1	0.27
Clarke 4, 5 + 10 m SAS (forbs)	32	+7	8	2	2	0.30
Clarke 5, 5 + 10 m SAS (forbs)	29	−2	9	11	0	0.50
Clarke 1, 5 m SAS (graminoids)	11	+2	4	2	0	0.46
Clarke 2, 5 m SAS (graminoids)	10	+2	5	3	0	0.62
Clarke 3, 5 m SAS (graminoids)	10	+3	4	1	0	0.45
Clarke 4, 5 m SAS (graminoids)	10	+3	5	2	0	0.58
Clarke 5, 5 m SAS (graminoids)	9	+3	4	1	0	0.50
Clarke 1, 5 + 10 m SAS (graminoids)	11	+1	3	2	0	0.38
Clarke 2, 5 + 10 m SAS (graminoids)	10	+1	4	3	0	0.54
Clarke 3, 5 + 10 m SAS (graminoids)	11	+2	4	2	0	0.46
Clarke 4, 5 + 10 m SAS (graminoids)	11	+4	6	2	0	0.62
Clarke 5, 5 + 10 m SAS (graminoids)	10	+2	4	2	0	0.50

Table 3 continued

Summit, sample area (life form)	Species richness in 2011	Change (+/−) since 2004	No. new species	No. species not found in 2011	No. species same frequency	T_{veg}
Clarke 1, 5 m SAS (shrubs)	5	+1	1	0	0	0.20
Clarke 2, 5 m SAS (shrubs)	5	+2	2	0	1	0.40
Clarke 3, 5 m SAS (shrubs)	9	−1	1	2	0	0.27
Clarke 4, 5 m SAS (shrubs)	8	+2	2	0	0	0.25
Clarke 5, 5 m SAS (shrubs)	11	+2	2	0	0	0.18
Clarke 1, 5 + 10 m SAS (shrubs)	6	+1	1	0	0	0.17
Clarke 2, 5 + 10 m SAS (shrubs)	9	+2	2	0	0	0.22
Clarke 3, 5 + 10 m SAS (shrubs)	13	+1	1	0	0	0.08
Clarke 4, 5 + 10 m SAS (shrubs)	14	+5	3	0	0	0.25
Clarke 5, 5 + 10 m SAS (shrubs)	16	+3	3	0	0	0.19

and shrub species contributing to the increases in both the 5 and the 5 + 10 m SAS. The most dramatic decreases in species richness across the study were among forb species at Clarke 3 and 5 (−4 and −6 species respectively) within the top 5 m SAS (Table 3).

Species and vegetation turnover

At the quadrat level, mean individual species turnover (T_{sp}) was highest at Clarke 1 and 2, and lower at Clark 3 and 4 (0.67, 0.72, 0.59, 0.25 Clarke 1–4 respectively). Mean T_{sp} over these four sites was relatively high, 0.65. Most forb species had relatively low turnover (T_{sp} between 0 and 0.5), but there were a few exceptions where new occurrences or absences in some quadrats produced complete turnover ($T_{sp} = 1.0$) at one or more sites (Table 4). For example, *Euphrasia alsa*, *Scleranthus biflorus* and *S. singuliflorus* had either very high or very low T_{sp}, where less than three occurrences in either 2004 or 2011 produced very high or complete turnover. *Geranium potentilloides*, a common forb species from lower altitudes in the region, was a new occurrence in the quadrats, appearing in 2011 once at Clarke 4 (Table 4). The prominent snowgrass, *Poa* sp., was present in every quadrat at each site and this did not change between 2004 and 2011 (Table 4). The inconspicuous hook sedge, *Uncinia* sp. was not present in the quadrats in 2011, but this species was recorded within the SAS at the two highest sites. The larger shrub species recorded at the lower altitude sites (*Prostanthera cuneata* and *Phebalium ovatifolium*) showed no turnover whatsoever. *Epacris microphylla*, a prominent shrub present at all sites, also showed no change or any turnover at the three highest sites (Clarke 1–3), and only a minor change at Clarke 4. *Kunzea muelleri*, a common larger alpine shrub, also showed no change between 2004 and 2011 (Table 4). Other shrub species had low turnover values, mostly as a result of fewer records in quadrats in 2011.

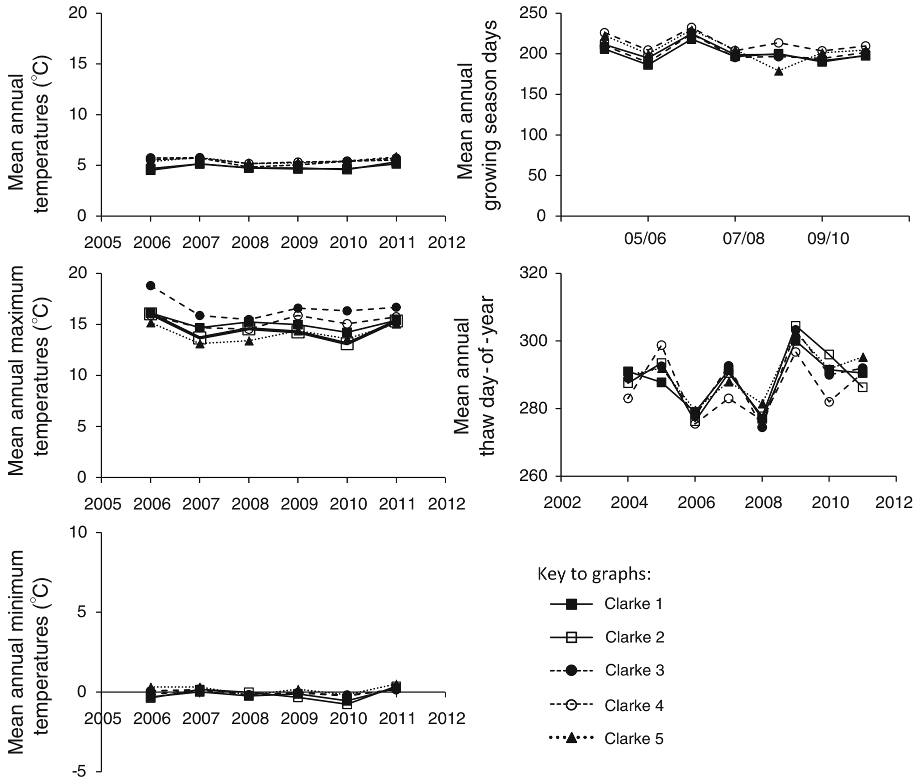

Fig. 3 Climate parameters derived from buried temperature loggers (10 cm soil depth) at the five summit sites (Clarke 1–5) over the period of study from 2004 to 2011

Vegetation turnover (T_{veg}) across the five sites within the 5 m SAS were between 0.31 and 0.40 (Table 3) with no clear trends with site altitude. Within the 10 m SAS (not including the 5 m SAS) T_{veg} values were between 0.32 and 0.45 across the five sites (Table 3). Overall vegetation turnover in the quadrats was similar to that of the SAS, T_{veg} between 0.25 and 0.47. Kosciuszko endemic species had higher turnover, especially within the 5 + 10 m SAS (between 0.20 and 0.60). Forb turnover was fairly similar across summits and SAS of different areas (between 0.27 and 0.5) as was graminoid turnover, although the T_{veg} values were overall slightly higher (between 0.38 and 0.62). Shrub species at the 5 m and the 5 + 10 m SAS showed considerably lower T_{veg} values (between 0.08 and 0.40). Exploratory analyses of the data revealed no clear relationships with the T_{veg} values of any life form and site altitude.

Discussion

Short-term changes in species richness and variation through sampling scale

The short-term increases in species richness across the summits on the Mt Clarke ridge between 2004 and 2011 are consistent with the trends from similar monitoring studies in the European Alps (Grabherr et al. 1994; Walther et al. 2005; Pauli et al. 2007; Holzinger et al. 2008;

Table 4 The frequency, change (+/−) is species richness between 2004 and 2011, the species turnover (T_{sp}) for species recorded in the 1 m^2 quadrats at sites Clarke 1–4, and the overall frequency, change and T_{sp} for the four summits combined

Species	Family	Life form	Clarke 1			Clarke 2			Clarke 3		
			Frequency	Change +/−	T_{sp}	Frequency	Change +/−	T_{sp}	Frequency	Change +/−	T_{sp}
Acctosella vulgaris[a]	Polygonaceae	Forb				1	−4	0.80	9	+2	0.40
Agrostis sp.	Poaceae	Graminoid	9	+8	0.89	11	NEW	1.00	5	NEW	1.00
Asperula gunnii	Rubiaceae	Forb							5	0	0.33
Brachyscome spathutulata subsp. *spathutulata*	Asteraceae	Forb	2	0	0.00	1	NEW	1.00			
Carex breviculmis	Cyperaceae	Graminoid	15	NEW	1.00	11	NEW	1.00	15	+13	0.94
Carex hebes	Cyperaceae	Graminoid	1	−15	0.94	6	−8	0.75	5	−9	0.73
Celmisia costiniana	Asteraceae	Forb	7	−2	0.22	12	0	0.00	8	−4	0.33
Chionogentias muelleriana subsp. *alpestris*	Gentianaceae	Forb				4	0	0.00	1	NEW	1.00
Craspedia costiniana	Asteraceae	Forb	15	−1	0.06	11	−3	0.21	3	NEW	1.00
Craspedia maxgrayi	Asteraceae	Forb	1	NEW	1.00	4	0	0.00			
Craspedia sp. B	Asteraceae	Forb	NR	−1	1.00				NR	−7	1.00
Empodisma minus	Restionaceae	Shrub				5	−1	0.17	2	0	0.00
Epacris microphylla	Epacridaceae	Shrub	6	0	0.00	8	0	0.00	1	0	0.00
Erigeron bellidioides	Asteraceae	Forb							3	−5	0.63
Erigeron nitidus	Asteraceae	Forb	2	+1	0.50	4	+1	0.25			
Euphrasia alsa	Scrophulariaceae	Forb				2	0	0.00			
Euphrasia collina subsp. *diversicolor*	Scrophulariaceae	Forb				3	+1	0.33	NR	−2	1.00
Ewartia nubigena	Asteraceae	Forb	4	0	0.40	3	+1	0.75	NR	−1	1.00
Garanium potentilloides	Geraniaceae	Forb									
Grevillea australis	Proteaceae	Shrub							NR	−1	1.00
Hypochoeris radicata[a]	Asteraceae	Forb									

Table 4 continued

Species	Family	Life form	Clarke 1			Clarke 2			Clarke 3		
			Frequency	Change +/−	T_{sp}	Frequency	Change +/−	T_{sp}	Frequency	Change +/−	T_{sp}
Kunzea mueleri	Myrtaceae	Shrub									
Leucopogon montanus	Epacridaceae	Shrub									
Luzula acutifolia subsp. *nana*	Juncaceae	Graminoid									
Luzula alpestris	Juncaceae	Graminoid							2	NEW	1.00
Luzula australasica subsp. *dura*	Juncaceae	Graminoid	5	NEW	1.00	10	NEW	1.00			
Luzula novae-cambriae	Juncaceae	Graminoid							1	NEW	1.00
Luzula sp.	Juncaceae	Graminoid	NR	−3	1.00	NR	−8	1.00	NR	−6	1.00
Lycopodium fastigatum	Lycopodiaceae	Moss					0				
Melicytus sp.	Violaceae	Shrub							2	−2	0.50
Microseris lanceolata	Asteraceae	Forb	9	0	0.00	5	−1	0.17	NR	−3	1.00
Oreomyrrhis eriopoda	Apiaceae	Forb				4	−1	0.20	2	−4	0.67
Pentachondra pumila	Epacridaceae	Shrub				6	−2	0.25			
Phebalium ovatifolium	Rutaceae	Shrub							4	0	0.00
Pimelea alpina	Thymelaeaceae	Shrub				4	0	0.00	6	−1	0.14
Plantago euryphylla	Plantaginaceae	Forb							NR	−1	1.00
Poa sp.	Poaceae	Graminoid	16	0	0.00	16	0	0.00	16	0	0.00
Podolepis robusta	Asteraceae	Forb									
Prasophyllum alpestre	Orchidaceae	Geophyte				1	0	0.00	5	+4	0.80
Prasophyllum sp.	Orchidaceae	Geophyte				NR	−3	1.00			
Prasophyllum tadgellianum	Orchidaceae	Geophyte							2	+1	0.50
Prostanthera cuneata	Lamiaceae	Shrub									
Ranunculus graniticola	Ranunculaceae	Forb							4	+1	0.60
Ranunculus gunnianus	Ranunculaceae	Forb							1	0	0.00

Table 4 continued

Species	Family	Life form	Clarke 1			Clarke 2			Clarke 3		
			Frequency	Change +/−	T_{sp}	Frequency	Change +/−	T_{sp}	Frequency	Change +/−	T_{sp}
Ranunculus muelleri	Ranunculaceae	Forb	NR	−1	1.00	1	−2	0.67			
Rytidosperma nudiflorum	Poaceae	Graminoid							14	+1	0.20
Scleranthus biflorus	Caryophyllaceae	Forb	NR	−2	1.00				NR	−1	1.00
Scleranthus singuliflorus	Caryophyllaceae	Forb	2	+1	0.50	1	−4	1.00	2		0.67
Trisetm spicatum subsp. *australiense*	Poaceae	Grass	12	+3	0.25	6	+1	0.17	9	−3	0.25
Unicinia sp.	Cyperaceae	Graminoid	NR	−2	1.00	NR	−3	1.00			
Viola betonicifolia subsp. *betonicifolia*	Violaceae	Forb							8	−1	0.45

Species	Family	Life form	Clarke 4			Clarke 1–4		
			Frequency	Change +/−	T_{sp}	Frequency	Change +/−	T_{sp}
Acctosella vulgaris[a]	Polygonaceae	Forb	5	+2	0.40	15	0	0.50
Agrostis sp.	Poaceae	Graminoid	10	NEW	1.00	35	+34	0.97
Asperula gunnii	Rubiaceae	Forb	10	+2	0.36	15	+2	0.35
Brachyscome spathutulata subsp. *spathutulata*	Asteraceae	Forb	6	−1	0.70	9	0	0.62
Carex breviculmis	Cyperaceae	Graminoid	5	NEW	1.00	46	+44	0.98
Carex hebes	Cyperaceae	Graminoid	9	−4	0.53	21	−36	0.74
Celmisia costiniana	Asteraceae	Forb	13	+1	0.08	40	−5	0.15
Chionogentias muelleriana subsp. *alpestris*	Gentianaceae	Forb	NR	−2	1.00	5	−2	0.50
Craspedia costiniana	Asteraceae	Forb	11	NEW	1.00	40	+10	0.41
Craspedia maxgrayi	Asteraceae	Forb	NR	−1	1.00	5	0	0.33
Craspedia sp. B	Asteraceae	Forb	NR	−7	1.00	NR	−15	1.00
Empodisma minus	Restionaceae	Shrub	1	0	0.00	8	−1	0.11
Epacris microphylla	Epacridaceae	Shrub	7	+1	0.14	22	+1	0.05

Table 4 continued

Species	Family	Life form	Clarke 4			Clarke 1–4		
			Frequency	Change +/−	T_{sp}	Frequency	Change +/−	T_{sp}
Erigeron bellidioides	Asteraceae	Forb	2	−1	0.75	5	−6	0.67
Erigeron nitidus	Asteraceae	Forb	4	0	0.40	10	+2	0.36
Euphrasia alsa	Scrophulariaceae	Forb				2	0	0.00
Euphrasia collina subsp. *diversicolor*	Scrophulariaceae	Forb	NR	−3	1.00	3	−4	0.75
Ewartia nubigena	Asteraceae	Forb	NR	−1	1.00	7	−1	0.64
Garanium potentilloides	Geraniaceae	Forb	1	NEW	1.00	1	NEW	1.00
Grevillea australis	Proteaceae	Shrub	6	+2	0.57	6	+1	0.63
Hypochoeris radicata[a]	Asteraceae	Forb	NR	−1	1.00	NR	−1	1.00
Kunzea mueleri	Myrtaceae	Shrub	10	0	0.00	10	0	0.00
Leucopogon montanus	Epacridaceae	Shrub	4	+2	0.50	4	+2	0.50
Luzula acutifolia subsp. *nana*	Juncaceae	Graminoid	NR	−1	1.00	NR	−1	1.00
Luzula alpestris	Juncaceae	Graminoid	5	NEW	1.00	7	NEW	1.00
Luzula australasica subsp. *dura*	Juncaceae	Graminoid				15	NEW	1.00
Luzula novae-cambriae	Juncaceae	Graminoid				1	NEW	1.00
Luzula sp.	Juncaceae	Graminoid	NR	−5	1.00	NR	−22	1.00
Lycopodium fastigatum	Lycopodiaceae	Moss	NR	−2	1.00	NR	−2	1.00
Melicytus sp.	Violaceae	Shrub	1	NEW	1.00	3	−1	0.60
Microseris lanceolata	Asteraceae	Forb	4	−2	0.33	18	−6	0.25
Oreomyrrhis eriopoda	Apiaceae	Forb	4	0	0.00	10	−5	0.33
Pentachondra pumila	Epacridaceae	Shrub				6	−2	0.25
Phebalium ovatifolium	Rutaceae	Shrub				4	0	0.00
Pimelea alpina	Thymelaeaceae	Shrub	3	−2	0.40	13	−3	0.19
Plantago euryphylla	Plantaginaceae	Forb				NR	−1	1.00
Poa sp.	Poaceae	Graminoid	16	0	0.00	64	0	0.00

Table 4 continued

Species	Family	Life form	Clarke 4			Clarke 1–4		
			Frequency	Change +/−	T_{sp}	Frequency	Change +/−	T_{sp}
Podolepis robusta	Asteraceae	Forb	NR	−1	1.00	NR	−1	1.00
Prasophyllum alpestre	Orchidaceae	Geophyte				6	+4	0.67
Prasophyllum sp.	Orchidaceae	Geophyte	NR	−1	1.00	NR	−4	1.00
Prasophyllum tadgellianum	Orchidaceae	Geophyte	2	+1	0.50	4	+2	0.50
Prostanthera cuneata	Lamiaceae	Shrub	4	0	0.00	4	0	0.00
Ranunculus graniticola	Ranunculaceae	Forb				4	+1	0.60
Ranunculus gunnianus	Ranunculaceae	Forb				1	0	0.00
Ranunculus muelleri	Ranunculaceae	Forb				1	−3	0.75
Rytidosperma nudiflorum	Poaceae	Graminoid	1	NEW	1.00	15	+2	0.25
Scleranthus biflorus	Caryophyllaceae	Forb	1	0	0.00	1	−3	0.75
Scleranthus singuliflorus	Caryophyllaceae	Forb				5	−3	0.82
Trisetm spicatum subsp. *australiense*	Poaceae	Grass	1	−1	0.50	28	0	0.25
Unicinia sp.	Cyperaceae	Graminoid				NR	−5	1.00
Viola betonicifolia subsp. *betonicifolia*	Violaceae	Forb				8	−1	0.45

$N = 16$ at each summit. The highest frequency possible for each species is 16

NEW new species to quadrats in 2011, *NR* not recorded in 2011

[a] Exotic species

Erschbamer et al. 2011). The magnitude of the species richness increase on a single summit (up to 17 new species not previously recorded in 2004) is within the range of increases reported from Europe (Holzinger et al. 2008), however, future surveys of the summits at Mt Clarke will reveal whether these are merely short-term fluctuations or part of longer-term trends (Erschbamer et al. 2011). The largest changes (mostly increases) in species richness were at the lower mountain sections (10 m SAS), and moderate changes occurred at the whole of summit scale (5 + 10 m SAS), where the observed changes across summits equate to an increase of almost one extra species per year, taking into account species absences. This is in line with recent findings from Europe where, at the continent scale, Gottfried et al. (2012) report an increase in species numbers and abundance of species that predominantly grow at lower elevation mountain summits, in response to climate warming. In contrast, the observed change in species richness at the very top of the Australian summits (the 5 m SAS) was approximately 0.2 species per year. At the whole summit scale, including data across all summits, total mean species richness in 2011 had increased by about 12 % since 2004; whereas at the very top of each summit, changes were more subtle and total mean species richness across all summits had only increased by 4.4 %. Climate variables measured on site did not change significantly over this time and so these observed changes in species richness are more likely a result of species responses to longer-term increases in temperatures, declines in snowpack (Green and Pickering 2009), or possibly positive biotic interactions (Callaway et al. 2002; Venn et al. 2009) facilitating the co-existence of many species on the summits, whereby lower temperatures on summits (compared to lower mountain environments) are negated by individuals sheltering next to one another. Continued warming trends may, however, alter or reverse such plant–plant interactions leading to an increase of negative (competitive) interactions (Venn et al. 2009) and stagnating species richness. The recent, large increases in regional precipitation may have resulted in a pulse of recruitment (Venn and Morgan 2009), but are unlikely to result in large changes in species migration and subsequent species richness at the summits within the same year/growing season. At the 1 m^2 quadrat scale, changes in total species richness between 2004 and 2011 were subtle, and with no appreciable mean net increase or decrease in species numbers across summits Clarke 1–4. Over future sampling intervals of 5–7 years, appreciable changes to species richness are likely to be at the larger spatial scales at these summits, not just because of the larger area and therefore a greater chance of encountering more species, but because many high elevation species in Australia are large themselves (broad leaved herbs with leaves up 20 cm, and shrubs with diameters up to 1.5 m). Whereas at smaller scales, the 1 m^2 quadrat level, total species richness may be limited by the physical size of individual plants, and smaller changes over time are expected through species losses and gains countering each other.

Turnover dynamics between 2004 and 2011

The high proportion of perennial species among the Australian alpine flora (Costin et al. 2000) and the relatively tall and closed vegetation structure, which may act to reduce the availability of micro-habitats for colonisers, are the most likely explanations for the lack of pattern and the overall moderate values of vegetation turnover within the larger SAS areas. Slow growing perennials may also integrate climatic changes that occur over longer periods better than short-lived species. Although there has been much variation in the annual snow amount (metre-days), the general trend is an overall decline with a 30 % reduction over the past five decades (Green and Pickering, 2009; Green, 2010) with the date of snow melt also having advanced by 2.75 days per decade (Green 2010). The downward trend in depth of snow is associated with increasing temperature rather than reduced precipitation (Nicholls 2005). Therefore longer-term increases in temperature and snowpack declines (Green and Pickering 2009) may be key determinants of turnover dynamics in these systems. Recent turnover in European mountain summits has also been moderate in magnitude with, on average, increasing species richness in temperate and boreal regions, but strikingly in stagnation or decreases on the Mediterranean mountains; the latter consisting of very open vegetation where water availability in summer is an important factor (Pauli et al. 2012). Climatic water balance also appears to be the key driver of species' (often downhill) niche-tracking on Californian summits, despite twentieth century warming (Crimmins et al. 2011).

In the Snowy Mountains, the tenacity of the grass tussocks, larger forbs and shrubs may prevent many dispersing species from entering the community through the effects of competition (Venn et al. 2009; Venn et al. 2011). Additionally, attached leaf litter surrounding *Poa* tussocks and many Asteraceae forbs and ground litter from shrubs effectively insulate soils and meristematic regions close to the ground, to the benefit of the individual, whilst preventing new seedlings from establishing (Dullinger et al. 2003; Körner 2003; Buckeridge et al. 2010; Myers-Smith et al. 2011). However, at the higher summits, facilitative (positive) effects of the standing vegetation are more likely to play a role in sheltering and protecting new species from the harsher climatic conditions at high altitudes (Callaway 1995; Callaway et al. 2002), and potentially creating establishment opportunities for typically lower altitude species.

Naturally long-lived species will show little turnover over short time periods, as demonstrated by many of the alpine shrubs in this study. Shrub population dynamics may also offer additional insights into future vegetation change, given the differential growth rates between species and recognised expansion with respect to land-use legacies and climate warming in this region (McDougall 2003; Scherrer 2003; Scherrer and Pickering 2005). Surprisingly however, the total number of shrub species increased over the study period at the whole summit scale, with marked increases occurring at Clarke 4 (Fig. 2). Additionally, three individuals of *Podocarpus lawrencei* (Podocarpaceae), a distinctive, slow growing and extremely long-lived shrub species (up to 400 year) (McDougall et al. 2012), were recorded for the first time in 2011 within the 5 + 10 m SAS at Clarke 3 and 5, thereby challenging the idea that shrub species are mostly static in the landscape and regenerate clonally, whereas some species have the potential to migrate to suitable habitats faster than previously thought. At the quadrat scale, turnover in most shrub species was small, although a new occurrence of *Melicytus* sp. was recorded at Clarke 4. Over time, new shrub occurrences combined with the obvious decaying branches of senescing shrubs, will act as indicators of directional and/or cyclical vegetation change. Shrubs may therefore demonstrate the longer-term effects of climatic change, whereas many graminoid and forb species may be too short-lived or decay too quickly to leave evidence of their establishment/decline within a seven-year sampling interval.

The largest declines in species richness were among forb species within the top 5 m SAS at some of the lower sites, Clarke 3 and Clarke 5 (declines of 18 and 25 % respectively). None of the species which contributed to these particular declines were locally endemic and they were all present in either the lower SAS on those summits or at other sites. Until species are repeatedly absent from future re-surveys, perhaps as a result of climatic changes affecting the summits differentially according to altitude, local extinctions of the summit flora are unlikely in the short-term. Longer-term predictions however, should include measures of population dynamics and identification of species ranges that are still occupied through species resilience, but which in future may become climatically unsuitable (Dullinger et al. 2012) and disappear once certain thresholds are exceeded, creating an extinction debt.

Individual species losses from quadrats did not contribute to the species absence from any of the summits. Species turnover and apparent losses at small spatial scales may also indicate identification issues surrounding certain genera. Whilst the data indicate substantial declines and losses of several species, substantial increases of closely related species occurred concurrently (Table 2). This was particularly evident in genera such as *Carex*, *Luzula* and *Prasophyllum* where accurately identifying individuals to species was at times impossible in the field because flowering material was not available. Additionally, on several occasions in 2011 the closely related and difficult to distinguish species did occur together in the same plot. The values presented here are therefore conservative in terms of changes in species numbers; if several individuals of the difficult to distinguish species were together in the same plot and could not be identified further, they were classed as one taxonomic unit. Every effort was made accurately to identify, record and match species data between the sampling years. Subsequent re-surveys will determine whether complete species turnover in 2011 were genuine losses or gains, or indeed misidentifications.

Factors governing species richness change at Mt Clarke

The inter-annual variability in climate in the Snowy Mountains over the period of this study does not reflect the longer-term trends in climate warming for the region; increasing temperatures (Nicholls 2005) and around a 30 % reduction in snow (metre days) over the past five decades in combination with snowmelt having advanced by 2.75 days per decade (Green and Pickering 2009; Green 2010).The predicted effects of long term climate change for the region, however, include a lengthening of the growing season, increased end of season variability in snow cover and an increase in mean minimum temperatures (Hennessey et al. 2003), all of which could potentially make higher altitude habitats more suitable for typically lower altitude species (Venn and Morgan 2005). The overall general increase in species richness across the summits recorded during this re-survey and the marked increase in shrub and graminoid species, indicate that the vegetation may be responding to one or more environmental factors present at these sites. However, patterns in species richness and co-existence are determined by a host of interacting factors including rainfall, microsite availability (Zobel et al. 2000; Venn and Morgan 2009), species interactions (positive and negative) (Choler et al. 2001; Cavieres et al. 2006; Venn et al. 2009) and the dispersal and recruitment potential of species in the regional species pool (Dirnböck and Dullinger 2004), a thorough discussion of which is beyond the scope of this study. Bear in mind that species and life forms will respond to environmental stimuli and predicted changes across the altitudinal gradient of sites differently. For example, a large component of the herbaceous vegetation across the study sites at Mt Clarke are Asteraceae forbs, which in general have reproductive and dispersal traits synonymous with successful colonisation (Venn 2007; Venn and Morgan 2010). However, only the taller, mat-forming and more vigorous genera of this family (*Craspedia*, *Celmisia*, *Podolepis*) are predicted to be competitive with environmental change (Venn et al. 2011), although colonisation may be slow. Contrary to expectation, these genera did not show clear patterns of increases at any spatial scale between 2004 and 2011, indicating that perhaps longer intervals between samples may be needed to detect change and that even widespread, common species with relatively well understood biology might not demonstrate directional change or migration predictably. Overall, the specific environmental factors that may determine species enrichment or species decline across the altitudinal gradient of sites at Mt Clarke remain undetermined.

Conclusions

Species richness changes over short time scales may not reflect the longer-term trends or be indicative of longer-term trends in climate. Here, the variation in climate between 2004 and

2011 showed no directional change for any parameters except recent rainfall and the increases/decreases in species richness across the summits were not apparently related to short-term variation in climate. Climatic variation over the past few decades is therefore more likely to explain changes in species richness across the sites. Over the short-term, changes in species richness could not be predicted from site altitude, but increases in species richness, particularly consisting of shrub and graminoid species were more pronounced at the lower altitudes. These results suggest shrub migration onto the lower SAS of the summits is underway, whereas dramatic changes to the uppermost summit vegetation at these sites seems unlikely in the short term. Given that the local lower elevation species pool is dominated by expanding shrubby vegetation, over longer time periods shrubs are expected to continue to increase in abundance at the lower summit sites, potentially causing decreases in overall species richness at those sites. Results from this re-survey do not suggest that Kosciuszko endemic species are any more or less threatened by the short-term variation in climate than the more widespread species, however, future surveys will reveal whether these species become more marginalised or continue to turn over at moderate rates across the gradient of sites at Mt Clarke.

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Appendix

See Tables 5 and 6.

Table 5 Spatial scales and statistics used to compare species richness between 2004 and 2011

Sampling scale	Total area across summits (m^2)	Mean area per summit (m^2)	Number of replicates for test	Statistical tests
5 m SAS	16,602	3,220	20 20 4 5	Linear regressions between mean climatic parameters and species richness One-way ANCOVA of SR change and climate parameters, altitude as a covariate Paired *t* tests Linear regressions between altitude and species richness change (+/−)
10 m SAS	41,912	8,382	20 20	Linear regressions between mean climatic parameters and species richness One-way ANCOVA of SR change and climate parameters, altitude as a covariate Paired *t* tests
5 + 10 m SAS	57,713	11,543	5	Linear regressions between altitude and species richness change (+/−)
1 m^2 quadrats	64	1	16 4	Paired *t* tests Linear regressions between altitude and species richness change (+/−)

Replicates sometimes included the aspects within SASs from sites depending on the statistical test used

Table 6 Results for the statistical tests performed on species richness data comparing differences between 2004 and 2011 at various spatial scales

Site/sampling scale/data	Statistical test	n	Results		
			Mean ± 1 SE		Statistics
			2004	2011	
Clarke 1/5 m SAS	Paired t test	4	21.75 ± 1.43	21.25 ± 0.96	$t = 0.26$, $P = 0.83$
Clarke 2/5 m SAS	Paired t test	4	22.75 ± 2.16	23.00 ± 3.20	$t = -0.14$, $P = 0.9$
Clarke 3/5 m SAS	Paired t test	4	31.25 ± 2.51	31.75 ± 2.48	$t = -0.2$, $P = 0.836$
Clarke 4/5 m SAS	Paired t test	4	28.75 ± 0.74	31.00 ± 0.71	$t = -2.18$, $P = 0.12$
Clarke 5/5 m SAS	Paired t test	4	31.50 ± 1.44	30.25 ± 1.34	$t = 0.95$, $P = 0.41$
Clarke 1/10 m SAS	Paired t test	4	21.00 ± 1.54	25.00 ± 2.18	$t = -1.46$, $P = 0.24$
Clarke 2/10 m SAS	Paired t test	4	25.75 ± 1.85	28.50 ± 1.35	$t = -2.20$, $P = 0.11$
Clarke 3/10 m SAS	Paired t test	4	30.50 ± 1.03	34.50 ± 2.19	$t = -1.12$, $P = 0.34$
Clarke 4/10 m SAS	Paired t test	4	23.25 ± 2.27	34.75 ± 1.47	$t = -4.00$, $P = 0.03^{a}$
Clarke 5/10 m SAS	Paired t test	4	28.50 ± 1.60	32.25 ± 2.30	$t = -3.38$, $P = 0.04^{a}$
Clarke 1/1 m^2 quadrats	Paired t test	16	6.26 ± 0.32	6.66 ± 0.48	$t = -1.38$, $P = 0.18$
Clarke 2/1 m^2 quadrats	Paired t test	16	8.94 ± 1.19	8.75 ± 0.95	$t = 0.42$, $P = 0.68$
Clarke 3/1 m^2 quadrats	Paired t test	16	9.56 ± 0.86	8.43 ± 0.89	$t = 1.62$, $P = 0.13$
Clarke 4/1 m^2 quadrats	Paired t test	16	8.56 ± 0.88	9.12 ± 0.47	$t = -0.75$, $P = 0.46$
All sites/5 m SAS/SR change	Linear regression against altitude	5			$R^2 = 0.09$, $F = 0.32$, $P = 0.61$
All sites/10 m SAS/SR change	Linear regression against altitude	5			$R^2 = 0.31$, $F = 1.33$, $P = 0.33$
All sites/5 + 10 m SAS/SR change	Linear regression against altitude	5			$R^2 = 0.01$, $F = 0.04$, $P = 0.86$
All sites/1 m^2 quadrats/SR change	Linear regression against altitude	4			$R^2 = 0.52$, $F = 2.14$, $P = 0.28$
All sites/5 m SAS/SR 2011	Linear regression against temp. means	20			$R^2 = 0.23$, $F = 5.93$, $P = 0.03^{a}$
All sites/10 m SAS/SR 2011	Linear regression against temp. means	20			$R^2 = 0.42$, $F = 12.89$, $P = 0.002^{a}$
All sites/5 m SAS/SR 2011	Linear regression against max. temp. means	20			$R^2 = 0.00$, $F = 0.04$, $P = 0.84$
All sites/10 m SAS/SR 2011	Linear regression against max. temp. means	20			$R^2 = 0.12$, $F = 2.46$, $P = 0.13$
All sites/5 m SAS/SR 2011	Linear regression against min. temp. means	20			$R^2 = 0.18$, $F = 3.99$, $P = 0.06$
All sites/10 m SAS/SR 2011	Linear regression against min. temp. means	20			$R^2 = 0.09$, $F = 1.94$, $P = 0.18$

Table 6 continued

Site/sampling scale/data	Statistical test	*n*	Results		
			Mean ± 1 SE		Statistics
			2004	2011	
All sites/5 m SAS/SR 2011	Linear regression against mean season days	20			$R^2 = 0.09$, $F = 1.89$, $P = 0.18$
All sites/10 m SAS/SR 2011	Linear regression against mean season days	20			$R^2 = 0.18$, $F = 3.93$, $P = 0.06$
All sites/5 m SAS/SR 2011	Linear regression against mean thaw day	20			$R^2 = 0.01$, $F = 0.18$, $P = 0.67$
All sites/10 m SAS/SR 2011	Linear regression against mean thaw day	20			$R^2 = 0.01$, $F = 0.24$, $P = 0.63$
All sites/5 m SAS/SR change	ANCOVA temp. means (altitude)	20			df = 1, $F = 0.00$, $P = 0.96$
All sites/5 m SAS/SR change	ANCOVA max. temp. means (altitude)	20			df = 1, $F = 0.04$, $P = 0.96$
All sites/5 m SAS/SR change	ANCOVA min. temp. means (altitude)	20			df = 1, $F = 0.03$, $P = 0.86$
All sites/5 m SAS/SR change	ANCO VA mean season days (altitude)	20			df = 1, $F = 0.00$, $P = 0.98$
All sites/5 m SAS/SR change	ANCO VA mean thaw day (altitude)	20			df = 1, $F = 0.07$, $P = 0.79$
All sites/10 m SAS/SR change	ANCOVA temp. means (altitude)	20			df = 1, $F = 2.10$, $P = 0.17$
All sites/10 m SAS/SR change	ANCOVA max. temp. means (altitude)	20			df = 1, $F = 0.33$, $P = 0.57$
All sites/10 m SAS/SR change	ANCOVA min. temp. means (altitude)	20			df = 1, $F = 0.02$, $P = 0.90$
All sites/10 m SAS/SR change	ANCO VA mean season days (altitude)	20			df = 1, $F = 2.49$, $P = 0.14$
All sites/10 m SAS/SR change	ANCO VA mean thaw day (altitude)	20			df = 1, $F = 0.04$, $P = 0.85$

Results of linear regressions between the differences (species richness change +/−) between years with altitude and climate parameters. ANCOVA tests were used to determine separately whether these climate parameters explained change in species richness using altitude as a covariate

[a] Statistically significant result ($P < 0.05$)

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