Long-term Vegetation Changes on Alpine Summits in Response to Global Drivers of Change

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Statement of Authorship and Ethics

Except where reference is made in the text of the thesis, this thesis contains no material published elsewhere or extracted in whole or in part from a thesis submitted for the award of any other degree or diploma. No other person's work has been used without due acknowledgment in the main text of the thesis. This thesis has not been submitted for the award of any degree or diploma in any other tertiary institution.

None of the research undertaken in connection with this thesis required approval by a University Ethics Committee. Permission was granted to conduct research under a Parks Victoria Access Agreement and the Flora and Fauna Guarantee Act 1988 (permit no.: 10010228).

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Iris Tara Hickman

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Acknowledgement of Country

I acknowledge the traditional owners of the land where I live and on which I conducted the fieldwork for this thesis. I wish to acknowledge the Wurundjeri people, the traditional custodians of Melbourne, where I live and where the La Trobe University Bundoora campus is located. The Daung wurrung, Dhudhuroa, Gunaikurnai, Taungurung, Waywurru and Jaitmatang people are the traditional custodians of the Victorian Alps, where this study was conducted. I pay my respects to their Elders, past and present, and their enduring connection to the land and plants that I worked on.

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Abstract

Contemporary climate warming and altered disturbance regimes are predicted to drive the expansion of warm-adapted species in alpine ecosystems worldwide, posing a significant threat to alpine endemic plants. Most evidence for plant distribution shifts comes from revisiting sites, but such studies are relatively scarce in the southern hemisphere, particularly in the marginal alpine ecosystems of the Australian Alps. This thesis aims to understand the responses of Australian alpine vegetation on summit areas to global change drivers over an 18-year period.

The studies in this thesis used a revisitation approach on 14 alpine summits where permanent plots were established in 2004 and 2012 to investigate long-term vegetation dynamics. Resurveys were completed in 2012, 2017 and 2022. Plant functional traits were utilised to assess species responses to varying abiotic conditions. However, 11 summits were burnt in the 2007 fires after the first survey. This thesis aimed to assess summit vegetation floristic changes over time (Chapter 2) and broad vegetation changes in response to global drivers of change (Chapter 3). It also examined meso-topographically driven microhabitats (Chapter 4), which may contribute to alpine species' resistance to climate change by providing local micro-refugia on summits.

This thesis offers invaluable insights and addresses critical knowledge gaps concerning the response of Australian alpine summit vegetation to global drivers of change. Recent rapid changes, including regional warming and altered fire regimes, have diversified summit vegetation responses. The longer growing seasons increased shrub and graminoid cover, while fire temporally boosted forb and graminoid cover due to post-fire succession within the local species pool. There were elevation-dependent changes in cover and composition: higher elevations were dominated by forbs and had the most pronounced changes in composition. Interestingly, there was little evidence of new species migrating upslope. Hence, alpine summits may exhibit resilience by limiting novel species establishment, yet future changes are likely without effective climate action, compounded by invasive species, fires, and recreational impacts.

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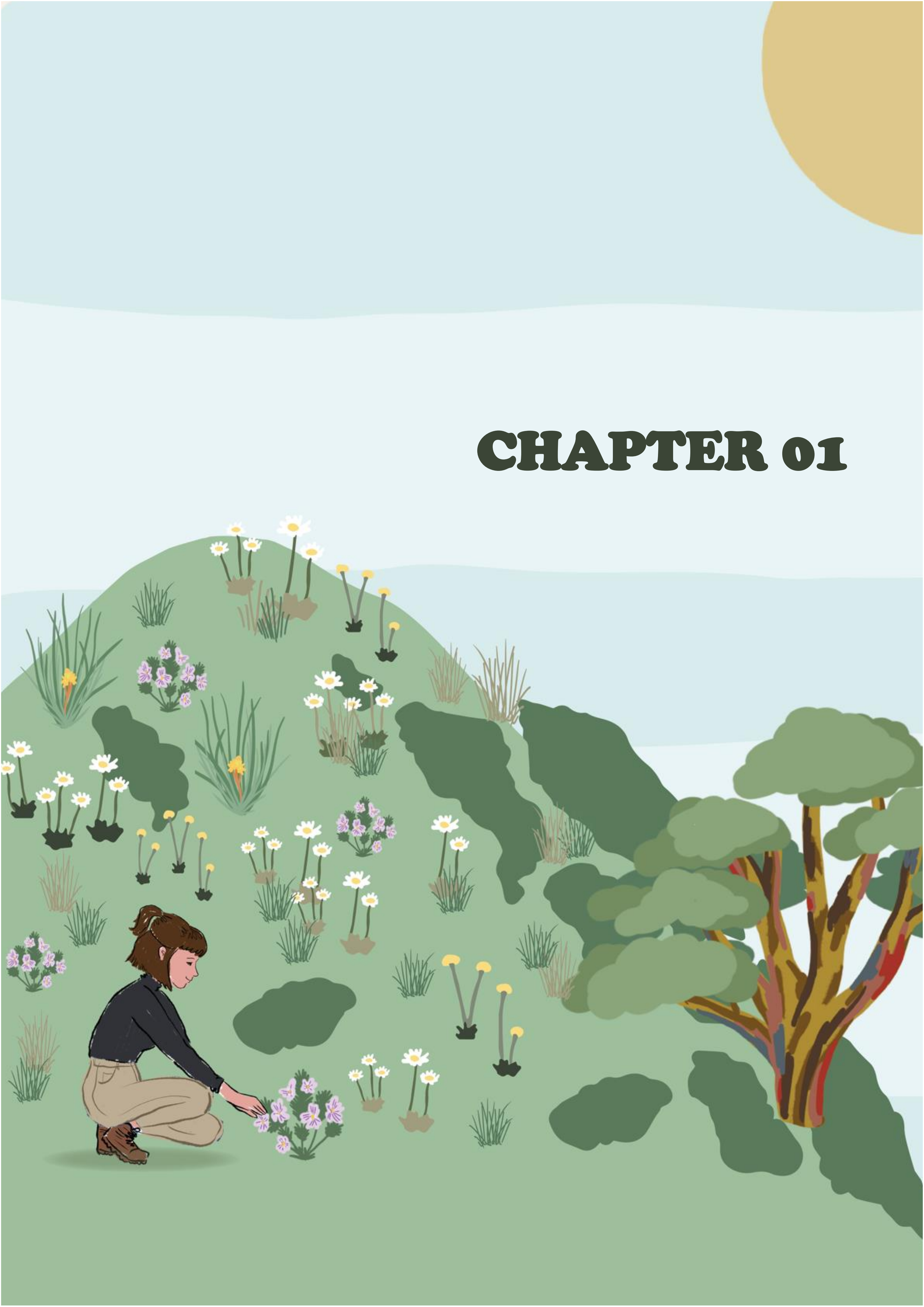
CHAPTER 01



Chapter 1: Introduction

1.1 Alpine ecosystems

Globally, alpine regions occupy only 2.6% of terrestrial areas (excluding Antarctica) (Körner 2003). Alpine vegetation is characterised by strict climatic parameters, steep environmental gradients, and geographical restrictions (Körner 2003; Testolin *et al.* 2020). Furthermore, the interaction between topography, solar radiation, wind, plant stature, snow accumulation and water distribution create diverse meso- and micro-climates (Körner and Hiltbrunner 2021). These strong and variable environmental filters influence community assembly, leading to sharp transitions between vegetation types over relatively small spatial scales (Körner 2003; Venn and Green 2018). This high geodiversity drives mosaics of alpine vegetation types that support high biodiversity of specialised endemics with the capacity for physiological adaptation to the associated climatic features (Figure **1.1**, Körner 2003; Mcdougall and Walsh 2007; Niittynen *et al.* 2020).

Figure 1.1 An example of the high number and diversity of endemic species in high mountain environments in an alpine herbfield at Kosciuszko National Park, Australia.

1.2 Threats to alpine environments

Alpine environments are increasingly subject to anthropogenic impacts and are considered one of the most sensitive ecosystems globally to climate change (Gottfried *et al.* 2012). The most significant threats to alpine vegetation include climate warming, invasive species, and land use changes, such as cattle grazing management and commercial tourism (Venn *et al.* 2017). Climate-related pressures are expected to intensify with climate warming, more extreme weather events, decreased rainfall and snow cover, and a decline in extremely low temperatures (Hennessy *et al.* 2008; Doherty *et al.* 2024). As a result, the principal ecosystem abiotic drivers that dictate alpine community assembly will be modified substantially (Venn *et al.* 2011; Williams *et al.* 2015). This is predicted to profoundly impact alpine biodiversity, community composition and structure, and ecosystem function more broadly (Elmendorf *et al.* 2012).

1.3 Effects of climate change on alpine mountain summit vegetation

Contemporary climate change is particularly relevant for mountain summit alpine vegetation. Alpine species already living at the extreme edge of their tolerances (such as those located on mountain summits) have little ability to track their climatic niche upslope and are predicted to be very sensitive to changes in climate (Grabherr *et al.* 1994; Theurillat and Guisan 2001). Additionally, more frequent heatwaves and a longer growing season will increase abiotic stress, as well as competition from the expansion and upslope migration of native and exotic invasive, more warm-adapted species (Gottfried *et al.* 2012), ultimately increasing the likelihood of local species extinction (Kammer *et al.* 2007; Pauli *et al.* 2012; Stöckli *et al.* 2012; Steinbauer *et al.* 2018). The global consensus is that climate change will reduce the extent, frequency, and distribution of alpine specialists and lead to the expansion of generalist species (Dirnböck *et al.* 2011).

Projected changes in climate may not be experienced evenly over alpine landscapes. This is because, in alpine environments, the variation in topography over small spatial scales creates a mosaic of microhabitats that vary in their microclimatic conditions (Figure **1.2** Scherrer and Korner 2009; Körner and Hiltbrunner 2021). The topographic heterogeneity of alpine areas can induce differential responses to regional climate change at metre-scale resolutions, analogous to the variations observed in species responses across broader spatial and temporal dimensions (Dobrowski 2011; Scherrer and Körner 2011; Suggitt *et al.* 2018; Oldfather *et al.* 2024), potentially influencing the direction and rate of local community shifts in response to climate warming. Consequently, to understand alpine plant life, it is essential to consider the diverse living conditions created by the interplay of geodiversity, plant height, solar radiation, and wind (Körner and Hiltbrunner 2021).

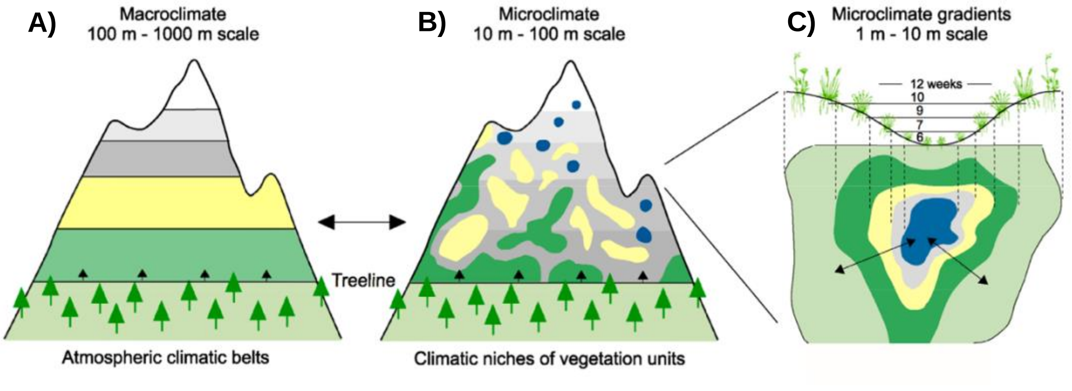


Figure 1.2 Alpine vegetation patterns are created by variations in topography (microclimate) that are not captured by air temperatures from weather stations (macroclimate) as described by Korner & Hiltbrunner (2021). A) The mountain macroclimate, which is driven by atmospheric climate belts. B) The mosaics of thermal habitats provided by the steep climatic gradients at fine spatial scales, C) with a zoomed-in example. Large differences in the growing season can occur across exposure gradients (e.g., North versus South aspect).

1.4 Australian alpine environments

Like their overseas counterparts, Australian alpine ecosystems have distinctive plant communities adapted to cold conditions. Alpine vegetation covers approximately 0.2% of the Australian continent and is listed on the Australian National Heritage Register under the federal Environment Protection and Biodiversity Conservation Act 1999 (Costin 2000; Australian Government 2023). However, unlike other alpine environments, Australian mainland alpine summits are ancient, typically flat-topped, and comparatively low (the highest point is Mt Kosciuszko, 2228 m) with little topographical relief (**Figure 1.3,** Venn *et al.* 2017). They lack nival zones but have deep, well-developed soils unique to Australia and considered to be of international significance (Costin 1955). The long snow-free periods create a relatively long growing season supporting more productive vegetation than in the northern hemisphere (Costin 2000; Venn *et al.* 2017). Furthermore, lower-elevation mountain communities are at higher risk of the effects of climate warming due to already being at their climatic limits (Theurillat and Guisan 2001). These qualities make the Australian Alps significant locally and internationally, requiring targeted study.

Figure 1.3 Mount Bogong summit (1986 m) is Victoria's highest mountain, showcasing the characteristically topographically flat nature of Australian mountains.

1.5 Climate change in the Australian Alps

The effects of contemporary climate change are evident in the Australian Alps, with higher temperatures and a reduction in snow cover having been recorded (Scherrer and Pickering 2005; Griffin and Hoffmann 2012; Wahren *et al.* 2013; Verrall *et al.* 2023). Temperature changes result from changes in albedo, implying that faster warming in winter might be dominated by a decrease in albedo from declines in natural snowfall and snowpack (Ji *et al.* 2022). Furthermore, alpine regions have experienced increased climate-related disturbance regimes (fire and drought) (Hennessy *et al.* 2008; Doherty *et al.* 2024). Fire was typically thought to be infrequent in alpine areas, occurring once or twice per century, but the past two decades have seen repeated, extensive fires that have burnt most of the Australian Alps (Williams *et al.* 2008; Godfree *et al.* 2021). This is likely to continue; extreme events such as fire and drought are expected to increase in frequency and severity under climate change scenarios (Hennessy *et al.* 2008). The combination of disturbance—defined by its frequency, severity, and extent—with warming temperatures and declining rainfall is expected to affect plant recruitment, growth, and persistence, leading to local extinctions (Fairman *et al.* 2017; Malanson *et al.* 2019; Naccarella *et al.* 2020). This highlights the importance of understanding factors other than climate warming affecting extant species' population dynamics.

The warmer conditions and more extreme events are expected to facilitate the expansion and upslope migration of more warm-adapted species in Australia (Camac *et al.* 2021). Lower elevation species have already been recorded establishing in Australian alpine environments

(Johnston and Pickering 2001; Pickering and Hill 2007; Venn *et al.* 2012, 2014; Pickering *et al.* 2014; Verrall *et al.* 2021). This includes exotic species (Johnston and Pickering 2001; Pickering and Hill 2007), encroachment of native shrubs (Verrall *et al.* 2021) and increased native graminoid cover (Venn *et al.* 2014; Verrall *et al.* 2021). In addition to climate-induced changes, altered fire regimes, i.e. shorter fire return intervals, are expected to facilitate shrub establishment and encroachment by creating bare ground and removing competitors (Wahren *et al.* 2013; Camac *et al.* 2017). Moreover, because shrubs are the most flammable vegetation component in the alps, their encroachment in alpine vegetation will strengthen the feedback between shrubs, warming and fire (shrub-fire feedback summarised in **Figure 1.4**) (Williams *et al.* 2006; Fraser *et al.* 2016; Venn *et al.* 2016; Camac *et al.* 2017). The invasion of woody species into alpine environments could result in biotic homogenisation, which changes the structure and composition of alpine communities (Venn *et al.* 2014; Evangelista *et al.* 2016; Verrall *et al.* 2021).

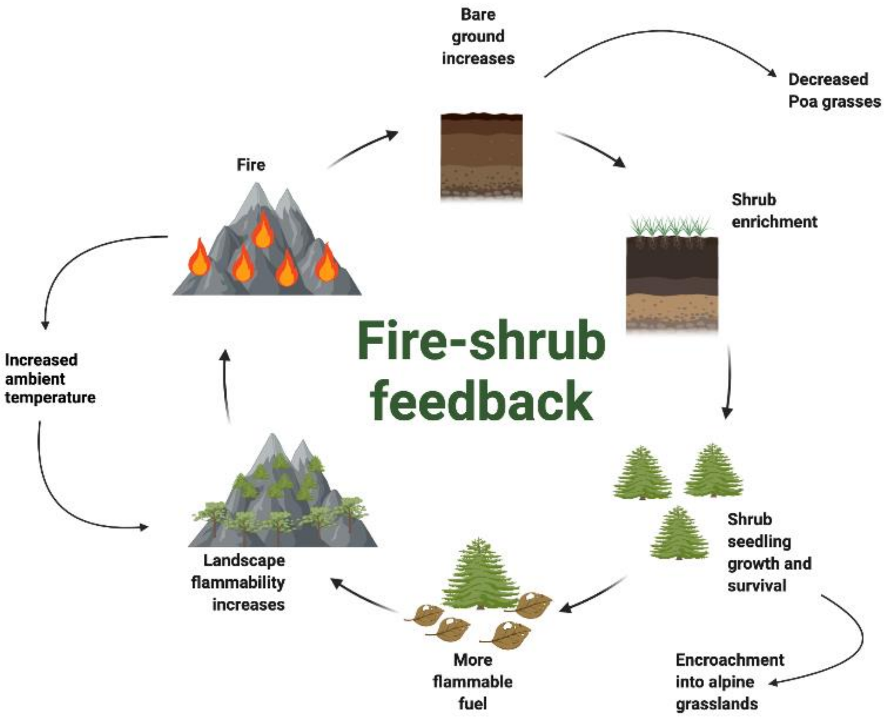


Figure 1.4 The potential fire-shrub feedback cycle on mountains as described by Camac *et al.* (2021). A warmer climate will increase shrub species' growth and cover. Increased fire frequencies will create more bare ground opportunities for obligate shrubs to recruit and establish, which will increase landscape flammability.

1.6 Monitoring change in alpine environments

To understand the processes driving alpine vegetation dynamics, long-term ecological monitoring approaches are required to distinguish natural variability from community changes caused by climate warming (Stöckli *et al.* 2012). Short-term vegetation responses and climate oscillation can conceal long-term dynamics in alpine vegetation (Müller *et al.* 2010). Moreover, time-lag processes influence biotic responses to climate change. Lags can occur due to limitations on a species' ability to disperse and establish, as well as the development of extinction debts (Alexander *et al.* 2018; Camac *et al.* 2021). However, the majority of our understanding of climate-induced alpine vegetation dynamics originates from the northern hemisphere, particularly Europe (Verrall and Pickering 2020). Studies from the southern hemisphere are lacking, including in the marginal alpine ecosystems of the Australian Alps (Verrall and Pickering 2020).

In Australia, predicting species response to climate change is based on data from the resurvey of monitoring sites (e.g. McDougall *et al.* 2005; Hoffmann *et al.* 2010; Venn *et al.* 2012; Wahren *et al.* 2013; Pickering *et al.* 2014; Verrall *et al.* 2021) and field experiments data (e.g. (Wahren *et al.* 2013; Camac *et al.* 2015; Slatyer *et al.* 2022). However, most studies of the impacts of global change on Australian alpine vegetation are typically based on short-term, manipulative experiments (Camac *et al.* 2021), which, by their nature, lack information about the rate of change (Camac *et al.* 2015; Morgan *et al.* 2016), making it difficult to forecast long-term changes and assess the severity the extinction scenarios (Camac *et al.* 2021).

1.7 Aims

This thesis aims to understand the responses of alpine vegetation in summit areas to global change drivers over 18 years in Victoria, Australia. To investigate alpine summit vegetation dynamics, this thesis used two different revisitation approaches on 14 alpine summits (line intercept and floristic quadrats) at permanent plots established between 2004 and 2012 by Venn (2007). Vegetation resurveys were completed in 2012, 2017 and 2022. Plant functional traits were also utilised to assess species responses to varying abiotic conditions. Over the last two decades, seven summits were burnt once (2007), and two summits were burnt three times (2003, 2007 and 2013). Fires in the alps introduce another element to the research, where shorter fire-return intervals are expected to facilitate the encroachment of shrubs into alpine areas.

The specific questions asked in this thesis were:

1. How does summit vegetation composition change over time? (Chapter 2)
2. What are the broad vegetation changes in response to global drivers of change (climate warming, fire, and elevation)? (Chapter 3)
3. How does the variation in microhabitats, driven by differences in topography, contribute to the assembly of alpine summit vegetation communities, and potentially influence their response to climate warming? (Chapter 4)

1.8 Structure of thesis

This thesis consists of three data chapters (Chapters 2-4), framed by an introduction (Chapter 1) and a synthesis (Chapter 5). Data chapters were written as stand-alone manuscripts intended for publication in scientific journals. These three chapters are, therefore, separate but logically connected manuscripts. Consequently, there is repetition between chapters when describing the study region and design. Formatting differs slightly between chapters, reflecting the journal guidelines relevant to each chapter. Since these are co-authored manuscripts, chapters use the term ‘we’ rather than ‘I’. However, the majority of work was completed by the author of this thesis (ITH), including conceptualisation, data collection (2022), undertaking statistical analyses and leading the writing of manuscripts. This project involved the collection of two datasets: a floristic dataset using quadrats and a line intercept dataset. These datasets are used separately in different chapters of this thesis:

- Chapter 2 describes changes in floristic composition over time using the floristic quadrat dataset and is being prepared for submission to the *Journal of Vegetation Science*.
- Chapter 3 investigates broad vegetation changes in response to local drivers of change (fire and warming) using the line intercept dataset. This chapter is currently in press with *Arctic, Antarctic, and Alpine Research*.
- Finally, Chapter 4 uses only the 2022 floristic dataset to examine the importance of microhabitat heterogeneity driven by meso-topography on summits. This chapter is being prepared for submission to the *Australian Journal of Botany*.
- Chapter 5 summarises the findings from each study.

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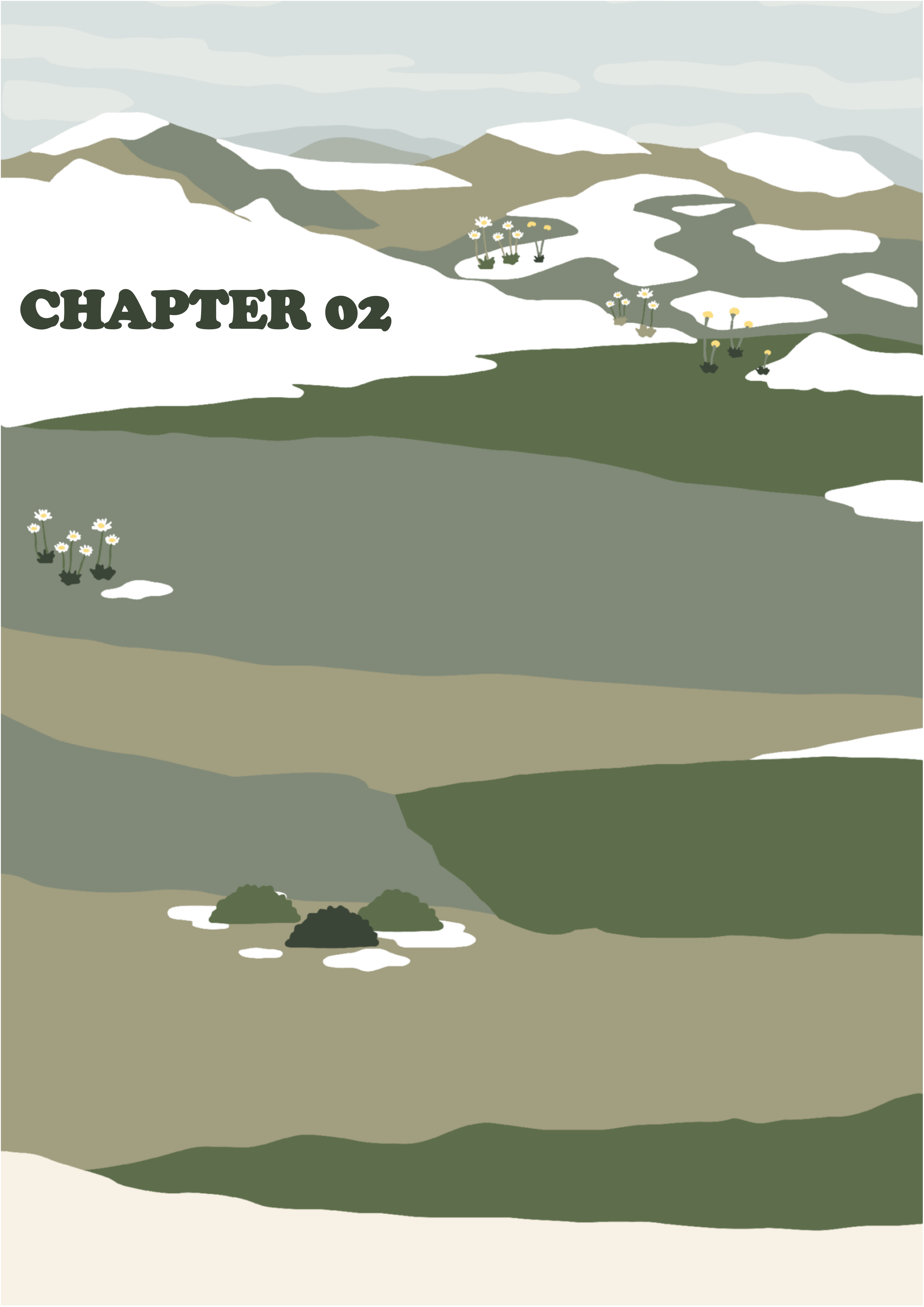
CHAPTER 02



Chapter 2: Alpine summit plant composition dynamics over time

2.1 Details, author contributions and declaration

This chapter consists of a paper that is in preparation for submission to the *Journal of Vegetation Science*, which was co-authored with my supervisor and co-supervisors. The details of this paper are:

Hickman, I.T., Venn, S.E., Williams, R.J., & Morgan, J.W. (in preparation). Plant community shifts in alpine summit vegetation are driven by changes in the abundance of resident species rather than by species turnover. *Journal of Vegetation Science*.

Author contributions for this paper are as follows:

Author	**Contribution**	**Percent contribution**
ITH	conceptualisation, project administration, investigation, data collection (2022), data analysis, writing, reviewing and editing.	90%
JWM	conceptualisation, data collection (2004-2022), project administration, investigation, reviewing and editing.	5%
SEV	conceptualisation, data collection (2004-2022), reviewing and editing.	4%
RJW	conceptualisation, reviewing and editing.	1%

2.2 Paper’s title

Plant community shifts in alpine summit vegetation are driven by changes in the abundance of resident species rather than by species turnover

2.3 Abstract

Questions: Alpine plant species living at the extreme edge of their tolerances (e.g. mountain summits) are predicted to be very sensitive to changes in climate and have limited ability to track their climatic niche upslope. More frequent heatwaves and a longer growing season will increase abiotic stress during the growing season, and competition from the expansion and upslope migration of native and exotic invasive, more warm-adapted species is also likely. This study examines changes in the composition of Australian alpine vegetation over two decades, providing insights into these dynamics in a natural setting.

Location: Victorian Alpine Bioregion, Victoria, Australia.

Methods: This study revisited 14 Australian alpine summits with permanent plots originally established between 2004 and 2012. Vegetation surveys were repeated in 2012, 2017, and 2022. Over this two-decade period, the summits were also impacted by fires.

Results: We found that alpine summits are experiencing directional floristic composition shifts attributed to changes in dominant species within the local species pool. Fire was the key driver of vegetation change on alpine summits due to post-fire successional processes. There were no elevation-dependent changes in composition. However, the highest elevation summit had the most pronounced composition changes. Interestingly, there was little evidence of new species migrating upslope to summits, suggesting time-lag processes may limit species' ability to disperse, migrate, and establish on summits.

Conclusions: Closed alpine vegetation may provide some resistance to compositional change by limiting the establishment of novel species. However, further vegetation changes seem imminent without effective climate action, and this will be further compounded by threats such as fires, recreation, invasive species, and infrastructure development impacts.

2.4 Introduction

Climate change is modifying the environmental filter that dictates community assembly in alpine environments (Gottfried et al., 2012; Ernakovich et al., 2014; Graae et al., 2018). The decline in freezing temperatures and snow cover is expected to increase abiotic stress (e.g. earlier snowmelt exposing plants to more freezing events) and biotic competition, leading to the loss of endemic alpine species (Stöckli et al., 2011; Kammer et al., 2012; Pauli et al., 2012; Malanson & Fagre, 2013; Gottfried et al., 2012; Steinbauer et al., 2018; Kraft et al., 2015; Iseli et al., 2023). This will have profound implications for alpine community diversity, composition, structure, and ecosystem function (Elmendorf et al., 2012), potentially leading to collapse in some alpine ecosystems (Williams et al., 2015; Bergstrom et al., 2021).

The effects of climate change are particularly concerning for alpine species at the edge of their uppermost distribution (e.g. summits). Species occupying alpine summits have little ability to track their climatic niche upwards and are predicted to lose most of their habitat (Grabherr et al., 1994; Theurillat & Guisan, 2001; Pauli et al., 2003). Furthermore, lower-elevation summits are likely at higher risk due to species likely already being at their climatic limits (Theurillat & Guisan, 2001). With increasing temperatures and longer growing seasons, alpine summit communities worldwide have been increasing in species richness due to the upslope migration of warm adapted native and exotic invasives (e.g. colonisation) (Malanson & Fagre, 2013; Gottfried et al., 2012; Stöckli et al., 2011; Kammer et al., 2012; Pauli et al., 2012; Steinbauer et al., 2018). Increases in the abundance of these species have been at the expense of alpine endemics (i.e. extinction) (Erschbamer et al., 2011; Rumpf et al., 2018), a process termed "thermophilisation" (Gottfried et al., 2012). In response, alpine plant communities are predicted to lead to significant changes in alpine vegetation composition due to high turnover (Engler et al., 2011; Dullinger et al., 2012; Hulber et al., 2016) which can lead to biotic homogenisation (Verrall et al., 2021). However, some studies have found that changes in alpine vegetation composition are driven by the reorganisation of local species rather than species turnover through extinction and colonisation events (le Roux & McGeoch, 2008; Oldfather et al., 2024).

Australian alpine ecosystems, much like their overseas counterparts, host distinctive plant communities adapted to cold conditions, and the impacts of contemporary climate change on these ecosystems are increasingly evident. The Australian alpine areas are already experiencing higher temperatures and a reduction in snow cover (Scherrer and Pickering 2005; Griffin and Hoffmann 2012; Wahren et al. 2013; Verrall et al. 2023). In response to this, there have been obvious elicit shifts in vegetation detected via experimental warming (Hoffman et al., 2010; Jarrad et al., 2008; Wahren et al., 2013), across elevational gradients

(Pickering et al., 2008) and in short-term observational studies (Venn et al., 2012). However, empirical evidence of vegetation composition shifts in response to contemporary climate change is limited (but see Verrall et al. 2021). Moreover, discrepancies between observed change and modelled distribution shifts to climate change may arise due to time lags in species responses ("disequilibrium dynamics"; Svenning & Sandel, 2013). This is because alpine community assembly is also influenced by biotic factors such as competition/colonisation trade-offs (Korner, 2003; Kraft et al., 2015; Alexandra et al., 2018). Consequently, significant changes in alpine plant species diversity and community composition may be slow (Qin et al., 2022). This is particularly the case for ecosystems with high initial plant species richness that may exhibit high resistance to non-extreme climate and habitat changes (Tilman et al., 1996; Falk et al., 2019). As a result, clear signals of climate change effects on community composition may only be detected in the long term (Dullinger et al., 2004).

Shifts in alpine species ranges may also depend on the co-occurrence of other drivers of change (i.e. grazing, fire) (Barnosky et al., 2012; Camac et al., 2017; Ratajczak et al., 2018). In Australia, warmer conditions and more extreme events, such as fire, are expected to facilitate the expansion and upslope migration of warm adapted native and exotic invasives (Camac et al., 2021). For example, shorter intervals between fire events can facilitate shrub establishment by creating bare ground and reducing competitors (Wahren et al., 2013; Camac et al., 2017). Moreover, because shrubs are the most flammable vegetation component in the Australian Alps, the encroachment of shrubs could strengthen the feedback between shrubs, warming and fire (Williams et al., 2006; Fraser et al., 2016; Venn et al., 2016; Camac et al., 2017). Disentangling the effects of climate from other drivers of change can be challenging and has resulted in uncertainty surrounding alpine communities' response to climate change (Malanson et al., 2019; Camac et al., 2021). As such, to understand the processes driving alpine vegetation dynamics and to better forecast the future of alpine plants, long-term ecological monitoring approaches are required to distinguish the interplay between climate and other drivers (Stöckli et al., 2011; Venn et al., 2012).

In this study, we focus on detecting changes in Australian alpine vegetation composition over a two-decade on mountain summits. We used revisitation vegetation surveys conducted on 14 Australian alpine summits over 18 years to investigate changes in alpine vegetation community composition due to colonisation, extinction or reorganisation events. We specifically ask: i) Are there significant shifts in alpine summit vegetation composition over 18 years? ii) What is the rate and direction of change of alpine summit vegetation composition? iii) Is alpine summit vegetation composition dynamics driven by colonisation (new species from outside the study sites), extinction (loss of species from within a site), and/or re-ordering (change in relative abundance of species) processes? iv) Are lower-elevation summits more sensitive to change?

2.5 Materials and methods

2.5.1 Study sites

Permanent plots were established on 14 alpine summits in the Victorian Alpine Bioregion, that are part of the Australian Alps in south-eastern Australia (**Figure 2.1**). Australian mainland alpine summits are characteristically ancient, typically rounded or flat-topped, fully vegetated, and comparatively low in elevation with little topographical relief (Venn et al., 2017). All summits in this study lack nival zones but have well-developed organic, highly acidic soils (Wilson et al., 2022). Soils at summits are all ‘alpine humus’, generally shallow, stony, organic and acidic (pH 4-5) (Wilson et al., 2022). Consequently, they have high biomass with continuous, mostly perennial vegetation cover (Costin, 1954). Summit plant communities include alpine grasslands, herbfields, and open heathlands, with most summits characterised by shrubs, while the highest summits are dominated by herbs and graminoids typical of alpine herbfields (**Appendix I, Table S1**).

The Victorian Alpine Bioregion experiences a mid-latitude mountain climate that receives an even amount of precipitation year-round, with no dry season, cold winters with snow cover and relatively mild summers (Williams, 1987; Grose et al., 2019). The mean annual rainfall is 1781-2378 mm, mostly falling as snow in winter and early spring (June to September) (Bureau of Meteorology, 2022). Winter air temperatures commonly fall below freezing, ranging from -6 to 12 °C, while summer air temperatures range between 2 to 27 °C (Bureau of Meteorology, 2022). They experience frequent or periodic droughts (Wahren et al., 2013) and frosts (Williams, 1987) and historically were subjected to infrequent landscape fires (approximately every 50-100 years) (Williams et al., 2008).

The study area is of great cultural and spiritual significance for the Australian Alps First Peoples, including the Daung wurrung, Dhudhuroa, Gunaikurnai, Taungurung, Waywurru and Jaitmatang peoples. The region has been an important place for large-scale ceremonial gatherings (Flood, 1980). Post-European colonisation, free-ranging cattle were first introduced to the area in the 1850s (Lawrence, 1995). Study summits had been variously grazed in the snow-free season by domestic cattle, with grazing gradually banned from the region between the 1950s and 1990s and banned altogether in 2005 (**Appendix I, Table S1**) (Lawrence, 1995, DSE, 2005). Large feral herbivores, such as Sambar deer and horses, are known to be present in these areas (Brown et al., 2016; Tolsma & Shannon, 2018). Currently, the study area is listed on the Australian National Heritage Register under the Environment Protection and Biodiversity Conservation Act 1999 (EPBC Act). The primary land use is now nature and culture conservation and water production (Costin et al., 2000; Worboys & Good, 2011). However, some ski resorts operate on higher elevation summits, including Mount Buller and Mount Hotham, attracting high numbers of visitors (Pickering, 2011).

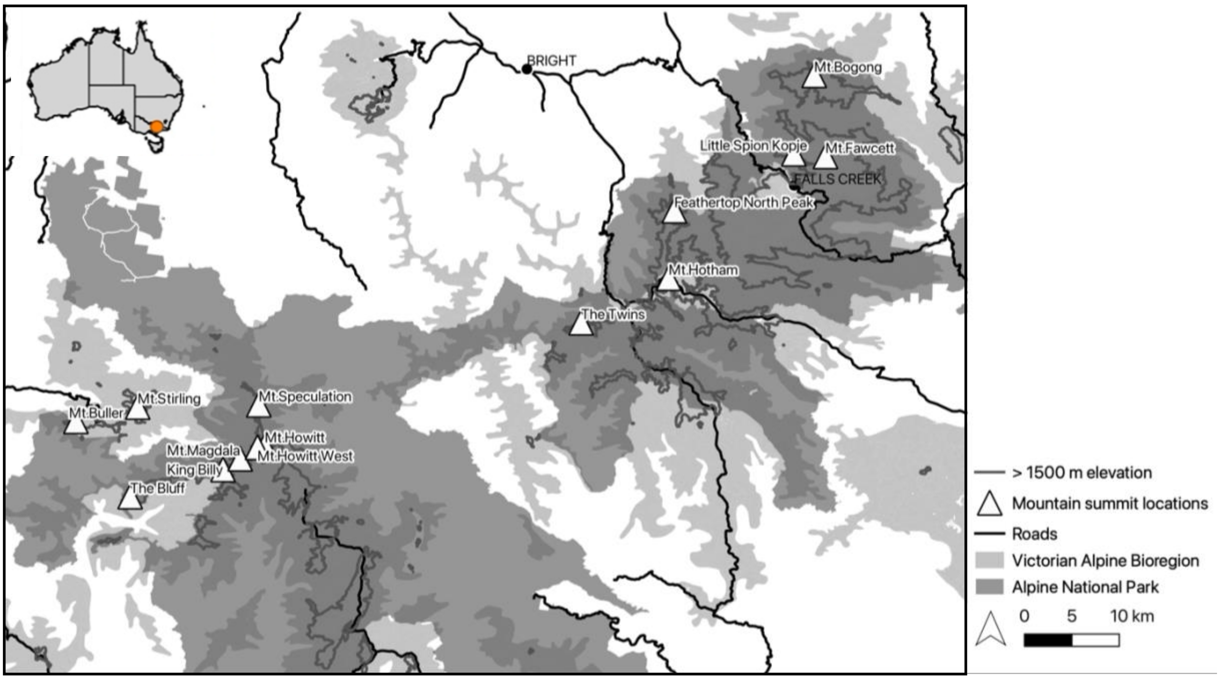


Figure 2.1 Location of the 14 study summits within the Victorian Alpine Bioregion that are part of the Australian Alps in south-eastern Australia. *Note: Mt Fawcett is the unofficial name of the mountain documented on the map.*

2.5.2 Revisitation study

This study revisits four-cornered plots permanently established on 14 mountain summits in Victorian Alpine Bioregion in 2004 and 2012. The plots encompassed the 5 m contour below the highest summit point and were divided into four quadrants by the four cardinal bearings (**Appendix I, Figure S1**, Venn, 2007). On summits with little topographic relief, the boundary of the summit survey area was extended to 50 m from the highest summit point. Summits that experience high recreational activities were avoided (Venn, 2007). Revisitation vegetation surveys were completed in late summer (January and February) of 2012, 2017 and 2022.

To investigate plant community compositional changes, five 1 m x 1 m quadrats were randomly placed into the four quadrants; there were a total of 20 quadrats per site (Venn 2007). All vascular plant species were recorded within each quadrat, and their percent cover was visually estimated to the nearest 5% (Venn, 2007). Species that were less than 5% were recorded as 0.5%. Between survey periods, taxonomic changes had occurred. All species names were updated to current nomenclature (https://vicflora.rbg.vic.gov.au/). Where species have been split into several taxa since the original survey (e.g. *Craspedia* spp.), these new species were subsumed into their original synonyms. This inevitably underestimates total species richness on alpine summits.

2.5.3 Environmental factors

The 14 alpine summits represent an elevational gradient ranging from 1668 m to 1950 m a.s.l. and are distributed over approximately 43 km of latitude and 87 km of longitude. On average, summits at higher elevations experience lower minimum and maximum temperatures than lower elevation summits. They also experience, on average, up to 215 mm more precipitation per year than lower elevation summits (**Appendix I, Table S1**).

To examine changes in climate at the study region, temperature data was obtained for each summit from historical gridded datasets available from the Scientific Information for Land Owners (SILO) (http://www.longpaddock.qld.gov.au /silo/index.html; Jeffrey et al., 2001). This database is a patched point database with a spatial resolution of grids have a spatial resolution of 0.05° × 0.05° (approximately 5 km × 5 km) (Jeffrey et al., 2001). The climate data (annual precipitation, maximum temperature, minimum temperature) between 2003 and 2022 was compared to climate data between 1961 and 1990, the climatological baseline period that is a 30-year "normal" period used for long-term climate change assessments (World

Meteorological Organization, 2017). Between 2003 and 2022, the mean annual maximum temperature increased by up to 0.70 °C, the mean annual minimum temperature increased by up to 1.40 °C, and the mean annual precipitation declined by up to 517 mm this baseline (**Figure 2.2**). Lower elevations experienced a greater rate of change in maximum temperature, while higher elevation summits experienced greater changes in minimum temperature and annual precipitation (**Figure 2.2**).

Following the baseline vegetation survey in 2004, most of the study summits were burnt to various degrees by fires (**Appendix I, Table S2**). In 2007, a large-scale fire burned 11 out of the 14 study summits. Furthermore, Feathertop North Peak (1850 m) and The Twins (1705 m) were burnt three times (2003, 2007, and 2013), and Mount Bogong (Hooker Plateau) (1950 m) and Mount Hotham (1900 m) remained unburnt.

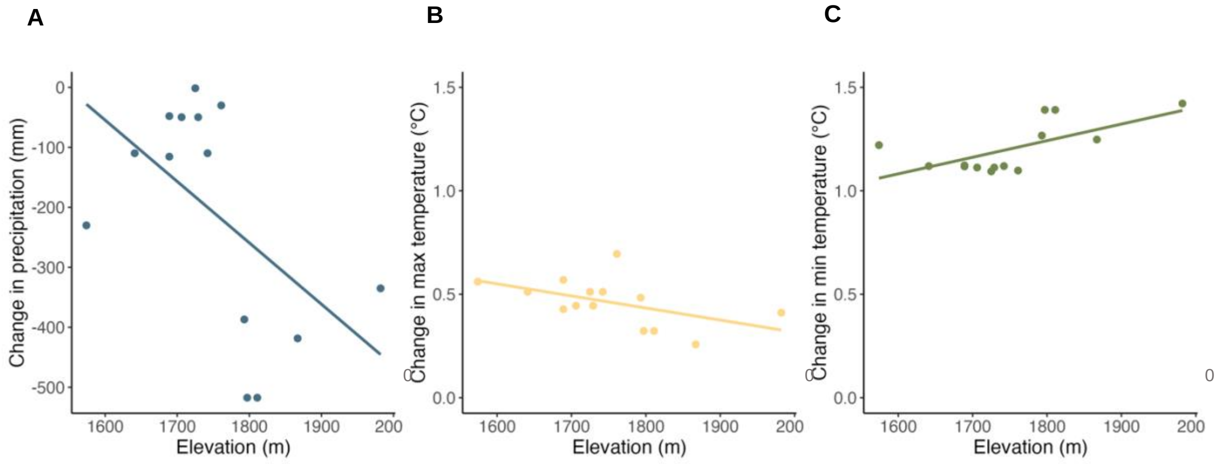


Figure 2.2 The change in (A) annual mean precipitation (mm) and (B) maximum and (C) minimum temperatures (°C) from the baseline period (1967–1990) in relation to elevation (m) for each study site (n=14). Trend lines are shown for each variable. Climate data was obtained from Scientific Information for Land Owners (SILO) (http://www.longpaddock.qld.gov.au /silo/index.html; Jeffrey et al., 2001).

2.6 Data analysis

Before the analysis, five singleton species were removed from the dataset that were only recorded in one quadrat in one year (**Appendix II, Table S3**) to minimise the effect of sampling bias (Legendre & Legendre, 2012). Before assessing the diversity dynamics, species accumulation curve models were conducted to calculate the cumulative number of species found at each site in 20 quadrats in 2004, 2012, 2017 and 2022 (Krebb, 2014; Oksanen et al., 2022). The results indicated adequate sampling and captured most species at approximately 20 quadrats (**Appendix II, Figure S2**).

2.6.1 Summit composition community change over time

To investigate significant shifts in alpine summit vegetation composition over 18 years, non-metric dimensional scaling (NMDS) ordinations were used. Two NMDS ordinations were constructed with the Bray–Curtis (B-C) similarity distance matrices of the square root transformed species abundances for each summit in each survey year (Bray & Curtis, 1957; Quinn & Keough, 2003). The first ordination was to explore how summit communities changed over time. The second ordination was to explore how individual summits changed over time using centroid between years and centroid arms to show the degree of compositional shift over time. Analysis of similarity (ANOSIM) was executed using 999 random permutations to test whether there had been a significant composition shift over time (Clarke, 1993). Influential species and environmental vectors driving variances between years and summits were investigated by fitting vectors of maximum correlation and overlaid if significant ($p < 0.01$ and $p < 0.05$, respectively) (Blackburn-Smith & Morgan, 2022). Ordinations were created using the “vegan” package (Oksanen et al., 2022).

To investigate the rate and direction of compositional changes, a time lag analysis was performed at the community and the individual summit level (Collins et al., 2000; Hallett et al., 2016). The floristic composition for each summit in each survey year was described by Euclidean distances, then regressed against the three-year time intervals (i.e. 2004 to 2012, 2004 to 2017, 2004 to 2022, 2012 to 2017, etc) (Hallett et al., 2016). Euclidean distance is described as a measure of community composition dissimilarity between two time points in a multi-dimensional space (Collins et al., 2000). Simple linear regression analyses were then used to summarise trends. The slope of this relationship indicated the rate and direction of composition change (Collins et al., 2000). A positive relationship suggests that community compositional changes are directional, i.e. points further apart are more dissimilar than those closer together. Conversely, a negative slope indicates community instability, resulting in low variance at longer time lags (Collins et al., 2000). A flat slope suggests stochastic changes in the community over time (Collins et al., 2000). The time lag analysis was completed using the “codyn” package (Hallett et al., 2016, 2018).

2.6.2 Summit community composition components

To investigate the components (colonisation, extinction, reordering) driving composition change on alpine summits, species turnover and change in rank abundance were calculated using the “codyn” package (Hallett et al., 2016, 2018; Avolio et al., 2019). Traditional diversity indices (such as species richness and Shannon index) poorly capture community dynamics (Collins et al., 2000; Tierney, 2024). A better approach for estimating diversity variation is using analogous temporal metrics, such as species turnover and rank abundance (Collin et al., 2000, 2008; Cleland et al., 2013). These indices quantify temporal variation in species richness in relation to abundance, which accurately detects how much communities vary over time and better informs species' extinction risks (Collin et al., 2000).

Species turnover (T_{sp}) represented the temporal analogue to species richness and was defined as:

$$T_{sp} = \frac{(A + B)}{C}$$

where A is species gained, B is species lost and C is the total species observed between consecutive years (Cleland et al., 2013). Low species turnover results are near 0.01, while complete species turnover is 1.0 (Venn et al., 2012). Turnover also involves calculating the proportion of species that appear (gain) or those that disappear (lost) which can be used to detect processes driving total turnover between time points (Hallett et al., 2014, 2016).

To examine the change in rank abundance over time (i.e. reordering), the change in species ranks based on their abundances was calculated using the “codyn” package (Hallett et al., 2014, 2016; Avolio et al., 2019). Rank change measures how much species abundances change over time relative to each other and is independent of species richness (Collins et al., 2008; Avolio et al., 2019). The average rank change (ΔR) was defined as:

$$\Delta R = \frac{\sum_{i=1}^{N}\left(\left|R_{i,t+1} - R_{i,t}\right|\right)/N}{N}$$

where $R_{i,t}$ represents the rank of species i at a survey year t. N represents the number of species shared between the different survey years and $R_{i,t+1}$ is the relative rank of species i

at survey year $t + 1$ (Hallett et al., 2016; Avolio et al., 2019). Rank change is bound between 0 and 0.5 (maximum rank changes) (Avolio et al., 2019).

To examine the change in species turnover and range change over time, the mean and 95% confidence intervals were calculated over time for each diversity index. The outcomes were compared by examining the overlap of 95% confidence intervals (i.e. 'inference by eye'; Cumming & Finch, 2005).

To determine the processes driving compositional changes, the correlation between all change measures (species turnover, species loss, species gain, rank change) was examined across all summits and time points (n = 36). Composition change over time was first determined using the Multivariate function in the "codyn" package (Avolio et al., 2019), which calculates change by creating a Bray-Curtis dissimilarity matrix, then obtains the pairwise distance between centroids of compared time periods (Avolio et al., 2019). Compositional change ranges from 0-1, where identical communities give 0 and completely different communities give 1 (Avolio et al., 2019). A pairwise comparison using Spearmen correlation was then used to examine the relationship between composition change and change measures (Avolio et al., 2019).

All analyses were calculated and plotted in R (RStudio Team, 2024).

2.7 Results

A total of 130 plant species from 33 families were recorded across the study area between 2004 and 2022 (**Appendix II, Table S4**). Of these species, 8% were exotic and 30% of native species were listed under the *Victorian Flora and Fauna Guarantee Act* 1988 (FFG Act). *Euphrasia crassiuscula* subsp. *glandulifera* and *Argyrotegium nitidulum* are also listed as Vulnerable under the federal *Environment Protection and Biodiversity Conservation Act* 1999 (EPBC Act). Graminoids comprised 21% of species, forbs 56%, shrubs 22% and one tree species.

2.7.1 Summit compositional change over time

The NMDS ordination shows there were significant differences in summit floristic composition over time ($p < 0.001$, $n = 14$, **Figure 2.3**). Summit floristic composition divergence occurred between 2004 and 2012, followed by homogenisation between 2012 and 2022. Elevation was a significant environmental correlate of between-site composition variation ($p = 0.001$) (**Figure**

2.3, Table 2.1). The summits with the greatest compositional shift over time were at both high (1900 m and 1950 m) and low elevation (1705 m and 1730 m) (**Appendix II, Figure S3**). Few changes in composition were seen at summits at 1870 m and 1710 m. Important discriminating species included alpine forb species *Celmisia costiniana, Brachyscome nivalis,* and *Euphrasia* spp., which were higher in abundance at higher elevation summits. At lower elevation summits, the important discriminating species included the alpine shrub *Hovea montana,* the alpine forb *Brachyscome rigidula,* and snow grass *Poa fawcettiae* (**Table 2.1**).

The time lag analysis of summit species composition changes over time revealed a small positive, but non-significant, relationship between Euclidean distance and time intervals (β = 2.87, R^2 = 0.02, p = 0.16, n = 14, **Figure 2.4**). Overall, this indicates a modest trend of increasing dissimilarity in species composition with increasing time intervals. This suggests species composition is experiencing a gradual but positive directional change over time. At the individual summit level, all summits experienced positive directional compositional change, except Mount Howitt (1740 m) and Mount Fawcett (1870 m) (**Appendix II, Table S5**).

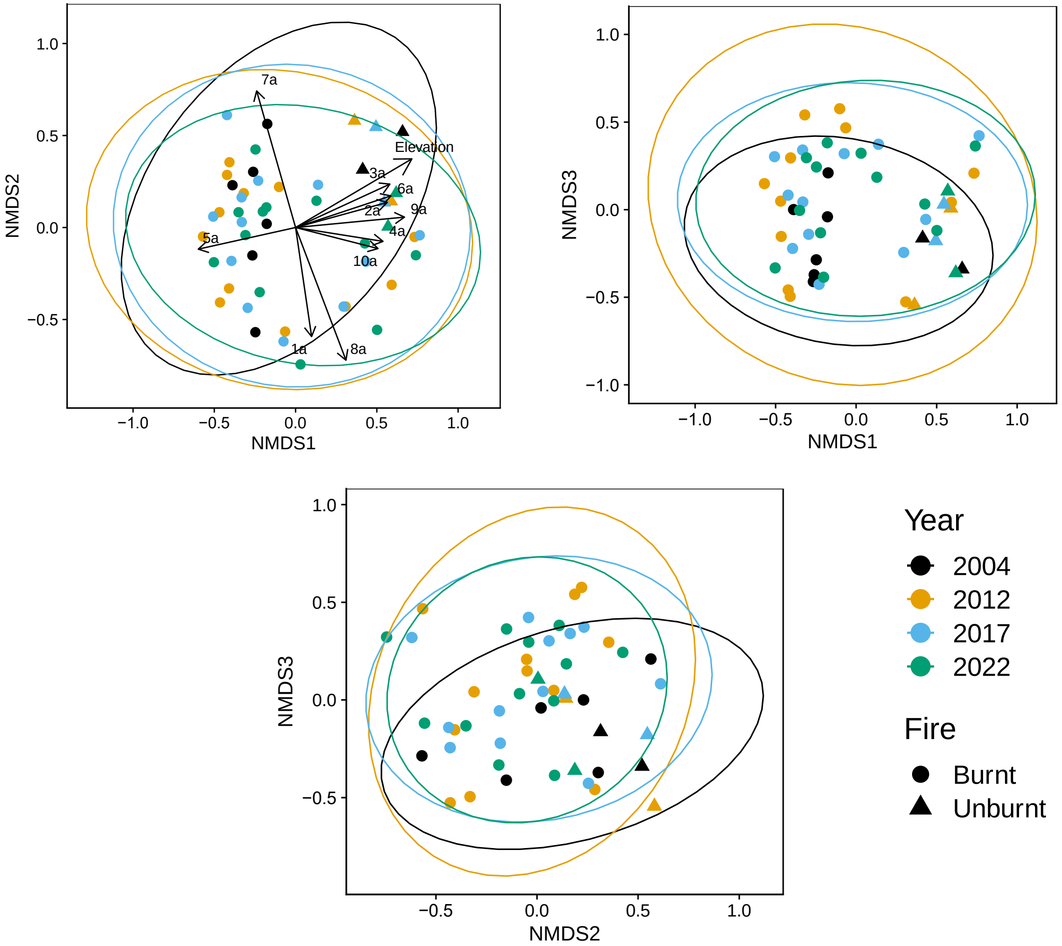


Table 2.1 Key indicator species ($p < 0.01$) and environmental ($p < 0.05$) vectors that correspond to the vector arrows in the NMSD plot, **Figure 2.3**.

Label	**Vector**	***p*-value**
1a	*Acrothamnus montanus*	< 0.001
2a	*Brachyscome nivalis*	< 0.001
3a	*Celmisia costiniana*	< 0.001
4a	*Euphrasia spp.*	< 0.001
5a	*Hovea montana*	< 0.001
6a	*Kunzea muelleri*	< 0.001
7a	*Poa fawcettiae*	< 0.001
8a	*Poa hothamensis*	< 0.001
9a	*Scleranthus singuliflorus*	< 0.001
10a	*Senecio pinnatifolius*	< 0.001
	Elevation	0.001

Figure 2.3 Floristic composition of the 14 mountain summits in Victoria. 3D NMDS ordination in which each symbol represents the composition of each summit in one survey year, with colours representing the 95% confidence ellipses of different years. Shapes represent different fire histories of summits. Ordinations are based on the percentage cover analysed using Bray–Curtis dissimilarity matrix (3D stress = 0.145). Top left ordination: NMDS1 vs. NMDS2 axes with the significant environmental and species vectors shown. Top right ordination: NMDS1 vs. NMDS3 axes. Bottom left ordination: NMDS2 vs. NMDS3 axes. Species are indicated by numbers corresponding to **Table 2.1**.

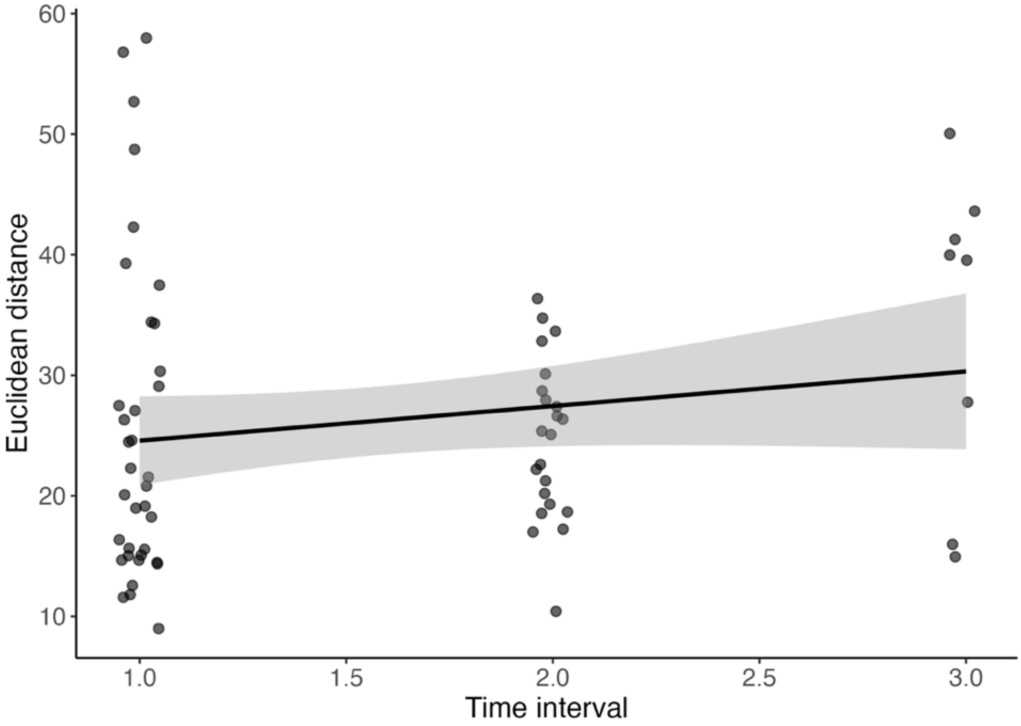


Figure 2.4 Time lag analysis showing the relationship between compositional changes (measured using Euclidean distance) and time intervals (2004, 2012, 2017 and 2024) for the study area. The scatter plot presents Euclidean distance for each summit for different time intervals. The solid line represents the regression model, with shaded areas indicating the 95% confidence intervals. ($\beta = 2.87$, $R^2 = 0.02$, $p = 0.16$).

2.7.2 Summit community composition components

At the community level, mean species total turnover was low (0.1 to 0.4) and did not change significantly over time (**Figure 2.5**). In 2012 and 2017, total turnover was attributed to species losses. In 2022, total turnover was attributed to species gains. There was a significant difference in mean species losses over time. Species losses declined from 0.263 in 2012 to 0.150 in 2015 (**Figure 2.5**). Then, it further declined in 2022 to 0.10. There was a small increase in the mean species gains from 2004 to 2022, from 0.174 to 0.260. However, this was not significant (**Figure 2.5**). At the individual summit level, there was no clear trend between elevation and turnover (**Appendix II, Figure S4**). Between 2004 and 2017, species turnover for six summits was attributed to species loss, with 1950 m (Mount Bogong Hooker Plateau) having the highest rate of losses (0.40) (**Appendix II, Figure S5**). At the same time, turnover for two summits experienced a gain in species (The Bluff 1710 m and Mount Hotham

1900 m). Between 2017 and 2022, greater species gain contributed to total species turnover at all summits.

At the community level, the change in community rank abundance over time was positive but low, indicating evidence of abundant species becoming more abundant (**Figure 2.5**). Change in community rank abundance corresponds to the directional change observed in the time lag analysis. The rank change was significantly higher in 2012 compared to 2017 and 2022. Rank change declined from 2012 to 2017, from 0.211 to 0.174. The rank change did not vary significantly from 2017 to 2022, indicating little change in abundant species during that period (**Figure 2.5**). At the individual summit level, there was no clear trend between elevation and change in rank abundance (**Appendix II, Figure S4**). Most sites exhibit relatively stable rank changes over the years, with some variability observed at specific elevations such as 1660 m, 1720 m, and 1805 m, suggesting different dynamics in species composition across these sites (**Appendix II, Figure S6**). Mount Buller (1805 m) experienced the highest rank change between 2004 and 2012 (0.26). Little Spion Kopje (1670 m) experienced the lowest rank change from 2012 to 2017 (0.11).

The correlation analysis revealed relationships between composition change and other measures of community dynamics (**Appendix II, Figure S7**). There was a strong positive correlation between species losses and composition change (r = 0.652, $p < 0.001$, **Appendix II, Figure S7**), indicating that the loss of species significantly altered community composition. Additionally, rank change is moderately positively correlated with composition change (r = 0.372, $p < 0.05$, **Appendix II, Figure S7**), suggesting that shifts in the relative abundance ranks of species contribute to changes in community composition.

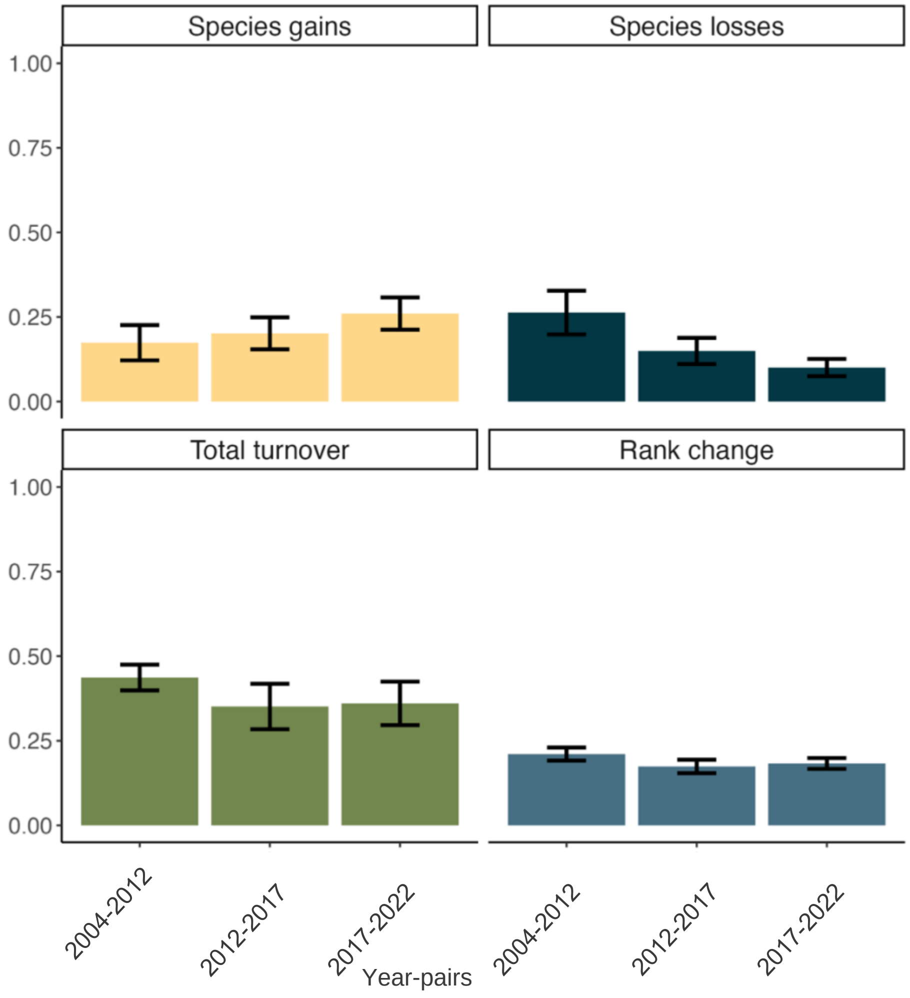


Figure 2.5 Mean species turnover (total, gains and losses) and rank change (± 95% CI) for the study area (*n* = 8 from 2004 to 2012 and *n* = 14 from 2012 to 2022) over time. Species turnover is bounded between 0 (low species turnover and 1 (complete turnover). The rank change indicates the degree of plant species reordering between time intervals and is bound between 0 and 0.5 (maximum rank changes) (Avolio *et al.* 2019).

2.8 Discussion

This study utilised a long-term dataset of repeated surveys to investigate vegetation changes on alpine summits, aiming to detect community compositional change over time. The findings indicate that, despite regional warming, decreased precipitation and fires over the past 20 years, there has been minimal change in species composition and community stability over time. However, the modest compositional changes identified between 2004 and 2012 were attributed to changes in the abundance of alpine species. Further investigation showed that species loss and reordering were the dominant processes on alpine summits. Notably, species reordering and species losses significantly increased between 2004 and 2012; however, overall, species turnover remained low. This suggests that the majority of change occurred between 2004 and 2012, most likely driven by the large-scale fire in 2007. This caused compositional drifts in resident summit species without leading to significant shifts over the long term. No clear trends were observed between elevation and vegetation dynamics over time.

2.8.1 Fire as a key driver of change in alpine summit composition

The 2007 fire that burnt 11 study summits was the key driver of alpine summit community change across the study period. Secondary succession resulted in modest positive directional change attributed to the re-assembly of local species. After the 2007 fire, secondary succession occurred, resulting in the initial loss of local species, followed by a herbaceous vegetation cover "pulse" and the recovery of summit community. This herbaceous pulse translated into compositional changes in the abundance of local species, resulting in compositional divergence and evident local community reassembly (i.e., reordering) between 2004 and 2012. Species driving this change included snow grasses (*Poa fawcettiae*, *Poa hothamensis)* and native forbs such as *Senecio pinnatifolius*. These species are known to be effective post-fire colonisers, and pyrogenic growth, flowering, and seed set have been documented for both Poa species (Yeates & Lee, 1997; Wahren et al., 2001) and *Senecio pinnatifolius (Walsh & McDougall, 2004).* Species gains at summits were predominantly driven by local forbs responding to disturbance, including *Stellaria pungens* and *Acaena novae-zelandiae*. However, two summits (1705 m and 1670 m) gained exotic herbaceous species not previously recorded (*Acetosella vulgaris*, *Cerastium vulgare)*. This result supports the work of other studies that found that the diversity and composition of Australian alpine vegetation are mostly unaffected by fire, and most alpine species are resilient to infrequent, large, intense fires and regenerate rapidly (Wahren et al., 2001; Walsh & McDougall, 2004*;* Williams et al., 2008; Camac et al., 2012). It also supports the “Initial Floristic Composition” hypothesis, whereby following disturbance, a community undergoes "progressive development" of local species that can be resistant to invasion (Egler, 1954). Consequently, the observed divergence-homogenisation dynamics can be attributed to secondary succession processes from local species colonising bare ground caused by the pyrogenic seed germination, resprouting and mast flowering (Williams et al., 2008).

2.8.2 Alpine summit vegetation stability over time

Despite regional warming, decreased precipitation, and fires over the past 20 years, the findings from this study suggest summit community composition stability over time. Community stability was reflected in the changes in species reordering, low turnover and minimal change in species composition over time. These findings are at variance with other findings which predict warmer conditions will facilitate colonisation events (i.e., thermophilisation) and lead to significant shifts in alpine community composition (Engler et al., 2011; Dullinger et al., 2012; Gottfried et al., 2012; Hulber et al., 2016). However, similar results have been found where community-level shifts are driven by changes in the abundance of resident species rather than species turnover (e.g., Oldfather et al., 2024). These findings were associated with dispersal lags and the demographic inertia of alpine plant communities, which enable fine-scale range shifts across landscapes (Alexander et al., 2018; Oldfather et al., 2024). Consequently, even over 18 years, the influence of global warming has not led to detectable patterns of local population extinction or colonisation.

A species' ability to migrate and establish is often constrained by its plant traits and abiotic and biotic interactions (Dullinger et al., 2012; Lenoir & Svenning, 2013; Alexander et al., 2018). Most herbaceous alpine species have poor long-distance dispersal ability and typically reproduce clonally or vegetatively (Korner, 2003; Morgan & Venn, 2017). As such, the dispersal of alpine species is generally restricted, possibly to avoid dispersing into unsuitable habitats off mountains or denser lower-elevation vegetation (Riibak et al., 2015). Invasive species may also experience time-lagging processes in alpine regions. For example, the invasion of woody species is limited due to their extended maturity time (Lenoir & Svenning, 2013). Conversely, invasive herbaceous species with smaller seeds can migrate upslope at a faster rate than invasive woody plants (Lenoir et al., 2008). However, germination and seedling establishment may be difficult for those species not adapted to an alpine climate (Graae et al., 2011). Thus, to establish themselves in the alpine environments, species need to arrive in sufficient numbers (Alexander et al., 2018). Consequently, local community re-assembly may be the norm in alpine environments.

Close neighbouring plants can also influence seedling establishment through neutral, competitive (negative), and facilitative (positive) interactions (Venn et al., 2009; HilleRisLambers et al., 2013). At high elevations, facilitative interactions with the standing vegetation can buffer the extreme alpine conditions and create favourable conditions for plant growth (Korner, 2003). However, in Australia, these interactions have been identified as primarily species-specific and dependent on an abiotic stress gradient (Venn & Morgan, 2009). This means that in lower-elevation mountains with closed alpine vegetation (such as summits in this study), seedling recruitment and establishment may be significantly reduced as competition for recruitment sites outweighs the facultative interaction benefits (Venn et al., 2009; Lembrechts et al., 2016; Angers-Blondin et al., 2018). For example, the high cover of snow grass (Poa species) has been shown to inhibit the establishment and growth of shrub seedlings (Williams & Ashton, 1987). As a result, these summits may have some resistance to change by limiting the establishment of novel species. However, seedling establishment will be possible where suitable conditions and microsites are available (Winkler et al., 2016; Niittynen et al., 2020), e.g. increasing fire frequency creating bare ground opportunities (Camac et al., 2017).

2.8.3 Impact of elevation on alpine summit plant communities

The 14 alpine mountain summits in this study represented an elevation gradient, which implies a gradient of environmental variables such as temperature, precipitation, snow cover duration and growing season length, soil moisture, wind speeds and UV radiation (Korner, 2003). While there were differences between sites, there were no apparent effects of elevation on community dynamics, which contrasts with other studies that found lower elevation summits were more likely to change in composition due to climatic change (Theurillat & Guisan, 2001). The variation between summits may be explained by the differences in plant communities and legacies, including land use, geology, and fire history (Estes & Vermeij, 2022). As such, thresholds for change at each summit may be governed by the underlying local plant communities and abiotic conditions (Green & Pickering, 2009).

The highest elevation summit, Mount Bogong (Hooker Plateau) (1950 m), had the most pronounced composition change, the largest species loss and some species gains (immigration). Species gains and losses were primarily a result of local species fluctuations. However, two alpine endemics, *Ewartia nubigena* and *Gentianella muelleriana,* were not recorded after 2004. Moreover, two new species found in 2017 and 2022, *Hypochaeris radicata* and *Acaena novae-zelandiae*, are widespread (non-native and native) species from the broader landscape. This finding is consistent with other alpine studies where lower elevation species were driving increased species richness in response to warming (Erschbamer et al., 2011; Venn et al., 2012; Lamprecht et al., 2018; Verrall et al., 2021). The loss of these two alpine species may be the first sign of local extinction processes, as predicted for alpine endemics globally (Dirnbock et al., 2011; Dullinger et al., 2012).

Most alpine species are inherently rare, highly restricted and have poor dispersal abilities. This combination of traits substantially increases their risk of local extinction due to climate change (Körner, 2003; Guisan & Thuiller, 2005; Cotto et al., 2017; Williams et al., 2015; Venn & Morgan, 2017). However, many alpine species are long-lived and reproduce vegetatively, which creates demographic inertia (De Witte et al., 2012). Together with lags in invasive species establishment, this may result in an extinction debt where extinctions take decades to be realised (Korner, 2003; Nomoto & Alexander, 2021). Extinction debts are predicted to be more frequent in alpine species from the highest elevations, with fewer opportunities to escape warming (Rumpf et al., 2019). However, alpine plants may have opportunities to utilise the various microclimate habitats within an alpine area (Korner & Hiltbrunner, 2021). For example, alpine species may reside in the cooler aspects of mountains or behind rocks. Consequently, Australian alpine species may resist climate change's impacts by relocating around mountains and other landscape features, such as rocks, rather than directly upslope (Korner & Hiltbrunner, 2021).

2.8.4 Regional implications

Ongoing climate change is modifying ecological conditions for many species, with the effects most noticeable at the edges of their geographical ranges (Grabherr et al., 1994; Theurillat & Guisan, 2001; Verrall et al., 2021). Alpine plant species are moving to higher elevations in response to these climatic changes (Grabherr et al., 1994; Theurillat & Guisan, 2001). Most of the evidence for the upward migration of alpine plants comes from the northern hemisphere (Malanson & Fagre, 2013; Gottfried et al., 2012; Stöckli et al., 2011; Kammer et al., 2012; Pauli et al., 2012; Steinbauer et al., 2018), while there is relatively little evidence for such shifts in the southern hemisphere (but see Auld et al., 2022). Understanding changes in Australian alpine species distributions is challenging but essential for identifying the contributions of various drivers, allowing for management actions to mitigate threats. However, attributing these changes to specific causes is complicated by historical land use impacts (Malanson et al., 2019; Camac et al., 2021). Many northern hemisphere examples of elevational range shifts involve species moving into a shrinking nival zone where new habitats become available (Malanson & Fagre, 2013; Gottfried et al., 2012; Stöckli et al., 2011; Kammer et al., 2012; Pauli et al., 2012; Steinbauer et al., 2018). In contrast, with their deep soils, Australian alpine mountains are already covered in dense vegetation (Costin, 1954), making new species establishment outside their current range due to climate change more limited (Alexander et al., 2018). Instead, future changes may be accelerated by disturbances from feral ungulates, fire (Doherty et al., 2024), and human activity. Therefore, understanding the interaction between climate and other factors, particularly disturbance, is crucial for predicting the future of alpine plants in Australia.

2.9 Conclusions

Using a revisitation approach, this study quantified detectable changes over the long term in alpine ecosystems expected to undergo substantial long-term shifts. The results indicate little compositional change over time. However, fires cause rapid vegetation changes due to successional processes and are mostly undergoing directional change driven by local species. Consequently, closed alpine vegetation, such as summits in this study, may have some resistance to change by limiting the establishment of novel species. However, vegetation changes seem imminent without effective climate action, and this will be further compounded by threats such as fire, recreation, development, and invasive species impacts. Additional assessments will be necessary to understand the interplay between fire and climate warming.

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CHAPTER 03

Chapter 3: Summit vegetation response to global drivers of change

3.1 Details, author contributions and declaration

This chapter consists of the paper that is currently under review at the *Arctic, Antarctic, and Alpine Research* Journal and was co-authored with my supervisor and co-supervisors. Permission to include the unpublished version of this paper in this thesis can be found in Appendix V. The details of this paper are:

Hickman, I.T., Venn, S.E., Camac, J.S., & Morgan, J.W. (in press). Alpine summit vegetation cover change over 18 years: divergent trajectories driven by climate warming and fire. *Arctic, Antarctic, and Alpine Research*.

Author contributions for this paper are as follows:

Author	**Contribution**	**Percent contribution**
ITH	conceptualisation, project administration, investigation, data collection (2022), data analysis, writing, reviewing and editing.	90%
JWM	conceptualisation, data collection (2004-2022), project administration, reviewing and editing.	5%
SEV	conceptualisation, data collection (2004-2022), reviewing and editing.	1%
JSC	data analysis, reviewing and editing.	4%

3.2 Paper under review

Long-term alpine summit vegetation cover change: divergent trajectories driven by climate warming and fire

Abstract

Alpine summit vegetation, the highest point of species geographical distributions, are vulnerable to climate change (thermal niche contraction), and there is evidence of change in northern hemisphere summits. However, summits are experiencing multi-faceted change due to warming and increasing fire frequency. Little is known about how these factors are affecting alpine summit vegetation. We used a revisitation approach to capture the long-term (18 years) dynamic changes in Australian alpine plant summit community patterns and to understand the mechanisms of change. We found vegetation change was influenced by climate and moderated by site-specific factors. There was increased shrub cover over time; however, summit vegetation was largely stable unless disturbed. Fire-disturbed summits experienced higher instability in their vegetation cover over time. Linear mixed-effect models indicated that as time since fire increased and the growing degrees accumulated, there was a strong positive effect on forb and graminoid cover and a negative effect on shrub cover. Forb cover was higher at cooler, wetter, higher-elevation summits. These findings indicate the multifaceted nature of change that must be accounted for in alpine vegetation studies. We show alpine summit vegetation will respond multi-directionally to a warming climate and changing fire regimes, with outcomes likely contingent on life history characteristics.

Introduction

Alpine vegetation occurs above the bioclimatic treeline, characterised by low temperatures, short growing seasons, complex terrain and microclimates that support high biodiversity and endemism (Elsen & Tingley, 2015; Körner, 2003; Perrigo et al., 2020). Alpine plants, often long-lived, cryophilic perennials, are predicted to be sensitive to the changing parameters of climate, such as rapid warming that is lengthening the growing season and reducing snow cover (Adler et al., 2023; Alatalo et al., 2016; Graae et al., 2018). Macroscale changes in climate are also increasing disturbance regimes, e.g. fire and drought (Adler et al., 2023; De Boeck et al., 2018; Williams et al., 2008). As a result, alpine ecosystems have experienced broad climate-induced vegetation changes, including increased annual primary productivity and the loss of alpine endemics (Elmendorf, Henry, Hollister, Björk, Boulanger-Lapointe, et al., 2012; Gottfried et al., 2012; Steinbauer et al., 2018; Stöckli et al., 2012). The effects of climate change are particularly concerning for alpine species at the limit of their uppermost distribution (i.e., summits), as those occupying alpine summits have little ability to track their climatic niche upwards and are predicted to run out of suitable habitat (Grabherr et al., 1994; Pauli et al., 2012; Theurillat & Guisan, 2001).

Climate change is causing ecological boundaries in high mountains to shift, with some alpine regions experiencing an upward expansion of treelines (Harsch et al., 2009) and the expansion and densification of woody plants, especially tall shrubs, which is predicted to increase (Camac et al., 2017, 2021; Elmendorf, Henry, Hollister, Björk, Bjorkman, et al., 2012; Myers-Smith et al., 2019). Shrub encroachment and expansion in high mountain environments will alter albedo, soil temperature, nutrient cycling, carbon dynamics and species composition, potentially creating feedbacks to global climate (Myers-Smith et al., 2011; Pearson et al., 2013; Williamson et al., 2016). However, landscape factors such as topography, disturbance, and biotic interactions may modulate the rate of shrub expansion and lead to ‘time lags’ in response to climate change (Alexander et al., 2018; Angers-Blondin et al., 2018). Therefore, investigations into the drivers of shrub encroachment are necessary to project future vegetation change in alpine environments and resulting feedbacks on ecosystem functions.

Understanding the synergistic and antagonistic interactions among climate, vegetation, and fire is particularly important for predicting the likelihood (or probability) of ecosystem transformation (Adler et al., 2023; Bowman et al., 2009; Folke et al., 2004). Warmer conditions are expected to facilitate shrub expansion and upslope migration, and fire may aid shrub encroachment by removing competitors (Camac et al., 2017; Elmendorf, Henry, Hollister, Björk, Bjorkman, et al., 2012; Wahren et al., 2013). Because shrubs are the most flammable vegetation component in alpine habitats, especially in Australia, their encroachment and expansion could strengthen positive feedbacks between warming, fire, and shrubs, thus accelerating landscape changes (Camac et al., 2017; Fraser et al., 2016; Higuera et al., 2008; Venn et al., 2016; Williams et al., 2008). However, negative climate-fire-shrub feedbacks may also emerge, hindering shrub expansion (Camac et al., 2017; Fairman et al., 2017). For example, frequent fires can reduce the recruitment of obligate seeding woody plants (trees and some shrubs) and their subsequent growth (Bradstock et al., 2014; Enright et al., 2015; Fairman et al., 2017). Understanding these potential feedbacks is critical to understanding how global change drivers may amplify or diminish vegetation responses in alpine regions through complex fire-vegetation interactions.

Here, we use a revisitation approach to investigate the long-term dynamics of vegetation states in Australian alpine summit vegetation. Alpine ecosystems in Australia are an ideal place to examine climate-fire-shrub feedbacks as they have been subject to repeated, extensive fires over the past two decades, with most of the Australian Alps having experienced more than one fire since 1939 (Godfree et al., 2021; Williams et al., 2008). The high abundance of shrub species in Australian alpine vegetation also contributes to its landscape flammability (Fraser et al., 2016; Williams et al., 2006). Furthermore, the region has experienced increases in mean annual temperatures, annual precipitation declines (Wahren et al., 2013), and snow cover reductions (Hennessy et al., 2008). However, little is known about how these factors affect alpine summit vegetation.

In this study, we used permanent transect data from 2004 to 2022 to capture the dynamic changes in alpine summit plant functional groups and understand the mechanisms of change. To understand the processes driving alpine vegetation dynamics, long-term ecological monitoring approaches are required to distinguish between natural temporal variability and community changes caused by environmental drivers of change (Stöckli et al., 2012; S. Venn et al., 2012). This is because short-term vegetation responses and climate oscillation can conceal long-term dynamics in alpine vegetation (Müller et al., 2010). Moreover, biotic/vegetation responses to climate change can be lagged. Lags can occur due to limitations on a species' ability to disperse and establish, as well as the development of extinction debts (Alexander et al., 2018; Camac et al., 2021). Specifically, we asked: (1) What is the likelihood of vegetation states transitioning to a different vegetation state over time (i.e. are shrubs out-competing other vegetation/substrate states over time), and how do these transitions vary between burnt and unburnt alpine mountain summits? (2) How does vegetation cover across different summits respond to environmental factors such as warming, fire and elevation (i.e. does fire and warming promote shrubification)?

Materials and Methods

Study sites

Permanent transects were established on 14 mountain summits with alpine vegetation situated above the bioclimatic limits of tree growth in the Australian Alpine Bioregion (**Figure 3.1**). Australian mainland alpine summits are characteristically ancient, typically rounded or flat-topped, fully vegetated, and comparatively low in elevation (study summits ranged from 1666 m to 1970 m a.sl.) with little topographical relief (Venn et al. 2017). Furthermore, compared to other alpine areas, Australian summits lack nival zones and contain 'alpine humus' soils; well-developed organic, highly acidic soils of international significance (Wilson et al., 2022). Consequently, Australian summits have high biomass with continuous, mostly perennial vegetation cover (Costin, 1954).

The alpine summits in this study experience a mild, mid-latitude mountain climate. The mean annual rainfall is 1781-2378 mm, mostly falling as snow in winter and early spring (June to September) (Bureau of Meteorology, 2022, Station No. 083084, 083085, 083024, 083094). Winter air temperatures commonly fall below freezing, ranging from -6 to 12 °C, while summer air temperatures range between 2 to 27 °C (Bureau of Meteorology, 2022). They experience frequent or periodic droughts (Wahren et al., 2013) and frosts (Williams, 1987) and are subject to recurrent landscape fire (approximately every 50-100 years) (Williams et al., 2008).

Shrubs and graminoids dominate most summits (open to closed heathlands) (**Appendix I, Table S1**). However, the highest summits are dominated by forbs and graminoids (alpine herbfield). Open heathlands are a highly flammable plant community relative to alpine tussock grassland (Fraser et al., 2016; Williams et al., 2006).

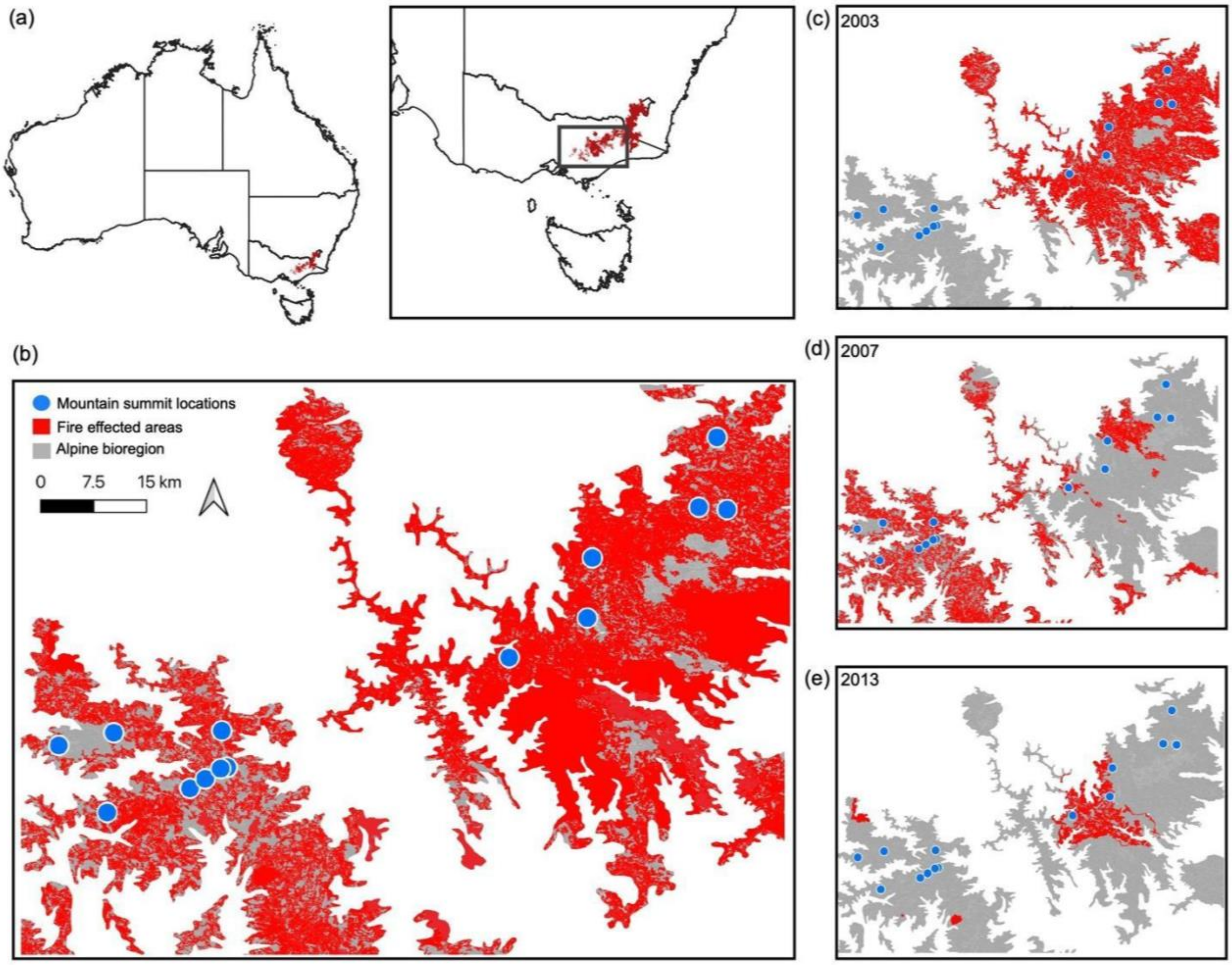

Figure 3.1 The study area with the recent Australian Alpine Bioregion fire history that affected the study summits. Left: (a) Location of the study area in south-eastern Australia and (b) study summits shown in relation to the total area affected by recent fires in the Australian Alpine Bioregion. Right: Study summits in relation to areas affected by the recent fires in (c) 2003, (d) 2007, and (e) 2013.

Study design

Permanent transects were established on 10 mountain summits in Australian Alpine Bioregion, south-eastern Australia in 2004 (Venn 2007) and four summits were established in 2012 (**Figure 3.1**). The Line Intercept Transect (LIT) method was used to assess fine-scale changes in summit dominant vegetation state (i.e. functional groups) and substrate state cover over time (Kent, 1992). Four permanent LITs were positioned at each summit. The transects were positioned within the upper 5 m contour line of the highest summit point and followed the four cardinal bearings (**Appendix I, Figure S1**; Venn 2007). On summits with little topographic relief, the boundary of the summit survey area was extended to 50 m from the highest summit point. Summits often targeted for recreational activities were avoided (Venn 2007). All summits have a variable history of domestic free-ranging cattle grazing, first occurring in the 1850s and progressively banned between the 1950s and 1993 (**Appendix I, Table S1**). Some sites were burnt in landscape-scale bushfires in 2003, 2007 and 2013 (**Appendix I, Table S2**). Vegetation surveys were completed in midsummer (January - February) of 2004, 2012, 2017 and 2022. The dominant structural type intercepting the transect every 10 cm along was recorded as either a lifeform (shrub, forb, graminoid) or a substrate condition when there was no vegetation cover (bare ground, litter, rock).

Summit-level environmental factors

To investigate the response of summit vegetation cover to drivers of change, we analysed the environmental factors at the summit level, including elevation, fire, and climate warming.

Climate warming

To estimate the effects of climate warming on summit vegetation cover, we calculated cumulative growing degrees (CGD) during the snow-free growing period (Russelle et al., 1984). Cumulative growing degrees provide a metric of the changing thermal niche dimension and measures the total heat accumulation above a 0 °C threshold (i.e. base temperature) (Körner et al., 2023; Russelle et al., 1984). This serves as a cumulative index of growing time and, thus, the amount of energy available for plant growth. To calculate CGD, we used modelled temperature (degrees Celsius) data for each summit from 1999 to 2022 from historical gridded datasets available from the Scientific Information for Land Owners (SILO) patched point database with a 0.05° (~5 km) spatial resolution (http://www.longpaddock.qld.gov.au/ silo/index.html; Jeffrey et al., 2001). While this resolution may seem large, it is appropriate for our study because the summits are distributed over approximately 43 km of latitude and 87 km of longitude. This scale allows us to capture regional temperature variations that influence CGD in summit environments. Additionally, we acknowledge that this resolution may be the only available data for our analysis.

To estimate the effects of climate warming on summit vegetation cover, we calculated cumulative growing degrees (CGD) during the snow-free growing period (Russelle et al., 1984). Summit CGD was defined as:

$$CGD = \sum_{i=1}^{n} \left(\frac{Tmax_{tj} + Tmin_{tj}}{2}\right) \tag{1}$$

where $Tmin$ is the daily minimum air temperature and $Tmax$ is the daily maximum air temperature for each day, i, above the threshold of 0 °C, n, in the growing season (October-March) of a particular year, t, for each summit, j. A threshold of 0 °C was chosen because of the strong link with the physiology and growth of alpine plant species (Löffler & Pape, 2020).

The CGD over 23 years (1999–2022) was used for analysis of summit vegetation cover change. The CGD was determined from 1999 to 2022 to generate a time series that is pertinent to the vegetation surveys to examine the climate history prior to each survey. We selected 1999 to 2004 as our baseline and subsequently summed the CGD between survey periods (i.e. 1999-2004, 2005-2012, 2013-2017 and 2018-2022).

Fire

Summits were affected by fire to various degrees (**Figure 3.1**). Between 2003 and 2022, all summits experienced fires (except Mt. Bogong and Mt. Hotham). Notably, two summits (Feathertop and The Twins) were burnt three times within this period (2003, 2007, and 2013). At a local scale, fire was patchy across the summits. To quantitatively assess the impact of fire on vegetation coverage, we used a fire-history dataset which contained the spatial extent of fires across the study region (DEECA, 2022). This dataset records each instance an area was burned, providing a continuous overlay of all fires recorded since 1900. However, the precise localities of fires were unknown for six summits. In these cases, we conducted detailed surveys of burnt vegetation. These surveys were completed immediately following the 2007 fires using the four permanent LITs. Burnt and unburnt vegetation were recorded at 10 cm intervals. This data was used to analyse the effects of fire on summit vegetation cover (**Appendix I, Table S2**).

Elevation

The study summits represent an altitudinal gradient, ranging from 1668 m to 1970 m. Consequently, they may vary in precipitation, evapotranspiration, solar radiation, and soil properties (Körner, 2003, **Appendix I, Table S1**). We incorporated elevation to account for these correlated variables.

Data analysis

To examine changes in the dominant vegetation on alpine summits over time, we utilised state and transition models (STMs). Subsequently, we developed hierarchical models to statistically estimate environmental factors (e.g. growing degree days, time-since-fire, elevation) that affected transitions in vegetation on these summits.

Australian alpine summit structural state and transition model

State and transition models (STM) can assist in describing resilience and event-driven dynamics (Bestelmeyer et al., 2009; Westoby et al., 1989; Williams, 1990b). A state transition represents the abrupt and unexpected shift into an alternative state, which can only be reversed slowly, if at all (Scheffer et al., 2009). Many STMs describe state resilience in terms of plant community structure observed over time or associated with disturbances such as fires or grazing (Bestelmeyer et al., 2009; Williams, 1990b). Here, we used data-driven STMs to detect shifts in ecosystem states, often observable with a change in dominant lifeforms (Scheffer et al., 2001), in unburnt and burnt summits.

We defined an ecosystem state as a vegetation cover type, i.e. lifeform (forb, graminoid, or shrub) or substrate (bare ground, litter, or rock). A shrub was defined as an evergreen, perennial woody plant. Shrubs were typically low-statured, prostrate dwarf shrubs (0.10 - 0.5 m) or tall shrubs (0.5 - 1.3 m). Dominant dwarf shrub species include *Hovea montana* (Fabaceae) and *Kunzea muelleri* (Myrtaceae), and dominant tall shrub species include *Grevillea australis* (Proteaceae), *Acrothamnus montanus* (Ericaceae), and *Podolobium alpestre* (Fabaceae). Alpine summits were typically dominated by facultative seeder shrubs (e.g. *Hovea montana, Kunzea muelleri*) and some obligate seeder species (e.g. Grevillea australis). Facultative seeder species are capable of vegetative resprouting via stem laying or root-suckering and are thought to have a lifespan of > 50 years (Williams & Ashton, 1988; Williams, 1987). Obligate seeder species are readily killed by fire but can regenerate prolifically from seed in fire-affected soils (Gill, 1981). They are considered to live to approximately 50 years before senescence (Williams & Ashton, 1988; Williams, 1987). Graminoids were herbaceous monocot angiosperms with grass-like morphology, typically tussock-forming grasses, rushes, or sedges (Körner, 2003). The most abundant graminoid species on summits were the tussock snowgrasses of the *Poa* genera (Poaceae). Forbs were defined as herbaceous dicot that was not a graminoid (Körner, 2003). Dominant forb species in alpine summits include alpine specialist species in Asteraceae: *Celmisia costiniana, Leptorhynchos squamatus* subsp. *alpinus*, and *Craspedia* spp., and the exotic species *Hypochaeris radicata*. Of these species, some are rhizomatous plants forming extensive colonial carpets, and others are individual rosette species. Lastly, substrates were defined as either rock, bare ground, or litter, representing distinct abiotic components within the ecosystem that moderate community dynamics and resilience (Bestelmeyer et al., 2009).

Using data from 2004 and 2022, state and transition stages were quantified for individual points across the LIT structural survey data for the 10 summits. The 2004 state was then compared to the 2022 state. This was then related to the fire surveys completed post the 2007 fire. We described the probability of a vegetation lifeform or substrate undergoing a transition from 2004 to 2022 from a conditional distribution (Samuels, 2003):

$$P(B,F) = \frac{P(A,B,F)}{P(B,F)} \tag{2}$$

where A is the lifeform or substrate observed in 2022 and B is the lifeform or substrate observed in 2004 at a point along the LIT. *F* is the fire history of summits during the study period. Thus, the probability of change was calculated as the proportion of points at a given site, given the fire history, divided by the total number of points along a transect. A transition of a given lifeform or substrate indicated structural change where a threshold was crossed (Scheffer et al., 2001). Probabilities of state and transitions were displayed through a schematic structural change model.

Factors influencing summit vegetation transitions

Using the full dataset (14 summits), we examined vegetation structural type response to summit-level environmental factors (elevation, fire, warming) over four time points (2004, 2012, 2017, 2022). We focused on forb, graminoid, and shrub dynamics and built multiple hierarchical models to examine environmental factors influencing transitions in lifeform states. For each model, we used Bayesian inference and fitted models using the R package brms (Bürkner, 2021) in R 4.3.3 (R Core Team, 2024).

Prior to analysis, we first tested for collinearity between variables with a determinant of the correlation matrix. We assessed the correlation between variables using the Pearson correlation value (threshold of $r < 0.7$) (Dormann et al., 2013). To compare the magnitude of effects between covariates with different units, we centred all covariates on their associated means and divided them by one standard deviation (Gelman & Hill, 2007). The advantage of centring and standardising is that it allows for simpler interpretation, with intercepts interpreted as responses to average conditions and slope terms as partial dependencies conditional on other continuous variables being at their mean (Camac et al., 2017).

We constructed Bayesian Generalised Linear Mixed Models (GLMM) to analyse the data. Mixed effect models are appropriate for hierarchical data structures (e.g. transects nested within sites) as they can partition variation at multiple levels and account for observation error (Gelman & Hill, 2007; Kéry et al., 2012). Specifically, we ran the models using four chains, sampling 2000 interations. The first 1000 iterations of each chain were discarded and treated as warm-up/burn-in, leaving a total of 4000 posterior samples across chains (Camac et al., 2017). We determined chain convergence using the Brooks-Gelman-Rubin convergence diagnostic (Brooks & Gelman, 1998). Posterior inferences were then made using these 4000 samples. We assessed the adequacy of the models by posterior predictive checks, comparing replicated data generated under the fitted models to the observed data (**Appendix III, Figures S8-10**). Below, we describe the model structure and parameters used in these models.

Lifeform cover, Y_{jt}, and each summit, *j*, and each sample period, *t*, was modelled as random realisation from a binomial distribution:

$$Y_{jt} \sim Binomial(N_{trials}, P_{jt}) \tag{3}$$

$$logit(P_{jt}) = \alpha + \beta_1 \times E_j + \beta_2 \times F_{jt} + \beta_3 \times CGD_{jt} + \beta_4 \times (F_{jt} \times CGD_{jt}) + \varepsilon_j + \varepsilon_t \tag{4}$$

Here, P_{jt} is the estimated likelihood of a lifeform being intercepted on summit, *j*, at time, *t,* and N_{trials} is the total number of lifeforms or substrates along a line intercept transect. We modelled, P_{jt}, on the logit scale as a linear function of summit elevation (E_j), time-since-fire (F_{jt}) and cumulative growing degrees (CGD_{jt}). We included interactions between F_{jt} and CGD_{jt} because the impact of CGD_{jt} on vegetation cover will depend on how long a summit has remained unburnt. We also included random intercept effects for site, ε_j, and survey year, ε_t. Random effects were included for several critical reasons, including accounting for the non-independent structure of observations within sites and over time, estimating group-level effects and providing a means to predict new group levels (Camac et al., 2017). Model intercepts, α, and coefficients, β, were estimated using weakly informative student's t priors. These student's t priors are the brms package default priors (Bürkner, 2021). Partial dependency plots were then created for the average site and the average year. P_{jt} was modelled separately for forbs, graminoids and shrubs, but the three models are structurally similar. **Appendix III, Figures S11-13** show the conditional modes of the random effects (site and year) from the fitted models.

Results

Australian alpine summit structural change model

Over the duration of the 18-years survey period, there was a high persistence of vegetation states over time on summits, particularly shrubs. In the absence of fire, vegetation states were more likely to be stable, i.e. remain in the same state (the proportion of shrubs remaining stable was shrubs 0.71, forbs 0.50, graminoids 0.50, **Figure 3.2**) relative to summits that were burnt during the study period, with forbs experiencing the greatest decline in stability (shrubs 0.62, forbs 0.24, graminoids 0.43, **Figure 3.2**). Unburnt summits had higher bare ground patches (0.27) than burnt summits (0.13). Rock had similar stability between unburnt (0.29) and burnt (0.33) summits. Litter was not stable over time. Overall, there was higher vegetation community structural stability without disturbance.

Without fire, the highest number and proportion of state transitions occurred to the shrub state. For example, a high proportion of shrubs colonised and established in bare ground (0.28) and litter (0.28) and had grown over rock (0.39) over time (**Figure 3.2**). Shrubs also replaced forbs (0.22) and graminoids (0.22) over time. Despite this, forbs had the highest probability of colonising litter (0.38). Forbs also established in bare ground (0.23) and graminoids (0.18), but to a lesser degree than shrubs. This indicates a shift towards a shrubbier community in the absence of disturbances such as fire. By contrast, the fire-affected summits experienced more transitions between states, with the highest number and proportion of transitions occurring in graminoids (**Figure 3.2**). This included an overall shift to graminoids from forbs (0.42), litter (0.50), bare ground (0.38), rock (0.26) and shrubs (0.23).

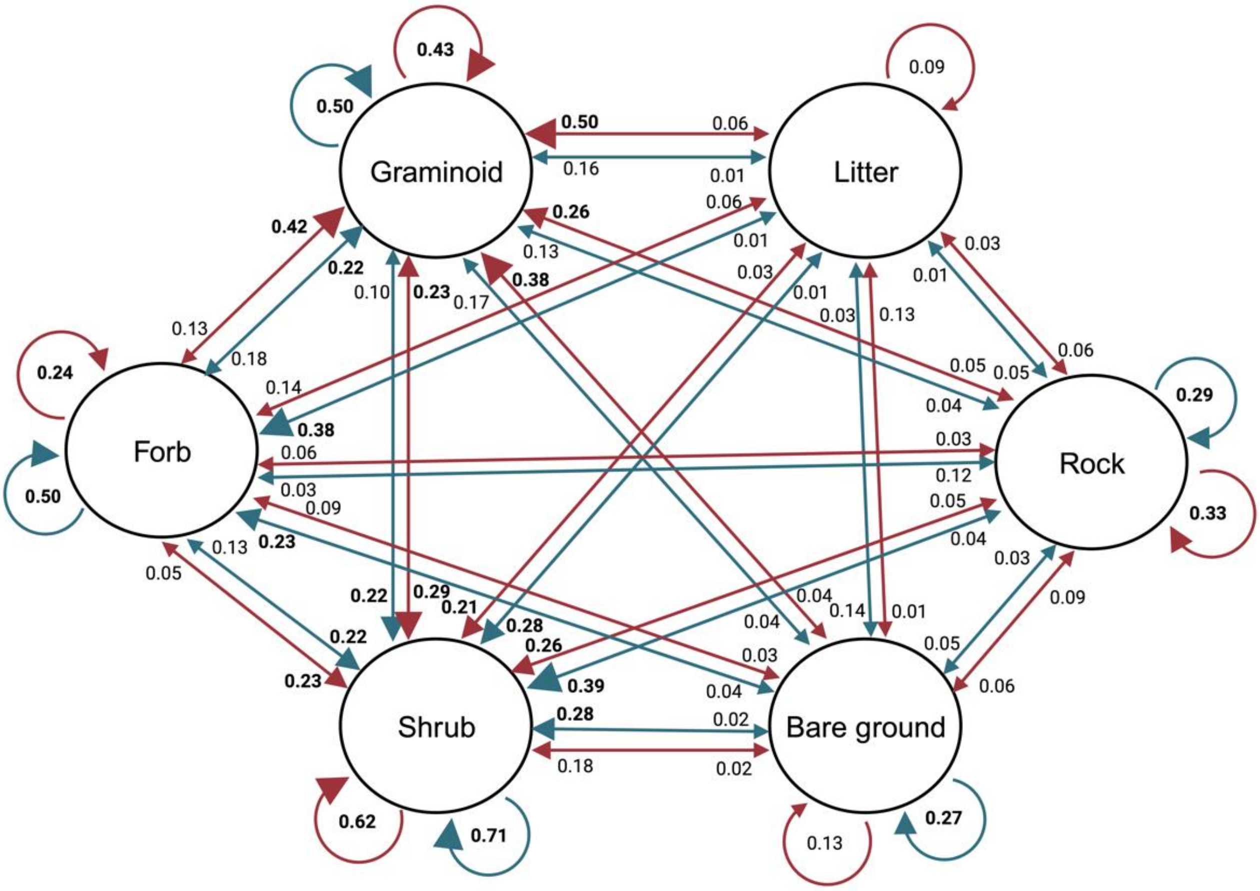

Figure 3.2 The structural change model summarises the proportion of change in alpine summit vegetation states in unburnt (blue) and burnt (red) mountain summits. The model identifies the key transitions from one state to another. Arrows indicate a state transition occurred between 2004 and 2022. The probability of change was shown for each state and transition, also reflected by the arrow thickness.

Drivers of alpine summit vegetation cover change

Across the 14 summits surveyed, we found that vegetation cover was strongly influenced by cumulative summer growing degree (CGD). However, this was dependent on time since fire. As time since fire (years) increased and growing time accumulated, there was a strong positive effect on forb (**Figure 3.3a**) and graminoid cover (**Figure 3.4a**) and a negative effect on shrub cover (**Figure 3.5a**). For instance, summits that have gone 83 years without fire have experienced an increase of 23% forb (**Figure 3.3c**) and 69% graminoid cover (**Figure 3.4c**) and a 26% decline in shrub cover (**Figure 3.5c**) with a 63,900 °C increase in cumulative growing degrees over 18 years. Conversely, recently burnt summits (4 years) experienced an increase of 7% forb (**Figure 3.3c**), 63% graminoid (**Figure 3.4c**) and 21% shrub cover (**Figure 3.5c**) with a 63,900 °C increase in cumulative growing degrees over 18 years.

Elevation had a positive influence on forb cover, with a predicted 33% increase at summits at 2000 m elevation compared to those at 1500 m (**Figure 3.3a, d**). In contrast, elevation showed no discernible effect on graminoid cover (**Figure 3.4a, d**) and shrub cover (**Figure 3.5a, d**).

Graminoid cover had higher unexplained variation among years than sites (**Figure 3.5b**), whereas forb (**Figure 3.3b**) and shrub cover (**Figure 3.4b**) had similar unexplained variation among sites and years. However, the year estimates had larger uncertainty for all models.

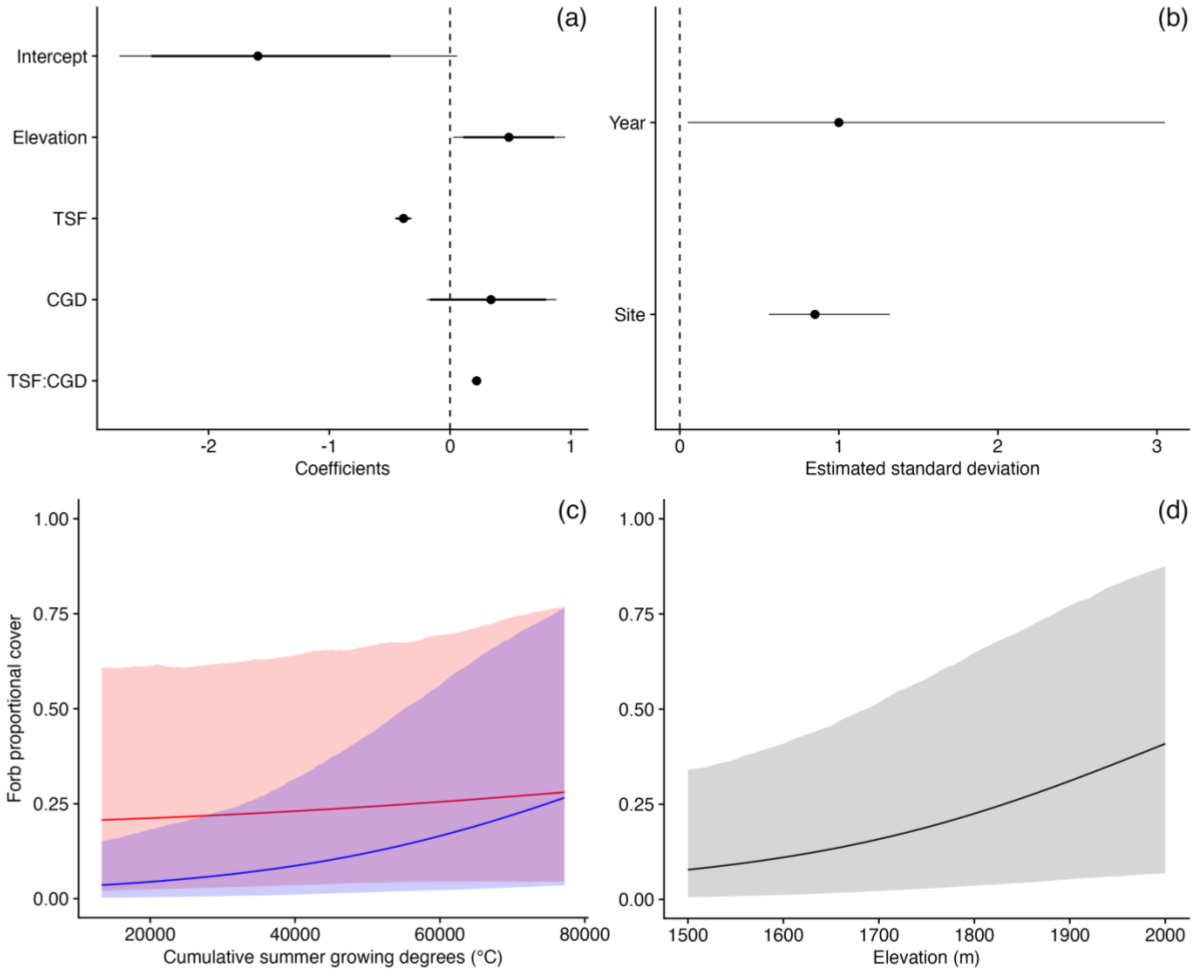

Figure 3.3 The effects of environmental factors on forb cover on Australian summits. (a) Centred and standardised model coefficients (on the logit scale) and the effects of (c) the interaction between time since fire and cumulative growing degrees (°C) at recently burnt summits (4 years) indicated in red and blue at long unburnt summits (83 years) and (d) elevation (m) for the average summit. (b) The model estimated standard deviation among sites and year. The significance can be determined if the 95% or 89% credible intervals cross the 0 line (dashed line). The predicted mean forb proportional cover as a function of the environmental factors at the average site and average year are shown. Thin error bars and shaded areas indicate 95% Bayesian credible intervals, and thick error bars indicate 89% Bayesian credible intervals.

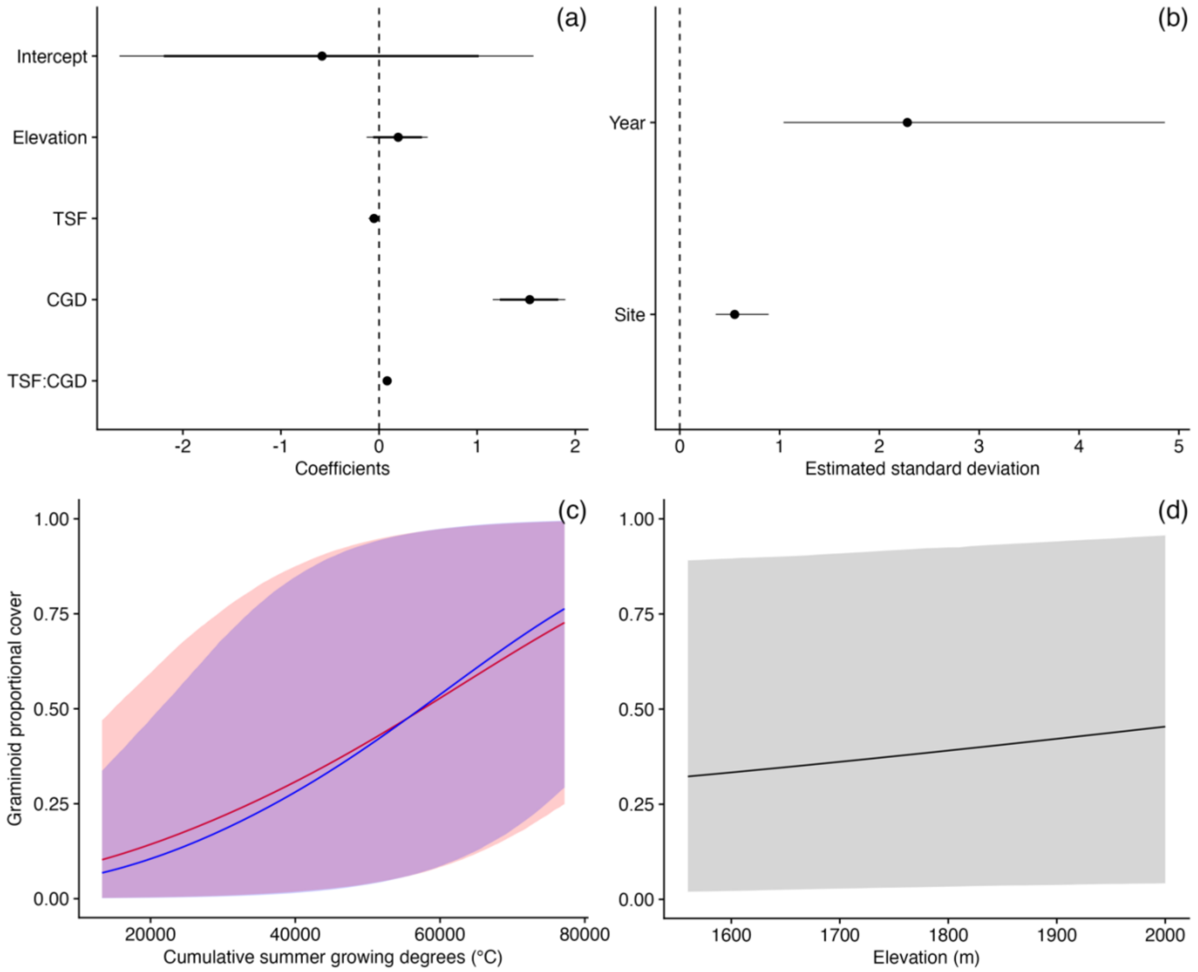

Figure 3.4 The effects of environmental factors on graminoid cover on Australian summits. (a) Centred and standardised model coefficients (on the logit scale) and the effects of (c) the interaction between time since fire and cumulative growing degrees (°C) at recently burnt summits (4 years) indicated in red and blue at long unburnt summits (83 years) and (d) elevation (m) for the average summit. (b) The model estimated standard deviation among sites and year. The significance can be determined if the 95% or 89% credible intervals cross the 0 line (dashed line). The predicted mean graminoid proportional cover as a function of the environmental factors at the average site and average year are shown. Thin error bars and shaded areas indicate 95% Bayesian credible intervals, and thick error bars indicate 89% Bayesian credible intervals.

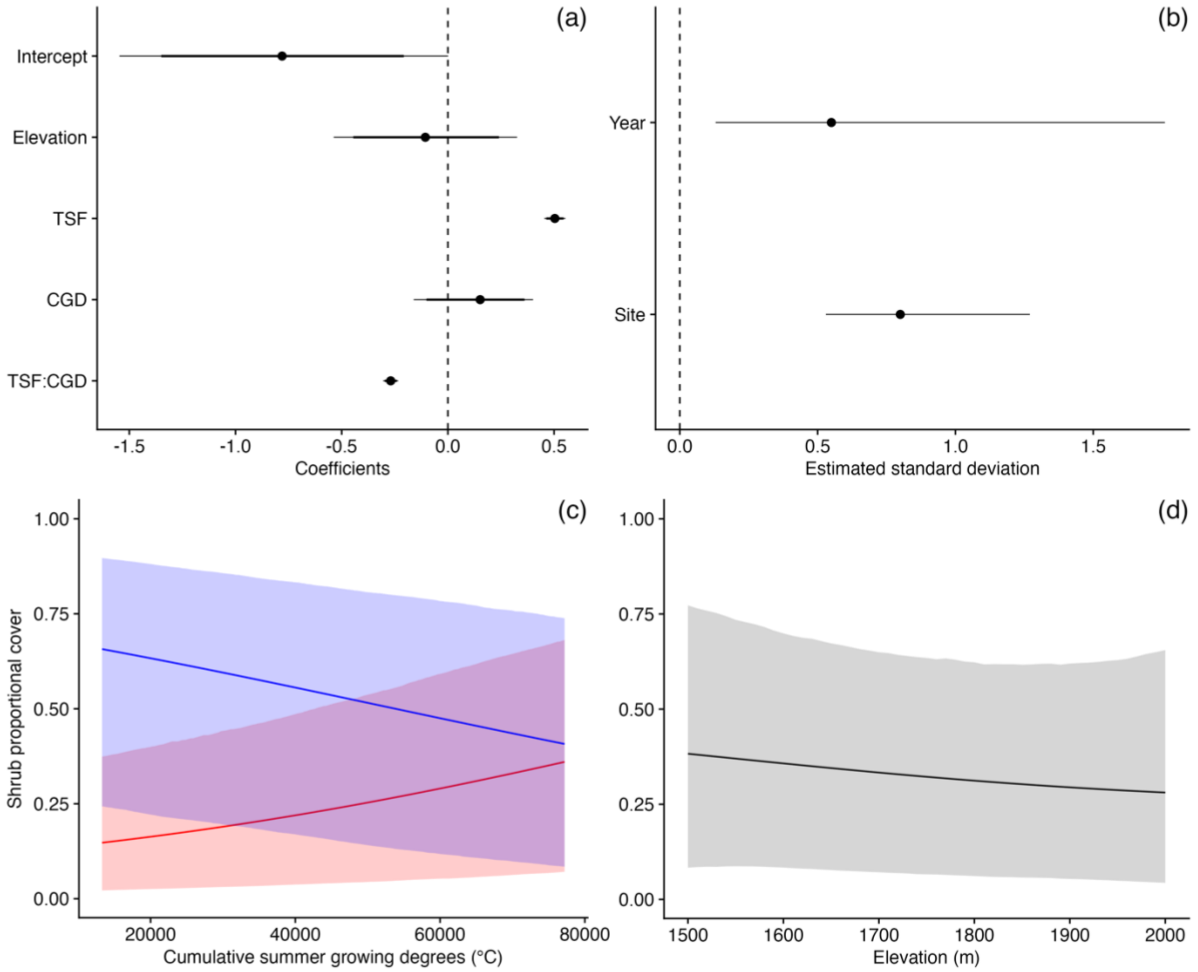

Figure 3.5 The effects of environmental factors on shrub cover on Australian summits. (a) Centred and standardised model coefficients (on the logit scale) and the effects of (c) the interaction between time since fire and cumulative growing degrees (°C) at recently burnt summits (4 years) indicated in red and blue at long unburnt summits (83 years) and (d) elevation (m) for the average summit. (b) The model estimated standard deviation among sites and year. The significance can be determined if the 95% or 89% credible intervals cross the 0 line (dashed line). The predicted mean shrub proportional cover as a function of the environmental factors at the average site and average year are shown. Thin error bars and shaded areas indicate 95% Bayesian credible intervals, and thick error bars indicate 89% Bayesian credible intervals.

Discussion

Here, we used a revisitation design to investigate alpine summit plant community dynamics and understand mechanisms of change. We showed distinct trajectories of change for dominant vegetation types on summits in response to global drivers of change. Specifically, we found the effect of cumulative growing degree days depended on fire occurrence. As time since fire increased and the growing degrees accumulated, there was a strong positive effect on forb and graminoid cover and a negative effect on shrub cover. These results indicate that alpine summit vegetation will respond multi-directionally to challenges posed by a warming climate and changing fire regimes, with outcomes likely contingent on life history characteristics (Williams & Ashton, 1988). These findings build on previous work in response to climate change and disturbance regimes, e.g., the 'Shrub-fire feedback model', Camac et al. (2017) and the 'Shrub-grass balance', Williams (1987). We summarise these dynamics in **Figure 3.6**. This highlight the need to consider the impacts of compounded perturbation on alpine vegetation under changing climates (Fairman et al., 2017).

On summits that are long-unburnt (83 years), we identified transitions of lifeforms and substrates to shrub and graminoid states over time. Shrub encroachment into alpine ecosystems has been observed in the European Alps (Dullinger et al., 2003; Hallinger et al., 2010; Rundqvist et al., 2011), the North American Alps (Dial et al., 2016; Myers-Smith et al., 2019; Myers-Smith & Hik, 2018), and other Australian alpine environments (Camac et al., 2017; Venn et al., 2012, 2014; Verrall et al., 2021; Wahren et al., 2013; Williams, 1990a), often at the expense of grassland species (Camac et al., 2015; McDougall, 2003; Wahren et al., 2013). The range expansion of woody species into alpine environments will result in biotic differentiation, which changes the structure, composition, and function of alpine communities (Evangelista et al., 2016; Venn et al., 2014; Verrall et al., 2021). Shrubs can modify ecosystem processes and magnify the effects of climate change by, for example, affecting snow depth and altering associated biological processes (Myers-Smith et al., 2011). Shrubs are often the tallest plants in alpine ecosystems, with long-lived dense canopies (Myers-Smith et al., 2011) that enable them to be competitively superior for light capture (Camac et al., 2017; Myers-Smith et al., 2011; Wahren et al., 2013). Similarly, increasing graminoids has implications for ecosystem processes such as modified biotic interactions by increasing intraspecific and interspecific competition (Alexander et al., 2015). The expansion of dominant alpine grass species has been attributed to their ability to tolerate drought and exploit the warmer climate (Griffin & Hoffmann, 2012). Consequently, as the climate continues to warm, the invasion by more competitive, dominant species will likely re-assemble short-statured alpine ecosystems such as grasslands, snowpatches, and herbfields (Gottfried et al., 2012; Williams et al., 2015).

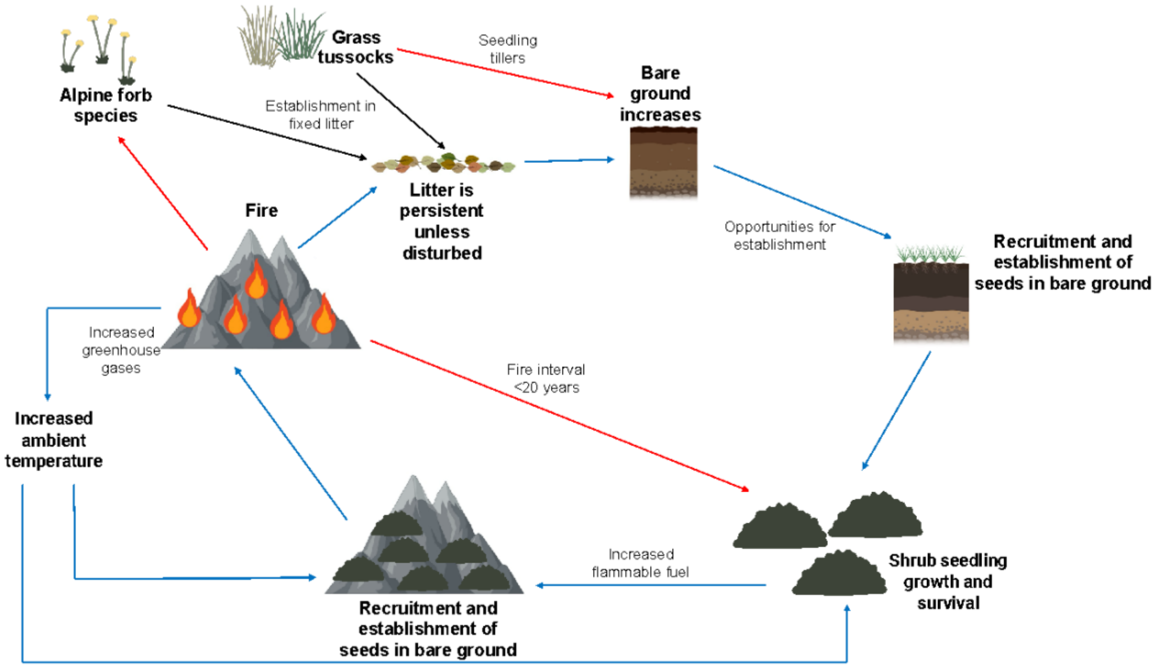

Figure 3.6 Diagrammatic summary of the major interactions and feedbacks involving disturbance (fire and climate warming) and regeneration of dominants in the alpine vegetation showing positive (blue) and negative (red) feedbacks, adapted from Camac et al. (2017) and Williams (1990b). A warmer climate and an increased frequency of extreme events, such as fires, will result in positive outcomes for shrub species, particularly for obligate seeder shrubs. Increased fire frequencies will create more bare ground for shrubs to recruit and establish, resulting in increased landscape flammability. Fire negatively affects forbs and reduces fixed litter required for the regeneration of forb species. Too frequent fire may negatively affect survival of shrubs – especially obligate seeders - with warming.

Under contemporary climate change, alpine environments are projected to experience an increase in fire frequency, severity and extent (Bradstock et al., 2014; Zylstra, 2018) and warming will improve growth and recruitment conditions for woody species (Myers-Smith & Hik, 2018). Despite the focus on shrub encroachment in alpine environments and some patches of long unburnt summits experiencing shrub encroachment in the state and transition model, the hierarchical models showed that shrub cover declined with increasing growing time on average. As such, variability in landscape features, dispersal dynamics, biotic interactions and demographic responses could lead to shrub encroachment being more spatially sporadic than previously thought (Alexander et al., 2018; Angers-Blondin et al., 2018; Camac et al., 2017; Myers-Smith & Hik, 2018; Tape et al., 2006; Williams, 1990b). While global warming will reduce low temperatures and snow cover (the principal abiotic drivers of alpine communities), the existing vegetation cover limits colonisations by limiting the number of ‘safe sites’ for establishment (Alexander et al., 2018; Angers-Blondin et al., 2018). This may reduce the likelihood that shrubs can expand their distributional ranges, i.e. ‘establishment-lag’, which could translate to community resilience to climate change (Alexander et al., 2018; Angers-Blondin et al., 2018). For example, in the absence of disturbance (i.e. bare ground), obligate seeder species, such as *Grevillea australis*, have limited opportunity to regenerate (Camac et al., 2017; Williams, 1990b, 1992). Furthermore, not all shrub types uniformly respond to warmer summer temperatures. Dwarf shrubs declined with long-term warming experiments, whereas tall shrubs increased throughout their range (Elmendorf, Henry, Hollister, Björk, Bjorkman, et al., 2012; Elmendorf, Henry, Hollister, Björk, Boulanger-Lapointe, et al., 2012). Consequently, observed declines in shrub cover with increasing growing time could result from demographic effects and senescence (Williams, 1990b). Overall, the realised extent of range shifts depends not only on climate suitability but also on biotic interactions within the community (Angers-Blondin et al., 2018; Camac et al., 2015; HilleRisLambers et al., 2013).

Other environmental elements, such as elevation and fire, were also identified as key factors driving summit vegetation changes. Notably, the effect of increasing growing time was found to be contingent on the presence of fire and was the primary catalyst for shifts in vegetation dominance on alpine summits. Burnt summits experienced greater instability of lifeform states, resulting in different trajectories of lifeforms compared to climate warming, particularly shrubs. Fire temporarily reduced shrub cover and increased graminoid and herb cover, resulting in a pyrogenic herbaceous vegetation cover pulse. Forb species such as *Stellaria pungens* (Caryophyllaceae) are known to be effective post-fire colonisers in Australian alpine areas (Doherty & Wright, 2006), and pyrogenic growth, flowering and seed set have been documented for snow grasses (Wahren et al., 2001). Fire, as one agent of disturbance, can affect vegetation productivity, structure, and composition (Bowman et al., 2014; Keeley et al., 2011). It can act as a positive catalyst for ecological boundary change (Camac et al., 2015; Körner, 2003), triggering seed release, reducing ground layer competition, and generating bare ground opportunities for a pulse of seedling establishment (Camac et al., 2017). Succession after land use disturbance, such as fire, can explain vegetation dynamics in Australian alpine vegetation (Kirkpatrick et al., 2002; Scherrer & Pickering, 2005; Williams, 1990a) and overseas (Brown et al., 2006; Roxburgh et al., 1988) and needs to be considered when investigating the relative contributions of different, co-occurring drivers of plant species range change over time.

However, fire did not promote a substantial increase in shrub cover on summits, as predicted by the shrub-fire feedback (Camac et al., 2017). This is in contrast with other studies that show shrubs can re-establish in bare ground patches resulting from such fires and, provided the fires are not too frequent, will eventually revert to a shrubby state given adequate time (Camac et al., 2017; Williams, 1992). Additionally, climate warming has improved growth and recruitment conditions (Myers-Smith & Hik, 2018), potentially enabling shrub species to attain reproductive maturity faster post-fire. Our findings may be the result from time-lag processes where changes lag behind climatic changes (Alexander et al., 2018). Such lags in shrub cover on summits post-fire may be explained by, for instance, variations in biotic interactions (Angers-Blondin et al., 2018; Dullinger et al., 2003). For example, competitive interactions post-fire with vigorous grass regrowth have been a key factor limiting shrub invasions in alpine environments, particularly infilling bare ground gaps (Angers-Blondin et al., 2018; Camac et al., 2017; Dullinger et al., 2003). Overall, the realised extent of range shifts depends not only on climate suitability but also on biotic interactions within the community (Angers-Blondin et al., 2018; HilleRisLambers et al., 2013).

The findings from this study and others (Evangelista et al., 2016; Graae et al., 2018; Grabherr et al., 1994; Pickering et al., 2014; Venn et al., 2014; Verrall et al., 2021; Williams et al., 2008) suggest that the vegetation in alpine regions is undergoing change driven by warming conditions and increased fire frequency. This is particularly concerning for alpine summit vegetation, as such areas are considered the most sensitive to climate change and contain many specialised and endemic species (Grabherr et al., 1994; Theurillat & Guisan, 2001). Of particular concern for alpine regions is the escalating severity and frequency of fire associated with climate change (Hennessy et al., 2008; Kampf et al., 2022; Zylstra, 2018); historically, these regions have experienced few fire events at century timescales (Higuera et al., 2008; Williams et al., 2008). Consequently, successional processes might compromise how we observe change (directional, with respect to climate). The predicted increase in fire frequency associated with climate warming may provide opportunities (i.e. via bare ground) for novel species, particularly shrubs, to establish on mountain summits (Camac et al., 2017). Warmer conditions are expected to facilitate shrub expansion and upslope migration, and fire may aid shrub encroachment by removing competitors (Camac et al., 2017; Elmendorf, Henry, Hollister, Björk, Bjorkman, et al., 2012; Wahren et al., 2013). Because shrubs are the most flammable vegetation component in alpine habitats, their encroachment could strengthen positive feedback between warming, fire, and shrubs, thus accelerating landscape changes (Camac et al., 2017; Fraser et al., 2016; Higuera et al., 2008; Venn et al., 2016; Williams et al., 2006). However, negative climate-fire-shrub feedbacks may also emerge, hindering shrub expansion (Camac et al., 2017; Fairman et al., 2017). Continuing to monitor alpine summit vegetation will assist in discerning which factors are driving alpine vegetation dynamics and whether shrubs will increase under a warming climate and shorter fire intervals (Alexander et al., 2018; Angers-Blondin et al., 2018; Camac et al., 2017, 2021).

Conclusions

Using a simple scientific design, this study sheds light on patterns and processes in Australian alpine mountain summit vegetation to infer long-term dynamics in vegetation state trends. The findings indicate the multifaceted nature of change that must be accounted for in alpine vegetation studies. We found that the effect of cumulative growing degrees on vegetation depended on fire. When time since the fire increased and growing degrees accumulated, there was a positive effect on forb and graminoid cover but a negative effect on shrub cover. These findings suggest that disturbance brings about changes in vegetation structure that may not be related to climate. Notably, fire-disturbed summits experienced higher vegetation instability, resulting from successional processes. Meanwhile, the lack of disturbance may result in declining shrub cover based on demographic responses. These findings demonstrate the value of maintaining long-term monitoring sites within alpine ecosystems (Williams et al., 2014), because vegetation change is invariably slow, and drivers of change may be sporadic (e.g. individual fires) or very gradual (e.g. rising temperatures).

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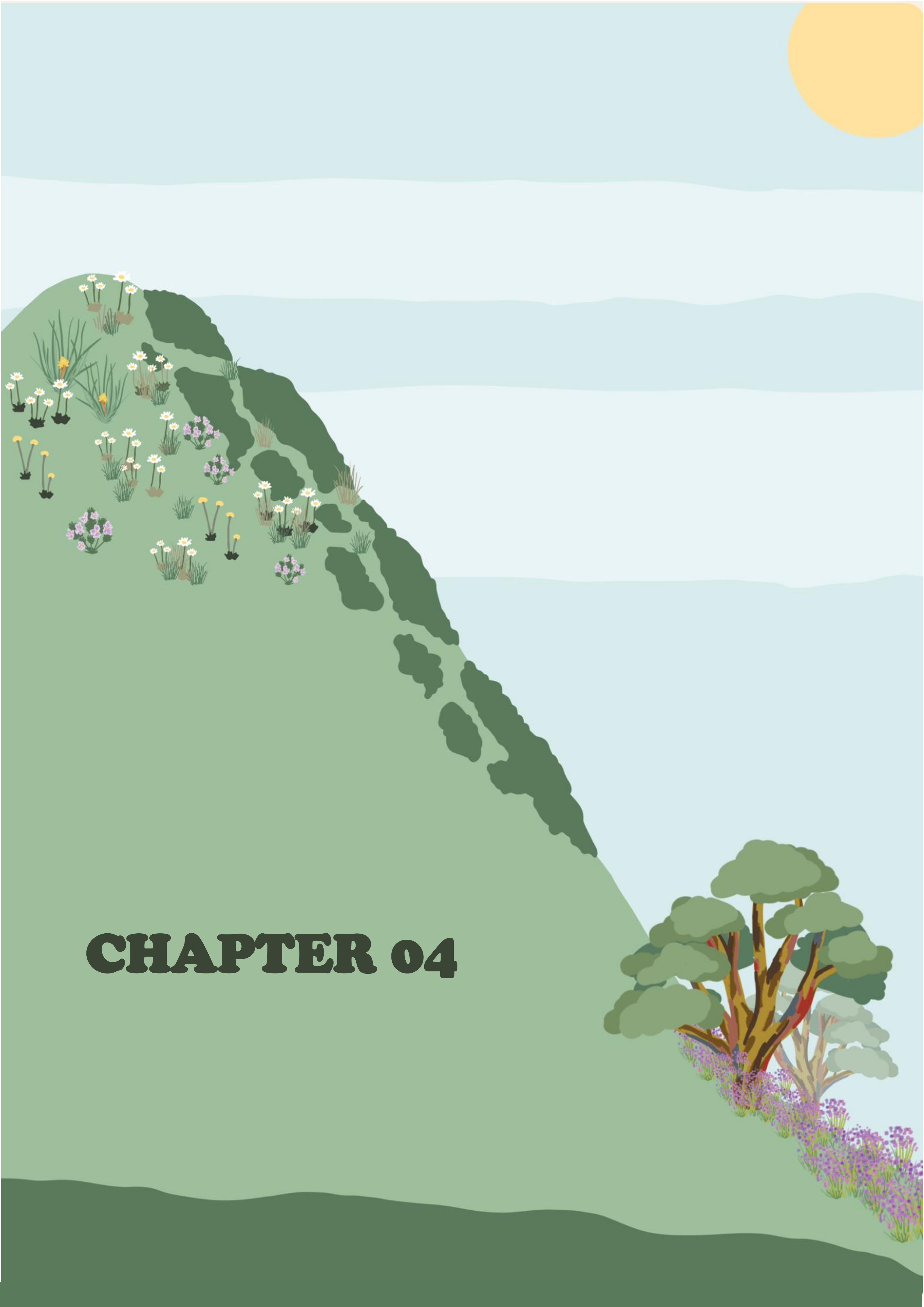

CHAPTER 04

Chapter 4: Topography's role on summit vegetation patterns

4.1 Details, author contributions and declaration

This chapter consists of a paper that is in preparation for submission to the *Australian Journal of Botany*, which was co-authored with my supervisor and co-supervisors. The details of this paper are:

Hickman, I.T., Venn, S.E., Camac, J.S., Williams, R.J., & Morgan, J.W. (in preparation). Topographic heterogeneity and its role in mediating climate change responses in Australian alpine summit vegetation. *Australian Journal of Botany*.

Author contributions for this paper are as follows:

Author	**Contribution**	**Percent contribution**
ITH	conceptualisation, project administration, investigation, data collection (2022), data analysis, writing, reviewing and editing.	85%
JWM	conceptualisation, data collection (2004-2022), project administration, reviewing and editing.	5%
SEV	conceptualisation, data collection (2004-2022), reviewing and editing.	4%
JSC	data analysis, reviewing and editing.	5%
RJW	conceptualisation, reviewing and editing.	1%

4.2 Paper's title

Topographic heterogeneity and its role in mediating climate change responses in Australian alpine summit vegetation

4.3 Abstract

Context: Complex topography creates fine-scale microclimate variations that can influence vegetation community assembly and likely drive how it responds to climate change. In high mountainous areas, topographic heterogeneity has been demonstrated to mediate responses to regional climate warming by creating small-scale variations in solar radiation, which directly impact temperature, water, and energy availability across landscapes. **Aims:** This study examines the influence of diverse topography on the distribution of vegetation on mountain summits to better understand the response of alpine plants to climatic change. **Methods:** We conducted vegetation surveys on 14 alpine summits in Victoria, Australia and used variations in topographic features (aspect, slope, elevation) to determine microclimates in solar radiation input. We then constructed eight hierarchical models to examine the influence of solar radiation on diversity, the cover of ecological groups (endemics, generalist, and exotic), and plant functional trait types. **Key results:** Our analysis revealed a muted effect of a solar radiation gradient on alpine summit vegetation patterns. However, areas of the landscape that experience more solar radiation tended to shift towards a shrubbier, stress-tolerant constituent of their community, while areas with less solar radiation shift towards a herbaceous community. **Conclusions:** These findings indicate that the factors driving alpine plant population and community dynamics vary greatly across the complex topography landscape typical of high-elevation mountain ecosystems. **Implications:** This demonstrates that the vegetation patterns due to fine-scale heterogeneity in solar radiation could mediate the direction of vegetation responses to climate change.

4.4 Introduction

Alpine ecosystems are predicted to be sensitive to contemporary climate change (Grabherr *et al.* 1994; Theurillat and Guisan 2001; Dirnböck *et al.* 2011). Globally, alpine environments are experiencing higher temperatures, decreased snowpack (Huss et al., 2017), longer growing seasons (Walker *et al.* 2006) and more frequent extreme events (e.g. heatwaves and fire; Adler *et al.* 2023). As a result, endemic alpine plants are experiencing increases in abiotic stresses combined with competition from expansion and upslope migration of native and exotic warm-adapted species (i.e. thermophilisation) (Gottfried *et al.* 2012; Pauli *et al.* 2012), thus increasing the probability of their long-term local extinction (Stöckli *et al.* 2011; Pauli *et al.* 2012; Dullinger *et al.* 2012; Steinbauer *et al.* 2018; Camac *et al.* 2021). The global consensus is that climate change will reduce the extent, frequency, and distribution of alpine specialists and lead to the expansion of generalist species (Dirnböck *et al.* 2011; Nomoto and Alexander 2021). This is most concerning for species at the highest latitudes and elevations (i.e. summits), which are the most exposed to the changing climate parameters and are most at risk of future habitat loss (Grabherr *et al.* 1994; Theurillat and Guisan 2001; Pauli *et al.* 2012). However, the variation in topography in high mountain environments creates a mosaic of habitats that vary in their microclimatic conditions (Scherrer and Korner 2009; Körner and Hiltbrunner 2021). This, therefore, may act as a compensatory force to mitigate the combined effects of abiotic and biotic stresses. Thus, these projected changes may not be experienced evenly over alpine landscapes.

Topography is a key determinant of climatic variation in high mountain environments. Topography creates differences in solar radiation that directly influence temperature and indirectly influence the availability of water and energy across landscapes, thus affecting the distribution of soil water and vegetation (Graae *et al.* 2011; Lenoir *et al.* 2013; Fan *et al.* 2019). In alpine ecosystems, topographic complexity (e.g. variation of slopes, aspect) at micro-, meso- and macro-scales (tens to thousands of meters) drives variability in the accumulation and redistribution of snow and water, leading to gradients in soil conditions, hydrology, decomposition, and nutrient cycling (Opedal *et al.* 2015; Hu *et al.* 2020). Consequently, landscapes with high local abiotic heterogeneity promote species coexistence at small spatial scales (Kraft 2015; Graae et al. 2018), driving local shifts in the distribution of plant species (Scherrer and Körner 2011; Moeslund *et al.* 2013; Winkler, Lamprecht, *et al.* 2016; Löffler and Pape 2020), plant functional traits (Choler 2005; Spasojevic and Suding 2012), communities (Graae *et al.* 2018), and ecosystem processes (Fan *et al.* 2016). This results in mosaics of vegetation types across the topographically heterogeneous landscapes of alpine environments (Scherrer and Körner 2011; Körner and Hiltbrunner 2021). However, despite the importance of topography for plant life, the patterns of variation attributed to topography are not well documented (Körner and Hiltbrunner 2021).

The topographic heterogeneity of alpine areas can induce differential responses to regional climate change at meter-scale resolutions, analogous to the variations observed in species responses across broader spatial and temporal dimensions (Scherrer and Körner 2011; Dobrowski *et al.* 2013; Suggitt *et al.* 2018a; Oldfather *et al.* 2024), potentially influencing the direction and rate of local community shifts in response to climate warming. Complex meso-topography can give rise to microclimates with mean temperatures that reach expected future climate change scenarios (Scherrer and Körner 2011; Dobrowski *et al.* 2013; Lenoir *et al.* 2013; Opedal *et al.* 2015; Graae *et al.* 2018). On the other hand, topographic heterogeneity can also buffer the direct effects of climate change (Graae *et al.* 2018; Suggitt *et al.* 2018a). For example, in mountainous areas, xeric (warm-adapted) species, such as shrubs and low-elevation species, may be found in warmer microsites with longer growing seasons (e.g. Winkler *et al.* 2016). Mesic (cold-adapted) species, such as alpine endemics, may be found in cooler microsites with prolonged snow cover (e.g. Kulonen *et al.* 2018). Hence, instead of large-scale shifts in elevation, shifts in species distributions locally across meso-topographic gradients may be an early biogeographic response to climate change (Oldfather 2018; Graae *et al.* 2018).

Complex topography may also lead to time lags in realised community change in response to climate change in heterogeneous landscapes (Alexander *et al.* 2018; Graae *et al.* 2018; Falk *et al.* 2019; Körner and Hiltbrunner 2021). The microsite variation can produce microrefugia for populations to persist locally as climate relics (Hampe and Jump 2011; Alexander *et al.* 2018). Consequently, extinction rates and range shifts may be overestimated if microrefugia are not considered in species distribution models (Scherrer and Körner 2011; Bütikofer *et al.* 2020) and potentially contribute to alpine species' resistance to climate change by providing local micro-refugia (Suggitt *et al.* 2018b; Körner and Hiltbrunner 2021). As such, understanding microclimate is essential for forecasting the broader effects of climate change on vegetation dynamics in alpine ecosystems.

This study aimed to ascertain whether the limiting conditions governing alpine vegetation dynamics are mediated by microsite heterogeneity driven by diverse topography on alpine summits. To investigate this, we first determined the microsite conditions driven by meso-topography heterogeneity on summits using modelled solar radiation. We also incorporated plant trait information to understand the potential consequences of climate change by quantifying the link between the environment and vegetation patterns (Bjorkman *et al.* 2018). Typically, species with resource-acquisitive traits display more rapid responses to environmental variations compared to those with more cautious resource-use traits (Soudzilovskaia *et al.* 2013; Oldfather *et al.* 2024). We specifically asked: i) How do these microsite conditions influence the diversity of alpine plant communities on mountain summits? ii) To what extent do these microsite conditions affect the distribution of endemic, generalist, and exotic species across alpine summit communities? iii) Can the observed patterns in species cover and growth forms be attributed to microsite heterogeneity? iv) How do plant functional traits correlate with specific microsite conditions, and what does this reveal about the adaptability of summit plants to climate change?

4.5 Methods

4.5.1 Study area

The study was conducted on 14 alpine summits in Victoria, south-eastern Australia, on the lands of the Daung wurrung, Dhudhuroa, Gunaikurnai, Taungurung, Waywurru and Jaithmatang peoples (**Figure 4.1**). While all summits are above the bioclimate treeline, they range over 290 m in elevation, approximately 43 km of latitude, and 87 km of longitude. Consequently, they vary in biotic and abiotic conditions, such as community types, precipitation, temperature, geology, and land use history (**Appendix I, Table S1**).

All summits in the study area experience a mid-latitude mountain climate that receives an even amount of precipitation year-round, with no dry season, cold winters, and relatively mild summers (Williams 1987; Grose *et al.* 2019). The mean annual rainfall is high (1781-2378 mm), falling as snow in winter and spring (Bureau of Meteorology 2022). Winter maximum air temperatures commonly fall below freezing, ranging from -6 to 12 °C, while summer maximum air temperatures range between 2 to 27 °C (Bureau of Meteorology 2022). Prevailing winds typically originate north-westerly to south-westerly (Williams 1987).

Australian mainland alpine summits are typically dome-shaped rather than conical peaks, which lack significant topographical relief (**Figure 4.1**). Summits also have near complete vegetation cover and high plant biomass compared to many other alpine ecosystems (Costin 2000; Pickering *et al.* 2008; Venn *et al.* 2017). However, the complex topography, microclimatic heterogeneity and geographic isolation of the study area have given rise to a species-rich flora with high endemism (Costin 2000). The alpine treeline ecotone is dominated by snow gum species (*Eucalyptus pauciflora*), forming a demarcation between the alpine and subalpine zones, ranging from 1700–1900 m a.s.l. depending on latitude, aspect, topography, and soils (Green and Pickering 2009; Venn *et al.* 2017).

The plant communities on summits include alpine grasslands, alpine herbfields and open heathlands. Shrubs and graminoids dominate all summits (open to closed heathlands). However, the highest summit is dominated by herbs and graminoids (alpine herbfield) (**Appendix I, Table S1**).

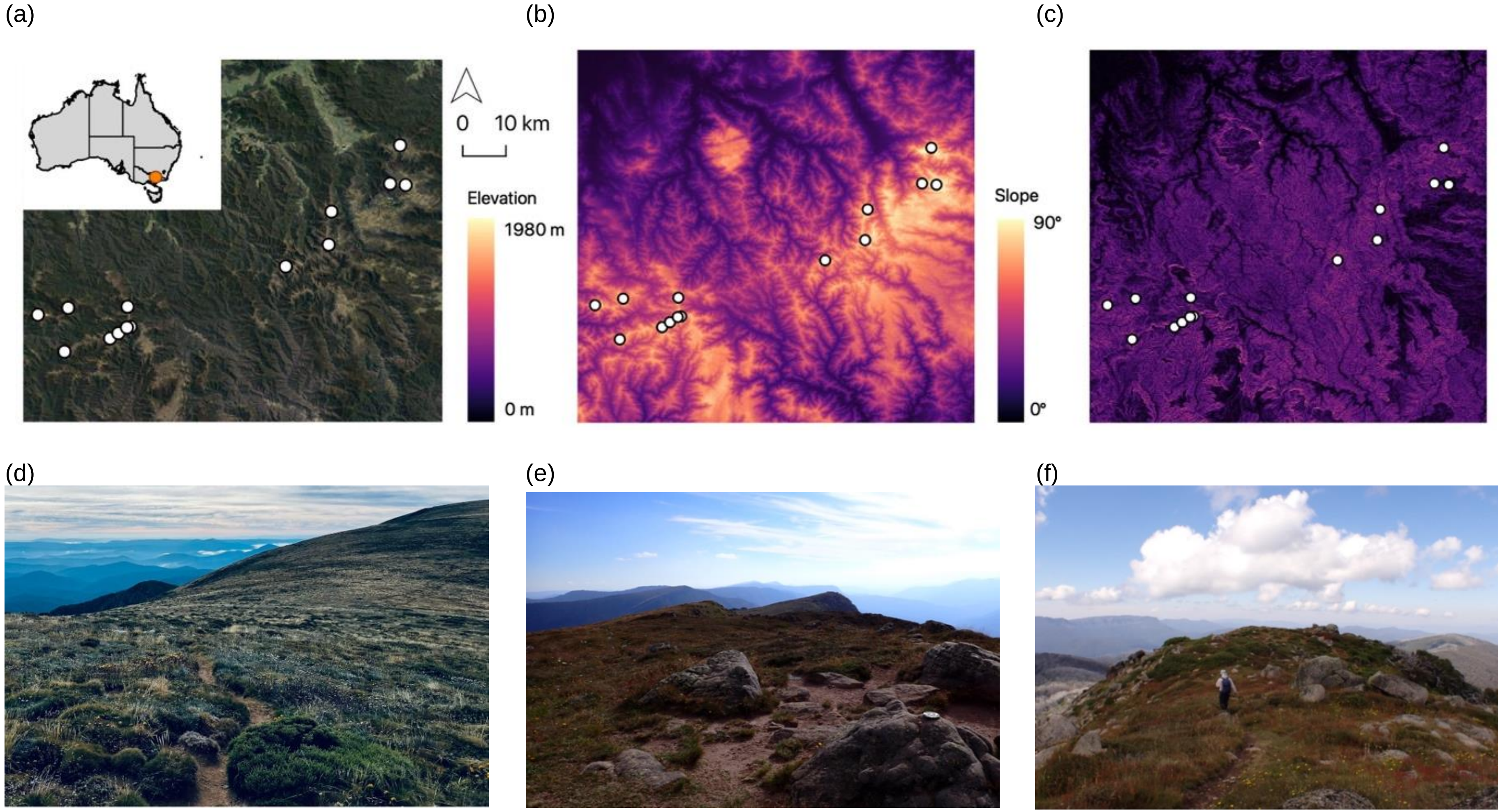

Figure 4.1 Location and characteristics of the study summit areas, including (a) location, (b) elevation and (c) slope of the study area and examples of the topographical variation of Australian alpine summits surveyed for (d) Mount Bogong (Hooker Plateau) (1950 m), (e) Mount Howitt (1740 m), and (f) Mt Stirling (Stanley Knob) (1750 m).

4.5.2 Study design

In 2022, vegetation surveys were conducted at four-cornered plots permanently established on 14 mountain summits by Venn (2007). The plots encompassed the 5 m contour below the highest summit point and were divided into four quadrants, by the four cardinal bearings (**Figure 4.2**; Venn 2007). On summits with little topographic relief, the boundary of the summit survey area was extended to 50 m from the highest summit point. Summit plot sizes ranged from 1141 m^2 to 10,000 m^2. Summits that experience high levels of recreational use were avoided (Venn 2007).

To investigate summit vegetation patterns associated with topographic features, five 1 m x 1 m quadrats were randomly placed into the four quadrants; there were a total of 20 quadrats per summit (**Figure 4.2**; Venn 2007). For each quadrant, the slope, aspect and elevation were measured. All vascular plant species were recorded within each 1 m^2 quadrat, and their percent cover was visually estimated to the nearest 5% (Venn 2007). Nomenclature follows the VICFLORA, Flora of Victoria (https://vicflora.rbg.vic.gov.au/). Following the surveys, species lists were checked, and genus level was recorded if species were not accurately and consistently identified.

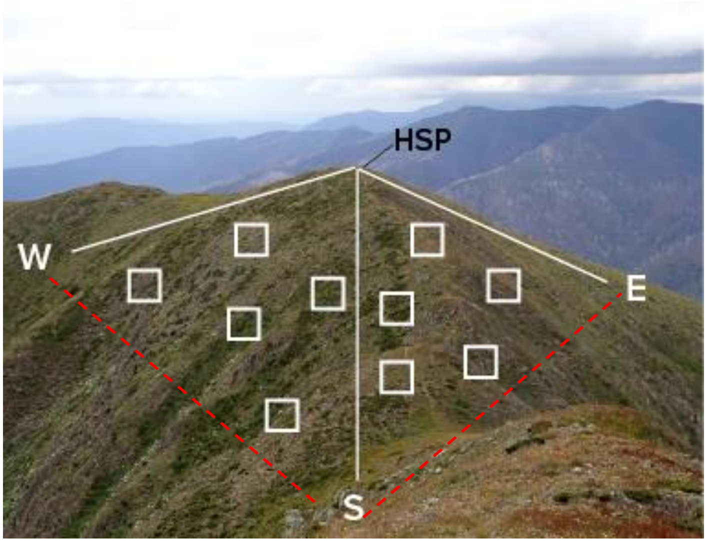

Figure 4.2 The layout of the sampling methodology for the summits. The summit plot, showing the quadrants from the highest summit point (HSP) and the five 1 m^2 quadrats within each quadrant. The plot encompasses the highest summit point (HSP) down to the 5 m contour line (dashed red line). Image of Mt Feathertop North Peak (not to scale).

4.5.3 Microclimatic heterogeneity

In alpine environments, the interaction between microtopography (e.g., aspect, slope, and relative elevation) and solar radiation is one of the key determinants of microclimatic variation at small spatial scales (Lenoir *et al.* 2013; Graae *et al.* 2018; Körner and Hiltbrunner 2021). Solar radiation has been used as a predictor variable in modelling temperature in complex terrain (Dobrowski *et al.* 2013). Differences in solar radiation due to aspect and slope generate local patterns in temperature, light, and moisture, which can contribute to species patterning (**Figure 4.3,** Löffler and Pape 2020). For example, in the Southern Hemisphere, northwest-facing slopes tend to be warmer and drier than southeast-facing slopes (Radcliffe and Lefever 1981). These differences in solar radiation due to topographical variation influence snow distribution, from near snow-free windswept Feldmark to long-lasting snow patches (Choler 2005; Venn *et al.* 2017; Rosbakh, Fernández-Pascual, *et al.* 2022). As a result, these topography-driven snow patterns strongly influence abiotic factors determining plant growing season, including surface-level temperature, moisture, and available light (Scherrer and Körner 2011; Winkler, Lamprecht, *et al.* 2016; Körner *et al.* 2021; Rixen *et al.* 2022; Körner *et al.* 2023).

To estimate this heterogeneity in topographically driven thermal microclimates, we approximated the cumulative summer solar radiation that sites were exposed to using the "NicheMapR" package (Kearney and Porter 2017). Specifically, we used the "micro_ncep" function (Kearney *et al.* 2020), which integrates functions of the "microclima" (Maclean *et al.* 2019), "elevatr" (Hollister 2023) and "RNCEP" (Kemp *et al.* 2012) packages to compute cumulative summer solar radiation (McCullough and Porter 1971) in each quadrant for each summit. The "NicheMapR" package accounts for local terrain effects to a spatial resolution of 30 m, including latitude, longitude, elevation, slope, and aspect (Kearney *et al.* 2020).

For each study summit plot, the aspect, slope, elevation and coordinates for each summit quadrant were inputted into the "micro_ncep" function. This was used to calculate the cumulative summer solar radiation from October 2021 to March 2022, assuming 0% shade and a clear sky. **Figure 4.4** demonstrates the variation in modelled cumulative summer solar radiation across the mesotopography features of the study summits. Here, the more north-facing a slope is, the more solar radiation it receives. In contrast, increasing slope was associated with less solar radiation.

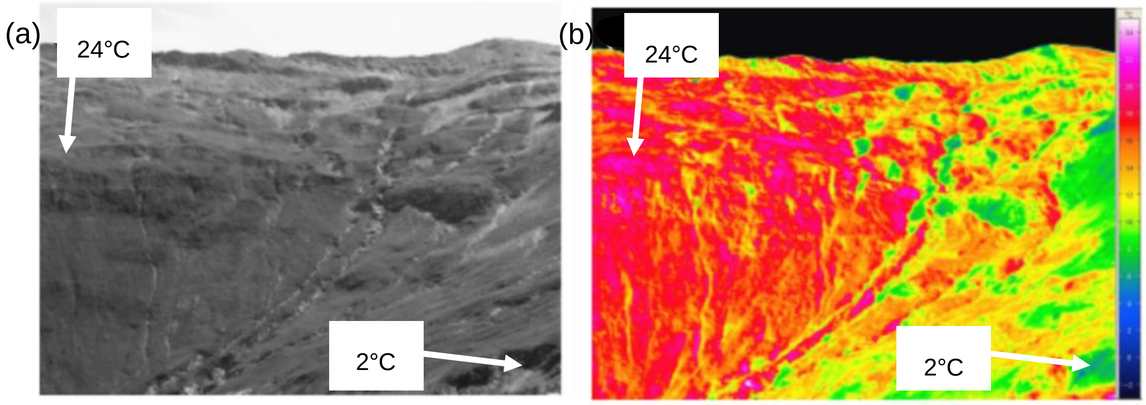

Figure 4.3 Example of an NNW facing slope in the Swiss Alps in summer. (a) Image of an ordinary, visible light, greyscale photograph taken by a digital camera and (b) shows the data for the same slope under full direct solar radiation using an infrared thermal camera. Dark blue represents cold (2°C) and magenta hot surface (24°C). Figures adapted from Scherrer & Körner (2011).

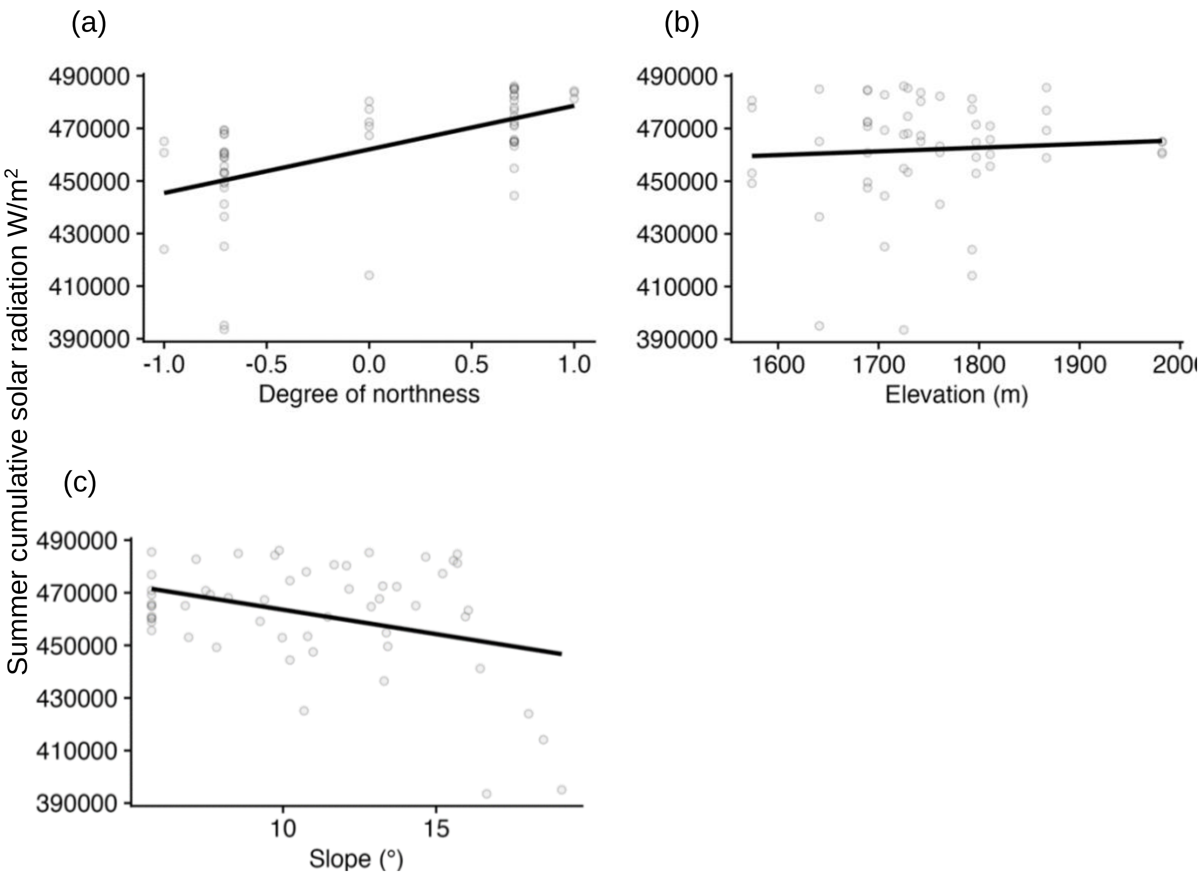

Figure 4.4 The relationship between meso-topography features, (a) degree of northness, (b) elevation and (c) slope of the Australian summits surveyed and the modelled cumulative summer solar radiation. The trend line is shown in black, and the grey dots represent summit quadrants.

4.5.4 Metrics of community change along a solar radiation gradient

4.5.4.1 Diversity indices

Diversity profiles were calculated to investigate diversity patterns across a solar radiation gradient. Local-scale diversity indices were generated from species cover estimates from each quadrat at each summit by calculating diversity based on Hill numbers (Hill 1973; Chao *et al.* 2019). Diversity based on Hill numbers are modified versions of the traditional Shannon and Simpsons indices, which give each index value in units of 'effective species number'. There is a consensus on using Hill numbers as the class of species diversity measure of choice (Ellison 2010).

To calculate diversity, we express S as the total number of species and p_i as the proportion of the total cover represented by species i. The parameter q determines the sensitivity of the measure to the relative abundance of species. Thus, $\sum_{i=1}^{S} p_i{}^q$ denotes the relative abundance of the individuals of species in the assemblage. When q = 0, D^0, is simply species richness, which counts species equally without regard to their relative abundance (Chao *et al.* 2019) and is defined as:

$$D^0 = \sum_{i=1}^{S} p_i{}^0 \qquad [1]$$

The measure for q = 1, D^1, is the exponential of Shannon's entropy index and considers individuals equally and weighs each species in proportion to its cover (Chao *et al.* 2019) and is defined as:

$$D^1 = \exp\left(-\sum_{i=1}^{S} q_i^1 \; ln\, p_i\right) \qquad [2]$$

Lastly, the measure for q = 2, D^2, is the inverse of Simpson diversity and disproportionately favours dominant species (Chao *et al.* 2019) and is defined as:

$$D^2 = 1/\left(\sum_{i=1}^{S} p_i^2\right) \qquad [3]$$

4.5.4.2 Ecological groups

To further investigate floristic patterns across a solar radiation gradient on summits, all species were classified as either endemic, generalist or exotic based on the VicFlora descriptions (www.vicflora.rbg.vic.gov.au). Endemic species were defined as restricted native species only found in alpine areas above the bioclimatic treeline (**Figure 4.5**). Generalist species were defined as a widespread native found across the alpine regions and lower elevations (**Figure 4.6**). Lastly, exotic species were defined as non-native species that are generalists, invasive, and widespread, occurring in high abundance on summits (**Figure 4.7**).

Figure 4.5 Example of alpine endemic species found on summits, left to right: Aciphylla glacialis (E), Craspedia adenophora (E), Scleranthus diander (E), and Euphrasia crassiuscula subsp. glandulifera (CR).

Figure 4.6 Example of generalist species found on summits, left to right: *Acaena novae-zelandiae*, *Olearia phlogopappa* subsp. *flavescens* (E), *Stellaria pungens* and *Rytidosperma pallidum*.

Figure 4.7 Exotic species found on summits, left to right: *Cerastium vulgare, Acetosella vulgaris* and *Hypochaeris radicata*.

4.5.4.3 Plant functional traits

Four plant functional traits associated with the distribution of species in high mountain areas were selected and measured: specific leaf area (SLA), plant height, leaf dry matter content (LDMC), and seed mass (**Table 4.1**) (Good *et al.* 2019; Myers-Smith *et al.* 2019). Variation in SLA in differing conditions means that SLA and its components (leaf mass per area and LDMC) are often, but not always, related to each other and to productivity gradients (Pérez-Harguindeguy *et al.* 2016). Consequently, to further improve our understanding of plant strategies from plant functional traits, we also measured LDMC. These traits are essential for various assembly processes and population dynamics, such as competition, facilitation, productivity, stress tolerance and longevity (Grime 1974; Westoby 1998; Weiher *et al.* 1999).

Trait data were obtained from each vascular species identified in all floristic surveys and were collected from mature, healthy individuals in the 2022 growing season. Where traits could not be collected in the field, the mean trait value was obtained from the Austrait database (Falster *et al.* 2021) from traits collected in alpine areas on the Australian Alps. To examine leaf traits, 10 healthy, undamaged, mature, non-senescent leaves were selected from at least 10 individuals from each species, stored in moist and cool sealed plastic bags and refrigerated prior to processing in a laboratory within 24 hours (Pérez-Harguindeguy *et al.* 2016). Leaves were then scanned using ImageJ software (Schneider *et al.* 2012) to quantify the one-sided leaf area (mm^2), and the fresh weight (mg) was recorded. To obtain leaf dry weight, leaves were oven-dried for 48 hrs at 80 °C (Pérez-Harguindeguy *et al.* 2016). Specific leaf area (SLA) was quantified by the one-sided area of a fresh leaf divided by its oven-dry mass (mg) (Pérez-Harguindeguy *et al.* 2016). Leaf dry matter content (LDMC) was quantified for each species by dividing the oven-dry weight (mg) by the fresh weight (g) (Pérez-Harguindeguy *et al.* 2016). The maximum plant height ($H_{\max}$) was obtained from VicFlora (vicflora.rbg.vic.gov.au). If information was not available, $H_{\max}$ was obtained by measuring the maximum stature of an individual from the ground of at least 10 individuals of a species (Pérez-Harguindeguy *et al.* 2016). Lastly, seed mass (mg) was quantified by the diaspore oven-dried mass of an average diaspore of a species (Pérez-Harguindeguy *et al.* 2016). At least 10 mature, plump seeds were collected from at least 10 plants of a species. Seeds were oven-dried for 48 hrs at 80 °C then weighed with a microbalance (Pérez-Harguindeguy *et al.* 2016). The mean values of each trait were calculated for each species (**Appendix IV, Table S6**).

Table 4.1 Specific details of the functional traits used in research investigating alpine community dynamics to climate change and the trait form favoured at low and high elevation environments.

Functional trait	**Description**	**Functional indicator**	**Trade-off**	**References**
Specific leaf area (SLA) (mm^2 mg-1)	Ratio of one-sided area of a fresh leaf to its oven dry mass.	Ecological strategy to stress/ disturbance/ avoidance, return on captured resources (light and nutrients), growth rate, plasticity	Leaf energy, water balance, leaf longevity, defence	Cornelissen et al. 2003; Westoby et al. 1998; Pérez-Harguindeguy et al. 2016; Good et al. 2019; Venn et al 2014; Pickering et al. 2014
Plant maximum height (m)	Distance between ground and upper boundary of main photo synthetic height.	Overall competitive ability for light. Vegetation dynamics, ecological strategy to environmental stress	Growth, maintenance of structure, water transport	Cornelissen et al. 2003; Westoby et al. 1998; Pérez-Harguindeguy et al. 2016; Pickering et al. 2014; Venn et al. 2011, 2014
Leaf dry matter content (LDMC) (mg g-1)	Average density of tissue. Ratio of oven-dry mass and fresh weight of the leaf.	Ecological strategy to stress/ disturbance/ avoidance, resource acquisition	Leaf energy, water balance, leaf longevity, defence	Cornelissen et al. 2003; Pérez-Harguindeguy et al. 2016; Good et al. 2019; Venn et al 2014;
Seed mass (g)	Oven-dry mass of an average seed of a species	Indicator of regeneration: fecundity, seedling survival, seed dispersal, seed production	Reproductive effort	Cornelissen et al. 2003; Westoby et al. 1998; Weiher et al. 1999; Pérez-Harguindeguy et al. 2016; Venn et al. 2011

4.5.5 Data analysis

In total, we built eight hierarchical models to examine the influence of a solar radiation gradient on the diversity, ecological group (endemics, generalist and exotic) and plant function trait types of Australian alpine summit communities. Prior to analysis, we first tested for collinearity between variables with a determinant of the correlation matrix. We assessed collinearity using the Pearson correlation value (threshold of $r < 0.7$) (Dormann *et al.* 2013). To compare the magnitude of effects between covariates with different units, we centred all covariates on their associated means and divided them by one standard deviation (Gelman and Hill 2007). The advantage of centring and standardising is that it allows for simpler interpretation, with intercepts interpreted as responses to average conditions and slope terms as partial dependencies conditional on other continuous variables being at their mean (Camac *et al.* 2017).

We constructed Bayesian Generalised Linear Mixed Models (GLMM) to analyse the data. Mixed effect models are appropriate for hierarchical data structures (e.g. transects nested within sites) as they can partition variation at multiple levels and account for observation error (Gelman and Hill 2007; Kéry *et al.* 2012; Camac *et al.* 2017). For each model, random effects were included for several critical reasons, including (i) accounting for the non-independent structure of observations within sites, (ii) estimating group-level effects and (iii) providing a means to predict new group levels (Camac *et al.* 2017). Additionally, all model coefficients, β, were estimated using an improper flat prior and intercepts, α, were estimated using weakly informative student's t priors (the default in "brms" package) (Bürkner 2021).

We used Bayesian inference and fitted models using the R package "brms" (Bürkner 2021) for each model in in R 4.3.3 (R Core Team 2024). Specifically, we ran the models using four chains, each sampling 4000 iterations. The first 1000 iterations of each chain were discarded and treated as warm-up/burn-in, leaving a total of 12000 posterior samples across chains (Camac *et al.* 2017). We determined chain convergence using the Brooks-Gelman-Rubin convergence diagnostic (Brooks and Gelman 1998). Posterior inferences were then made using these 12000 samples. We assessed the adequacy of the models by posterior predictive checks, comparing replicated data generated under the fitted models to the observed data (Camac *et al.* 2017, example of model checks are in **Appendix III, Figures S8-S10**).

Below, we describe the model structure and parameters used in these models.

4.5.5.1 Modelling summit diversity response to a solar radiation gradient

We built three hierarchical models to examine the response of Australian summit diversity (D_{ij}) across a solar radiation gradient (SR_{ij}) at each quadrat, i, at each site, j. First, Hill diversity D^0 was modelled from a Poisson distribution given its discrete count nature:

$$\begin{gathered} D_{ij} \sim \mathrm{Poisson}(\lambda_{ij}) \\ \log(\lambda_{ij}) = \alpha + \beta_1 \times \mathrm{SR}_{ij} + \varepsilon_j \\ \varepsilon_j \sim Normal(0, \sigma_j) \\ \alpha \sim Student - t(3, 2.4, 2.5) \\ \sigma_j \sim Student - t(3, 0, 2.5) \end{gathered} \qquad [4]$$

Then for D^1 and D^2, we assumed a Gamma distribution as both are positive, continuous values:

$$\begin{gathered} D_{ij} \sim Gamma(\alpha_{ij}, \phi) \\ \log(\alpha_{ij}) = \alpha + \beta_1 \times \mathrm{SR}_{ij} + \varepsilon_j \\ \varepsilon_j \sim Normal(0, \sigma_j) \\ \alpha \sim Student - t(3, 1.8, 2.5) \\ \sigma_j \sim Student - t(3,0,2.5) \\ \phi \sim Gamma(0.01, 0.01) \end{gathered} \qquad [5]$$

For all three models, the structure and parameter definitions are similar. Our response variable, α_{ij} and λ_{ij}, represents the log likelihood diversity for each quadrat, i, at each site, j. We modelled α_{ij} and λ_{ij} as a linear function of solar radiation, SR_{ij}. However, Equation 5, contains the scale parameter, ϕ. For both models, the parameter β_1 represents the varying effect of solar radiation across different sites j. The intercept, α_1, is the average log diversity per quadrat at a reference site. We included random intercept effects for site, ε_j. α_{ij} and λ_{ij} were modelled separately for D^0, D^1 and D^2. Partial dependency plots were created for the estimated average diversity at the average site.

4.5.5.2 Modelling the interaction between ecological groups and solar radiation

We built two hierarchical models to investigate whether the effect of solar radiation (SR_{ij}) on summit vegetation was dependent upon the ecological group (EC_s) of each species (S), i.e. alpine endemic, generalist, and exotic species. We included an interaction term between solar radiation and ecological groups to assist in capturing potential differences in how different species respond to varying levels of solar radiation, SR_{ij}. Our observations, O_{ij}, were binary (0 = absent, 1 = present) for each quadrat, i, at each summit, j. We modelled these binary observations across a solar radiation gradient as random realisations from a Bernoulli distribution:

$$
\begin{gathered}
O_{ij} \sim Bern(\rho_{ij}) \\
\mathrm{logit}\ (\rho_{ij}) = \alpha + \beta_1 \times \mathrm{SR}_{ij} + \beta_2 \times EC_s + \beta_3 \times (\mathrm{SR}_{ij} \times EC_s) + \varepsilon_j + \varepsilon_s \\
\varepsilon_j \sim Normal(0, \sigma_j) \\
\varepsilon_s \sim Normal(0, \sigma_s) \\
\alpha \sim Student - t(3, 0, 2.5) \\
\sigma_s \sim Student - t(3, 0, 2.5) \\
\sigma_j \sim Student - t(3, 0, 2.5)
\end{gathered}
\qquad [6]
$$

Here, ρ_{ij}, is the estimated probability of a summit species occurrence as a function of a solar radiation SR_{ij} gradient and ecological groups, EC_s, and their two-way interaction. The intercept, α, varies by site and species and is the log odds of species occurrence per quadrat at site j, assuming all other covariates are at their mean. β_1 is the effect of SR_{ij}, β_2 is the effect of EC_s, β_3 is the interactive effect of SR_{ij} and EC_s, Random intercept effects were included for site, ε_j, and species, ε_s.

Given a species was present, we then modelled the observed species' cover, C_{ij}. Prior to modelling, we applied the inverse logit transformation to C_{ij} using the *stats* package v.3.6.2 (R Core Team 2024) to ensure the response variable was on the probability scale suitable for modelling with a normal distribution. We could then utilise a normal distribution because values were boundless:

$$\begin{gathered}
\text{logit}(C_{ij}) \sim \text{Normal}(\mu_{ij}, \sigma) \\
\mu_{ij}, = \alpha + \beta_1 \times \text{SR}_{ij} + \beta_2 \times EC_s + \beta_3 \times (\text{SR}_{ij} \times EC_s) + \varepsilon_j + \varepsilon_s \\
\alpha \sim \textit{Student-t(3, 0, 2.5)} \\
\sigma \sim \textit{Student-t(3, 0, 2.5)}
\end{gathered} \tag{7}$$

We modelled the estimated species cover μ_{ij} in the same way we modelled ρ_{ij} in Equation 6. Here, the structure and parameter definitions are similar. σ is the standard deviation of the observation error. The intercept, α, varies by site and species and is the expected proportional cover of species per quadrat at site j, assuming all other covariates are at their mean. Partial dependency plots were created for μ_{ij} and ρ_{ij} for the average site and average species.

4.5.5.3 Modelling the interaction between plant functional traits and solar radiation

Lastly, to investigate the influence of solar radiation on plant functional traits of species present on summits, we investigated whether the effect of solar radiation (SR_{ij}) on species cover ($cover_{ij}$) was dependent on species plant traits: Leaf Dry Matter Content (LDMC_s), Specific Leaf Area (SLA_s), maximum height (H_s), and seed mass (mass_s). We applied the logit transformation mentioned above to $cover_{ij}$ prior to modelling. We could then utilise a normal distribution because values were boundless:

$$\begin{gathered}
logit(cover_{ij}) \sim Normal(\mu_{ij}, \sigma) \\
\mu_{ij} = \alpha + \beta_1 \times \text{SR}_{ij} + \beta_2 \times \text{LDMC}_s + \beta_3 \times \text{LDMC}_s \times \text{SR}_{ij} \\
+\beta_4 \times \text{SLA}_s + \beta_5 \times \text{SLA}_s \times \text{SR}_{ij} \\
+\beta_6 \times \text{H}_s + \beta_7 \times \text{H}_s \times \text{SR}_{ij} \\
+\beta_8 \times \text{mass}_s + \beta_9 \times \text{mass}_s \times \text{SR}_{ij} + \varepsilon_j + \varepsilon_s \\
\alpha \sim \textit{Student}-\textit{t}(3,-1.7,2.5) \\
\sigma \sim \textit{Student}-\textit{t}(3,0,2.5)
\end{gathered} \tag{8}$$

Here, our response variable, μ_{ij}, estimated species proportional cover for each quadrat, i, on each mountain summit, j, and σ is the standard deviation of the observation error. We modelled μ_{ij} as a linear function of solar radiation, SR_{ij}, and species traits, T_s, along with their two-way interaction. The intercept, α, varies by site and species and represents the expected proportional cover of species per 1 m^2 quadrat, i, and summit, j. This model has additional parameters; $\beta_2, \beta_4,\ \beta_6, \text{and}\ \beta_8$ representing the effect of plant traits that varies with species, s, and $\beta_3, \beta_5, \beta_7, \text{and}\ \beta_9$ represents the interactive effect of SR_{ij}, and traits. The formulation includes random intercept effects for site, ε_i and species, ε_s. μ_{ij} was modelled separately for forb, graminoid and shrub species, but the three models are structurally similar. Partial dependency plots were created for each trait and estimated species proportional cover for the average site and average species at low (380,000 W/m^2) and high (490,000 W/m^2) solar radiation.

4.6 Results

4.6.1 Diversity responses

In 2022, 102 species were found on the 14 alpine summits, including 77 alpine endemic species, 28 generalist species, and three exotic species. The average frequency of occurrence was 29.2 % of plots per species; 10 of the 102 species occurred as a singleton, and the highest frequency of occurrence was 73% for the sedge *Carex breviculmis*. There were 61 forbs, 23 graminoid species, 23 shrubs, and one tree species. The highest average cover was *Poa fawcettiae* (18.8%) and *Hovea montana* (10.1%).

The 1 m^2 quadrats averaged 10.8 species per plot (range 3-25) exhibited high diversity (average D^1 = 6.3; range1.3 - 18.1). However, there was considerable variability among sites. None of these diversity indices showed a single-factor relationship with cumulative summer solar radiation (**Appendix IV, Figure S14**). No conclusions could, therefore, be drawn about the influence of cumulative summer solar radiation on summit plant diversity. The variability across the 14 different sites for all diversity models was similar; the unexplained variation among sites in the D^0 model was 0.25 standard deviations (95% CI: 0. 0.16, 0.39; **Appendix IV, Figure S14**, the D^1 model was 0.26 standard deviations (95% CI: 0.17, 0.42; **Appendix IV, Figure S14**), and the D^2 model was 0.27 standard deviations (95% CI: 0.17, 0.43; **Appendix IV, Figure S14**).

4.6.2 Shifts in endemic, generalist and exotic species

There was no detectable effect of solar radiation on summit species probability of occurrence (**Figure 4.8**). However, the effect of solar radiation depended on the ecological group for species cover (**Figure 4.9a**). Specifically, the cover of generalist and exotic species declined with increasing solar radiation. For example, the predicted mean generalist species cover at low solar radiation (393,520 W/m) was 7%, whereas, at higher solar radiation (486,083 W/m), it was 5% (**Figure 4.9d**). Similarly, the predicted mean exotic species cover at low solar radiation (393,520 W/m) was 8%, whereas at higher solar radiation (486,083 W/m), it was 3% (**Figure 4.9e**). No detectable influence of solar radiation on endemic species cover was observed (**Figure 4.9a, c**). For the species occurrence and cover models, the unexplained variation was greater among species than sites (**Figure 4.8b**, **Figure 4.9b**, respectively).

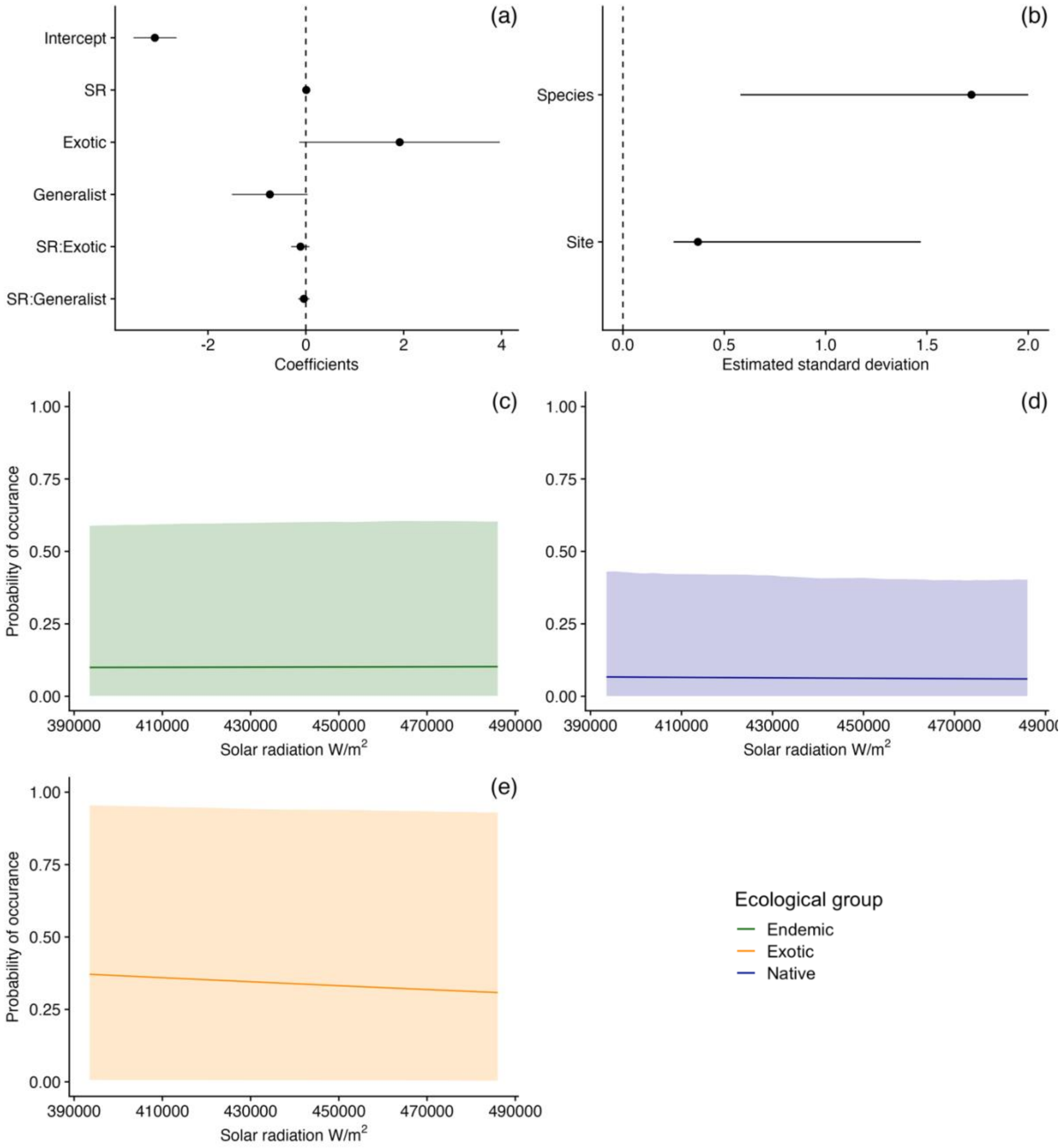

Figure 4.8 The occurrence probability of endemic (green), generalist (blue) and exotic (orange) species as a function of solar radiation. (a) Centred and standardised model coefficient and effects of solar radiation and ecological groups and two-way interactions. The intercept is interpreted as the average cover of an endemic species. The 95% significance can be determined if the 95% credible intervals cross the 0 line (dashed line). (b) The model estimated standard deviation among sites and species. All error bars and shaded areas indicate 95% Bayesian credible intervals.

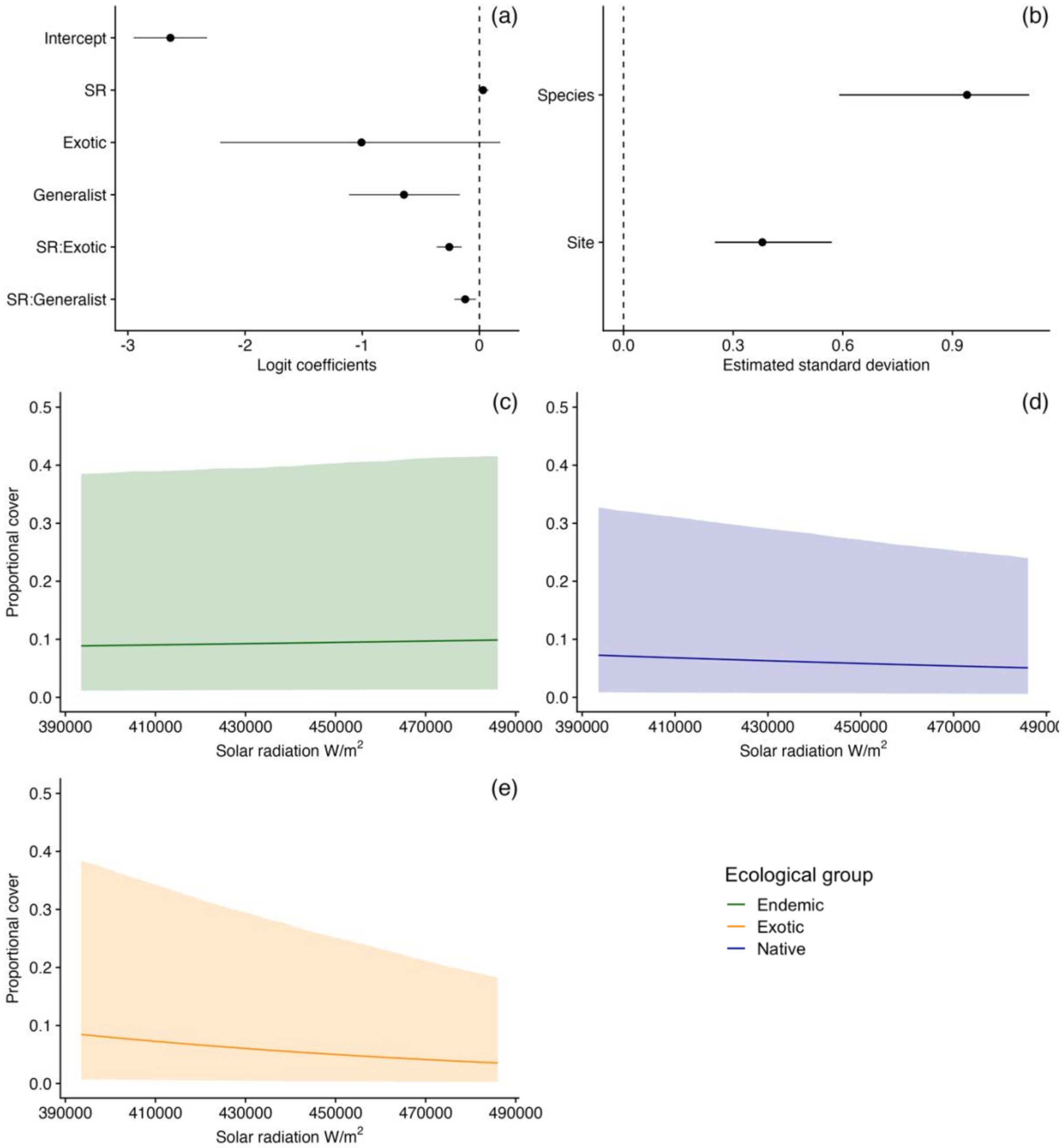

Figure 4.9 Species proportional cover as a function of solar radiation and species ecological group (endemic, generalist, exotic). (a) Centred and standardised model coefficient and effects of solar radiation and ecological groups and two-way interactions. The intercept is interpreted as the average cover of an endemic species. The 95% significance can be determined if the 95% credible intervals cross the 0 line (dashed line). (b) The model-estimated standard deviation among sites and species. (c-e) Mean species proportional cover as a function of solar radiation and ecological group (endemics, generalists, exotics) for the average site. All error bars and shaded areas indicate 95% Bayesian credible intervals.

4.6.3 Plant functional trait shifts

For shrub species, there was a significant increase in cover with increasing solar radiation. However, this effect was dependent on plant trait type (**Figure 4.10**). Notably, the interaction between solar radiation and mean specific leaf area (SLA) negatively affected shrub species cover (**Figure 4.10a**). For example, summit microsites that experience lower solar radiation (393,520 W/m) had 13% more cover of shrub species with higher SLA values (13 mm^2/mg) than species with lower SLA values (4 mm^2/mg). In comparison, microsites that experience high solar radiation (486,083 W/m) had 29% more cover of shrub species with lower SLA values (4 mm^2/mg) than species with higher SLA values (13 mm^2/mg) (**Figure 4.10d**).

Similarly, the interaction between solar radiation and mean seed mass had a negative effect on shrub species cover (**Figure 4.10a**). For example, summit microsites that experience lower solar radiation (393,520 W/m) had 20% more cover of shrub species with heavier seeds (18 mg) than species with lighter seeds (0.02 mg) (**Figure 4.10e**). In comparison, microsites that experience higher solar radiation (486,083 W/m) have 12% more cover of shrub species with lighter seeds (0.02 mg) than species with heavier seeds (18 mg) (**Figure 4.10e**). The two-way interaction with solar radiation and leaf dry matter content (LDMC) and height did not influence shrub species cover (**Figure 4.10a**).

For forb species, there was a significant decline in species cover with increasing solar radiation; this effect was not dependent on plant trait type (**Figure 4.11**). In contrast, for graminoid species, there was no detectable effect of solar radiation, plant traits and their two-way interaction on species cover (**Figure 4.12**). For all models, the amount of unexplained variation was substantially greater among species than sites (**Figure 4.10b, Figure 4.11b, Figure 4.12b**). Overall, solar radiation did not strongly mediate the effects of traits on Australian summit species cover.

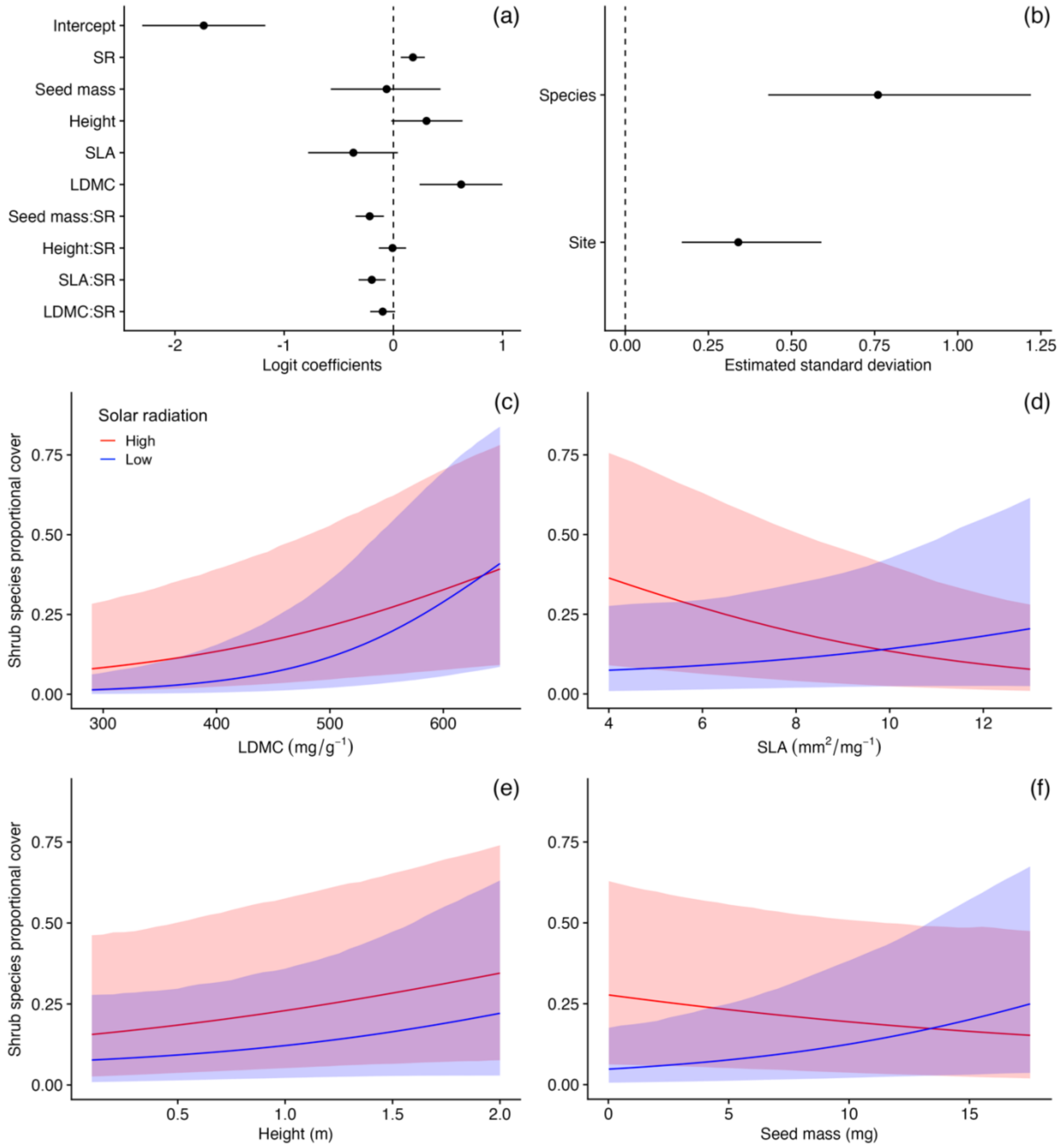

Figure 4.10 Shrub species proportional cover as a function of solar radiation and mean plant functional traits and their interactions. (a) Centred and standardised model coefficients (on the logit scale) and effects of solar radiation, (c) Leaf Dry Matter Content (LDMC), (d) Specific Leaf Area (SLA), (e) maximum plant height (Hmax) and (f) seed mass and the two-way interactions effects for the average site and average species. The 95% significance can be determined if the 95% confidence intervals cross the 0 line (dashed line). (b) Model standard deviation of random effects (on the logit scale): site and species. All error bars and shaded areas indicate 95% Bayesian credible intervals. The predicted mean shrub species' proportional cover at low solar radiation is indicated in blue (393,524 W/m^2) and red at high solar radiation (486,083 W/m^2).

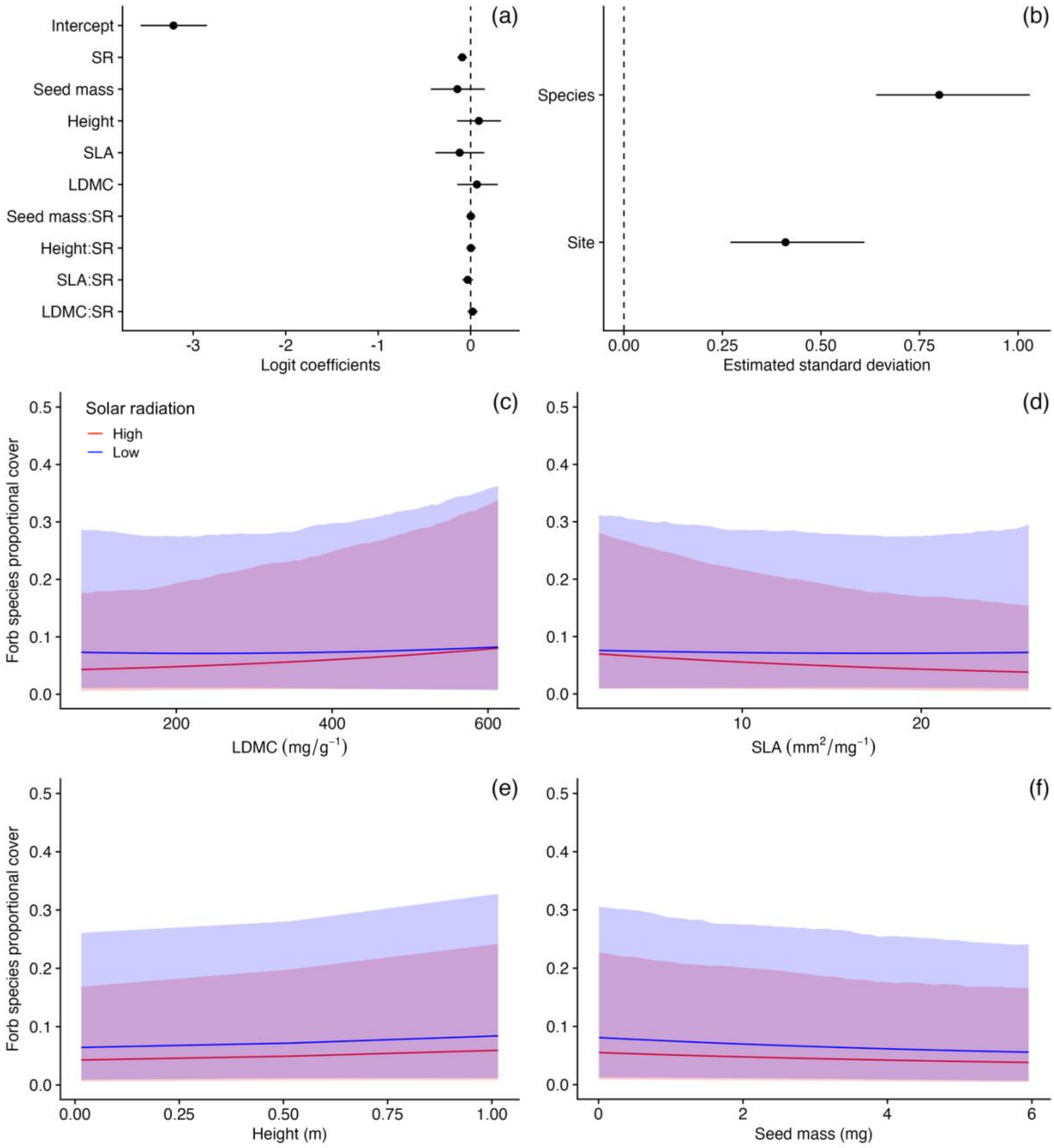

Figure 4.11 Forb species proportional cover as a function of solar radiation and mean plant functional traits and their interactions. (a) Centred and standardised model coefficients (on the logit scale) and effects of solar radiation, (c) Leaf Dry Matter Content (LDMC), (d) Specific Leaf Area (SLA), (e) maximum plant height (H_{max}) and (f) seed mass and the two-way interactions effects at the average site and average species. The 95% significance can be determined if the 95% confidence intervals cross the 0 line (dashed line). (b) Model standard deviation of random effects (on the logit scale): site and species. All error bars and shaded areas indicate 95% Bayesian credible intervals. The predicted mean forb species proportional cover at low solar radiation is indicated in blue (393,524 W/m^2) and red at high solar radiation (486,083 W/m^2).

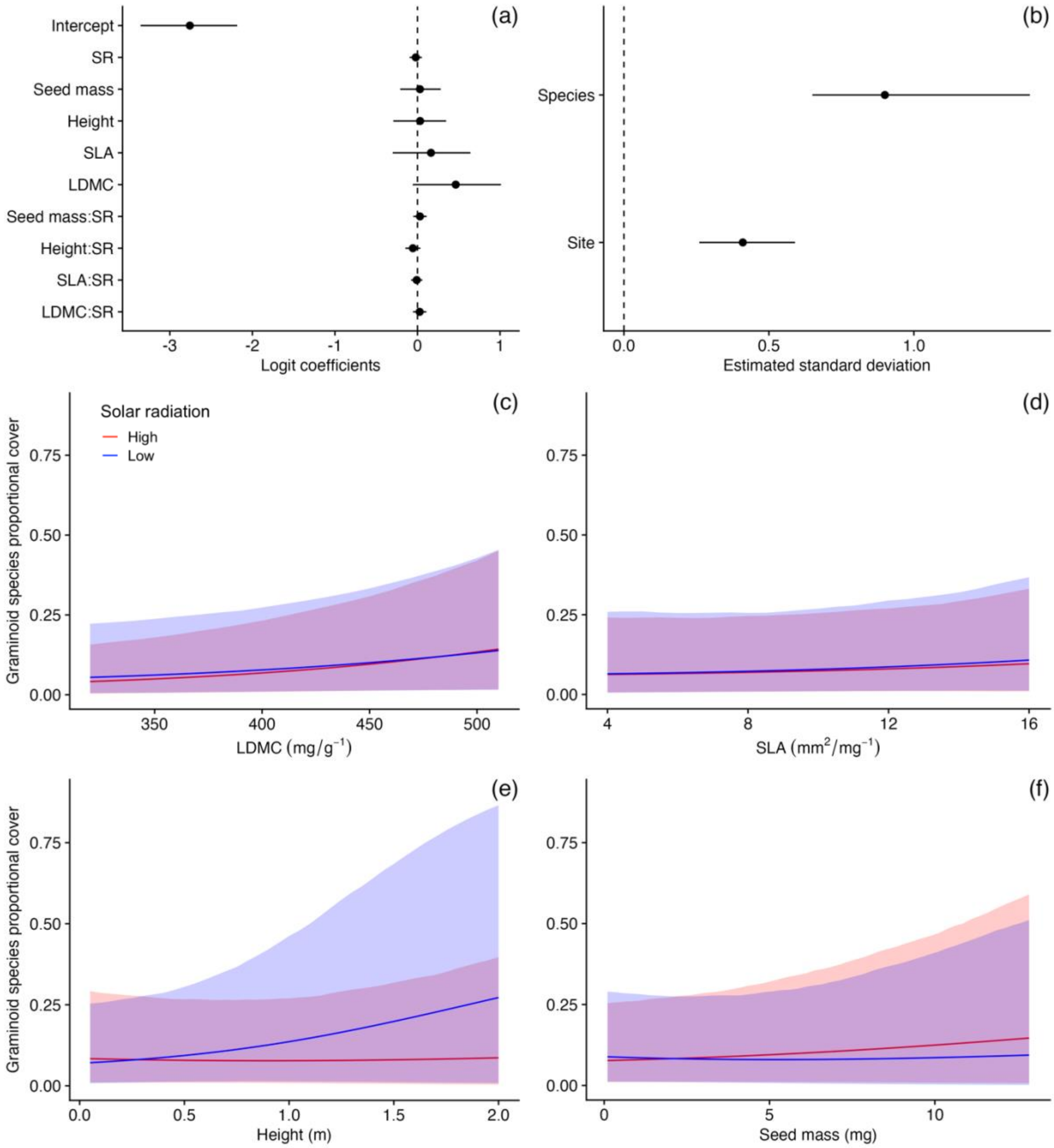

Figure 4.12 Graminoid species proportional cover as a function of solar radiation and mean plant functional traits and their interactions. (a) Centred and standardised model coefficients (on the logit scale) and effects of solar radiation, (c) Leaf Dry Matter Content (LDMC), (d) Specific Leaf Area (SLA), (e) maximum plant height (Hmax) and (f) seed mass and the two-way interactions effects at the average site and average species. The 95% significance can be determined if the 95% confidence intervals cross the 0 line (dashed line). (b) Model standard deviation of random effects (on the logit scale): site and species. All error bars and shaded areas indicate 95% Bayesian credible intervals. The predicted mean graminoid species proportional cover at low solar radiation is indicated in blue (393,524 W/m^2) and red at high solar radiation (486,083 W/m^2).

4.7 Discussion

This study investigated the effects of meso-topography on plant community composition on Australian mountain summits. Overall, there were few effects of meso-topography on alpine summit vegetation when using differences in modelled solar radiation as our metric of meso-topographic impacts on the environment. However, there was evidence of shifts in generalist, exotic, forb, and shrub species' cover across this solar radiation gradient. Additionally, shrub functional trait effects shifted across a solar radiation gradient, notably specific leaf area (SLA) and seed mass. This suggests that the direct impacts of solar radiation on the availability of water and energy in these systems influence community patterns at fine spatial scales (Graae *et al.* 2011; Lenoir *et al.* 2013; Fan *et al.* 2019; Löffler and Pape 2020). These findings align with the expectation that the factors limiting alpine vegetation dynamics are influenced by microsite variability caused by complex topography (Choler 2005; Scherrer and Körner 2011; Graae *et al.* 2018; Körner and Hiltbrunner 2021).

The physical characteristics of plant species, such as life form, combined with species distributions and local environmental factors, can reveal the processes underpinning patterns in alpine vegetation (Lavorel and Garnier 2002; Venn *et al.* 2014). The observed shifts in species lifeforms across a solar radiation gradient demonstrate differences in species distributions on alpine summits and indicate adaptations to local microclimate (Garnier *et al.* 2015). Here, shrub species were more abundant in areas with higher solar radiation, i.e. greater energy input. Forb species were more abundant in areas with less solar radiation, i.e. less energy input. These results are consistent with studies investigating the effects of topographical variation on alpine plant communities (Tape *et al.* 2006; Danby and Hik 2007; Myers-Smith and Hik 2018; Oldfather *et al.* 2024). For example, woody species (i.e. xeric species) have been documented to be advancing on warmer aspects, where conditions favour enhanced nutrient cycling and productivity (Tape *et al.* 2006; Danby and Hik 2007). In alpine areas, shrubs are often the tallest plants, are long-lived and have dense canopies (Myers-Smith *et al.* 2011; Venn *et al.* 2014): traits often associated with resource-acquisitive strategies (Soudzilovskaia *et al.* 2013; Oldfather *et al.* 2024). These traits allow shrubs to be competitively superior and gain dominance in warmer, more favourable environments (Myers-Smith *et al.* 2011; Wahren *et al.* 2013; Camac *et al.* 2017). By contrast, mesic species, such as herbaceous alpine species, are found on colder aspects with prolonged snow cover (Kulonen *et al.* 2018). Thus, the increased cover of shrubs in more favourable microsites may be evidence of a ‘pathway of migration’ whereby warmer microsites provide niche space for novel species to disperse and establish (Winkler *et al.* 2016).

While there were differential responses of lifeforms across the solar radiation gradient, the functional traits of shrub species had the strongest interaction with microclimate conditions. The cover of shrub species across this gradient depended on their specific leaf area (SLA) and seed mass. This finding is significant as it demonstrates that shrub species are not responding uniformly to contemporary climate change. Summit areas experiencing higher solar radiation had a greater cover of shrub species with lower SLA values (i.e., tougher leaves), e.g. *Orites lancifolius and Hovea montana*, Shrub species with lighter seeds also were more abundance with higher solar radiation, e.g. *Olearia phlogopappa* subsp. *flavescens*. In comparison, areas with less solar radiation had a higher cover of shrub species with higher SLA (i.e., fleshier) and heavier seeds, e.g. *Melicytus angustifolius* subsp. *divaricatus*. Like vegetative traits, seed traits relate directly and indirectly to fitness and niche differences among species (Kraft *et al.* 2015). Variation in seed mass can reflect abiotic filtering effects on dispersal (e.g., lighter seeds are assumed to have lower terminal velocity; Schupp *et al.* 2019), germination (e.g., large-seeded species have a survival advantage over small-seeded species during seedling establishment; Moles and Westoby 2004), persistence in the soil (e.g., smaller seeds persist longer in soil; Benvenuti 2007), and competition (e.g., Rosbakh *et al.* 2022). Our findings of shifts towards smaller-seeded shrub species in areas with higher energy input are supported by the well-established ecological theory of the ‘seed size—competition trade-off’ (Leishman 2001) and life-history theory (Smith and Fretwell 1974). Plant growth and seed production are limited by low temperatures (Körner 2003; Zhang *et al.* 2019). Hence, small seeds may be resource-poor but disperse often enough to enable infrequent but successful recruitment (Henery and Westoby 2001; Laughlin 2023). In contrast, large-seeded species invest more into energy reserves than small-seeded species, contributing to greater seedling establishment rates and survival in resource-limited environments (e.g. extremely cold, nutrient-poor) (Westoby *et al.* 2002; Laughlin 2023). As a result, species with smaller seeds and higher seed production are likely to be more successful at dispersing into new suitable habitats compared to species with larger seeds (Marteinsdóttir and Eriksson 2014). However, larger seeds are more likely to survive the harsh conditions of alpine environments (Laughlin 2023).

In addition to shifts in seed mass, shrub species varied in specific leaf area (SLA) across the solar radiation gradient. Summit areas with more solar radiation had a higher cover of shrub species with lower SLA values (i.e., tougher leaves). In contrast, less solar radiation was associated with a higher cover of shrub species with higher SLA (i.e., fleshier leaves). Variation in SLA values has been connected to climatic variation where heat, cold and drought stress all tend to select for leaves with relatively small SLA values (Reich *et al.* 2003; Laughlin 2023). In alpine regions, species with small SLA values are more abundant in the early-snow-melt alpine areas (Choler 2005; Venn *et al.* 2014; Hickman 2023). Without the insulation provided by winter snow cover, plants are exposed to freezing air temperatures (Happonen *et al.* 2019). However, the thermal insulation of snowpack depends upon the consistency and thickness, which is affected by topography (Billings 1969; Elmendorf *et al.* 2015). Consequently, summit areas exposed to higher solar radiation may have less snow cover, resulting in shrub species protruding above the snow and subjected to extreme frost during winter and spring (Bliss 1962). This would explain the higher cover of shrub species with typically thicker and more robust leaf strategy (low SLA). Species with low SLA exhibit conservative leaf economics, enabling them to tolerate increased abiotic stresses (Cornwell and Ackerly 2009; Venn *et al.* 2014). By comparison, the increased snow cover and shorter growing seasons in summit areas receiving less solar radiation account for the observed shrub species with thinner leaves with higher surface area (high SLA). This leaf trait is better adapted to capture light efficiently in low-light environments, indicating high productivity and fast resource acquisition (Kudo *et al.* 1999; Venn *et al.* 2014). These results support other work demonstrating the adaptive ability of Australian alpine shrubs to resist freezing despite variable snow conditions (Venn and Green 2018).

Water availability can also influence the strength and direction of temperature–trait relationship of SLA (Bjorkman *et al.* 2018). Differences in solar radiation due to aspect and slope can generate local moisture patterns (Pierce *et al.* 2005). For example, higher solar radiation is associated with increased evapotranspiration rates and less snow cover, resulting in decreased water availability (Fan *et al.* 2019; Meira Neto *et al.* 2020), which can influence spatial variation in plant traits (Bjorkman *et al.* 2018). This study found shrub species with smaller SLA values more abundant in areas with higher solar radiation. This trait is associated with lower stomata surface area, which functions to improve water-use efficiency under water stress (Wellstein *et al.* 2017).

Local changes in water availability can also lead to shifts in species composition (Oldfather *et al.* 2024). Moisture limitations from reductions in snowpack have been found to drive large compositional shifts in exposed sites (Oldfather *et al.* 2024). In our study, we found more exotic and generalist species in summit areas with less solar radiation. In contrast, the cover of endemic species did not vary across the solar radiation gradient. This result is unexpected and contradicts other studies that found colonisation of species on warmer aspects (Winkler, Lamprecht, *et al.* 2016) and more alpine endemics on cooler aspects (Kulonen *et al.* 2018). In Mediterranean mountains, such as those in this study, the unfavourable aridity on the warmer aspects has been attributed to the weak or absent relationship (Winkler, Lamprecht, *et al.* 2016) Consequently, this trend may be due to the relationship between the cold and drought tolerance of alpine species (Pescador *et al.* 2016; Sierra-Almeida *et al.* 2016; Sumner *et al.* 2022). The physiological mechanisms for freezing tolerance (e.g., osmotic regulation) also promote drought tolerance (Pescador *et al.* 2016; Sumner *et al.* 2022). For example, the dominant Australian alpine grass, *Poa* spp., is considered to be relatively tolerant of droughts (Griffin and Hoffmann 2012; Sumner *et al.* 2022). Hence, certain alpine species may have a greater tolerance for drier conditions in areas receiving higher solar radiation compared to exotic and generalist species.

The muted effect of plant diversity on Australian mountain summit vegetation community patterns contradicts other studies that found significant shifts in diversity and species turnover with topography complexity (Moeslund *et al.* 2013; Opedal *et al.* 2015; Winkler, Lamprecht, *et al.* 2016). However, this was consistent with other findings from Australian alpine areas (Pickering *et al.* 2008; Verrall *et al.* 2021). Australian alpine summits are topographically flat, eroded and ancient, which potentially have little variation in solar radiation, indicating less topographical-driven abiotic effects (**Figure 4.1**). Hence, there may be little opportunity for species to move into other microhabitats, unlike their counterparts in other alpine areas, which have strong topographically driven floristic patterns. This suggests that coarser scale topography, i.e. elevation, remains the single most important factor in determining variation in the distributions of species and community attributes in Australian mountainous areas (Chytrý *et al.* 2024).

In conclusion, this study reveals that fine-scale heterogeneity in solar radiation can drive divergent community trajectories within a single landscape. Summit microsites that receive higher solar radiation tend to have a shrubbier, stress-tolerant plant species as community constituents. Microsites receiving relatively lower solar radiation and are possibly less exposed and snowier tend to have a more herbaceous community. Nevertheless, Australian alpine summits may lack microrefugia, potentially owing to the limited meso-topographical relief. Consequently, Australian alpine endemics may be more vulnerable to change compared to their counterparts in other alpine regions.

Future changes in summit vegetation communities driven by warming may depend on the interplay between rising temperatures, changes in snow distribution (Winkler, Chapin, *et al.* 2016; Oldfather *et al.* 2024) and water availability (Meentemeyer *et al.* 2001; Christiansen *et al.* 2017). Divergent community responses could be intensified by fine-scale climatic gradients, potentially enhancing the overall landscape's resilience by promoting greater genetic, population, and community diversity over time (Lawler *et al.* 2015; Graae *et al.* 2018). This contrasts with concerns that climate change might homogenise alpine landscapes, thereby reducing the system's capacity to adapt to further changes (Gao *et al.* 2019; Verrall *et al.* 2021). Subsequently, the complex topography of summits may cause time lags in actual community changes in response to climate change in heterogeneous landscapes (Alexander *et al.* 2018; Graae *et al.* 2018; Falk *et al.* 2019; Körner and Hiltbrunner 2021).

4.8 References

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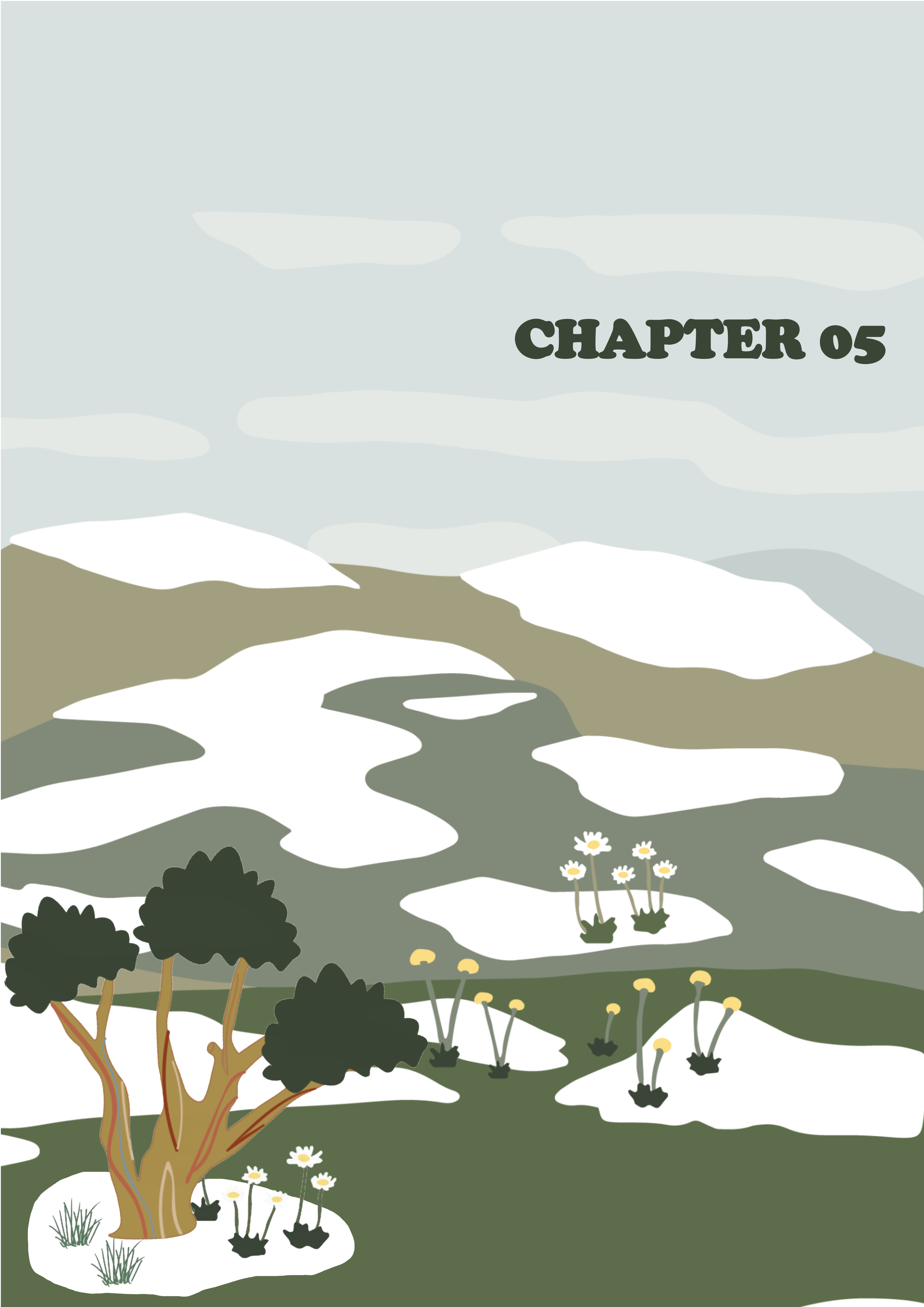
CHAPTER 05

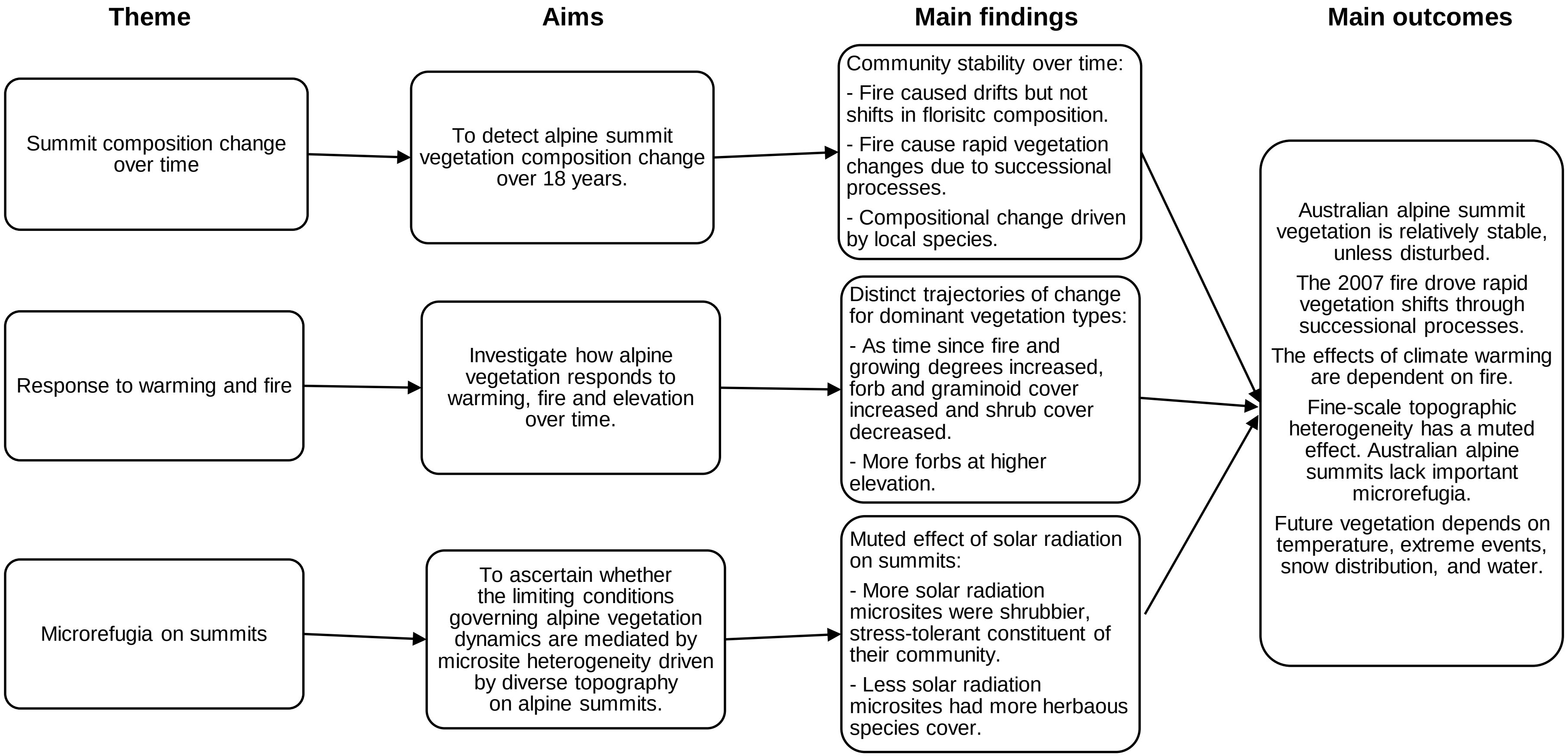


Chapter 5: Discussion

5.1 Overview

In this thesis, I aimed to understand the responses of Australian alpine summit vegetation to global change drivers over 18 years. Alpine species located on mountain summits are at the extreme edge of their tolerances, have little ability to track their climatic niche upslope and, thus, are predicted to be very sensitive to changes in climate (Grabherr *et al.* 1994; Theurillat and Guisan 2001). I had three objectives: (1) to understand how alpine summit vegetation composition was changing over time (Chapter 2), (2) how climate and disturbance influence the direction of vegetation change (Chapter 3), and (3) to determine whether meso-topography influences summit vegetation patterns which may provide microrefugia from climate change (Chapter 4). To achieve these objectives, I resurveyed vegetation on 14 Australian alpine summits using two different revisitation approaches (line intercept and floristic quadrats) at permanent plots established between 2004 and 2012 by Venn (2007). I collected and incorporated plant functional traits to assess species responses to varying abiotic conditions. Finally, using this long-term dataset, I developed a state and transition model and multiple hierarchical statistical models to estimate the vegetation change to fire, warming, elevation and small-scale variations in solar radiation. Specifically, I addressed five questions: i) Have there been significant changes in alpine summit vegetation composition over 18 years, and was this driven by colonisation, extinction and/or reordering processes? ii) What is the likelihood of vegetation states transitioning to a different vegetation state over time, and how do these transitions vary between burnt and unburnt alpine mountain summits? iii) How does vegetation cover across different summits respond to environmental factors such as warming and fire? iv) Are lower-elevation summits more vulnerable to change? v) How does microsite heterogeneity driven by diverse topography influence the alpine plant community vegetation patterns on mountain summits, and what does this reveal about the adaptability of summit plants to climate change?

This chapter synthesises the major findings of these combined studies, discusses the implications for management and limitations and provides suggestions for future research to advance our understanding of alpine vegetation's response to global drivers of change (**Figure 5.1**).



Summit composition change over time

To detect alpine summit vegetation composition change over 18 years.

Community stability over time:

- Fire caused drifts but not shifts in florisitc composition.
- Fire cause rapid vegetation changes due to successional processes.
- Compositional change driven by local species.

Response to warming and fire

Investigate how alpine vegetation responds to warming, fire and elevation over time.

Distinct trajectories of change for dominant vegetation types:

- As time since fire and growing degrees increased, forb and graminoid cover increased and shrub cover decreased.
- More forbs at higher elevation.

Microrefugia on summits

To ascertain whether the limiting conditions governing alpine vegetation dynamics are mediated by microsite heterogeneity driven by diverse topography on alpine summits.

Muted effect of solar radiation on summits:

- More solar radiation microsites were shrubbier, stress-tolerant constituent of their community.
- Less solar radiation microsites had more herbaous species cover.

Australian alpine summit vegetation is relatively stable, unless disturbed.

The 2007 fire drove rapid vegetation shifts through successional processes.

The effects of climate warming are dependent on fire.

Fine-scale topographic heterogeneity has a muted effect. Australian alpine summits lack important microrefugia.

Future vegetation depends on temperature, extreme events, snow distribution, and water.

Figure 5.1 Thesis structure, specific central chapter aims and main findings.

5.2 Summary of major findings

In **Chapter 2,** I used the floristic quadrat dataset from 2004 to 2022 to investigate changes in Australian alpine summit vegetation composition over time. I found that, despite regional warming, decreased precipitation, and fires over the past 20 years, there has been minimal change in species composition and community stability over time. However, the modest compositional changes identified between 2004 and 2012 were attributed to changes in the abundance of alpine species. Further investigation showed that species loss and reordering were the dominant processes on alpine summits. Notably, species reordering and species losses significantly increased between 2004 and 2012; overall, species turnover remained low. This suggests that the majority of change occurred between 2004 and 2012, most likely driven by the large-scale fire in 2007. This caused compositional drifts in resident summit species without leading to significant shifts over the long term.

In **Chapter 3**, I developed a state and transition model and hierarchical statistical models to estimate the vegetation change from fire, growing degrees days and elevation using the line intercept dataset from 2004 to 2022. Here, I found distinct trajectories of change for dominant vegetation types on summits in response to global drivers of change. I found the effect of cumulative growing degree days depended on fire occurrence. As time-since-fire increased and growing degrees accumulated, there was a strong positive effect on forb and graminoid cover and a negative effect on shrub cover. These results indicate that alpine summit vegetation will respond multi-directionally to challenges posed by a warming climate and changing fire regimes, with outcomes likely contingent on life-history characteristics. These findings build on previous work in response to climate change and disturbance regimes, e.g., the 'Shrub-fire feedback model' (Camac *et al.* 2017) and the 'Shrub-grass balance' (Williams 1990) . This study highlighted the need to consider the impacts of compounded perturbation on alpine vegetation under changing climates.

In **Chapter 4**, I developed hierarchical statistical models to estimate the effects of microsite heterogeneity, driven by diverse topography, on alpine summit vegetation and plant functional traits in 2022. Overall, meso-topography had a muted effect on alpine summit vegetation when differences in modelled solar radiation were used as the metric. However, there was evidence of shifts in generalist, exotic, forb, and shrub species' cover across this solar radiation gradient. Additionally, shrub functional traits shifted across a solar radiation gradient, notably specific leaf area (SLA) and seed mass. This suggests that the direct impacts of solar radiation on the availability of water and energy in these ecosystems influence community patterns at fine spatial scales. These findings show that the limiting conditions governing alpine vegetation dynamics are mediated by microsite heterogeneity driven by topography heterogeneity.

5.3 Management implications

5.3.1 Limiting novel plant establishment and shrub encroachment

In this thesis, I show that alpine vegetation is relatively stable through time unless disturbed. However, the combination of warming and increased fire frequency facilitates shrub encroachment on summits. I proposed that lags in novel species dispersal and establishment may provide alpine vegetation with some resistance to change. Australian summits are covered with dense, perennial, alpine vegetation, limiting the number of safe sites for novel species (Alexander *et al.* 2018). To prevent invasions from lower elevation species, it is imperative for land managers to limit bare ground opportunities and the spread of novel species. Infrastructure development, recreational use, feral ungulates, and fires are likely catalysts for change in Australian alpine vegetation, with exotic and shrub species increasingly spreading into mountainous areas (Pickering and Hill 2007; Myers-Smith *et al.* 2011; Iseli *et al.* 2023). Since these species require bare ground to establish (Williams 1992; Camac *et al.* 2017), minimising disturbance to alpine vegetation and controlling the spread of invasive species are crucial. Therefore, it is recommended that disturbance to alpine vegetation is minimised and that the spread of invasive species be controlled. However, facultative shrub species, which can spread vegetatively, may require more intensive management, such as mechanical removal treatment (Castillo-Garcia *et al.* 2024).

5.3.2 Continuing to monitor

Continuing to monitor alpine summit vegetation regularly is critical for understanding the severity of extinction scenarios for alpine plants (Pauli et al. 2015). To better understand the processes influencing alpine vegetation dynamics, long-term ecological monitoring methods assist in discerning natural variability from ecosystem dynamics due to a warming climate (Stöckli et al. 2011; Gitzen et al. 2012; Venn et al. 2012). In the context of Australian alpine species, where multiple factors such as recovery from grazing, droughts, fire, and warming contribute to shifts in species distributions, ongoing monitoring is particularly important. Given that most alpine plants are highly specialised, slow-growing, and long-lived perennials, which are resilient to short-term climatic fluctuations (Körner 2003; Nagy and Grabherr 2009; de Witte and Stöcklin 2010), continuous monitoring is crucial for understanding and managing their long-term survival in a rapidly changing environment.

5.4 Limitations

5.4.1 Global drivers of change

In Chapter 3, my goal was to untangle the effects of warming and fire on alpine vegetation on mountain summits. However, for a more thorough understanding, it is important to acknowledge the influence of other factors on alpine summit vegetation dynamics. Factors such as changes in snow duration and cover (Pickering *et al.* 2014; Oldfather *et al.* 2024), drought, and grazing history (Scherrer and Pickering 2005) also significantly impact alpine vegetation. Unfortunately, no reliable data on the history of natural snow or grazing in the study areas is available. However, I acknowledge that it is crucial to consider these factors alongside other global change drivers to comprehend the complexities of alpine summit environments.

5.4.2 Plant functional traits

In Chapter 4, I utilised plant functional traits to assess changes in alpine vegetation driven by microsite heterogeneity. The results from the hierarchical statistical models show that the amount of unexplained variation was substantially greater among species than sites. Although I used species-level averages, studies have indicated that there is less interspecific trait variation compared to intraspecific trait variation (Venn *et al.* 2014; Lim *et al.* 2017). Consequently, there may be a need to explore intraspecific variations of functional traits that could help explain the unexplained variation among species to microsite heterogeneity.

5.4.3 Topography effects on abiotic conditions

In Chapter 4, I explore microclimate heterogeneity driven by diverse topography on summits. I used modelled solar radiation as a proxy for changes in abiotic conditions. However, it is important to note that the solar radiation modelled using NicheMapR needs field validation to ensure accuracy and reliability. Field validation is essential to confirm that the modelled data accurately reflects the actual conditions experienced by alpine plants, which will enhance the robustness of any conclusions drawn about the effects of solar radiation on vegetation dynamics. It is worth noting that NicheMapR microclimate models predicted 85% of the variation in local conditions (Kearney *et al.* 2014).

5.5 Future directions

5.5.1 Microsite heterogeneity through time

In Chapter 4, I present a single-time snapshot of what the future may bring for alpine vegetation. However, it is important to investigate vegetation change over time within these microsites, given that the monitoring setup is fit for testing these predictions over the long term. This approach could significantly enhance our understanding of alpine vegetation responses to global drivers of change (Oldfather *et al.* 2024). Future studies could leverage the long-term dataset from 2004 to 2022 to investigate the interplay between climate warming and topographically mediated variation in local conditions. Understanding this relationship is crucial, as it will determine the overall impact of climate change on vegetation dynamics in alpine environments.

5.5.2 Time lag effects

Throughout this thesis, I suggest that time lags (e.g. “dispersal lags”, “establishment lags”, and “extinction lags”, Alexander *et al.* 2018) may be an important determinant of alpine summit vegetation resistance to change. Therefore, future research should investigate these time lag effects, particularly establishment lags, to better understand the factors limiting novel species' establishment in alpine communities on summits. In the context of Australian summit alpine vegetation, the closed alpine vegetation could inhibit the novel species seedling recruitment stage due to high competition (Graae *et al.* 2011; Lembrechts *et al.* 2016). Such studies could include a seed addition experiment of lower elevation species into differing microsite quality (e.g. Angers-Blondin *et al.* 2018). For example, microsites would consist of sowing seeds into patches of alpine grass, forbs, shrubs, bare ground, and litter, as well as differing future climate change conditions (warming, drought). These studies should be paired with translocation experiments, as interaction strengths have been shown to change with ontogeny (e.g. Gough, 2006). By examining how delays in species establishment influence vegetation dynamics, we can gain insights into alpine ecosystems' resistance to environmental changes. Understanding these processes is critical for predicting how alpine vegetation may respond to ongoing climate change and developing strategies to conserve these unique ecosystems.

5.6 Conclusion

The studies in this thesis examine the responses of alpine vegetation on mountain summits to a warmer and more extreme future Australian alpine climate. I show that, unlike other alpine ecosystems, Australian alpine summit vegetation is relatively stable, possibly due to high competition from resident vegetation that limits novel species establishment. I also emphasise the complex dynamics of Australian alpine mountain summit vegetation, highlighting that the effects of climate warming on vegetation are modulated by fire. These results underscore the importance of long-term monitoring in alpine ecosystems, where vegetation change can be slow and driven by infrequent or gradual factors. In addition, I show that fine-scale topographic heterogeneity has a muted effect on alpine summit vegetation, which lacks important microrefugia. The limited meso-topographical relief of Australian alpine summits may make them more vulnerable to climate change than other alpine regions. The future of summit vegetation will likely hinge on the interplay between rising temperatures, extreme weather events, shifts in snow distribution, and water availability. Without effective climate action, these changes will be exacerbated by invasive species, fires, and recreational pressures, accelerating ecological transformations.

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Appendix I: Site details

Table S1 Summary of site details, including abiotic features, year permanent plot established, the plant community type, and the cessation of cattle grazing. Information on environmental variables and disturbance regimes was obtained from Lawrence (1995), Department of Sustainability and Environment (2005) and Bureau of Meteorology (2022).

Study site	**Elevation (m)**	**Location**	**Year established**	**Plant community**	**Mean annual min temp in 2022 (°C)**	**Mean annual max temp in 2022 (°C)**	**Annual precip in 2022 (mm)**	**Size approx of plot (m^2)**	**Cessation of cattle grazing**	**Geology**
Mt Speculation	1660	-37.1253, 146.6433	2004	*Poa fawcettiae, Hovea montana* and *Podolobium alpestre* open grassy heathland	4.6	11.9	1843.1	3018	1960	Snowy Plains Formation
Little Spion Kopje	1670	-36.8263, 147.2815	2012	*Grevillea australis* and *Poa hothamensis* dominated open grassy heathland	2.8	9.3	2378.2	3195	1992	Cobungra Granite
King Billy (No. 2)	1690	-37.2024, 146.600	2004	*Poa fawcettiae, Hovea montana* and *Podolobium alpestre* open grassy heathland	4.2	11.2	1923.9	5928	1989	Bryce Plain Basalt
The Twins	1705	-37.027, 147.027	2012	*Grevillea australis and Poa hothamensis dominated low open grassy heathland*	4.7	12.4	1838.3	4979	1950s	Pinnak Sandstone
The Bluff	1710	-37.2346, 146.4899	2004	*Hovea montana* dominated closed heathland	5.0	12.4	1831	4130	1993	Snowy Plains Formation
Mt Howitt West Peak	1720	-37.1756, 146.6410	2012	*Poa fawcettiae* and *Hovea montana* dominated low open grassy heathland	4.1	11.1	1780.9	2378	1991	Snowy Plains Formation

Mt Magdala	1730	-37.1897, 146.6212	2004	*Poa fawcettiae and Hovea montana* open grassy heathland	4.2	11.2	1923.9	4260	1992	Snowy Plains Formation
Mt Howitt	1740	-37.1746, 146.6494	2012	*Poa fawcettiae, Kunzea muelleri* and *Hovea montana* dominated low open-closed grassy heathland	4.6	11.9	1843.1	5906	1991	Snowy Plains Formation
Mt Stirling (Stanley Knob)	1750	-37.1279, 146.49893	2004	*Poa fawcettiae* and *Podolobium alpestre* dominated open grassy heathland	4.6	11.8	2044.4	3614	1960	Mount Stirling Granodiorite
Mt Buller (West Knob)	1805	-37.1450, 146.42527	2004	Open *Poa fawcettiae* and *Hovea montana* dominated open-closed grassy heathland	4.5	11.6	2107.3	1380	1958	Mount Stirling Granodiorite/ Cobbannah Group
Feathertop North Peak	1850	-36.8911, 147.14060	2012	*Poa* spp., *Acrothamnus montanus* & *Grevillea australis* dominated low open grassy heathland	4.1	11.4	1948.4	1141	1950s	Pinnak Sandstone
Mt. Fawcett (unofficial name)	1870	-36.8294, 147.31925	2012	*Grevillea australis, Kunzea muelleri* and *Poa hiemata* dominated open grassy heathland	2.8	9.3	2378.2	10000	1992	Cobungra Granite
Mt Hotham	1900	-36.9745, 147.1322	2004	*Kunzea muelleri* dominated low alpine open heathland	3.6	10.5	1920.3	10000	1956	Pinnak Sandstone
Mt Bogong (Hooker Plateau)	1950	-36.7328, 147.3057	2004	*Celmisia costiniana* and *Poa fawcettiae* dominated tall grassy alpine herbfield	3.1	9.9	1973.2	10000	1950s	Complex gneiss/ Omeo Metamorphic Complex

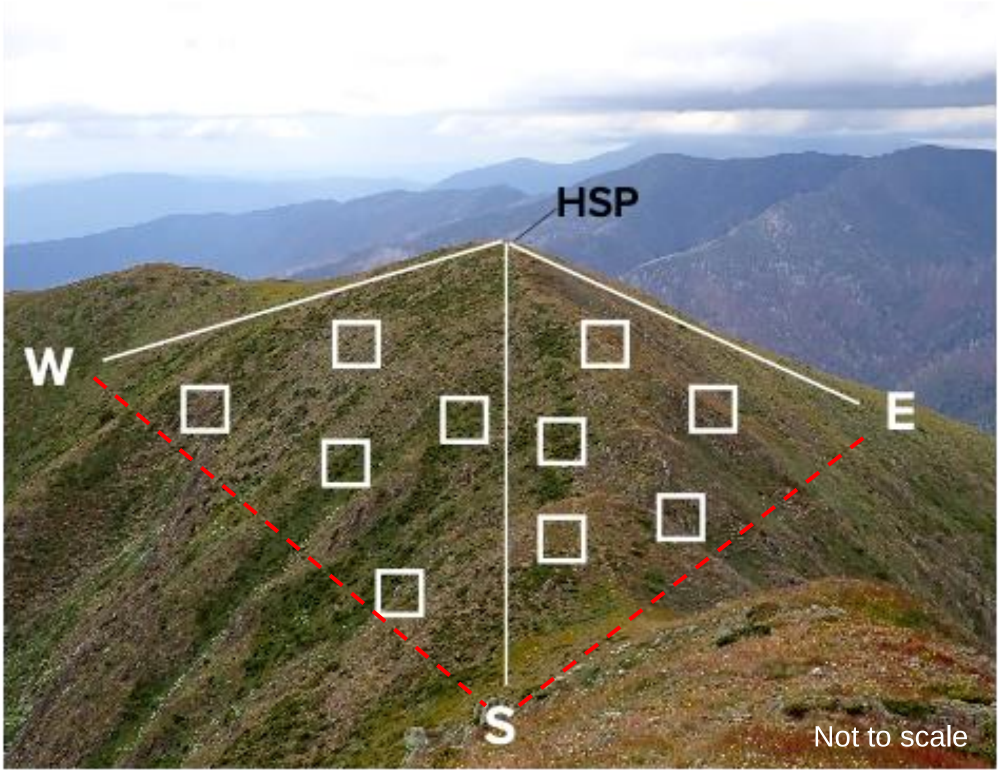


Figure S1 The layout of the sampling methodology of the summits. The layout of the sampling methodology of the summits. Showing the position of line intercept transects (solid white lines) and the five 1 m^2 quadrats in each quadrant. The plot encompasses the highest summit point (HSP) down to the 5 m contour line (dashed red line). Image of Mt Feathertop North Peak, Australia.

Table S2 Fire history of study summits.

Study site	**Elevation (m)**	**Year of last known recent fire/s**	**Total percent burnt from 2003 (%)**	**Fire history reference**
Mt Speculation	1660	2007	100	DEECA 2022
Little Spion Kopje	1670	2003	100	DEECA 2022
King Billy (No. 2)	1690	2007	63.54	Observed
The Twins	1705	2003, 2007, 2013	100	DEECA 2022
The Bluff (South Knob)	1710	2007	100	DEECA 2022
Mt Howitt West Peak	1720	2007	83.96	Observed
Mt Magdala	1730	2007	69.63	Observed
Mt Howitt	1740	2007	18.17	Observed
Mt Stirling (Stanley's Knob)	1750	2007	100	DEECA 2022
Mt Buller (West Knob)	1805	2007	100	DEECA 2022
Feathertop North Peak	1850	2003, 2007, 2013	100	Observed
Mt. Fawcett	1870	2003	100	DEECA 2022
Mt Hotham	1900	1939	0	DEECA 2022
Mt Bogong (Hooker Plateau)	1950	1939	0	DEECA 2022

Appendix II: Chapter 2 Supplementary Information

Table S3 Species changes to the dataset before analysis. This includes removing species that occurred only in one quadrat in one year, amalgamated species, and species name changes.

Year	Site	Elevation (m)	Quadrat	Species	New name	Cover
2004	Mt Stirling	1750	5	*Cotula.sp.*	Removed	5
2012	Mt Fawcett	1870	4	*Colobanthus affinis*	Removed	0.5
2022	King Billy	1690	2	*Asperula.scoparia*	Removed	1
2004	King Billy	1690	5	*Australopyrum.sp.*	Removed	0.5
2004	Mt Magdalla	1730	12	*Australopyrum.sp.*	Removed	5
All	All	All	All	*Bossiaea.foliosa*	*Bossiaea sericia s.l.*	
All	All	All	All	*Craspedia coolaminica, Craspedia glauca, Craspedia* (grey leaf, orange)	*Craspedia gracilis s.l.*	
All	All	All	All	*Craspedia* (green leaves orange), *Craspedia* (green leaves orange)	*Craspedia auranti*	
All	All	All	All	*Euphrasia (white), Euphrasia sp.*	*Euphrasia spp.*	
All	All	All	All	*Poa phillipsiana*	*Poa fawcettiae*	

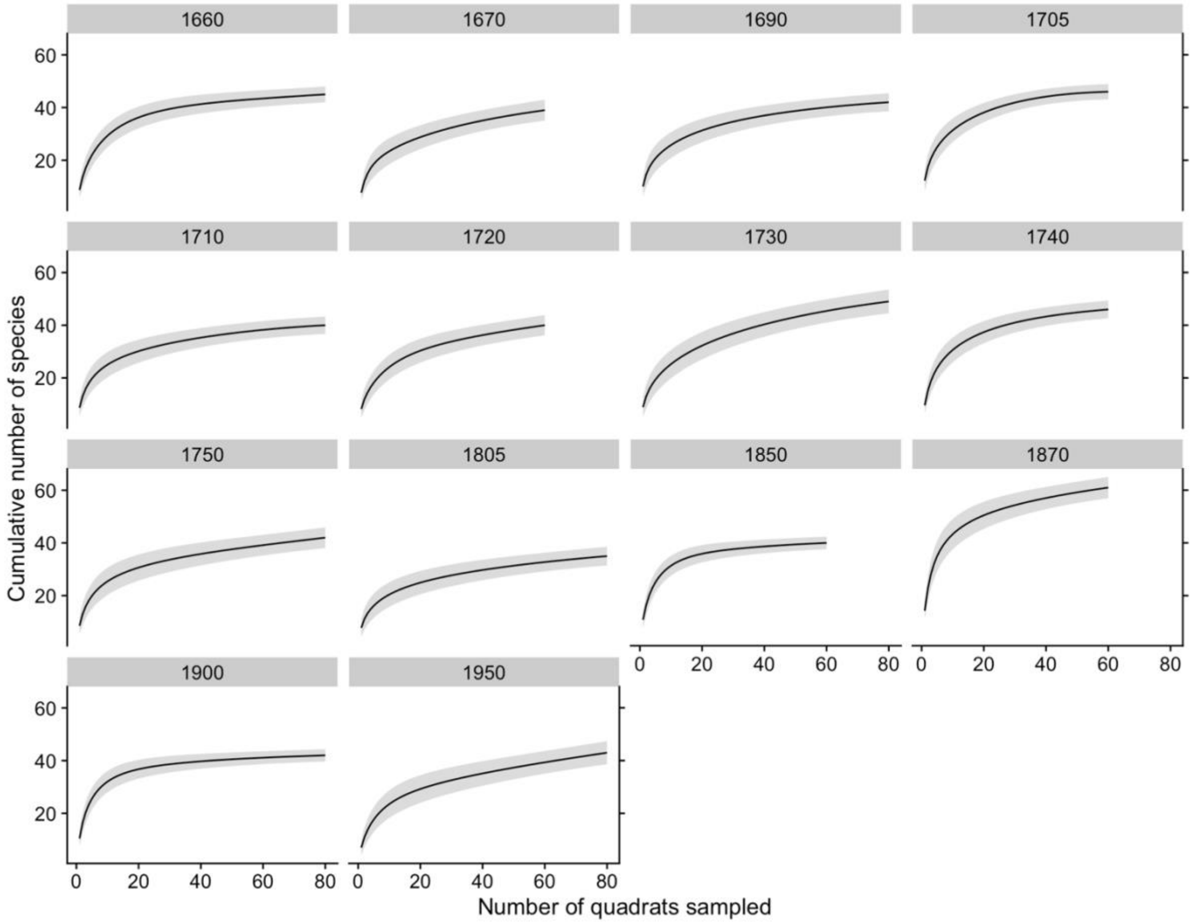


Figure S2 Species Accumulation Curve (SAC) model (+/- 95% confidence intervals) of all summits showing the cumulative number of species when the number of quadrats increases.

Table S4 Total plant species recorded at study summits between 2004 and 2022 and their family, conservation status (* indicated exotic species) and lifeform.

Species	**Family**	**Conservation status (Vic)**	**Lifeform**
Acacia siculiformis	Fabaceae		Shrub
Acaena novae-zelandiae	Rosaceae		Forb
Acaena sp.	Rosaceae		Forb
Acetosella vulgaris	Polygonaceae	*	Forb
Aciphylla glacialis	Apiaceae	EN (FFG)	Forb
Acrothamnus montanus	Ericaceae	EN (FFG)	Shrub
Agrostis capillaris	Poaceae	*	Graminoid
Agrostis venusta	Poaceae		Graminoid
Ajuga australis	Lamiaceae		Forb
Anthosachne scabra	Poaceae		Graminoid
Anthoxanthum odoratum	Poaceae	*	Graminoid
Aphanes arvensis	Rosaceae	*	Forb
Argyrotegium fordianum	Asteraceae		Forb
Argyrotegium nitidulum	Asteraceae	Rare (Vic), VU (EPBC)	Forb
Arthropodium milleflorum	Asparagaceae		Forb
Asperula gunnii	Rubiaceae		Forb
Asterolasia trymalioides subsp. trymalioides	Rutaceae		Shrub
Australopyrum velutinum	Poaceae	VU (FFG)	Graminoid
Austrostipa nivicola	Poaceae	EN (FFG)	Graminoid
Baeckea gunniana	Myrtaceae		Shrub
Baeckea utilis	Myrtaceae		Shrub
Bossiaea foliosa	Fabaceae		Shrub
Bossiaea sericea	Fabaceae		Shrub
Brachyscome nivalis	Asteraceae		Forb
Brachyscome rigidula	Asteraceae		Forb
Brachyscome spathulata	Asteraceae		Forb
Bulbine glauca	Asphodelaceae		Forb
Cardamine lilacina s.l.	Brassicaceae	EN (FFG)	Forb
Carex breviculmis	Cyperaceae		Graminoid
Carex hebes	Cyperaceae		Graminoid
Carpha nivicola	Cyperaceae	EN (FFG)	Graminoid
Celmisia costiniana	Asteraceae	EN (FFG)	Forb
Celmisia latifolia	Asteraceae	EN (FFG)	Forb
Celmisia pugioniformis	Asteraceae		Forb
Celmisia tomentella	Asteraceae	VU (FFG)	Forb
Cerastium glomeratum	Caryophyllaceae	*	Forb
Cerastium vulgare	Caryophyllaceae	*	Forb
Chrysocephalum semipapposum subsp.	Asteraceae		Forb
Colobanthus affinis	Caryophyllaceae	EN (FFG)	Forb
Coronidium monticola	Asteraceae		Forb
Cotula alpina	Asteraceae		Forb
Craspedia adenophora	Asteraceae	EN (FFG)	Forb

Craspedia aurantia	Asteraceae	EN (FFG)	Forb
Craspedia gracilis	Asteraceae		Forb
Crassula sieberiana	Crassulaceae		Forb
Deyeuxia monticola	Poaceae		Graminoid
Epacris glacialis	Ericaceae	EN (FFG)	Shrub
Epacris gunnii	Ericaceae		Shrub
Eucalyptus pauciflora subsp. niphophila	Myrtaceae		Tree
Eucalyptus pauciflora subsp. pauciflora	Myrtaceae		Tree
Euphrasia collina	Orobanchaceae		Forb
Euphrasia collina subsp. paludosa	Orobanchaceae		Forb
Euphrasia crassiuscula	Orobanchaceae		Forb
Euphrasia crassiuscula subsp. glandulifera	Orobanchaceae	CR (FFG), VU	Forb
Euryomyrtus ramosissima subsp.	Myrtaceae		Shrub
Ewartia nubigena	Asteraceae	EN (FFG)	Forb
Exocarpos nanus	Santalaceae		Shrub
Gentianella muelleriana subsp. muelleriana	Gentianaceae	Endemic	Forb
Gentianella muelleriana subsp. willisiana	Gentianaceae	VU (FFG)	Forb
Geranium potentilloides	Geraniaceae		Forb
Geranium spp.	Geraniaceae		Forb
Gonocarpus montanus	Haloragaceae		Forb
Goodenia hederacea subsp. alpestris	Goodeniaceae		Forb
Grevillea australis	Proteaceae		Shrub
Grevillea victoriae subsp. victoriae	Proteaceae	EN (FFG)	Shrub
Hovea montana	Fabaceae		Shrub
Hypochaeris radicata	Asteraceae	*	Forb
Kunzea muelleri	Myrtaceae		Shrub
Leionema phylicifolium	Rutaceae		Shrub
Leptorhynchos squamatus subsp. alpinus	Asteraceae	EN (FFG)	Forb
Leucochrysum albicans subsp. albicans	Asteraceae		Forb
Lomandra filiformis subsp. coriacea	Asparagaceae		Graminoid
Luzula acutifolia subsp. acutifolia	Juncaceae	EN (FFG)	Graminoid
Luzula modesta	Juncaceae		Graminoid
Luzula novae-cambriae	Juncaceae		Graminoid
Melicytus angustifolius subsp. divaricatus	Violaceae		Shrub
Microseris lanceolata	Asteraceae		Forb
Montia australasica	Montiaceae		Forb
Olearia brevipedunculata	Asteraceae	EN (FFG)	Shrub
Olearia frostii	Asteraceae	VU (FFG)	Shrub
Olearia phlogopappa subsp. flavescens	Asteraceae	EN (FFG)	Shrub
Oreomyrrhis eriopoda	Apiaceae		Forb
Orites lancifolius	Proteaceae		Shrub
Ozothamnus alpinus	Asteraceae	EN (FFG)	Shrub
Pappochroma bellidioides	Asteraceae		Forb
Pappochroma nitidum	Asteraceae	VU (FFG)	Forb
Pentachondra pumila	Ericaceae	EN (FFG)	Shrub
Phebalium squamulosum subsp. alpinum	Rutaceae	EN (FFG)	Shrub
Pimelea alpina	Thylemaeaceae		Shrub
Pimelea axiflora subsp. alpina	Thylemaeaceae	VU (FFG)	Shrub

Plantago euryphylla	Plantaginaceae		Forb
Poa annua	Poaceae	*	Graminoid
Poa fawcettiae	Poaceae		Graminoid
Poa hiemata	Poaceae		Graminoid
Poa hothamensis var. hothamensis	Poaceae		Graminoid
Podolepis robusta	Asteraceae		Forb
Podolobium alpestre	Fabaceae		Forb
Prasophyllum suttonii	Orchidaceae	Advisory list	Forb
Prasophyllum tadgellianum	Orchidaceae		Forb
Prostanthera cuneata	Lamiaceae		Shrub
Ranunculus eichlerianus	Ranunculaceae	EN (FFG)	Forb
Ranunculus graniticola	Ranunculaceae		Forb
Ranunculus muelleri	Ranunculaceae	EN (FFG)	Forb
Ranunculus victoriensis	Ranunculaceae	EN (FFG)	Forb
Rhodanthe anthemoides	Asteraceae		Forb
Rubus parvifolius	Rosaceae	*	Shrub
Rytidosperma alpicola	Poaceae	VU (FFG)	Graminoid
Rytidosperma erianthum	Poaceae		Graminoid
Rytidosperma nivicola	Poaceae	EN (FFG)	Graminoid
Rytidosperma nudiflorum	Poaceae		Graminoid
Rytidosperma oreophilum	Poaceae	EN (FFG)	Graminoid
Rytidosperma pallidum	Poaceae		Graminoid
Rytidosperma penicillatum	Poaceae		Graminoid
Rytidosperma pilosium	Poaceae		Graminoid
Scleranthus biflorus	Caryophyllaceae		Shrub
Scleranthus diander	Caryophyllaceae	EN (FFG)	Shrub
Scleranthus singuliflorus	Caryophyllaceae	EN (FFG)	Shrub
Senecio gunnii	Asteraceae		Forb
Senecio pinnatifolius var. alpinus	Asteraceae	EN (FFG)	Forb
Stackhousia monogyna	Celastraceae		Forb
Stellaria pungens	Caryophyllaceae		Forb
Stylidium armeria subsp. Armeria	Stylidiaceae		Forb
Stylidium graminifolium	Stylidiaceae		Forb
Stylidium montanum	Stylidiaceae	EN (FFG)	Forb
Trifolium repens	Fabaceae	*	Forb
Trisetum spicatum subsp. australiense	Poaceae		Graminoid
Viola betonicifolia subsp. betonicifolia	Violaceae		Forb
Viola hederacea	Violaceae		Forb
Wahlenbergia gloriosa	Campanulaceae		Forb
Xerochrysum subundulatum	Asteraceae		Forb

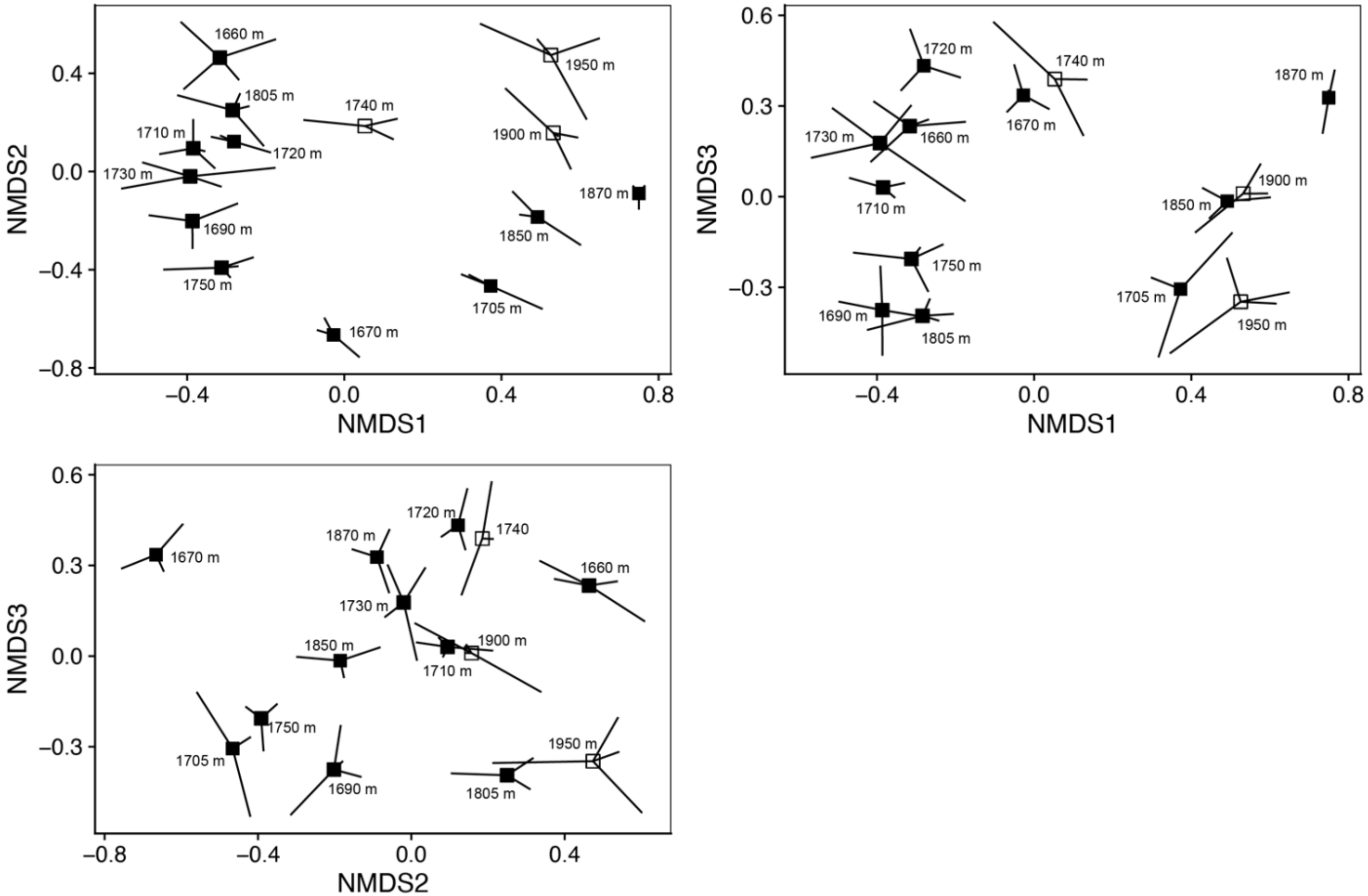


Figure S3 Floristic composition of the 14 mountain summits in Victoria. 3D NMDS ordination showing the centroid (symbol) between survey years for each summit. The length and directions of centroid arms show the degree of compositional change for each summit between 2004 and 2022. Open symbols represent unburnt sites, and closed symbols represent burnt sites. Ordinations are based on the percentage cover analysed using the Bray–Curtis dissimilarity matrix (3D stress = 0.145). Top left ordination: NMDS1 vs. NMDS2 axes with the significant environmental and species vectors shown. Top right ordination: NMDS1 vs. NMDS3 axes. Bottom left ordination: NMDS2 vs. NMDS3 axes.

Table S5 Time lag analysis results for 14 alpine summits in Victoria. Direction and rate of change are shown by the slope (β), and significant values at the $p < 0.05$ are shown with asterisks.

Elevation	***n***	***β***	***Df***	***R^2***	***p-value***
1660	80	15.847	118	0.022	0.107
1670	60	15.245	58	0.027	0.210
1690	80	1.062	118	0.000	0.986
1705	60	17.400	58	0.108	0.010*
1710	80	2.633	118	0.002	0.596
1720	60	33.885	58	0.000	0.952
1730	80	0.586	118	0.000	0.901
1740	80	-7.975	55	0.009	0.495
1750	80	5.911	118	0.033	0.047*
1805	80	9.636	118	0.016	0.166
1850	60	12.086	58	0.036	0.149
1870	60	-11.641	61	0.000	0.956
1900	80	0.367	118	0.002	0.668
1950	80	9.123	118	0.016	0.162

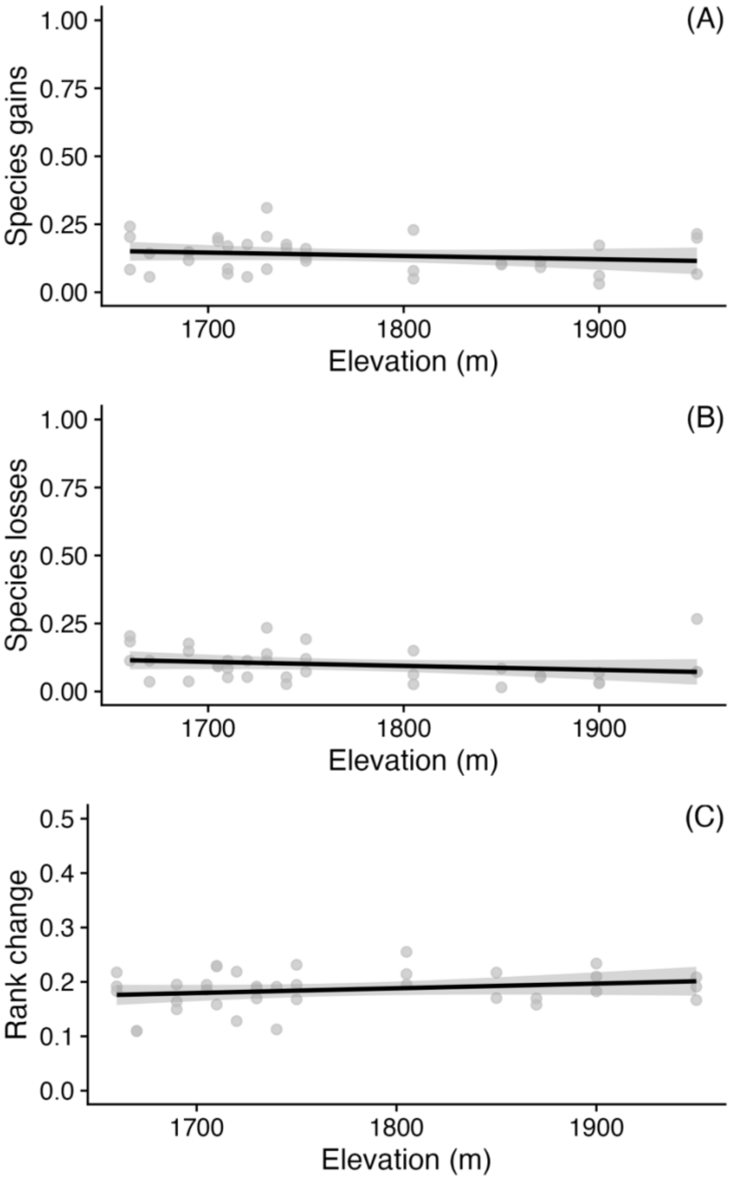


Figure S4 Species turnover: gains (A) and losses (B) and rank change (C) the elevational gradient (m) of the 14 Australian mountain summits. Grey dots represent the species turnover/rank change for each quadrat at each summit and the site level rank change in every year (2004 to 2022). A linear regression line, depicted in black, is fitted to the data with the 95% confidence intervals. Low species turnover results are near 0.01, and complete turnover is 1.0. Species rank change is bound between 0 and 0.5 (maximum rank changes allowed in the community) Avolio et al. (2018).

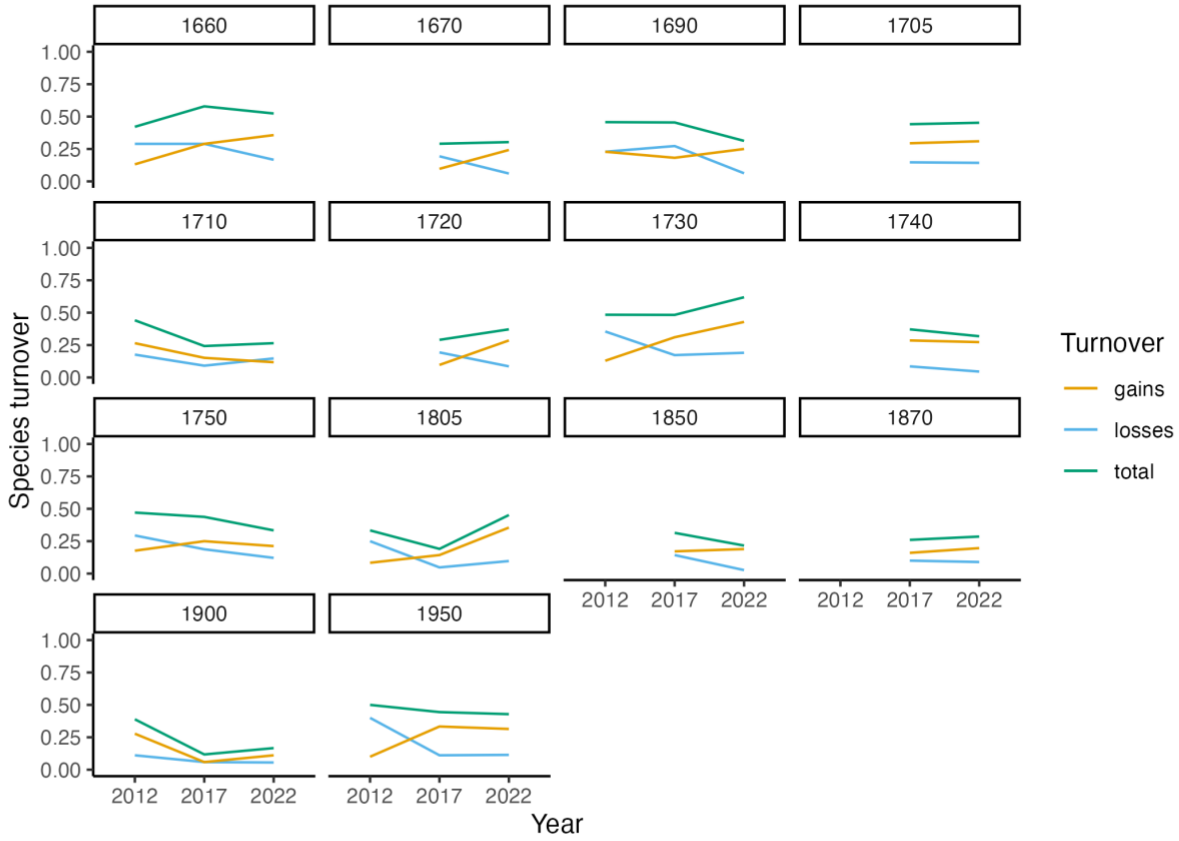


Figure S5 Species turnover (total, gains and losses) from 2004 to 2022 for each study summit (elevation m) in Victoria, Australia. Low species turnover results are near 0.01, and complete turnover is 1.0 (Avolio et al. 2018).

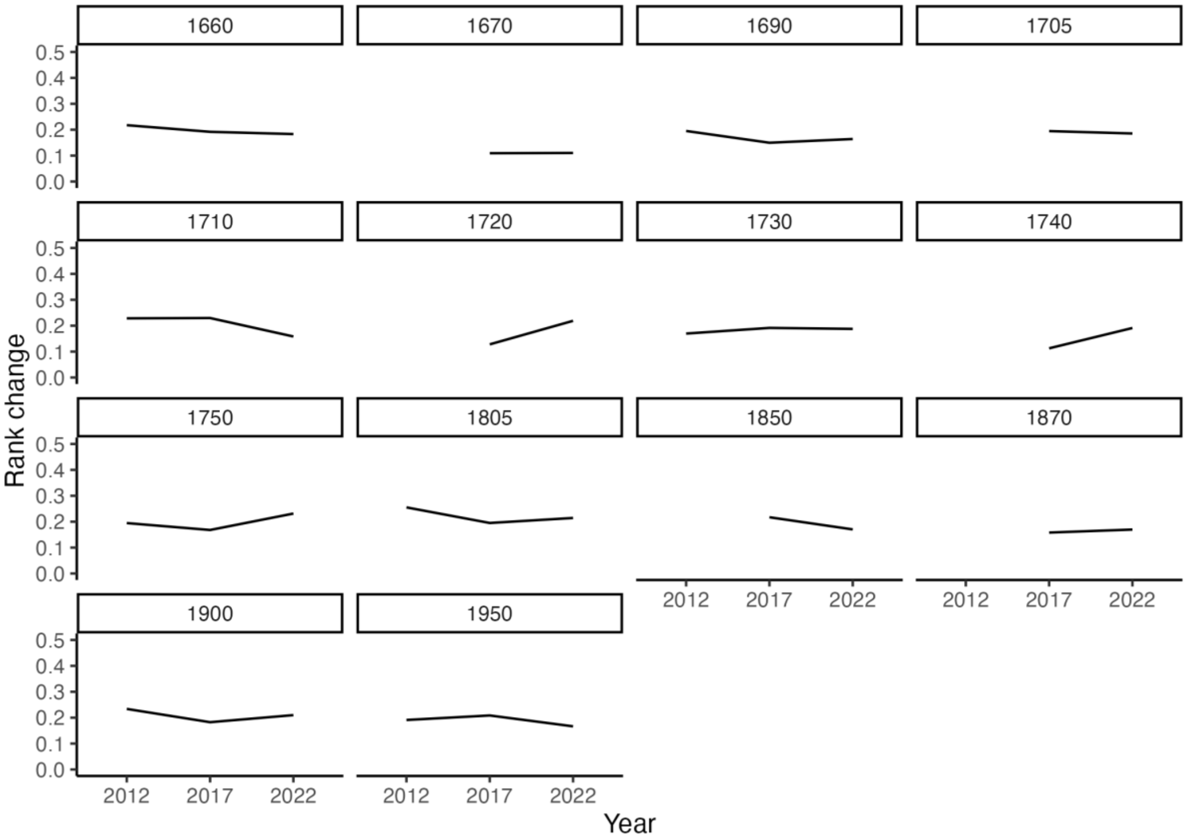


Figure S6 Species rank change from 2004 to 2022 for each study summit (elevation m) in Victoria, Australia. Species rank change is between 0 and 0.5 (maximum rank changes allowed in the community) (Avolio et al. 2018).

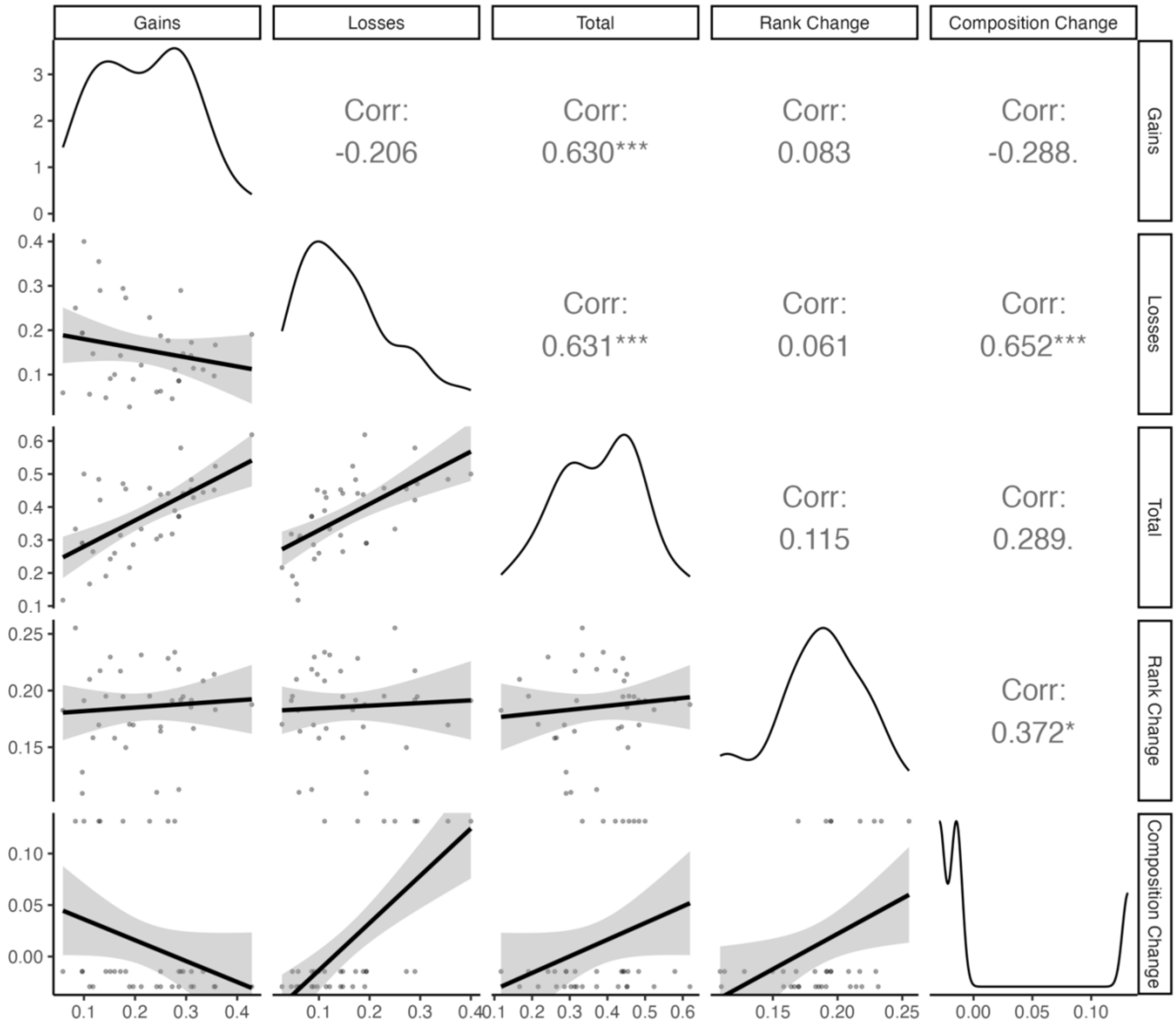


Figure S7 Correlations among measures of the 14 alpine summit vegetation community changes over time. Shown are the pairwise relationships between species total turnover, species gains, species losses, rank change, and composition change. The upper triangle of the matrix displays Pearson correlation coefficients, the lower triangle features scatter plots with regression lines and 95% confidence intervals, and the diagonal shows density plots for each variable. N = 36 for all correlations and histograms. Asterisks indicate levels of significance: * = p < 0.05, ** = p < 0.01, *** = p < 0.001.

Appendix III: Example model posterior predictive checks and random effects

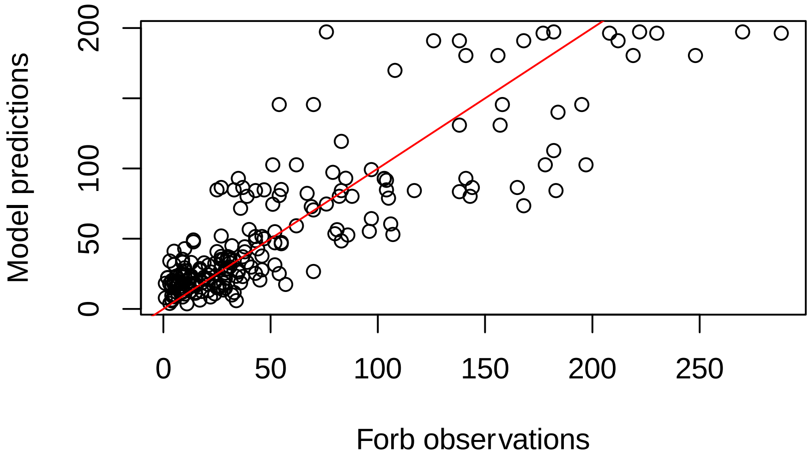


Figure S8 Forb model posterior predictive checks.

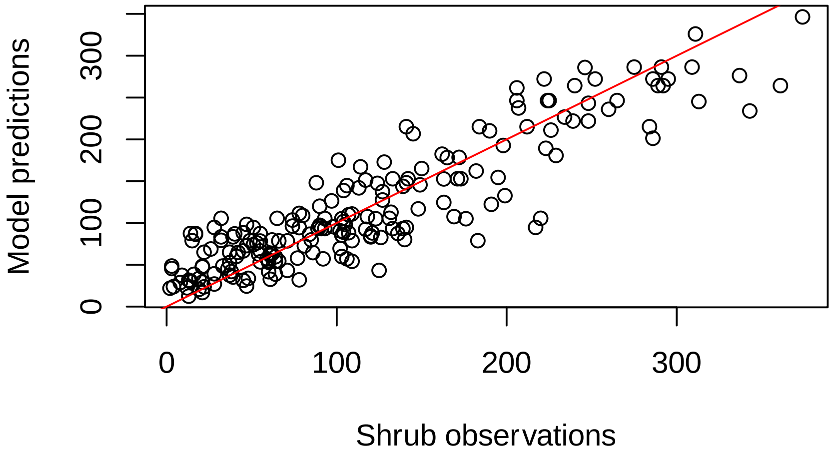


Figure S9 Shrub model posterior predictive checks.

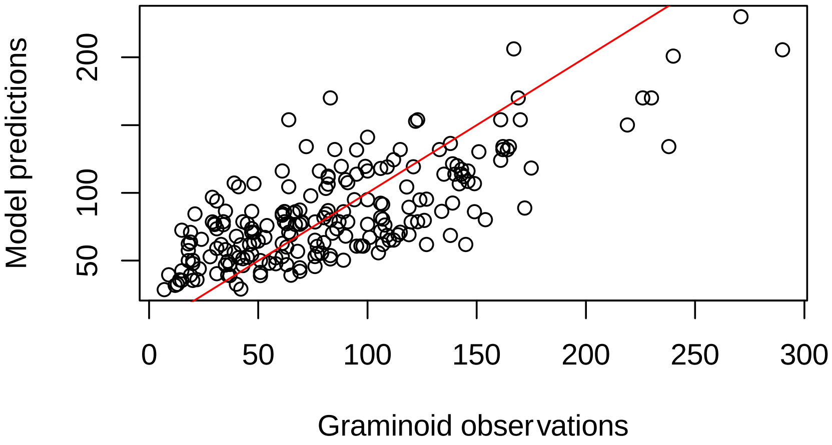


Figure S10 Graminoid model posterior predictive checks.

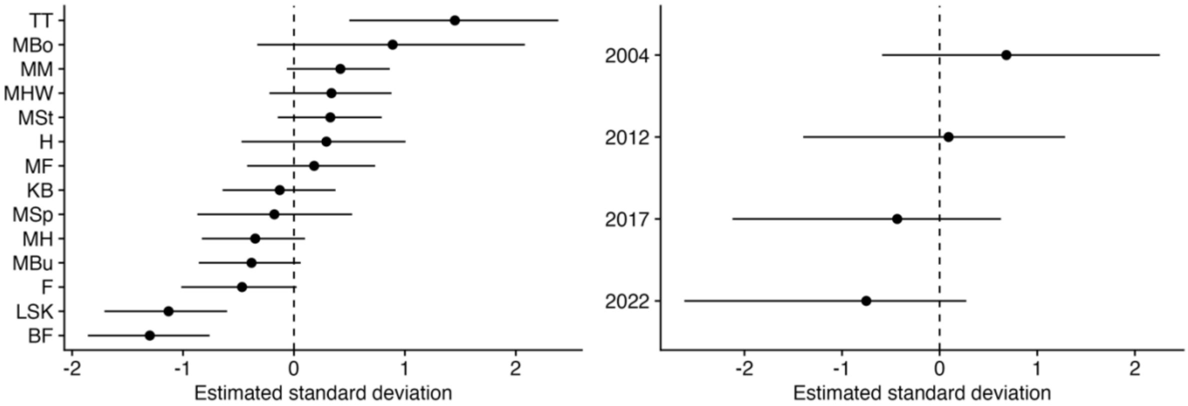


Figure S11 The conditional modes of the random effects (site and year) from the fitted forb model.

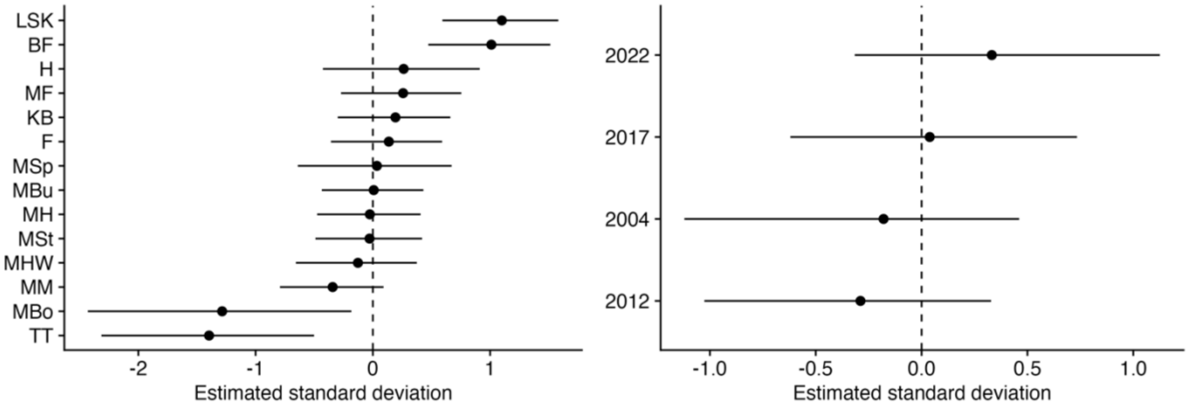


Figure S12 The conditional modes of the random effects (site and year) from the fitted shrub model.

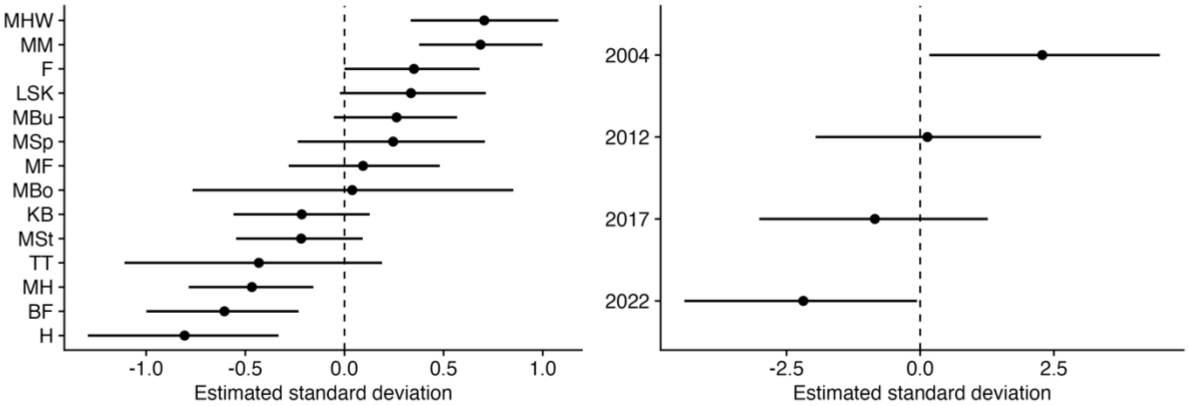


Figure S13 The conditional modes of the random effects (site and year) from the fitted graminoid model.

Appendix IV: Chapter 4 Supplementary Information

Table S6 Australian summit species and their plant functional traits: growth form, average Specific Leaf Area (SLA), average Leaf Dry Matter Content (LDMC), average seed mass, and maximum height (H_{max}).

Species	**Growth form**	**Average SLA (mm^2/mg^{-1})**	**Average LDMC (mg/g^{-1})**	**Average seed mass (mg)**	**H_{max} (m)**
Acacia siculiformis	Shrub	6.281	533.700	10.714	3.000
Acaena novae-zelandiae	Forb	13.121	341.372	1.706	1.500
Acetosella vulgaris	Forb	19.552	124.032	0.473	0.200
Aciphylla glacialis	Forb	6.746	357.222	5.148	0.600
Acrothamnus montanus	Shrub	8.041	525.000	12.201	0.500
Agrostis capillaris	Graminoid	16.455	366.784	0.090	0.700
Agrostis venusta	Graminoid	NA	479.167	0.127	0.300
Argyrotegium fordianum	Forb	14.544	329.051	0.087	0.030
Argyrotegium nitidulum	Forb	14.929	391.942	0.100	0.030
Ajuga australis	Forb	13.735	173.548	NA	0.500
Anthosachne scabra	Graminoid	9.659	392.448	8.542	1.200
Anthoxanthum odoratum	Graminoid	23.443	300.000	0.216	0.800
Aphanes arvensis	Forb	55.420	150.538	NA	0.300
Arthropodium milleflorum	Forb	21.046	180.079	1.254	1.300
Asperula gunnii	Forb	9.099	251.946	4.234	0.200
Asterolasia trymalioides	Shrub	5.224	455.748	2.372	0.500
Australopyrum velutinum	Graminoid	10.415	391.288	4.562	0.400
Austrostipa nivicola	Graminoid	14.929	391.942	11.432	0.800
Bossiaea foliosa	Shrub	8.026	412.500	2.826	1.500
Bossiaea sericea	Shrub	10.185	545.455	5.766	2.000
Brachyscome nivalis	Forb	6.594	262.797	0.486	0.150
Brachyscome rigidula	Forb	15.820	269.058	0.169	0.300
Brachysome spatulatha	Forb	13.304	147.665	0.239	0.300
Bulbine glauca	Forb	5.362	78.034	4.065	0.500
Cardamine lilacina	Forb	19.399	188.489	1.004	0.500
Carex breviculmis	Graminoid	15.207	357.618	1.035	0.100
Carex hebes	Graminoid	10.757	436.543	0.650	0.200
Celmisia costiniana	Forb	9.656	205.479	2.642	0.150
Celmisia latifolia	Forb	5.885	227.181	NA	0.260
Celmisia pugioniformis	Forb	4.761	387.645	2.793	0.200
Celmisia tomentella	Forb	6.866	310.656	4.628	0.200
Cerastium glomeratum	Forb	21.100	183.908	0.114	0.450
Cerastium vulgare	Forb	21.447	133.865	NA	0.500
Chrysocephalum semipapposum	Forb	NA	247.978	0.075	0.600
Colobanthus affinis	Forb	8.952	237.607	0.130	0.100

Coronidium monticola	Forb	23.307	229.938	0.181	0.350
Cotula alpina	Forb	11.865	256.923	0.227	0.040
Craspedia spp.	Forb	11.738	219.447	0.958	0.538
Crassula sieberiana	Forb	30.571	81.871	0.024	0.200
Deyeuxia monticola	Graminoid	6.630	345.401	0.255	0.900
Epacris glacialis	Shrub	8.860	518.182	NA	0.300
Epacris gunnii	Shrub	9.521	506.601	NA	1.000
Eucalyptus pauciflora	Tree	4.250	341.447	0.689	7.000
Euphrasia collina	Forb	9.809	233.873	0.188	0.600
Euryomyrtus ramosissima subsp. ramosissima	Shrub	11.807	496.000	NA	0.600
Ewartia nubigena	Forb	19.865	411.111	0.066	0.500
Exocarpus nanus	Forb	7.231	484.979	10.314	1.000
Gentianella muelleriana	Forb	20.320	181.686	0.396	0.250
Geranium potentilloides	Herb	12.891	261.058	1.519	1.000
Gonocarpus montanus	Herb	18.814	256.522	0.703	0.150
Goodenia hederacea	Herb	7.411	415.879	0.527	0.300
Grevillea australis	Shrub	5.455	406.306	8.192	1.200
Hovea montana	Shrub	5.314	540.884	17.386	0.500
Hypochaeris radicata	Herb	19.562	147.419	0.867	0.800
Kunzea muelleri	Shrub	8.013	622.222	2.435	0.300
Leionema phylicifolium	Shrub	6.720	416.541	NA	1.600
Leptorhynchos squamatus	Herb	10.769	373.500	0.114	0.500
Leucochrysum albicans	Herb	9.420	453.571	1.343	0.500
Leucochrysum alpinum	Herb	21.569	132.353	1.147	0.500
Lomandra filiformis subsp. coriacea	Graminoid	4.376	386.937	NA	0.470
Luzula acutifolia	Graminoid	8.300	345.944	0.330	0.050
Luzula modesta	Graminoid	9.243	365.385	0.427	0.300
Luzula novae-cambriae	Graminoid	14.468	326.205	0.460	0.300
Melicytus angustifolius	Shrub	12.149	296.104	12.452	2.000
Microseris lanceolata	Herb	19.795	137.785	3.252	0.500
Montia australasica	Herb	14.507	160.500	0.752	0.030
Olearia brevipedunculata	Shrub	8.802	524.462	NA	1.000
Olearia frostii	Shrub	8.468	403.326	0.860	0.400
Olearia phlogopappa subsp. flavescens	Shrub	9.047	412.227	NA	1.400
Oreomyrrhis eriopoda	Herb	8.346	303.302	4.539	0.300
Orites lancifolius	Shrub	4.179	485.043	6.883	2.000
Ozothamnus alpinus	Shrub	6.431	505.037	0.538	1.000
Pappachroma bellidoidies	Forb	9.173	269.141	0.248	0.160
Pappochroma nitidum	Forb	10.799	265.865	0.764	0.160
Pentachondra pumila	Shrub	8.970	646.154	1.219	0.100
Phebalium squamulosum	Shrub	6.280	486.667	NA	1.300

Pimelea alpina	Shrub	11.071	365.789	2.613	0.150
Pimelea axiflora	Shrub	10.144	416.346	2.619	1.000
Plantago euryphylla	Forb	8.741	157.469	0.319	0.110
Poa annua	Graminoid	15.086	303.226	0.209	0.300
Poa fawcettiae	Graminoid	15.234	505.917	0.359	0.600
Poa hiemata	Graminoid	7.407	468.403	0.350	0.600
Poa hothamensis	Graminoid	12.957	475.053	0.434	0.300
Podolepis robusta	Forb	13.077	163.105	1.017	0.600
Podolobium alpestre	Shrub	11.920	565.060	2.536	1.300
Prasophyllum sp.	Forb	22.891	133.127	0.007	0.300
Prostanthera cuneata	Shrub	6.708	391.935	1.133	1.000
Ranunculus graniticola	Forb	23.235	234.701	3.569	0.250
Ranunculus muelleri	Forb	7.995	266.824	1.591	0.062
Ranunculus victoriensis	Forb	12.235	227.787	0.968	0.180
Rhodanthe anthemoides	Forb	13.495	261.039	1.513	0.300
Rubus parvifolius	Shrub	20.973	390.752	3.220	1.000
Rytidosperma alpicola	Graminoid	13.216	422.906	1.106	0.300
Rytidosperma erianthum	Graminoid	NA	501.250	1.398	0.300
Rytidosperma nudiflorum	Graminoid	5.739	458.672	1.275	0.300
Rytidosperma oreophilum	Graminoid	6.255	406.822	NA	0.500
Rytidosperma pallidum	Graminoid	5.354	425.480	1.397	1.800
Rytidosperma penicillatum	Graminoid	11.936	359.464	1.016	0.700
Rytidosperma pilosum	Graminoid	14.807	NA	1.469	0.150
Scleranthus biflorus	Forb	2.224	322.631	0.552	0.120
Scleranthus diander	Forb	NA	443.038	NA	0.100
Scleranthus singuliflorus	Forb	9.773	440.000	1.004	0.240
Senecio gunnii	Forb	25.602	111.675	0.342	1.000
Senecio pinnatifolius	Forb	8.426	229.425	0.288	1.000
Stackhousia monogyna	Forb	18.063	181.135	3.799	0.600
Stellaria pungens	Forb	19.906	283.715	5.410	0.600
Stylidium graminifolium s.l.	Forb	10.364	207.723	0.235	0.750
Trifolium repens	Forb	32.699	200.262	0.589	0.300
Trisetum spicatum	Graminoid	11.032	433.611	0.377	0.600
Viola betonicifolia	Forb	15.368	219.225	1.365	0.450
Viola hederacea	Forb	19.058	284.091	NA	0.150
Wahlenbergia gloriosa	Forb	15.390	247.668	0.025	0.300
Xerochrysum subundulatum	Forb	10.750	264.018	0.878	0.450

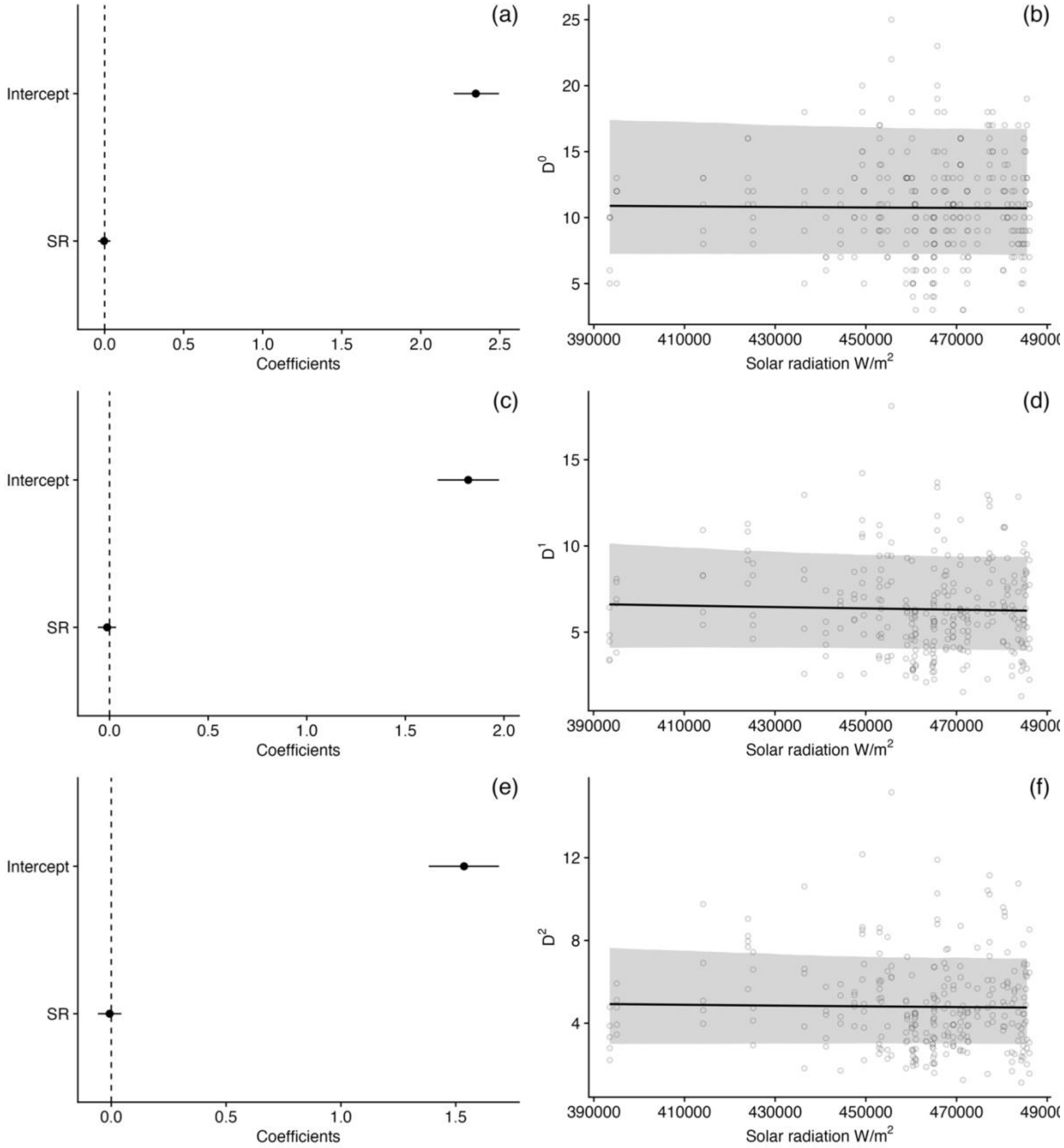
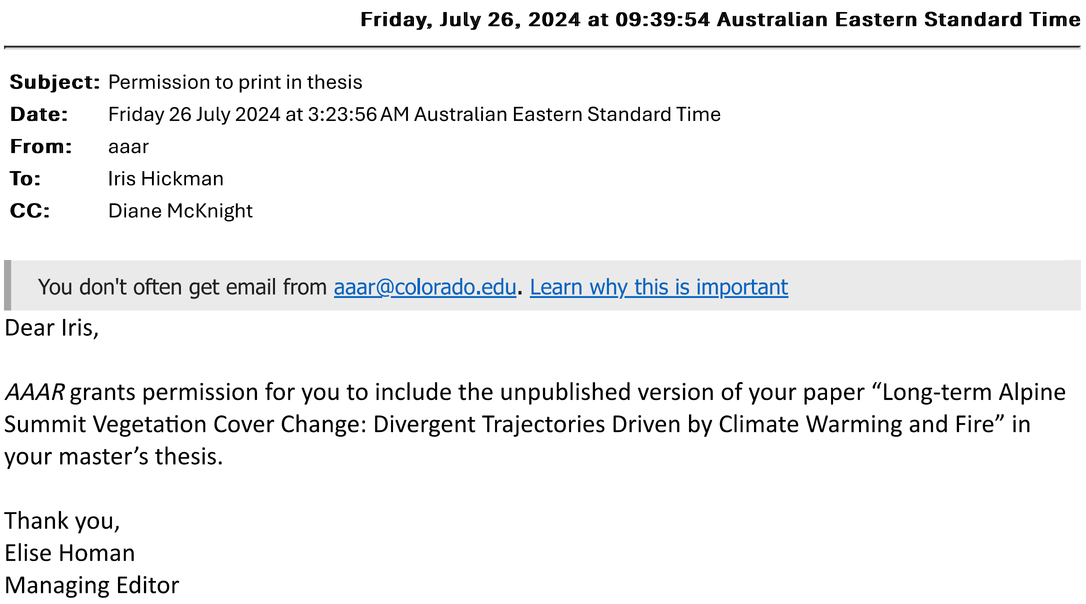


Figure S14 The effects of solar radiation on Australian summit α-diversity. (a, c, and e) Centred and standardised model coefficients and effects of solar radiation in 2022. The 95% significance can be determined if the 95% credible intervals cross the 0 line (dashed line). Mean diversity indices, based on the Hill numbers (b) q = 0 (D0), (d) q = 1 (D1), (f) q = 2 (D2) as a function of solar radiation at the average site. All error bars and shaded areas indicate 95% Bayesian credible intervals.

Appendix V: Chapter 3 Permission from Journal



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