# Assessing alpine vegetation dynamics using long-term ecological monitoring amidst rapid climate change



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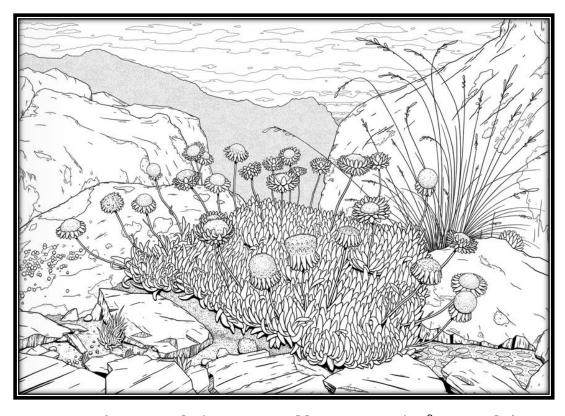
**Doctor of Philosophy** 

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# Statement of originality

This work has not previously been submitted for a degree or diploma at any university. To the best of my knowledge, the thesis contains no material previously published or written by another person except where references are made in the thesis.

(Signed):	
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10 October 2022	



Leucochrysum alpinum (F.Muell.) R.J.Dennis & N.G.Walsh

Artwork by Caleb Connell

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## **Abstract**

Alpine ecosystems occur above the bioclimatic treeline and support cryophilic plant communities with high endemism, which are governed by low temperatures and short growing seasons. However, the climate of many alpine ecosystems is changing rapidly with warming temperatures, declining snow cover and lengthening growing seasons. Alpine vegetation dynamics in response to changes in climate over recent decades have been observed via long-term ecological monitoring techniques, but such studies are less common in the southern hemisphere including in the marginal alpine ecosystems of the Australian Alps. Therefore, the scale, ecological processes and implications of climate-induced dynamics are less clear for this important ecological, cultural and socioeconomic region. The central aim of this thesis is to understand the responses of vegetation in the largest contiguous alpine area in the Australian Alps, the Kosciuszko alpine area, to climate change over recent decades across varying spatial scales.

To assess the status, distribution, themes and evolution of research examining alpine vegetation in relation to climate change, a multi-component bibliometric literature review was conducted (Chapter 2). Globally, there were 3,143 publications relating to climate change and alpine vegetation, with research on this topic exceeding the rate of increase apparent for research in general, which likely reflects the pronounced changes observed recently in alpine ecosystems. However, geographic disparities were apparent when continental alpine areas were compared with research outputs. Temporally, there was a shift in research from treelines to grasslands, largely driven by increasing research about the Tibetan Plateau, but there are still relatively few studies on cryophilic and periglacial communities. Traditional, field-based ecological monitoring techniques were often used, but increasingly remote sensing techniques are providing valuable insights. The review highlights the importance of this topic, changes in methods and technology, and important thematic and geographic research gaps including relatively limited research in the southern hemisphere.

Beginning at the microscale (metres), microclimate and vegetation dynamics along snowmelt gradients over 13 years were assessed in critically endangered snowpatch communities in the Kosciuszko alpine area (Chapter 3). Specifically, snowmelt zones were delineated using continuous soil temperature monitoring while vegetation composition was assessed using data from of 84 permanently-marked 1 m² quadrats surveyed in 2007 and 2013, combined with new data from a survey in 2020 conducted as part of this thesis. Microclimatic changes were most pronounced in the late melt zone, where growing seasons have lengthened and temperatures have warmed, with the initially distinct microclimates of each melt zone becoming more similar over time. Alongside these microclimatic changes, there was increasing cover of graminoids and

declining cover of snowpatch specialists in the mid and late melt zones, but diversity remained relatively stable across the three surveys. There were changes in composition as well as community-weighted traits and strategies, with vegetation increasingly dominated by taller species with larger leaves resulting in a shift from ruderal-tolerant to stress-tolerant compositions over time. With the climate continuing to warm, the loss of defining abiotic and biotic characteristics of snowpatches may lead to ecosystem collapse via replacement by a novel ecosystem.

Moving up to mesoscale dynamics (hectares), microclimate and vegetation dynamics of common alpine plant communities were assessed over 15 years along an elevation gradient in the Kosciuszko alpine area (Chapter 4). Specifically, microclimatic data were obtained from continuous soil temperature monitoring. Vegetation composition data were obtained from permanently-marked plots on five ~ 1 ha summits surveyed in 2004 and 2011, along with new data from a survey in 2019 conducted as part of this thesis. At this mesoscale, soil temperatures increased through time and were correlated to air temperatures. While species richness increased over time, diversity declined as a result of biotic homogenisation driven by the increasing cover of generalist and thermophilic graminoids and shrubs via densification and in-filling. There were also elevation-dependant changes in cover and composition with increasing dominance of shrubs at lower elevations and graminoids at higher elevations, with the most pronounced changes in composition at higher elevations. As climate-induced vegetation dynamics intensify with further warming, there are important implications for increasing potential for novel biotic interactions along elevation gradients as well as increasing biomass and landscape flammability in this alpine area.

Finally, to understand macroscale (kilometres) and longer-term dynamics over three decades in response to climate change and the landscape-level wildfires in 2003, changes across the whole Kosciuszko alpine area (~455 km²) were assessed (Chapter 5). Changes in climate were identified including increasing temperatures (1910-2019), precipitation (1900-2019) becoming more seasonally variable and declining snow cover (1954-2021), with the most rapid changes in recent decades. Then, vegetation cover and zonation were modelled using optimised random forest classification of Landsat growing season composites for 1990, 2000, 2010 & 2020. Concurrent with recent changes in climate, the cover of woodlands has increased via densification at lower elevations but there has been treeline stasis, except where wildfires resulted in treeline recession. Heathlands were mostly replaced by woodlands at lower elevations and shrublines have advanced upslope, however wildfire led to suppression of upslope movement in burnt areas as grasslands replaced burnt heathlands at higher elevations. Small increases in the cover of screelands were associated with drought and loss of vegetation during the less extensive 2020 wildfires. Finally,

wildfire led to increasing cover of grasslands, which recovered rapidly in areas burnt in 2003 but were replaced by heathlands and woodlands by 2020. With increasing landscape flammability and fire weather conditions associated with climate change in this alpine area, some vegetation dynamics may be incremental in response to relatively gradual climatic changes while others may be transformative in response to wildfires.

Overall, this thesis provides novel insights and addresses important knowledge gaps regarding how alpine vegetation responds to climate change, particularly in the Australian Alps. Specifically, the climate has changed rapidly over recent decades with warmer temperatures, lengthening growing seasons, more variable precipitation and declining snow cover, all of which are abiotic determinants of alpine vegetation. In response, there has been increasing cover of generalist and thermophilic competitive taxa and subsequent declines in cryophilic taxa. Climate-induced responses may be amplified along elevation and snowmelt gradients, with fire regulating woody advances upslope but not encroachment via densification at lower elevations. With the cumulative loss of abiotic and biotic conditions that governed the distribution of alpine vegetation in the past, as well as the increasing risk of wildfire, the stability and persistence of the Kosciuszko alpine flora is in question. Without effective climate action alongside the mitigation of threats such as invasive species, wildfire and recreation impacts, further vegetation changes seem imminent.

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## Acknowledgements

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# **Glossary and abbreviations**

Term	Abbreviation	Definition and relevant references	
Above sea level	a.s.l.	Elevation or height of land above sea level	
Advance		Upslope movement of vegetation over time	
Alpine		High elevation treeless vegetation that occurs above the	
•		bioclimatic treeline (Körner, 2003)	
Competition		Availability of resources that promote plant production,	
		with competition-adapted species able to thrive in such	
		conditions (Grime, 2006)	
Cryophilic		Plants able to thrive at lower temperatures	
Cryptogam		Plant or plant-like organism that reproduces via spores	
Densification		Process of plants increasing in density causing	
		increasing overlapping cover of vegetation over time, or	
		in reference to increasing density or dominance of one	
_		vegetation type over time	
Ecotone		Grouping of ecosystems within a bioclimatic belt that	
		experience relatively similar climatic and environmental	
<b>T</b>		conditions, and are distinct from surrounding landscapes	
Ecosystem		A biological network of interacting organisms and their	
FIN'~ C 4	ENICO	physical environment	
El Niño-Southern	ENSO	Irregular periodic variations in convection and winds	
Oscillation Fire		driven by sea temperature gradients in the Pacific Ocean	
riie		Anthropogenic and deliberately ignited fires to manage landscapes	
Forest Fire	FFDI	•	
Danger Index	LLDI	Index calculated from vegetation dryness, air temperature, wind speed and humidity	
Forb		Herbaceous dicot angiosperm other than a graminoid	
1.010		(Körner, 2003)	
Graminoid		Herbaceous monocot angiosperm with grass-like	
Oraninolu		morphology (Körner, 2003)	
In-filling		Process of plants occupying inter-tussock spaces or	
B		within the canopy of shrubs causing increasing	
		overlapping vegetation cover	
Indian Ocean	IOD	Irregular variations in convection driven by oscillations	
Dipole		of sea temperatures in the Indian Ocean	
Generalist		Plants that thrive in a wide variety of environmental	
		conditions	
Kosciuszko	KAA	The largest, highest and most species rich contiguous	
alpine area		alpine ecotone in Australia, delimited in this thesis as	
		the contiguous area above 1,700 m surround Mount	
		Kosciuszko	
Long term	LTEM	Systematically and regularly collection of ecological	
ecological		data from a particular site or set of sites for more than 10	
monitoring		years (Lindenmayer et al., 2012)	
Macroclimate		Overall climate of a large area (>100 m <sup>2</sup> ). Commonly	
		quantified gridded climate models using data from	
Miono alima at a		weather stations (Körner & Hiltbrunner, 2021)	
Microclimate		Localised climatic conditions of small area (1 – 10 m <sup>2</sup> )	
		that may differ from macroclimatic conditions.  Commonly quantified by soil temperature loggers in	
		alpine ecosystems (Körner & Hiltbrunner, 2021)	
Macroscale		Large spatial sampling scale spanning over kilometres	
iviacioscale		Large spatial sampling scale spanning over knothetres	

Term	Abbreviation	Definition and relevant references
Mesoscale		Intermediate spatial sampling scale spanning over
		hectares
Microscale		Small spatial sampling scale spanning over metres
Plant community		Collection or association of plant species covering a
		discernible and continuous area, forming an ecosystem
_		or may be part of a larger ecosystem
Tree		Woody plant greater than 3 m in height often with stem diameters at breast height of greater than 10 cm (Körner, 2012)
Treeline		High elevation limit of tree distribution where the
		realised niche of treeline species demarcates the lower
		boundary of the alpine ecotone (Körner, 2012)
Thermophilic		Plants able to thrive at higher temperatures
Recession		Downslope movement of vegetation over time
Remote sensing		Detecting and monitoring the physical characteristics of
		an area by measuring its reflected and emitted radiation
Ruderal		at a distance using satellite or aircraft
Ruderai		Disturbance that limits or removes plant biomass, with ruderal-adapted species able to thrive in such conditions
Shrub		Woody, multi-stemmed plant less than 3 m in height
Sindo		often with stem diameters at breast height of less than 10
		cm (Körner, 2012)
Specialist		Plants that only thrive in a confined range of
•		environmental conditions
Southern Annular	SAM	North-south movement of westerly low-pressure
Mode		systems from the Antarctic polar vortex
Stasis		Lack of upslope or downslope movement of vegetation over time
Stress		Conditions that limit plant production, with stress-
G :		adapted species able to thrive in such conditions
Suppression		Slower rate of upslope movement of vegetation over time
Wildfire		Uncontrolled burning of vegetation, often as a result of dry lightning ignition
Zonation		Bioclimatic division of ecotones, ecosystems and vegetation types, often along environmental gradients

#### **Glossary References**

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## Published and under review papers included in the thesis

This thesis includes three peer-reviewed published papers (Chapters 2, 3 and 4) and a paper currently under review (Chapter 5). I am first author on all papers, and my specific contributions to the co-authored papers are outlined at the front of each chapter. Acknowledgements of those contributing to the research are also included for each paper. The bibliographic details for the papers are as follows:

- Chapter 2: **Verrall, B.**, & Pickering, C. M. (2020). Alpine vegetation in the context of climate change: A global review of past research and future directions. *Science of the Total Environment*, 748, 141344. doi.org/10.1016/j.scitotenv.2020.141344
- Chapter 3: **Verrall, B.**, Green, K., & Pickering, C. M. (2022). Temporal dynamics in alpine snowpatch plants along a snowmelt gradient explained by functional traits and strategies. *Oecologia*, 1-17. doi.org/10.1007/s00442-022-05297-3
- Chapter 4: **Verrall, B.**, Green, K., & Pickering, C. M. (2021). Dynamics in plant diversity and composition on Australian alpine summits over time. *Biodiversity and Conservation*, 30(6), 1855-1880. doi.org/10.1007/s10531-021-02171-1
- Chapter 5: **Verrall, B.**, Norman, N., Mackey, B., Fisher, S. & Dodd, J. (in review). Decadal alpine vegetation dynamics modelled using Landsat timeseries amidst rapid climate change in Australia.

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# Other academic outputs completed during candiature

Conference presentations based on research in this thesis

- **Verrall, B.**, Green, K., & Pickering, C. M. (2019). Climate change induced trends in alpine vegetation over the last 15 years in the Australian Alps. 4th International Mountain Conference, Innsbruck, Austria. 10<sup>th</sup> September 2019.
- Verrall, B., Green, K., & Pickering, C. M. (2021). Are we losing snowpatches to climate change? Australian Institute of Alpine Studies Conference, Mount Hotham, Australia. 18<sup>th</sup> November 2021.
- **Verrall, B.**, Green, K., & Pickering, C. M. (2022). Temporal dynamics in alpine snowpatch plants along a snowmelt gradient explained by functional traits and strategies. 5<sup>th</sup> International Mountain Conference, Innsbruck, Austria. 12<sup>th</sup> September 2022.
- Verrall, B., Green, K., & Pickering, C. M. (2022). Modelling decadal treeline vegetation dynamics using Landsat timeseries amidst rapid climate change and fire in Australia. 5th International Mountain Conference, Innsbruck, Austria. 12th September 2022.

During my PhD, I contributed to other projects resulting in additional academic outputs utilising skills obtained from the thesis research. These outputs include:

#### Published papers

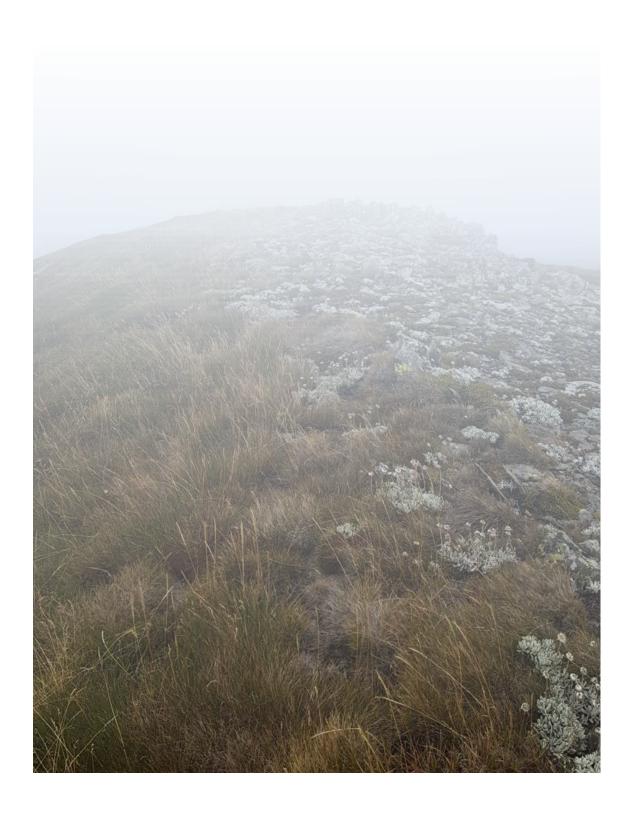
- **Verrall, B.**, & Pickering, C. M. (2019). Recovery of subalpine grasslands 15 years after landscape level fires. *Australian Journal of Botany*, 67(5), 425-436. doi.org/10.1071/BT19020
- Nalau, J., & Verrall, B. (2021). Mapping the evolution and current trends in climate change adaptation science. *Climate Risk Management*, 32, 100290. <a href="https://doi.org/10.1016/j.crm.2021.100290">doi.org/10.1016/j.crm.2021.100290</a>
- Hewitt, J., Lawson, C., **Verrall, B.**, & Grealish, L. (2022). Implementing voluntary assisted dying laws in healthcare: Exploring beliefs to identify implementation hurdles. *Research in Nursing & Health*, 1-14. doi.org/10.1002/nur.22287

#### Government reports and submissions

- Verrall, B., & Pickering, C. M. (2020). Impacts of Mountain Biking in Natural Areas: A Case Study of Kincumba Mountain Regional Reserve. Confidential report to Central Coast Council, New South Wales, Australia.
- Pickering, C.M., Mackey, B., Norman, P. and **Verrall, B.** (2021). Eleven reasons why increasing bed numbers in resorts within Kosciuszko National Park will have severe negative consequences economically, environmentally or socially. Submissions to the Amendment to the Kosciuszko National Park Plan of Management and the Snowy

Mountains Special Activation Precinct Draft Masterplan, NSW Government, Sydney.

Verrall, B., Smith, I., & Pickering, C.M. (2022). Assessment of Extent and Environmental Impacts of Unauthorised Trails at Westleigh Park. Report for the Hornsby Shire Council, Sydney, Australia.



## **Chapter 1: Introduction**

#### 1.1: Overview

Global change has caused widespread and diverse impacts on the biosphere in recent history, with anthropogenic climate change threatening many species, communities and ecosystems around the world (IPBES, 2019; IPCC, 2018, 2021). Understanding the impacts of climate change on mountain ecosystems is particularly important as they cover more than a tenth of global land area (Körner et al., 2011), provide water resources to nearly half of the global human population and support high biodiversity and endemism (Perrigo et al., 2020; Winkler, 2020). Transitions in major ecotones on mountains reflect changing climatic conditions along elevation gradients, with alpine ecosystems located above the bioclimatic treeline extending up to the physiological limit of plant life (Körner, 2003; Nagy & Grabherr, 2009). Since alpine ecosystems are primarily governed by low temperatures and short growing seasons, they are among the most responsive ecosystems globally to climate change (Dirnböck et al., 2011; Grabherr et al., 2010; Winkler et al., 2019).

Due to the importance of climatic factors over biotic interactions in determining alpine plant distributions, rapid changes in climate over recent decades are the primary agent of change in alpine ecosystems (Nagy & Grabherr, 2009). While there are some generalised responses of alpine vegetation to climate change in Europe (Gottfried et al., 2012; Steinbauer et al., 2018), there seem to be regional trends in vegetation dynamics (Pauli et al., 2012). Commonly, increasing species richness and vegetation cover has been recorded in response to climate change and is mostly driven mostly by increases in thermophilic taxa (Gottfried et al., 2012; Grabherr et al., 2010; Kullman, 2010; Lamprecht et al., 2018; Petriccione & Bricca, 2019). However, responses of alpine vegetation to climate change also seem to be specific to plant species, growth form and community (Gritsch et al., 2016; Liberati et al., 2019; Matteodo et al., 2016). Most insights on climate-induced alpine vegetation dynamics are from the northern hemisphere, particularly Europe, and elsewhere are less defined but have wide ranging implications for these ecological, cultural and socioeconomical significant ecosystems (Verrall & Pickering, 2020).

This introductory chapter begins with a brief synopsis of climate change and related impacts on the biosphere. Then, an overview of the importance and characteristics of mountains is provided, with a particular focus on alpine ecosystems including climatic and biotic characteristics and how these ecosystems are generally responding to climate change. Next, the different types of methods used to assess climate and vegetation dynamics in alpine ecosystems are summarised, emphasising the importance of long-term ecological monitoring. This is followed by an assessment of the ecology of the Kosciuszko alpine area in Australia including its historical,

climatic and biotic characteristics. Finally, this chapter concludes with the aims and structure of the thesis.

## 1.2: Climate, climate change and the biosphere

Climate is determined by the long-term averages (≥ 30 years) in weather conditions including temperature, precipitation, atmospheric pressure, humidity and wind. At any given time, climate is a representation of the current state of the climate system, which is determined by complex interactions among the atmosphere, hydrosphere, cryosphere, lithosphere and biosphere (Hartmann, 2016). In the past, the climate system has fluctuated over decades to millennia due to internal dynamics as well as external radiative forcings resulting in different weather patterns that persist for an extended period. These external forcings include variations in solar radiation, changing parameters of the Earth's orbit, internal variability in the climate system, plate tectonics and changes to atmospheric composition due to volcanic aerosols (Houghton, 2015; Zachos et al., 2001). In the past, the planet has periodically entered phases of climatic warming or cooling as a result of an imbalance of the climate system (Hartmann, 2016; Houghton, 2015). Eight cycles of climatic warming and cooling have occurred over the past 800,000 years (Barker et al., 2011), but the warming trend since the mid-19<sup>th</sup> century is occurring at a rate unprecedented in the past 10 millennia and is unequivocally influenced by anthropogenic activities (IPCC, 2021, 2022).

The emission of greenhouse gases is the primary driver of recent climate change, but modifications of land-use, environmental pollution, ecosystem degradation and destruction are also contributing factors. These activities have introduced additional external forcings resulting in imbalances in the climate system during a period where internal forcings would result in stable or cooling climatic conditions (IPCC, 2021, 2022). Anthropogenic carbon dioxide emissions have increased rapidly over the past two centuries to levels unprecedented in the past 66 million years (Zeebe et al., 2016). Concurrently, there has been a 1.09 °C rise in the global mean surface temperatures in 2011-2020 above those for 1850-1900, with the International Panel on Climate Change (IPCC) reporting that it is extremely likely (95% certainty) that anthropogenic emissions are the primary cause of this recent climate warming (IPCC, 2022). Anthropogenic emissions have caused an enhanced greenhouse effect where the rate of climate change is accelerating (Houghton, 2015; Loarie et al., 2009), with the 25 warmest years on record occurring since 1990 (GISTEMP Team, 2022; Lenssen et al., 2019). If emissions continue at the current rate, temperatures will continue to increase at approximately 0.20 °C per decade, reaching 1.50 °C between 2030 and 2052, which will have extraordinary impacts on the biosphere (IPCC, 2018). Since greenhouse gases persist in the atmosphere for centuries to millennia (Solomon et al., 2010), and there has been limited success so far in reducing emissions (Jackson et al., 2017; Lamb et al.,

2021), the multifaceted impacts of climate change on the biosphere will increase over coming decades (IPCC, 2022; Parmesan & Yohe, 2003; Sala et al., 2000; Warren et al., 2011).

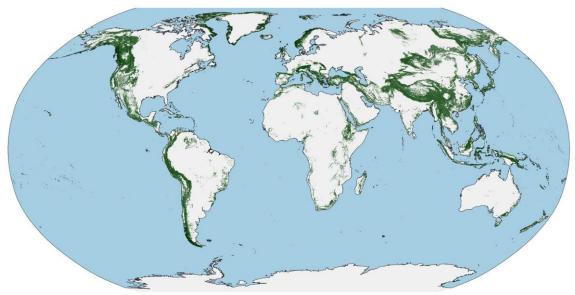
Currently, the planet is experiencing the sixth-wave of mass extinction (Barnosky et al., 2011), with the loss of biodiversity occurring at an extraordinary rate due to global change and anthropogenic activities (Ceballos et al., 2015; De Vos et al., 2015), where climate change is among the greatest threats to biodiversity globally (IPBES, 2019; IPCC, 2022). Several recent extinctions have been directly attributed to climate change (Cahill et al., 2013; Penuelas et al., 2013), with climate-induced biodiversity loss a key driver of degraded ecosystem structure, composition and function (Hisano et al., 2018; Hong et al., 2022; Kattel, 2022; Walther et al., 2002). Furthermore, it is extremely likely (95% certainty) that recent climate change has led to shifts in the geographic ranges, phenology, migration patterns, abundances and biotic interactions of many species (IPCC, 2022). These cumulative and intensifying impacts could lead to ecosystem collapse where the resilience and adaptation capacity of biota is eclipsed (Jackson & Canadell, 2021), and this could result in the degradation of ecosystem functions and services (Hooper et al., 2012; Pecl et al., 2017). Not all ecosystems are equally vulnerable or responsive to climate change (Li et al., 2018), but some are already facing climate-induced collapse (Bergstrom et al., 2021; Jackson & Canadell, 2021; Le Breton et al., 2022). Mountain ecosystems are among the most vulnerable to climate change (Engler et al., 2011; Gonzalez et al., 2010; Rogora et al., 2018), with widespread ecological impacts already documented (Beniston et al., 1997; Gottfried et al., 2012; Guisan et al., 2019; Hock et al., 2019; Steinbauer et al., 2018).

#### 1.3: Mountain ecosystems

#### Characteristics and importance of mountains

Mountains are elevated sections of the planet's crust that are formed by tectonic uplift or volcanism over millions of years and are dynamically shaped by agents of erosion including wind, ice, water and gravity (Frisch et al., 2011). Rarely are they solitary, commonly forming elongated mountain ranges along tectonic plate margins or faults (Frisch et al., 2011). Globally, mountains are defined by the ruggedness including the prominence and relief of a landscape that creates elevation gradients (Körner et al., 2011), and are one of the most well represented landforms covering 12.3% of terrestrial land area (Snethlage et al., 2022). They occur on all continents and latitudinal zones and in a diversity of climates and biomes from deserts to tropical rainforests to polar tundra, supporting a wide variety of mountainous ecosystems (Körner, 2004; Körner et al., 2011; Snethlage et al., 2022) (Snethlage et al., 2022) (Figure 1. 1). The importance and nuances of mountain ecosystems has garnered global attention for centuries, with nearly 200,000 published articles in Web of Science and the establishment of global mountain institutions including the Global Mountain Biodiversity Assessment Network (GMBA), the Mountain

Research Initiative (MRI) and the Mountain Partnership (Gurgiser et al., 2022). Through these concerted efforts, mountains are now understood to be among the most ecologically, culturally and socioeconomically important ecosystems on the planet (Gret-Regamey et al., 2012; Kollmair et al., 2005; Perrigo et al., 2020; Wehrli, 2014).



**Figure 1. 1**: Global distribution of mountains (green shading) outside of Antarctica according to the Global Mountain Biodiversity Assessment (GMBA) Mountain Inventory v2 (Snethlage et al., 2022).

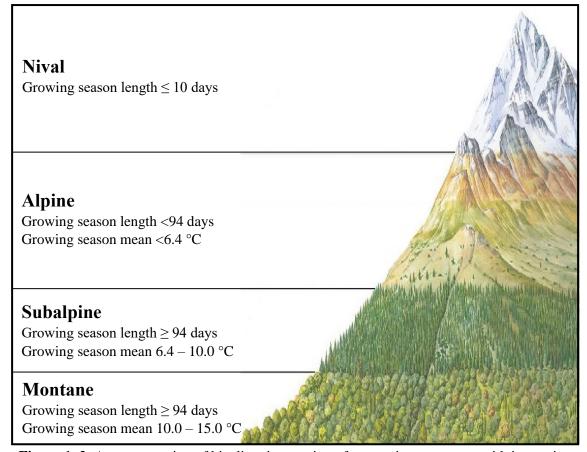
Of the global human population, only 7% resides directly within mountainous regions (Körner et al., 2011) but 15% resides within mountain forelands and ~50% is dependent on these ecosystems for water resources (Gurgiser et al., 2022; Körner & Ohsawa, 2005; Pomeroy et al., 2015; Winkler, 2020). Many industries including forestry, mining, hydroelectric energy production and tourism, among others, also rely on access to and use of mountain resources (Godde et al., 2000; Mengist et al., 2020; Wehrli, 2014). Additionally, mountains act as geographic boundaries that have driven ethnolinguistic diversification as well as providing spiritual and cultural significance as deities and sacred landscapes (Bernbaum, 2022; Meher-Homji, 2013; Slattery & Worboys, 2020). They also provide valuable ecosystem services such as the regulation of natural hazards (e.g. landslides and avalanches), capture moisture from the atmosphere, carbon storage, and provisioning of food, medicine and water among others (Palomo, 2017; Pomeroy et al., 2015). They are also of considerable ecological and conservation value, as mountains host almost half of the world's biodiversity hotspots and act as cradles, bridges, barriers and reservoirs for biodiversity (Körner, 2004; Perrigo et al., 2020). This is partly due to the complex topography of these ecosystems, which creates a heterogenous environment that has led to high biodiversity and endemism, but also the diversity of climates (Barry, 2008; Körner, 2003).

#### Climatic and biotic characteristics of mountains

Mountain climates can vary considerably among and within regions, but are largely determined by continentality, exposure to prevailing atmospheric circulations, latitude and elevation (Whiteman, 2000). The proximity of mountains to large bodies of water also influences their climates, with interior regions often experiencing more sunshine, less cloud and less precipitation than regions with maritime influences (Barry, 2008). Another factor that shapes the climates of mountain ecosystems is the relative exposure to winds and ocean currents, which are associated with prevailing atmospheric high- and low-pressure systems that form at different latitudinal belts (Whiteman, 2000). Furthermore, the latitude of mountain ecosystems also determines diurnal variations and the angle of incoming sunlight, and therefore, the quantity of solar radiation received (Barry, 2008). However, the most influential factor on mountain climates is elevation. With increasing elevation, temperature, atmospheric moisture and air density generally decrease, while precipitation, winds and solar radiation increase (Barry, 2008; Whiteman, 2000). Locations at higher elevations often have cooler climates due to typical dry adiabatic lapse rates of 6.5 °C per kilometre of elevation. Higher elevations are also subject to stronger winds due to less friction and topography-driven pressure differentials between air masses, and stronger solar radiation as the rate of atmospheric absorption and scattering is reduced (Whiteman, 2000). As a result, mountains often have distinct vertical climatic gradients which drive the biological zonation of ecosystems with clearly defined ecotones (Diaz et al., 2003; Körner et al., 2011).

Whilst only covering about an eighth of terrestrial land area, mountain ecosystems contain a relatively high proportion of global biodiversity (Körner, 2004; Snethlage et al., 2022). This is in part due to climatic variation, environmental heterogeneity, microhabitat differentiation and geographic isolation (Antonelli et al., 2018; Rahbek et al., 2019). These factors have resulted in steep ecological gradients, which are represented by the bioclimatic zonation of mountain ecosystems into montane (also referred to as lower montane), subalpine (also referred to as upper montane), alpine and nival (Körner et al., 2011) (Figure 1. 2). These ecosystems are largely determined by differences in mean growing season length and temperature (Körner, Paulsen & Spehn 2011), but the specific climatic parameters can vary among regions (Körner & Paulsen, 2004). In many regions, tall, dense and diverse montane forests transition into shorter, sparser and less diverse subalpine forests with increasing elevation. However, the most obvious biological transition is the climatic treeline, where the realised niche of treeline species demarcates the subalpine and alpine ecotone, along with the alpine and nival ecotone which occurs at the upper limits of plant life where there is permanent snow and ice (Körner, 2003, 2012; Körner et al., 2011). Furthermore, there may be zonation of ecosystems within each bioclimatic zone as a result of finer scale topographical, climatic and environmental heterogeneity (Grabherr et al., 2010). Considering that climate largely determines the zonation and extent of these ecosystems, the

effects of climate change on mountain ecosystems is of widespread concern (Guisan et al., 2019; Hock et al., 2019; Palomo, 2017).



**Figure 1. 2**: A representation of bioclimatic zonation of mountain ecosystems with increasing elevation based on climatic parameters described by Körner, Paulsen & Spehn (2011).

#### Climate change in mountains

Climate change has diverse impacts on mountain ecosystems across the world (Beniston et al., 1997; Hock et al., 2019; Pepin & Lundquist, 2008). Foremost, the climatic factors that define mountain ecotones and ecosystems are changing with warmer temperatures, and often declining snow cover and longer growing seasons (Notarnicola, 2020; Rangwala & Miller, 2012). Most mountains around the world are also warming faster at higher elevations, similar to amplified rates of warming recorded at higher latitudes in the Arctic (Jansen et al., 2020; Wang et al., 2016). This disproportionate phenomenon is known as elevation-dependent warming, and is largely driven by increases in daily minimum temperatures (Pepin et al., 2015; Rangwala & Miller, 2012). There are several mechanisms contributing to this elevation-dependant warming, such as complex interactions between convection and radiation as well as variations in environmental and climatic factors that are characteristic of mountain ecosystems (Table 1. 1). Considering the increasing effects of climate change, elevation-dependant warming has the potential to accelerate impacts on mountain biodiversity, cryosphere and hydrological regimes (Pepin et al., 2015; Pepin et al., 2022; Rangwala & Miller, 2012).

**Table 1. 1**: Mechanisms influencing elevation-dependant warming based on changes in climatic and environmental factors along elevation gradients (Rangwala & Miller, 2012).

Environmental/ Climatic Factor	Mechanism	Temperature Response
Decreases in snow/ice albedo	Increase surface absorption of solar radiation	Increase T <sub>max</sub>
Increases in daytime cloud cover	Decreases surface solar radiation	Decreases T <sub>max</sub>
Increases in night- time cloud cover	Increases downwelling longwave radiation	Increases T <sub>max</sub>
Increases in specific humidity	Increases downwelling longwave radiation	Increases T <sub>max</sub>
Increases in absorbing aerosols	Decreases surface insolation but increases mid- tropospheric heating Decreases albedo of clouds Decreases albedo of snowpack Decreases cloud cover	Increases T <sub>min</sub>
Increases in non- absorbing aerosols	Decreases surface insolation Increases cloud albedo and cloud lifetime	Decreases $T_{max}$ Increases $T_{min}$
Increases in soil moisture	Increases latent heat fluxes Decreases sensible heat fluxes during the day	Decreases diurnal temperature range Increases $T_{max}$

Note:  $T_{min}$  and  $T_{max}$  refers to mean minimum and maximum temperatures respectively.

Moreover, broad scale climate modelling suggests that mountain ecosystems will continue to experience increased warming and changes in precipitation regimes, with consequences for mountain ecosystems as well as those downslope (Hock et al., 2019). With warming temperatures in mountain ecosystems around the world, climate change has already resulted in changes in hydrology (Somers & McKenzie, 2020; Viviroli et al., 2011), cryosphere loss (Huss et al., 2017), and altered natural hazard regulation (Schneiderbauer et al., 2021). With climate change altering abiotic conditions in mountain ecosystems, there have been a range of impacts on plant biodiversity (Dullinger et al., 2012; Engler et al., 2011; Guisan et al., 2019), biotic interactions (Alexander et al., 2018; Anthelme et al., 2014; Vandvik et al., 2020) and physiological processes (Pellissier et al., 2018; Sumner & Venn, 2021).

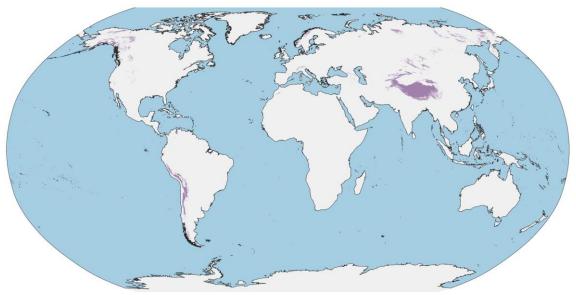
Often vegetation dynamics over time have been assessed to quantify the biotic impacts of climate change on mountain ecosystems (Hock et al., 2019). This reflects the role of flora as primary biotic and structural components of terrestrial ecosystems, as they are sessile and have specific requirements for growth and reproduction in addition to being relatively slow growing and long-lived organisms in comparison to many types of fauna (Malanson et al., 2019). However, attributing vegetation responses in mountain ecosystems to climate change can be complicated with other types of anthropogenic disturbances also occurring such as changing land-use practices (Gehrig-Fasel et al., 2007; Lindenmayer et al., 2020; Mackenzie et al., 2021; Palombo et al., 2013). Clearer links between climate change and vegetation responses can be drawn in higher elevation ecotones, as they are more sensitive to climate change with more clearly delineated

climatic parameters (Körner et al., 2011; Malanson et al., 2019), and there has often been less intensive anthropogenic land-use in the past than at lower elevations (Nagy & Grabherr, 2009). Alpine ecosystems provide important opportunities to examine vegetation responses to climate change (Gottfried et al., 2012; Grabherr et al., 2010; Rixen & Wipf, 2017; Steinbauer et al., 2018), with alpine vegetation including highly specialised, cryophilic and climate-sensitive plants (Körner, 2003; Lütz, 2013).

## 1.4: Alpine ecosystems

Distribution, climatic and biotic characteristics of alpine ecosystems

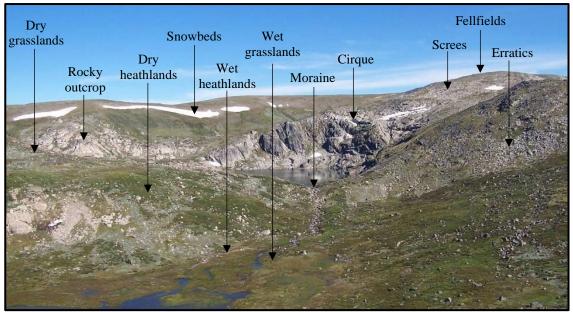
Alpine ecosystems are the only terrestrial ecosystems that have a global distribution from the tropics to the poles despite only covering around 3% of terrestrial land (Körner, 2003; Testolin et al., 2020). The northern hemisphere contains nearly 85% of global alpine area, with the majority found in Asia (73%) across the Tibetan Plateau, Himalayas, Kunlun Shan, Nyainqentanglha Shan and Bayan Har Shan (Testolin et al., 2020) (Figure 1. 3). North America contains 9% of global alpine area, mainly in the north-west of the continent in the Mackenzie Mountains, Brooks Range, Coast Mountains, Saint Elias Mountains and Rocky Mountains. Europe contains smaller and less contiguous alpine areas representing 2% of global alpine area, which are largely confined to the Scandinavian Mountains, Jotunheimen, European Alps, Greater Caucasus and Ural Mountains. In the Southern Hemisphere, 15% of global alpine area is confined to the Andes of South America, specifically in the Cordillera Occidental, Cordillera Oriental, Central Volcanic Zone, Cordillera Frontal and Cordillera Patagonia. However, less than 1% of global alpine area occurs in Oceania, and apart from the Southern Alps of New Zealand, most are small and geographically isolated fragments such as the Tasmanian Central Plateau, Mauna Loa, Mauna Kea and the Australian Alps (Körner, 2003; Testolin et al., 2020).



**Figure 1. 3**: Global distribution of alpine ecosystems (purple shading) according to Testolin et al. (2020).

Alpine ecosystems vary in elevation, latitude, air density, snow cover duration, precipitation, wind exposure and seasonality, but are generally characterised by cold, harsh climates (Körner, 2003; Nagy & Grabherr, 2009). All alpine ecosystems share some broad climatic factors including lower atmospheric pressure resulting in lower  $CO_2$  content, amplified levels of solar radiation and erratic weather (Körner, 2003). While the elevation at which alpine ecosystems occur varies with latitude (Testolin et al., 2020), the climatic conditions at the lower boundary of this ecotone are relatively similar, and the boundary is often demarcated by a treeline (Körner, 2012). At these bioclimatic treelines, the global mean duration of the growing season tends to be  $167 \pm 77$  days, with mean growing season temperatures of  $6.7 \pm 0.8$  °C (Körner & Paulsen, 2004). There is also a diversity of microclimates within alpine ecosystems driven by variations in topography, substrate, solar radiation, snow cover and exposure to winds (Körner, 2003; Scherrer & Körner, 2011). Similar to the bioclimatic zonation of mountain ecotones, macroclimatic and microclimatic variations along environmental gradients in alpine ecotones generate microhabitat differentiation, and determine the distribution, structure, processes and functions of alpine vegetation (Nagy & Grabherr, 2009).

Alpine ecosystems support disproportionately high biodiversity, accounting for 4% of dicots globally while covering less than 3% of terrestrial land area (Körner, 2003). They also contain high endemism including highly specialised cryophilic plants, with species adapted to the diverse range of habitats available in alpine ecosystems (Körner, 2003; Nagy & Grabherr, 2009). Alpine ecosystems support a diversity of vegetation types, communities and growth forms (Grabherr et al., 2010), with their dominance and extent determined by evolutionary strategies and adaptations to the environmental and climatic conditions (Körner, 2003; Lütz, 2013; Nagy & Grabherr, 2009). Generally, alpine plants can be categorised into one of four general growth forms; (1) low stature heath or prostrate woody shrubs, (2) graminoids such as sedges and tussock forming grasses, (3) acaulescent rosette perennial forbs, and (4) cushion plants (Körner, 2003). These common growth forms are arranged into a mosaic of vegetation communities across the diversity of microhabitats in alpine ecosystems (Figure 1. 4). Generally, at lower elevations with higher soil moisture content, deeper soils and milder climatic conditions, vegetation cover is higher and often consists of closed heathlands and grasslands. In contrast, at higher elevations where soil moisture is lower, soils shallower and climatic conditions are more extreme, including at the alpine-nival ecotone, vegetation cover is often sparse with cryophilic vegetation consisting of open grasslands, cushion plants and prostate heathlands that grow among the rocky outcrops, screes, erratics, periglacial areas, snowbeds and fellfields (Costin et al., 2000; Körner, 2003). Furthermore, many alpine plants have developed physiological adaptations to combat the climatic and environmental stressors including increased stomatal control to limit desiccation, freezing-point depression, supercooling and freezing tolerance (Körner, 2003; Lütz, 2013).



**Figure 1. 4**: Mosaic of alpine vegetation and microhabitats surrounding a glacial cirque in the Australian Alps (source: C. Pickering).

#### Impacts of climate change on alpine ecosystems

Alpine ecosystems are among the most vulnerable to climate change, with diverse impacts already documented (Grabherr et al., 2010; Guisan et al., 2019; Hock et al., 2019). In the northern hemisphere, increasing air temperature is occurring at three times the global warming rate but there are no clear trends in precipitation over recent decades due the variable influences of changing atmospheric circulations and regional climate drivers (Hock et al., 2019). However, globally there have been marked declines in snow cover, permafrost, glacial area and mass (Barry, 2011; Beniston et al., 2018; Bibi et al., 2018; Huss et al., 2017; Notarnicola, 2020; Stewart, 2009). These impacts are expected to continue under varying emission scenarios, with warmer temperatures leading to more precipitation falling as rain leading to further declines in snow cover and glaciers as well as thawing permafrost (Hock et al., 2019). Furthermore, rapidly changing climatic conditions in alpine ecosystems have already resulted in the increasing frequency and magnitude of natural hazards including avalanches, glacier collapse, glacial lake outburst, flooding, geomorphic instability and landslides, as well as wildfire in some regions, all of which are projected to intensify from further warming (Hock et al., 2019).

In response to changing climatic conditions in alpine ecosystems, widespread climate-induced ecological changes have occurred over the past century. The distribution of plant and animal species has changed in many alpine regions (Hock et al., 2019), prompting changing diversity and composition within and among alpine ecosystems (Lamprecht et al., 2018; Steinbauer et al., 2018). With increasing temperatures and lengthening growing seasons, there have been widespread changes in phenology (Inouye, 2020; Shen et al., 2015; Wells et al., 2022) as well as woody encroachment and upslope advances (Brandt et al., 2013; Dial et al., 2016; Hallinger et

al., 2010; Hansson et al., 2021; Myers-Smith & Hik, 2018), shrubline advances (Dial et al., 2016; Hallinger et al., 2010; Myers-Smith & Hik, 2018), with thermophilic vegetation replacing cryophilic vegetation in many regions (Gottfried et al., 2012; Kullman, 2010; Petriccione & Bricca, 2019; Rosbakh et al., 2014; Rumpf et al., 2018). Typically, insights about climate-induced dynamics in alpine ecosystems have been obtained through manipulative experiments that simulate future climate change, space-for-time substitutions derived from sampling along environmental gradients, and long-term ecological monitoring using repeat sampling to track dynamics over time, but these are mostly from the northern hemisphere (Elmendorf et al., 2015; Verrall & Pickering, 2020). Furthermore, climate change is predicted to have major impacts on alpine species abundances, distributions, composition and ecosystem functions globally in coming decades (Alexander et al., 2018; Dirnböck et al., 2011; Dullinger et al., 2012; Engler et al., 2011; Ernakovich et al., 2014; IPCC, 2018). Therefore, continued assessment and monitoring of alpine ecosystem dynamics over long periods is imperative to understand how these vulnerable ecosystems are responding to climate change including more studies on alpine ecosystems in the southern hemisphere (Pauli et al., 2015; Venn et al., 2017).

## 1.5: Long-term ecological monitoring

Theoretical basis and application in alpine ecosystems

Ecosystem dynamics are influenced by an array of biotic and abiotic factors over different spatial and temporal scales (Gitzen et al., 2012; Müller et al., 2010). Therefore, insights for specific ecosystem dynamics can only be obtained from appropriate research timescales and designs (Figure 1. 5). Assessing the current state of ecosystems, seasonal dynamics and/or pre- and postimpact assessments require traditional ecology methods that span over relative short periods (Lindenmayer & Likens, 2010). Since climatic conditions are influenced by seasonality and climate drivers, ecosystems can generally regulate shorter-term oscillations (Sofaer et al., 2017). The ability of ecosystems to remain at equilibrium with changing climatic conditions depends on their resistance to perturbation, as well as resilience, which is the speed at which ecosystems recover (Chapin et al., 2011; Ives & Carpenter, 2007). However, sustained changes to climatic conditions over several decades may outpace the resistance and resilience of an ecosystem, leading to disequilibrium where ecosystems are forced to transition or collapse (Bergstrom et al., 2021; Jackson & Canadell, 2021). Since ecosystem dynamics and processes in response to anthropogenic climate change can occur over years to centuries (Garcia et al., 2014; Heimann & Reichstein, 2008; Walther et al., 2002), longer-term research timescales are required to reduce the noise of the inherent intraannual and interannual climatic variability and associated ecological responses (Gitzen et al., 2012). Climate change can also amplify the frequency and severity of abrupt disturbance events such as wildfires and heat waves (IPCC, 2021, 2022), and baseline ecological data can permit the monitoring of ecosystem recovery (Gitzen et al., 2012).

Concurrently, there has been widespread use of Long-Term Ecological Monitoring (hereafter referred to as 'LTEM') to understand the impacts of climate change and other types of anthropogenic disturbances (Gitzen et al., 2012; Jackson & Canadell, 2021; Müller et al., 2010). For alpine ecosystems, LTEM has been a common method in research assessing the impacts of climate change (Verrall & Pickering, 2020), including field-based sampling and remote sensing of vegetation over years to decades to centuries (Gottfried et al., 2012; Hansson et al., 2021; Knoflach et al., 2021; Petriccione & Bricca, 2019; Rixen & Wipf, 2017; Stöckli et al., 2011).

Temporal scale	Ecosystem process	Research timescales
Millennia	Glaciation	Pologopology
Millennium	Bog succession	Paleoecology
Century	Forest succession	
Decade	Dune succession	Long-term ecological monitoring
Year	Lake turnover	
Month	Plankton succession	
Day	Algal bloom	T 4'4'11
Hour	Storms	Traditional ecology
Second	Photosynthesis	

**Figure 1. 5**: Timescales for various ecosystem dynamics and the associated research timescales required to assess these dynamics (adapted from (Müller et al., 2010)).

While there has been widespread monitoring of the atmosphere and cryosphere in alpine ecosystems, particularly in Europe (Beniston et al., 2018), initiatives to detect the impacts of climate change on alpine ecosystems are relatively sparse (Pauli et al., 2015). In response, alpine LTEM initiatives have been established over recent decades but most are also in Europe (e.g. Alatalo et al., 2020; Grabherr et al., 2010; Kullman, 2010; Petriccione & Bricca, 2019; Porro et al., 2022; Wieser et al., 2019), North America (e.g. Danby et al., 2011; Scharnagl et al., 2019; Spasojevic et al., 2013; Swerhun et al., 2009) and Asia (e.g. Bhattarai et al., 2021; Hamid et al., 2020; Liu et al., 2018; Sigdel et al., 2018; Zhou et al., 2019), with few in South America (e.g. Bokhorst et al., 2017; Duchicela et al., 2021; Pelayo et al., 2021), Africa (Carbutt & Thompson, 2021), or Oceania (e.g. Kirkpatrick et al., 2017; Wahren et al., 2013). Increasingly remote sensing techniques are being utilised to monitor alpine ecosystems, particularly those in remote and rugged regions, with advancing satellite technology and decades of spectral data allowing the analysis of vegetation dynamics in response to climate change (T. Chen et al., 2022; Chhetri & Thai, 2019; Franke et al., 2019; Verrall & Pickering, 2020). However, most alpine LTEM relies on traditional field-based methods of resampling permanently marked vegetation plots, with soil temperature often recorded as surrogated for the microclimates experienced by alpine plants (Björk & Molau, 2007; Wundram et al., 2010).

To provide insights into local, regional and global vegetation dynamics with climate change, some international monitoring networks have been established. This includes the International Tundra Experiment (ITEX) (Molau & Mølgaard, 1996) where manipulative experiments involving opentop chambers are used to enhance the temperatures experienced by Arctic and alpine tundra vegetation, while the Mountain Invasion Research Network (MIREN) (Haider et al., 2022) monitors the invasion of non-native plant species into many mountain ecosystems. However, the Global Observation Research Initiative in Alpine Environments (GLORIA) (Pauli et al., 2015) is the only international LTEM network that explicitly focuses on monitoring alpine microclimate and vegetation dynamics, where summits along an elevation gradient from the subalpine-alpine ecotone to the alpine-nival ecotone are sampled through time. A prototype of the multi-summit approach of GLORIA was tested in 1998 in Austria, with a further 17 European target regions established by 2001 (Pauli et al., 2015). By 2014, the GLORIA network expanded to every continent except Antarctica, with over 115 registered target regions. Current protocols include continuous (every few hours) monitoring of soil temperatures to measure changes in microclimatic variables such as the duration snow cover, length of the growing season and mean temperatures. Additionally, summit vegetation is surveyed every 5 to 10 years at varying spatial scales to assess changes in cover and composition over time (Pauli et al., 2015).

#### Insights from GLORIA and other alpine LTEM

Repeat surveys of GLORIA target regions in Europe provide strong evidence for climate-induced alpine vegetation dynamics over recent decades, with regionally specific responses (Gottfried et al., 2012; Nicklas et al., 2021; Pauli et al., 2012). Divergent responses along elevation gradients within and among target regions have also been found, with increasing cover via colonisation at higher elevations while encroachment and species turnover drive changes at lower elevations (Rumpf et al., 2018; Rumpf et al., 2019). In boreal and temperate Europe, species enrichment has been driven by upslope migration of thermophilic species, while diversity has stagnated or is in decline in the Mediterranean (Fernández Calzado & Molero Mesa, 2013; Gottfried et al., 2012; Lamprecht et al., 2021; Lamprecht et al., 2018; Pauli et al., 2012). Comparatively, there has been considerable species turnover in North American target regions (Malanson & Fagre, 2013), while there have been increases in vegetation cover (Salick et al., 2019) and compositional thermophilisation (Gigauri et al., 2016) in Asian GLORIA sites. There appears to be a growing 'extinction debt' in alpine plants, with sharp declines in diversity predicted as climatic thresholds are eclipsed in many regions (Alexander et al., 2018; Dirnböck et al., 2011; Dullinger et al., 2012; Lamprecht et al., 2018). In contrast to the situation in the northern hemisphere where the diversity of target regions have provided broad and comparative insights, there are few target regions and published GLORIA studies from the southern hemisphere (Pauli et al., 2015). Across two target regions in South America, compositional changes were found to be influenced by increasing plant cover at higher elevations via colonisation of bare ground by graminoids and forbs, as well as species enrichment at lower elevations (Carilla et al., 2018; Lencinas et al., 2021). Changing composition has also been recorded in the only target region in Australia, with increasing species richness and cover of graminoids and shrubs (Venn et al., 2012; Venn et al., 2014).

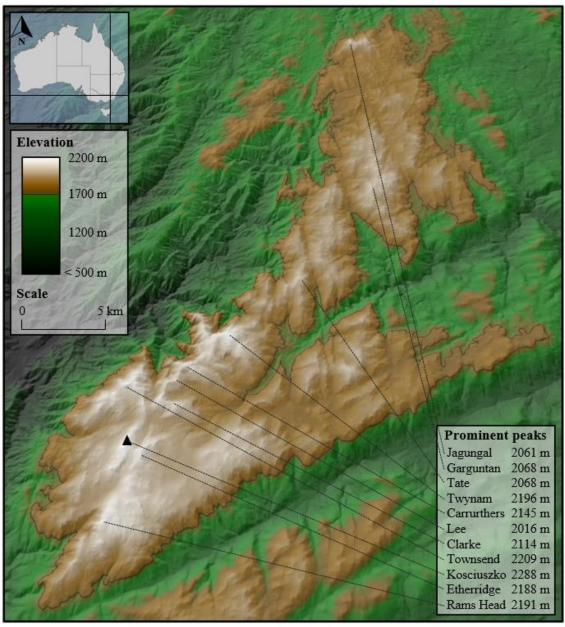
Aside from the GLORIA network, there are other important LTEM sites that have been established in alpine ecosystems around the world. These include many sites used to monitor alpine treeline dynamics in response to climate change (Broll & Keplin, 2005; W. R. Chen et al., 2022; Harsch et al., 2009; Holtmeier & Broll, 2020). As a result of enhanced monitoring, treeline dynamics have been shown to be influenced not only by low-temperature growth limitations, but also disturbance regimes, seed dispersal mechanisms, biotic interactions and microclimatic sheltering as well as seedling mortality and establishment (Harsch & Bader, 2011; Körner, 2012). The latest global reviews of treeline dynamics found advancement at 66% of sites but recessions were rarely recorded (Hansson et al., 2021). Recently, the power of remote sensing techniques has permitted the monitoring of treeline dynamics over larger and more remote areas (Franke et al., 2019), but such applications are limited in the southern hemisphere (Chhetri & Thai, 2019). Other alpine LTEM sites have focused on assessing the response to declining snow cover and lengthening growing seasons (Bokhorst et al., 2013; Rixen et al., 2022), including on cryophilic vegetation associated with snowpatches (Gritsch et al., 2016; Matteodo et al., 2016). Generally, as snowpatches become less persistent, the microclimate that shaped composition has rapidly changed with increases in species richness and vegetation cover via encroachment from adjacent areas (Sandvik & Odland, 2014; Schöb et al., 2009). Whether focused on experimental manipulation of climate, invasive species, changes in summit vegetation, treelines and/or cryophilic vegetation associated with snowpatches, most insights from alpine LTEM have come from the northern hemisphere (Chhetri & Thai, 2019; Hansson et al., 2021; Pauli et al., 2015; Steinbauer et al., 2018). However, valuable contributions are beginning to emerge from alpine ecosystems in the southern hemisphere, including in Australia.

#### 1.6: Kosciuszko alpine area

#### Importance of this alpine area

Australia contains some of the oldest continental crust of the planet and has experienced billions of years of weathering and millions of years of tectonic stability, resulting in mountains covering just 2.7% of the country (Hall, 2011; Snethlage et al., 2022). The Great Dividing Range spans much of the eastern coast of Australia and is the largest and highest mountain range. However, alpine ecosystems cover less than 0.02% of Australia and occur as small, isolated fragments in the south-east of continent in the highest mountains of New South Wales, Victoria and Tasmania (Green & Stein, 2015). The highest, largest and most diverse alpine area in the Australian Alps

surrounds the summit Mount Kosciuszko (-36.4559, 148.2635), which the highest mountain in Australia at 2,228 m above sea level (hereafter referred to as "a.s.l") (Costin et al., 2000). In this thesis, the Kosciuszko alpine area is defined as the contiguous area surrounding Mount Kosciuszko above 1,700 m a.s.l., which encapsulates the lower bound of the alpine-treeline ecotone across this 455 km² area (Green & Stein, 2015) (Figure 1. 6). This alpine area contains all of the mountains above 2000 m in Australia, spanning a semi-continuous ridgeline from Rams Head in the south-west to Jagungal in the north-east known as the Main Range (Slattery & Worboys, 2020).



**Figure 1. 6**: Location, topographical relief and extent of the Kosciuszko alpine area (grey outline of contiguous brown to white shading) surrounding Mount Kosciuszko (black triangle).

This alpine area is conserved within the 6,900 km<sup>2</sup> of Kosciuszko National Park, which is classified as an IUCN Category II protected area and as a UNESCO Biosphere Reserve due in

part to its unique alpine biota, important ecological processes, economic and scientific importance (Slattery & Worboys, 2020). This alpine area is one of Australia's most important watersheds as it contains the headwaters of the Snowy River and numerous tributaries to major rivers including the Murray and Murrumbidgee, and provides around \$3.8 billion dollars in water resources and hydroelectricity annually (Slattery & Worboys, 2020). Snow cover is scarce and ephemeral in Australia but the Kosciuszko alpine area supports the deepest and most persistent snowpack in the country (Fiddes et al., 2015; Pepler et al., 2015; Thompson, 2016), with adjacent subalpine areas providing the most extensive and reliable snow tourism option that generates ~\$880 million annually (NIEIR, 2013). Furthermore, the Kosciuszko alpine area is distinguished from other alpine areas around the world due to its distinctive geology, glacial history, soils, land-use history, climate, flora and fauna (Costin, 1967; Costin et al., 2000; McVean, 1969).

#### Geology, soils and paleoclimate of the Kosciuszko alpine area

Contrasting the active mountains of nearby New Guinea and New Zealand where rapid orographic uplift and glacial activities are ongoing, the Kosciuszko alpine area is considerably older and has experienced relatively stable climatic and environmental conditions (Costin, 1967; Lorrey & Bostock, 2014; Luning et al., 2020). During the Ordovician period (~ 450 million years ago), the Kosciuszko alpine area was submerged under a vast sea that covered much of eastern Australia, and extensive sediments were deposited that currently persist as slates, phyllites, quartzites and schists (Browne, 1967). Folding, uplifting and sedimentation continued into the early Devonian period (~ 420 million years ago) when granitic intrusions rose this area above sea level, which was followed by ~ 350 million years of relative stability and weathering that resulted in the characteristic paleoplain surface of this alpine area (Costin et al., 2000). During the Tertiary period (65-2 million years ago), there was significant uplift where this area was raised to present day elevations. These gradual geomorphic processes led to the uncharacteristic formation of deep, porous alpine soils with high organic matter content that are akin to montane soils in other regions (Costin, 1954; Wilson et al., 2022). Soils have developed in the Kosciuszko alpine area with little influence from underlying bedrock (Costin, 1954), with widespread deep alpine humus soils on across the paleoplain surface and deep fen peats in topographical depressions. There are also small tracts of skeletal lithosols on high elevation, steep and exposed slopes (Wilson et al., 2022), which is similar to alpine soils from other regions (Costin, 1954; Jenny, 1941; Körner, 2003). Several factors have promoted the development of soils in the Kosciuszko alpine area including a recurrent supply of aeolian distributed sediment from the west and relatively intense nutrient cycling by soil fauna, deep-rooting flora and mycorrhizal fungi (Costin, 1954; Wilson et al., 2022).

Starting about two million years ago during the Pleistocene period, a global period of cooling occurred where the Kosciuszko alpine area underwent at least two distinct glaciations beginning approximately 60,000 and 32,000 years ago (Barrows et al., 2001). The later glaciation was less extensive and occurred as three distinct advances with the most recent occurring around 17,000 years ago where summer temperatures were probably 5 – 8 °C below present (Barrows et al., 2001; McKenzie, 1997). However, these relatively mild Pleistocene conditions resulted in comparatively weak glaciations during phases of global glacial advancement, and the Kosciuszko alpine area has been free from glaciers for about 15,000 years (Barrows et al., 2001). During these periods of glaciation, the cover of alpine fellfields and grasslands extended over much South Eastern Australia above 1000 m (Martin, 1986; McKenzie, 1997). The climate then began to warm, with summer temperatures 3,500 years ago approximately 2.5 °C below present (Thomas et al., 2022). Over the past 2000 years, temperature and snow cover have fluctuated with historical climate events including the Roman Warm Period (~2270-1620 years ago), Medieval Warm Period (~1070-770 years ago) and Little Ice Age (~720-170 years ago) (McGowan et al., 2018). However, anthropogenic climate change has caused rapid increase in temperatures and decline in snow cover over the past century in the Australian Alps (McGowan et al., 2018), and there has been a concurrent decline in alpine vegetation and subsequent expansion of subalpine woodlands (Thomas et al., 2022).

#### Climate of the Kosciuszko alpine area

The present-day climate of the Kosciuszko alpine area is truly alpine in nature with mean growing season temperature at the treeline of approximately 7.9 °C, growing seasons length generally more than 150 days and approximately 170 freeze-thaw cycles per annum (Costin, 1954; Costin et al., 2000; Green & Pickering, 2009a; Green & Stein, 2015; Körner & Paulsen, 2004). Mean annual temperatures are 4.7 °C, with mean monthly minimum temperatures below freezing from May through October (Thredbo Automated Weather Station, 1967-2021, 1,957 m a.s.l.). In the colder months, a marginal snowpack forms usually by late May and becomes discontinuous in October but snow cover, depth and thaw date are variable among years and within the alpine area (Duus, 1992; Fiddes et al., 2015; Nicholls, 2005; Rasouli et al., 2022; Thompson, 2016). When snow begins to rapidly melt in spring, large snowpatches become apparent in semi-regular positions in nivation hollows on lee aspects of high elevation ridgelines and can persist into the following autumn (Edmonds et al., 2006; Green & Pickering, 2009a). Generally, prevailing westerly winds redistribute snow by scouring the windward western aspects and ridgelines, which then deposits onto the leeward south-eastern aspects (Costin et al., 1973). Since the Kosciuszko alpine area contains the highest mountains on the landmass, it is subject to strong winds with a mean speed of 25 km/h and a maximum mean wind gust speed of 142 km/h (Thredbo All Weather Station, 1967-2021, 1957 m a.s.l).

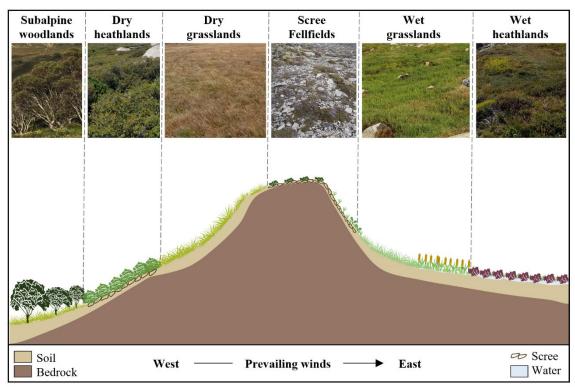
Mean annual precipitation is approximately 1430 mm with spring the wettest season (Thredbo Automated Weather Station, 1967-2021, 1,957 m a.s.l). The majority of precipitation falls as snow during the colder months but occasional snowfalls can occur during summer (Costin et al., 2000; Green, 1998). However, precipitation can vary considerably (650 – 2550 mm per annum) among years due to the influence and interactions of climate drivers such as the Indian Ocean Dipole (IOD), North-West Cloud Bands (NWCB), Subtropical Ridge (STR), Southern Annular Mode (SAM) and El Niño-Southern Oscillation (ENSO) (Pepler et al., 2015). Wetter conditions tend to occur during negative IOD and entrenched NWCB that infuses moisture into cut-off low pressure atmospheric circulations, which originate from the Antarctic polar vortex (McGowan et al., 2021). Furthermore, the orientation of the Main Range runs perpendicular to the prevailing, precipitation bearing westerly winds causing orographic precipitation and a resultant rain shadow to the east (Green, 1998). Drier conditions tend to occur when there is a lack of moisture supply from typical evaporative source regions during El-Niño, positive IOD and when the STR is further south, which can result in extended periods of drought (Holgate et al., 2020; Van Dijk et al., 2013). These extended periods of drought often result in more severe and frequent wildfires in the surrounding subalpine and montane ecotones, which can on occasion extend into the alpine area (Williams et al., 2008).

Globally, wildfires at and above treeline are rare but can occur in the tropics (Bader et al., 2007) northwest North America (Hock et al., 2019) and Australia (Kirkpatrick & Bridle, 2013; Williams et al., 2008). There is limited evidence of Indigenous cultural burning in this alpine area (Dodson et al., 1994), but wildlife is an undoubted agent of disturbance at treeline where inter-fire intervals were ~ 140 years over the past millennia (Williams et al., 2008). However, anthropogenic fire severity and frequency increased considerably over the past two centuries following colonisation (Costin et al., 2000; Dodson et al., 1994; Zylstra, 2006). Alongside altered anthropogenic fire regimes, landscape-level wildfires burning over 100 km<sup>2</sup> of alpine vegetation occurred in 1939 and then in 2003 (Williams et al., 2008). Generally, wildfires have been initiated by lightning strikes at lower elevations during prolonged periods of drought, and smaller tracts of this alpine area burnt in 1973, 1978, 1979, 1981, 1991, 2020 (NSW Government, 2022). Wildfires in the Kosciuszko alpine area have previously caused a mosaic of burnt and unburnt patches of vegetation ranging from square meters to square kilometres, driven primarily by the differential flammability of growth forms, wind tunnelling and fire spotting (McDougall et al., 2015; Williams et al., 2008). Shrubs are far more flammable than graminoids, with landscape flammability and fuel loads seemingly the limiting factor in fire propagation in this alpine area during the 2003 wildfire (Fraser et al., 2016; McDougall et al., 2015; Williams et al., 2008).

### Flora of the Kosciuszko alpine area

The Kosciuszko alpine area contains a diversity of plant species, growth forms, vegetation types and communities. While nearly all the species of plants are only found in Australia, they often have similar traits to those in other countries, with distant genetic links to alpine vegetation in New Zealand and New Guinea as well as lowland Australian species (Kirkpatrick, 1982; McDougall & Walsh, 2007). There are 204 species of angiosperms and eight species of pteridophytes, of which 10% (21 species) are endemic to the Kosciuszko alpine area and around 30 are found exclusively above treeline (Costin et al., 2000). Unlike many alpine areas globally, the treeline of the Kosciuszko alpine area is comprised of a single broadleaved and evergreen angiosperm species (Eucalyptus niphophila) with limited seed dispersal mechanisms (Green, 2009). Six species are the only representative of their genus and 20 are the only representative of their family in this alpine area, but many species are members of the Asteraceae, Poaceae, Cyperaceae, Apiaceae or Ranunculaceae families (Costin et al., 2000). Currently, four species are threatened and are listed either as vulnerable (Argyrotegium nitidulum, Ranunculus anemoneus and Rytidosperma pumilum) or endangered (Carex raleighii) under the Threatened Species Conservation Act 1995 (NSW Government, 2001). In addition to the native flora, there are least 46 invasive plant species in the Kosciuszko alpine area, with many restricted to disturbed areas such as walking trails and eroded sites (Mallen-Cooper, 1990; McDougall et al., 2005). At least 14 species of invasive plants are now established in this alpine area, and increasing diversity and cover over time presents as an emerging threat (Costin et al., 2000; Schroder et al., 2015).

The dominant growth form in the Kosciuszko alpine area is forbs with 116 species, followed by 56 species of graminoids, 33 species of shrubs and seven species of cryptogams (Costin et al., 2000). These species and growth forms can be arranged into broad vegetation types including woodlands, wet heathlands, wet grasslands, dry heathlands, dry grasslands and fellfields (Costin et al., 2000; Mackey et al., 2015; Walsh & McDougall, 2004). The composition, extent and distribution of these vegetation communities and types is determined by varying soil moisture content, nutrient availability, microclimate, topography, exposure and duration of snow cover (Costin, 1954; Costin et al., 2000; McVean, 1969) (Figure 1. 7). Vegetation cover in the Kosciuszko alpine area is relatively high when compared to other alpine areas globally, as deep humic soils, absence of large ungulate grazers, gentle topography, ephemeral snow cover, high precipitation and mild temperatures result in near complete vegetation cover (Costin et al., 2000). Conversely, there is sparse vegetation cover in fellfields due to extreme climatic conditions and shallow lithosols, and is more comparable to other alpine vegetation types globally. Furthermore, alpine vegetation types can be split into distinct communities including heathlands, sod tussock grasslands, fens and bogs, tall and short alpine herbfields, snowpatch (synonymous with "snowbed") feldmark (synonymous with "fellfield"), windswept feldmark (Costin et al., 2000).



**Figure 1.7**: Generalisation of the distribution of vegetation types in the Kosciuszko alpine area due to varying climatic and environmental conditions, as shown in this schematic cross section of a ridgeline.

The most common community is tall alpine herbfields, which forms on well-drained alpine humus soils (Table 1. 2). It is dominated by tussock-forming graminoids including species of *Poa* and has high diversity with approximately ~100 species of forbs occupying inter-tussock spaces and interspersed shrubs. Shallower and rockier soils support large tracts of heaths, with ~30 species of shrubs as well as graminoids and forbs. Seepage zones of low relief support fens and bogs, which contain approximately 50 species of cryptogams, graminoids, forbs and shrubs. However, the remaining communities are more specialised and have limited distributions (Costin et al., 2000). Short alpine herbfields and snowpatch feldmark are associated with areas of late lying snowpatches, with both communities listed as critically endangered under the Biodiversity Conservation Act 2016 (Duretto, 2019a, 2019b). Collectively, these endangered communities contain approximately 30 species of cryptogams, dwarf forbs and graminoids but not shrubs. Snowpatch feldmark occurs the leeside of exposed ridgelines in areas covered by large snowpatches for most of the year with sparse vegetation and shallow lithosol soils, while the short alpine herbfields often occur immediately downslope of large snowpatches, on deep soils and depends on snowmelt water from the snowpatches throughout the growing season (Costin et al., 2000). The rarest community is windswept feldmark, which is also listed as listed as critically endangered under the Biodiversity Conservation Act 2016 (Eldridge, 2015). It occurs on exposed ridgelines above 2000 m a.s.l., and contains around 20 species of dwarf shrubs, graminoids and forbs (Costin et al., 2000).

**Table 1. 2:** Overview of vegetation communities of the Kosciuszko alpine area based on mapping conducted south of Mount Tate (see Figure 1.6) in 1966 (CSIRO, 1972).

Community	Extent	Preference	Diagnostic Taxa
Tall alpine herbfields	63.46%	Well-drained alpine humus soils	Celmisia costiniana, Celmisia pugionformis, Poa spp., Craspedia spp., Leucochrysum alpinum
Heaths	26.12%	Sheltered, well-drained soils near rock outcrops, moraines and cirques	Kunzea muelleri, Nematolepis ovatifolium, Grevillea australis, Prosanthera cuneata, Oxylobium ellipticum
Fens and bogs	6.01%	Permanently wet, almost level sites	Carex gaudichaudiana, Sphagnum cristatum, Epacris paludosa, Richea continetis, Astelia spp.
Short alpine herbfields	0.85%	Wet sites below snowpatches and on wet, semi-bare surfaces	Plantago glacialis, Plantago muelleri, Neopaxia australasica, Psychrophila introloba, Ranunculus niphophilus
Snowpatch feldmark	1.74%	Shallow, rocky soils associated with snowpatches	Coprosma niphophila, Colobanthus nivicola, Ranunculus anemoneus, Epilobium tasmanicum
Windswept feldmark	0.30%	Shallow, rocky soils with high wind-exposure	Epacris gunnii, Epacris petrophila, Veronica densifolia, Euphrasia collina subsp. lapidosa, Ranunculus acrophilus
Other	1.53%		Rock screes, outcrops, lakes and eroded areas

### Fauna of the Kosciuszko alpine area

The Kosciuszko alpine area also supports a diversity of fauna but unlike many other alpine ecosystems, mammals are relatively uncommon and the majority are small, ranging from 15 g to 3500 g (Green & Osborne, 2012). These include Tachyglossus aculeatus (Short-beaked Echidna), Burramys parvus (Mountain Pygmy-possum), Antechinus agilis and A. swainsonii (Agile and Dusky Antechinus), Mastacomys fuscus (Broad-toothed Rat), Rattus fuscipes (Southern Bush Rat) and Tadarida australis (White Striped Mastiff Bat). All these species, except Tadarida australis, have been recorded in winter (Green & Osborne, 2012). However, large native marsupial herbivores such as Vombatus ursinus (Common wombat), Macropus giganteus (Eastern grey kangaroo) and Macropus rufogriseus (Red-necked wallaby), are largely excluded from this area in the colder months, as they are poorly adapted for deep snow and are only occasionally recorded in the snow-free months (Green, 2016; McVean, 1969). Other native vertebrates living in this alpine area include seven species of skinks, two species of snakes and two species of frogs (Green & Osborne, 2012). Common Aves found in this area are Anthus novaeseelandiae (Richard's Pipits) and Corvus mellori (Little Ravens), although there are other species that visit during the snow-free months including *Anas superciliosa* (Pacific Black Duck) and Falco cenchroides (Nankeen Kestrel) (Green & Osborne, 2012). In addition to native vertebrates, there is a ~200-year history of introduced animals (not native to Australia and originally brought to Australia during colonisation) in this area. This includes *Bos taurus* (Cattle) and *Ovis aries* (Sheep) which were deliberately herded into the alpine area during the snow-free months from the early 1800s, where their extensive grazing and trampling resulted in extensive damage to vegetation and soils prior to their being banned in the alpine area in 1958 (Costin et al., 2000; Good & Johnston, 2019). Currently, there are a range of introduced animals that access and damage this alpine area during the warmer months such as *Equus caballus* (Horse), *Dama dama* (Fallow Deer), *Cervus unicolor* (Sambar Deer), *Cervus elaphus* (Red Deer) and *Sus scrofa* (Pig), while *Vulpes vulpes* (Red Fox), *Felis catus* (Cat) and *Lepus capensis* (Hare) are found year-round (Green & Osborne, 2012).

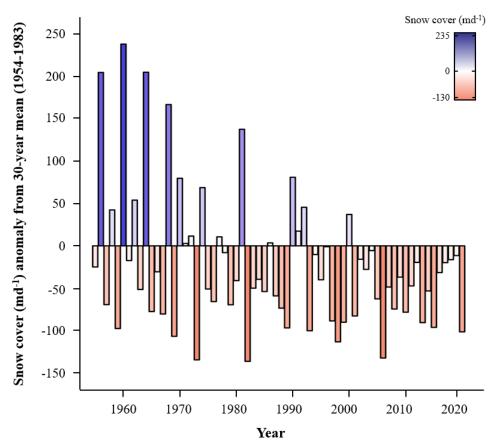
In contrast to the low numbers of native vertebrate herbivores, arthropods (invertebrates) are well represented in the Kosciuszko alpine area, where they fulfil important ecological functions such as nutrient cycling and pollination. Important invertebrate herbivores that can occur in large numbers include phytophagous insects such as native grasshoppers, and the larvae of *Oncopera alpina* (Swift Moths) and *Lomera caespitosae* (Alpine Case Moths) (Costin, 1954; Green & Osborne, 2012). There are at least 175 families and 990 species of insects recorded above 1,700 m a.s.l in the Snowy Mountains, with common species from Plecoptera (stoneflies), Coleoptera (beetles), Lepidoptera (moths and butterflies), Diptera (flies) and Collembola (springtails), with Orthoptera (grasshoppers) and Hymenoptera (ants, wasps and bees) particularly well established in this alpine area (Green & Osborne, 2012). Endemic insects to the Kosciuszko alpine area include four species of Plecoptera, *Oxycanus oreades* (a sub-brachypterous Swift Moth) and *Kosciuscola tristis* (Kosciuszko Alpine Thermocolour Grasshopper) although further surveys are required to more fully document the diversity and distribution of insects in this alpine area (Edwards & Green, 2011; Green & Osborne, 2012).

### Anthropogenic land use and climate change impacts in this alpine area

In comparison to many alpine ecosystems that have experienced several centuries of anthropogenic impacts, there have been relatively less intensive land-use practices in the Kosciuszko alpine area (Costin, 1967; Slattery & Worboys, 2020). Foremost, the Kosciuszko alpine area is a place of Indigenous cultural significance for Ngarigo, Wagalu and Djilamatang, and surrounding Nations would congregate for trade and ceremony in addition to feasting on Agrostis infusa (Bogong Moth) aestivating over summer and harvesting the common and widespread Microseris longifolia (Yam Daisy) (Flood, 1973; Slattery & Worboys, 2020). However, there is very limited evidence of permanent occupation or intensive land-use practices, including Indigenous cultural burning practices, in this alpine area (Williams et al., 2008), although fire was used sparingly to manage access routes and hunting grounds in the adjacent subalpine and montane areas (Dodson et al., 1994; Slattery & Worboys, 2020; Zylstra, 2006).

Colonisation led to altered fire regimes and a range of large non-native ungulates were introduced to the region in the early 1800s for agricultural purposes leading to eutrophication, damage to sensitive vegetation and soil erosion until grazing was finally banned in 1958 (Costin, 1954; Dodson et al., 1994; Good & Johnston, 2019). These impacts were severe and widespread, as the Kosciuszko alpine area evolved in the absence of frequent fire and extensive trampling or grazing by ungulates (Costin, 1954; Good & Johnston, 2019; Green & Osborne, 2012). However, introduced animals, such as horses, deer, pigs, hares, foxes, cats and foxes are still causing impacts in this area, particularly during the snow-free period (Green & Osborne, 2012; NSW Government, 2021). Without effective management of these introduced animal populations, the Kosciuszko alpine area is experiencing increasing degradation and disturbance (Cairns, 2019; Claridge, 2016; Driscoll et al., 2019; Hone, 2012). However, management and removal of introduced animals is a contentious issue in the Australian Alps, particularly for horses as they are an icon of colonial cultural identity (Hagis & Gillespie, 2021; Pickering & Norman, 2020). Nevertheless, introduced animals are placing considerable pressures on native flora and fauna through the destruction and degradation of vegetation and waterways, as well as increased predation and competition for resources with native animals (Driscoll et al., 2019; Green & Osborne, 1981; Schulz et al., 2019; Worboys, 2018).

Alongside land-use changes and rising anthropogenic emissions, the climate of the Kosciuszko alpine area is changing rapidly (Hughes, 2003; McGowan et al., 2018; Nicholls, 2005). Generally, the area has become warmer and precipitation more variable, causing declining snow cover Figure 1. 8). Mean temperatures have increased by 0.1° C per decade over the past century (Sritharan et al., 2021) but have accelerated to 0.3° C per decade since 1970 (Thredbo All Weather Station, 1967-2021, 1957 m a.s.l) (McGowan et al., 2018). With warming temperatures, there has been a concurrent 25% decline in snow depth at treeline between 1954 and 1993 (Slater 1995) and a further 15% reduction in the decade up to 2013 (Davis 2013). Growing seasons are lengthening as autumn and spring snow cover are rapidly declining, with warmer temperatures leading to accelerated ablation and more precipitation falling as rain (Fiddes et al., 2015; McGowan et al., 2021; Thompson, 2016; Thompson & Paull, 2017). While the maximum snow depth has declined by 10% from 1962 – 2002 (Nicholls, 2005), the number of heavy snowfall (>10 cm) days has remained stable over time but there has been a loss of five light snowfall (<10 cm) days per decade (Fiddes et al., 2015). This area has also experienced four droughts since 1980 (1982 – 1983, 1994 – 1998, Millennium Drought 2002 – 2010, 2018 – 2020) (Holgate et al., 2020; Wang et al., 2021), with fires often occurring during in the adjacent subalpine and montane areas during these drier periods (Williams et al., 2008).



**Figure 1. 8**: Latest snow cover anomalies derived from calculating snow metre-days (md<sup>-1</sup>) that incorporates snow depth and duration from Spencers Creek Snow Course (1830 m a.s.l) records, located at treeline in the south-east of the Kosciuszko alpine area (generated for the thesis).

Such changes in climate in the Australian Alps over recent decades have led to a considerable increase in Forest Fire Danger Index (FFDI), particularly in spring (Dowdy, 2018). This increasing fire risk is amplified by earlier onset of the fire season (Clarke et al., 2013), increasing landscape flammability in the surround subalpine and montane forests (Fraser et al., 2016; Zylstra, 2013; Zylstra, 2018) and increased risk of pyrocumulonimbus wildfires (Di Virgilio et al., 2019). Since the cover and composition of alpine vegetation has historically responded to natural climatic fluctuations over recent millennia (Dodson et al., 1994; McKenzie, 1997; Thomas et al., 2022), the ecological impacts of a rapidly changing climate is of growing concern in the Kosciuszko alpine area (Venn et al., 2017), with alpine ecosystems among the most vulnerable to climate change in Australia (Bergstrom et al., 2021; Hughes, 2003; Laurance et al., 2011). In response, specific LTEM sites were established in the Kosciuszko alpine area to understand and monitor how alpine vegetation is responding to climate change, in line with global initiatives (Pauli et al., 2015) as well as regional priorities.

### Long-term ecological monitoring in the Kosciuszko alpine area

There are a few LTEM studies in the Kosciuszko alpine area, with one of the first and longest running studies established in 1959 to assess the recovery of vegetation from agricultural grazing

and burning using permanent transects and photoquadrats (Wimbush & Costin, 1979), and was later adapted to monitor recovery from drought (Scherrer & Pickering, 2005). Overall, palatable species including *Aciphylla glacialis*, *Aciphylla simplicifolia*, *Chionochloa frigida* and *Ranunculus anemoneus* were almost grazed to extinction, but vegetation had mostly recovered 15 years after the cessation of grazing, but cover also declined by ~ 30% during drought (Scherrer & Pickering, 2005; Wimbush & Costin, 1979). The Wimbush and Costin (1979) LTEM alongside other monitoring in the Australian Alps more generally (Wahren et al., 1994; Wahren, Papst, et al., 2001; Wahren, Williams, et al., 2001) as well as in the Central Plateau of Tasmania (Bridle et al., 2001) proved that alpine vegetation responds rapidly to changing environmental conditions and highlighted the values of such approaches for these alpine areas. Therefore, as global LTEM networks were established in alpine and tundra ecosystems at the end of the last millennium (Molau & Mølgaard, 1996; Pauli et al., 2015), similar sites were established in the Kosciuszko alpine area to monitoring impact of climate change and other ecological threats including monitoring specialist cryophilic plants and communities (Green & Pickering, 2009b), as well as broader scale changes in vegetation along summits (Pickering et al., 2008).

Climate change is listed as a key threatening process for two critically endangered snowpatch plant communities within the Kosciuszko alpine area (Duretto, 2019a, 2019b), as the persistence of these communities is intrinsically linked periglacial processes and melt water from late-lying snowpatches (Costin et al., 2000; Williams et al., 2015). A LTEM protocol was developed to monitor soil temperatures and vegetation along environmental snowmelt gradients (Green & Pickering, 2009b) to assess the impact of declines in snowpatches with warming temperatures in the Kosciuszko alpine area (Green & Pickering, 2009a; Sánchez-Bayo & Green, 2013). Soil temperatures have been continuously monitored along snowmelt gradients within seven snowpatches since 2003, while vegetation was surveyed in 2007 (Green & Pickering, 2009b; Venn et al., 2011) and 2013 (Pickering et al., 2014). These assessments demonstrated that the duration of snow cover is a strong environmental filter for vegetation cover, composition and functional traits, with the transition between communities occurring over metres along snowmelt gradients (Green & Pickering, 2009b; Venn et al., 2011). As temperatures increased and growing seasons lengthened, there was increasing cover of tall, tussock forming graminoids and subsequent declines in snowpatch specialist species, associated with changes in communityweighted plant height and leaf area (Pickering et al., 2014). However, further monitoring is required to determine if changes defining biotic and abiotic characteristics of these critically endangered communities will lead to collapse in the future via replacement of a novel ecosystem (Bergstrom et al., 2021; Williams et al., 2015).

Another LTEM project in the Kosciuszko alpine area specifically established to assess climate change impacts, is the only GLORIA site in Australia (Pickering et al., 2008). Five summits along

an elevation gradient from the treeline to one of the highest summits in Australia (Mount Clarke - see Figure 1. 6) were selected for monitoring using the GLORIA protocols (Pauli et al., 2015). Since 2004, soil temperatures have been continuously monitored on the five summits, and vegetation was surveyed in 2004 (Pickering & Green, 2009; Pickering et al., 2008) and 2011 (Venn et al., 2012; Venn et al., 2014). The microclimate of each summit was relatively distinct, with elevation-dependant vegetation distributions where lower elevations were dominated by closed heathlands near the treeline which transitioned to tall alpine herbfields with small tracts of windswept feldmark on the most exposed areas at higher elevations (Pickering & Green, 2009; Pickering et al., 2008). The results from the first repeat sampling in 2011 indicated that species richness had increased with newly recorded graminoids and shrubs, as well as increasing overlapping cover of vegetation of graminoids and forbs at the shrub-dominated lower elevation summits (Venn et al., 2012). As temperatures increased and growing season lengthened, there was a shift in community-weight functional traits to species with greater leaf area and specific leaf area but lower plant height and leaf dry matter content (Venn et al., 2014). While there seems to be an elevation-dependant impact of climate change on vegetation dynamics on the summits, further monitoring is required to determine if there has been ongoing species enrichment and compositional changes (Pickering & Green, 2009; Pickering et al., 2008; Venn et al., 2012; Venn et al., 2014).

Following landscape-level fires that burnt large but irregular tracts of tall alpine herbfields, heathlands and some areas of critically endangered windswept feldmark (Eldridge, 2015) in 2003 during the Millennium Drought (2002 – 2010) along parts of the ridgeline of the Main Range in Kosciuszko alpine area, an opportunistic LTEM project was established. As altered fire regimes have had considerable and diverse impacts on this alpine area (Good & Johnston, 2019; Wilson et al., 2022; Wimbush & Costin, 1979), six permanently marked quadrats were used to assess changes in burnt and unburnt tall alpine herbfield and windswept feldmark from 2004 to 2018 (Pickering & Venn, 2013; Venn et al., 2016; Verrall, 2018). Furthermore, as large areas of subalpine vegetation surrounding this alpine area burnt in 2003, there were several projects monitoring recovery of treeless subalpine vegetation (Bear & Pickering, 2006; McDougall et al., 2015; Verrall & Pickering, 2019; Walsh & McDougall, 2004). These different studies found divergent recovery trajectories among subalpine and alpine vegetation dependant plant communities, among growth forms and among species with different fire regeneration strategies. In the subalpine, species richness had mostly recovered one-year post-fire where resprouting graminoids recovered swiftly but obligate seeding shrubs were slower to recover (McDougall et al., 2015; Walsh & McDougall, 2004). Overall, subalpine vegetation cover and composition had recovered to similar pre-fire condition after 10 years, except for lower cover of groundwater dependant fire sensitive species (Dracophyllum continentis and Sphagnum cristatum)

(McDougall et al., 2015) and shrub encroachment (*Grevillea australis* and *Hovea montantus*) into grasslands (Verrall & Pickering, 2019). However, recovery was much slower for alpine vegetation cover, with some recover after nine years for tall alpine herbfield (dry alpine grasslands) and 12 years for windswept feldmark (Pickering & Venn, 2013), but species and functional composition convergence occurred with areas of the critically endangered windswept feldmark becoming more similar to adjacent areas of tall alpine herbfield (Venn et al., 2016; Verrall, 2018). However, most of these studies have limited spatiotemporal scope with conclusions drawn from small vegetation plots, and hence the resilience of vegetation in this alpine area to fire is still unclear (Camac et al., 2021; Venn et al., 2017).

### 1.7: Aims

This thesis will examine climatic and vegetation dynamics along varying spatiotemporal scales and environmental gradients in the Kosciuszko alpine area building on two existing LTEM projects. Additionally, a novel monitoring approach for this alpine area will examine climatic and vegetation dynamics using remote sensing, gridded climate data and snow course records. Considering the 25 warmest years on record have occurred since 1990 (GISTEMP Team, 2022; Lenssen et al., 2019), and the historical climate-induced responses of alpine vegetation in this area (Dodson et al., 1994; Martin, 1986; McKenzie, 1997; Thomas et al., 2022), LTEM projects in the Kosciuszko alpine area have already been provided important insights (Pickering et al., 2014; Venn et al., 2016; Venn et al., 2014). Therefore, it is important to continue and expand the spatiotemporal scale of monitoring in the Kosciuszko alpine area, as well as incorporating new methods and sources of data as the climate continues to warm. Alongside global trends, this alpine area has already experienced rapid increases in temperature, longer growing season and a declining snowpack Figure 1. 8), resulting in changes in vegetation cover and composition (Pickering et al., 2014; Venn et al., 2014). With further declines in snow cover and warmer temperatures predicted in this area (Di Luca et al., 2018; Olson et al., 2016), climate-induced responses of different species, growth forms, vegetation communities and types over different spatiotemporal scales is unclear (Camac et al., 2021).

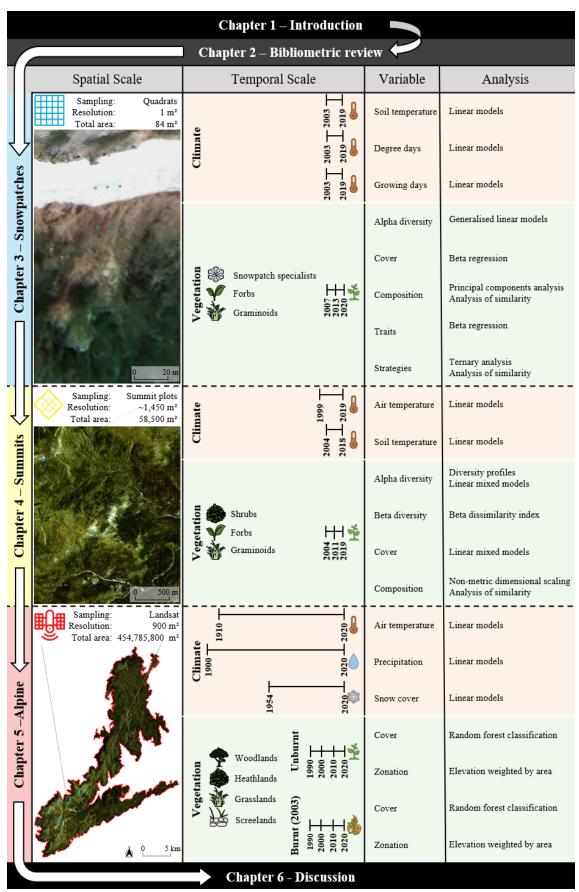
Therefore, the results section of this thesis begins with reviewing current literature on climate change and alpine vegetation using a multi-component bibliometric methodology. Then, soil temperature and vegetation data from field-based repeat surveys of two LTEM projects were analysed to assess the latest dynamics in microclimate and composition at the microscale in snowpatches (metres) and at the mesoscale on summits (hectares). Finally, a novel remote sensing approach is applied to this alpine area to monitor longer-term changes on the macroscale in broad vegetation types including in response to the 2003 wildfires, as well as assessing climatic changes

over the past century. Using these different sources of data, the thesis will address the following questions:

- 1) What is the current state of research on alpine vegetation in the context of climate change? (Chapter 2)
- 2) How is climate changing in the Kosciuszko alpine area? (Chapter 3, 4 & 5)
- 3) Are there differing responses of vegetation along environmental gradients in the Kosciuszko alpine area? (Chapter 3, 4 & 5)
- 4) Are there differing responses of vegetation at different sampling scales in the Kosciuszko alpine area? (Chapter 3, 4 & 5)
- 5) What vegetation is increasing and decreasing in response to climate change in the Kosciuszko alpine area? (Chapters 3, 4 & 5)
- 6) What are the benefits, limitations and implications of LTEM when assessing vegetation dynamics? (Chapters 3, 4 & 5)

### 1.8: Structure of the thesis

The structure of this thesis is in accordance with Griffith University policy on the inclusion of papers within a PhD thesis (Appendix A). It consists of six chapters (Figure 1. 9): an overall introduction (Chapter 1) and discussion (Chapter 6), a review chapter (Chapter 2), and three results chapters based on field and remote sensing climate and vegetation data (Chapters 3, 4 & 5). Chapter 2 reviews alpine vegetation in the context of climate change, which is followed by empirical results chapters where the spatial and temporal scales of sampling increase from Chapter 3 to 5. Chapter 3 assesses temporal dynamics in alpine snowpatch vegetation along a snowmelt gradient. Then, Chapter 4 assesses dynamics in alpine summit vegetation over time. Finally, Chapter 5 assesses decadal alpine vegetation dynamics using Landsat timeseries. Chapters 2 to 5 are in the form of published papers or papers currently under review that are formatted to meet the requirements of peer-reviewed academic journals. Consequently, there may be some overlap amongst these chapters, including in the introduction, methods, discussions and reference lists with other parts of the thesis. Additionally, there may be some differences in terminology (e.g. vegetation cover/plant cover). Tables, figures, references and supplementary materials of Chapters 2 to 5 were formatted to the specifications of each journal, and may not be consistent across chapters. Details of each paper and author contributions are also given at the beginning of the Chapters 2 to 5. At the time of thesis submission, Chapters 2, 3 and 4 consist of published peer-reviewed academic journal articles, while Chapter 5 is the latest version of the manuscript.



**Figure 1.9**: Overview of structure the thesis, highlighting the broad methodology (bibliometric review, climate data, vegetation plots or remote sensing), the spatiotemporal scale, vegetation types, response variables and analysis for each chapter.

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# Chapter 2: Alpine vegetation in the context of climate change

## 2.1: Objectives

In Chapter 1, I summarised the background, general literature, aims and structure of the thesis. The following four chapters present my research in the form of papers with their own introductions, aims, methods, results, discussions and reference lists.

First, I conducted a bibliometric literature review to examine 'Alpine vegetation in the context of climate change: A global review of past research and future directions'. This included assessing 3,143 publications to determine who does research and where was research conducted, how this relates to the distribution of alpine area globally, and what vegetation types were studied. Additionally, research trends were examined including in common themes and methods over recent decades. The review also examined the underlying literature by identifying the most highly-cited publications on which this field of knowledge is based.

This review summaries the broad academic context and justification for the following three chapters, by providing a topology of climate change and alpine vegetation research, including identifying emerging research directions and methods, and thematic and geographic gaps in the literature. The results highlighted the need for more research using traditional research methodologies including LTEM, as well as adapting technological advances in remote sensing techniques to provide larger temporal and spatial scale analysis. It also highlighted the need for more research focusing on cryophilic and periglacial vegetation, extreme climatic events and research in the unique alpine ecosystems of the southern hemisphere.

### 2.2: Details, author contributions and declaration

This chapter consists of the published version of a paper and supplementary material co-authored with my principal supervisor. The citation of this paper is:

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Author contributions	for t	this pa	aper	are	as	foll	ows:
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**BV** conceptualisation (lead), project administration (lead), data collection and analysis (lead), writing (lead), reviewing and editing (lead).

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## 2.3: Published paper

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#### Review

# Alpine vegetation in the context of climate change: A global review of past research and future directions



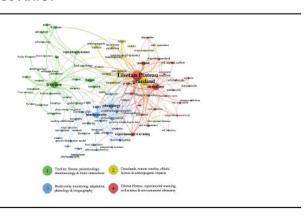
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#### HIGHLIGHTS

- The extent and state of climate change and alpine vegetation research are unclear.
- A multicomponent bibliometric analysis is applied to this research.
   Four broad research themes are identified.
- Four broad research themes are identified, and interrelations are explored.
- Research focus has shifted towards grasslands and the Tibetan Plateau.
- Periglacial vegetation presents as an avenue for future research.

#### GRAPHICAL ABSTRACT



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### ABSTRACT

Climate change is causing extensive alterations to ecosystems globally, with some more vulnerable than others. Alpine ecosystems, characterised by low-temperatures and cryophilic vegetation, provide ecosystems services for billions of people but are considered among the most susceptible to climate change. Therefore, it is timely to review research on dimate change on alpine vegetation including assessing trends, topics, themes and gaps. Using a multicomponent bibliometric approach, we extracted bibliometric metadata from 3143 publications identified by searching titles, keywords and abstracts for research on 'dimate change' and 'alpine vegetation' from Scopus and Web of Science. While primarily focusing on 'alpine vegetation', some literature that also assessed vegetation below the treeline was captured. There has been an exponential increase in research over 50 years, greater engagement and diversification in who does research, and where it is published and conducted, with increasing focus beyond Europe, particularly in China. Content analysis of titles, keywords and abstracts revealed that most of the research has focused on alpine grasslands but there have been relatively few publications that examine specialist vegetation communities such as snowbeds, subnival vegetation and fellfields. Important themes emerged from analysis of keywords, including treelines and vegetation dynamics, biodiversity, the Tibetan Plateau as well as grasslands and meadows. Traditional ecological monitoring techniques were important early on, but remote sensing has become the primary method for assessment. A key book on alpine plants, the IPCC reports and a few papers in leading journals underpin much of the research. Overall, research on this topic is increasing, with new methods and directions but thematic and geographical gaps remain particularly for research on extreme climatic events, and research in South America, in part due to limited capacity for research on these rare but valuable ecosystems © 2020 Elsevier B.V. All rights reserved.

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# **Supplementary materials**

Refer to the <u>full copy of this paper</u> available from the Elsevier website.

# Chapter 3: Temporal dynamics in alpine snowpatch vegetation

## 3.1: Objectives

The review in the previous chapter highlighted research trends and priorities for alpine vegetation in the context of climate change. This included demonstrating how LTEM remains a critical method for examining responses of vegetation to changing climatic conditions, but LTEM is relatively scarce in the alpine areas of the southern hemisphere. It also highlighted how specific types of alpine vegetation such as cryophilic and periglacial communities have received relatively little research attention globally.

Therefore, the first results chapter of the thesis starts with LTEM at the microscale (metres), where changes in microclimate and vegetation composition of critically endangered snowpatch plant communities were assessed in the Kosciuszko alpine area. Specifically, temporal vegetation dynamics were explored over a 13-year period using three surveys (2007, 2013, 2020) of 84 permanently marked 1 m² vegetation quadrats along snowmelt gradients. Furthermore, microclimate data along snowmelt gradients was recorded from continuous soil temperature monitoring (2003 – 2020). I led the project and field team for the latest survey in 2020, which provided an additional ~ 6,250 plant composition records from 52 species as well as another seven years of soil temperature data (~ 900,000 records). These data were then incorporated with those from the previous vegetation surveys (2007 and 2013) for analysis.

Microclimatic data from soil temperature loggers were assessed along snowmelt gradients and used to assign vegetation quadrats into early, mid and late melt zones. Then, changes in plant diversity, cover, composition, traits and strategies over the three survey periods were assessed to see how cryophilic plant communities and species have responded to changes in climatic conditions. Specifically, temporal dynamics in microclimate were assessed with linear models, diversity, cover and community-weighted functional traits were assessed with generalised linear models using beta regression, and composition and community-weighted plant strategies were assessed with principal component analysis and analysis of similarity (Figure 1. 9).

### 3.2: Details, author contributions and declaration

This chapter consists of a published version of a paper and supplementary materials that was coauthored with my external supervisor and principal supervisor. The citation of this paper is:

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Author contributions for this paper are as follows:

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- **KG** conceptualisation (co-lead), project administration (co-lead 2007, 2013; supporting 2020), data collection (co-lead 2007, 2013; supporting 2019), reviewing and editing (supporting).
- **CMP** conceptualisation (co-lead), project administration (co-lead 2007, 2013; supporting 2020), data collection (co-lead 2007, 2013; supporting 2020), writing (supporting), reviewing and editing (supporting).

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## 3.3: Published paper

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#### **COMMUNITY ECOLOGY - ORIGINAL RESEARCH**



# Temporal dynamics in alpine snowpatch plants along a snowmelt gradient explained by functional traits and strategies

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#### Abstract

Alpine snowpatches are characterised by persistent snow cover, short growing seasons and periglacial processes, which has resulted in highly specialised plant communities. Hence, these snowpatch communities are among the most threatened from climate change. However, temporal dynamics in snowpatch microclimate and plant composition are rarely explored, especially in the marginal alpine environments of Australia. Seven snowpatches were categorised into early, mid and late snowmelt zones based on growing season length, with soil temperatures recorded from 2003 to 2020 and plant composition surveyed in 84 1 m<sup>2</sup> quadrats in 2007, 2013 and 2020. Microclimate, species diversity, plant cover and composition, along with community-weighted trait means and plant strategies were assessed to understand snowpatch dynamics in response to climate change. We found that growing season length and temperatures have increased in late melt zones, while changes were less consistent in early and mid melt zones. There were few changes in species diversity, but increases in graminoids and declines in snowpatch specialists in mid and late melt zones. Community-weighted plant height, leaf area and leaf weight also increased, particularly in mid and late melt zones, while plant strategies shifted from compositions of ruderal-tolerant to stress-tolerant. Here, we show that snowpatch communities are rapidly changing in response to longer growing seasons and warmer temperatures, with the greatest changes occurring where snow persists the longest. The results highlight the climate-induced loss of defining biotic and abiotic characteristics of snowpatches, as temporal convergence of compositions along snowmelt gradients threatens the distinctiveness of snowpatch plant communities.

 $\textbf{Keywords} \ \ Alpine \ snowbed \cdot Community-weighted \ trait \ means \cdot Competitor-stress-ruderal \ plant \ strategies \cdot Long-term \ ecological \ monitoring \cdot Plant-climate \ interactions$ 

### Introduction

Alpine ecosystems are directly governed by low temperatures with short growing seasons due to seasonal snow cover (Körner 2003). Consequently, they are among the ecosystems most threatened globally from climate change, as temperatures increase in many alpine regions resulting in declines in snow cover (Guisan et al. 2019; Huss et al. 2017). As the duration of snow cover is a strong environmental filter

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for plant composition (Körner 2003), the threat of climate change is amplified for cryophilic plant communities that are maintained by periglacial and nivation processes (Björk and Molau 2007). In topographical depressions on lee aspects of mountain ridgelines where snow accumulates throughout the winter, snowpatches may persist for months after the general thaw, supporting distinctive and highly specialised snowpatch (synonymous with 'snowbed' and 'snowbanks') species and communities (Billings and Bliss 1959; Björk and Molau 2007; Green and Pickering 2009a). Although research on snowpatch plant communities remains sparse (Verrall and Pickering 2020), they are considered among the most vulnerable alpine ecosystems to climate change (Gritsch et al. 2016; Matteodo et al. 2016). This includes Australia where alpine environments are already marginal and uncommon (Kirkpatrick et al. 2017; Pickering et al. 2014; Williams et al. 2015).

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# Supplementary materials

Refer to the <u>full copy of this paper</u> available from the Springer-Nature website.

# Chapter 4: Dynamics in alpine summit vegetation over time

# 4.1: Objectives

The previous chapter assessed the response of critically endangered snowpatch plant communities over strong snowmelt gradients but relatively small scales (metres). It demonstrated how increasing temperatures and lengthening growing seasons have resulted in changes in the plant communities with fewer cryophilic specialist and more thermophilic generalists.

In this next chapter, changes in climate and vegetation composition were assessed at the mesoscale (hectares) to see how climate conditions may alter more common plant communities within the Kosciuszko alpine area. Specifically, it assessed temporal vegetation dynamics in graminoid- and shrub-dominated alpine plant communities along an elevation gradient of five summits over a 15-year period with three surveys (2004, 2011, 2019) of permanently marked summit vegetation plots ( $\sim 1$  ha) as part of the GLORIA international monitoring network. Furthermore, microclimate data along the elevation gradient of summits was recorded from continuous soil temperature monitoring (2004 – 2018). I led the project and field team for the latest survey in 2019, which provided an additional  $\sim 14,700$  plant composition records from 88 species recorded over the five summits assessed (total area = 5 ha) as well as another seven years of soil temperature data ( $\sim 600,00$  records). These data were then incorporated with those from the previous vegetation surveys (2004 and 2011) for analysis.

Based on these vegetation and microclimate data from soil temperature loggers along with air temperatures from a proximal weather station, it was possible to assess trends in climate over a longer time period in addition to conducting targeted statistical analysis to compare changes in plant diversity but also cover and composition of summit vegetation. Specifically, temporal dynamics in microclimate were assessed with linear models, species richness and cover were assessed with linear mixed models, alpha and beta diversity is assessed using diversity profiles and dissimilarity indices, and composition was assessed with non-metric dimensional scaling and analysis of similarity (Figure 1. 9).

### 4.2: Details, author contributions and declaration

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Author contributions for this paper are as follows:

- **BV** project administration (lead -2019), investigation (lead -2019), data collection (lead -2019), data analysis (lead), writing (lead), reviewing and editing (lead).
- **KG** conceptualisation (co-lead), project administration (co-lead 2004, 2011; supporting 2019), data collection (co-lead 2004, 2011; supporting 2019), reviewing and editing (supporting).
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## 4.3: Published paper

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### **ORIGINAL PAPER**



# Dynamics in plant diversity and composition on Australian alpine summits over time

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### **Abstract**

High mountain environments are often characterised by low temperatures and short growing seasons, yet support high plant endemism and biodiversity. While such ecosystems are considered among the most vulnerable to climatic warming, the impacts of climate change on diversity and composition can be complex. To develop a deeper understanding of these dynamics, changes in vegetation over time along five alpine summits that are part of the Global Observation Research Initiative in Alpine Environment (GLORIA), were assessed including species richness,  $\alpha$ -diversity,  $\beta$ -diversity, vegetation and growth form cover as well as composition. The five summits of Mount Clarke in the Australian Alps were surveyed in 2004, 2011 and 2019. Despite increases in species richness over time, there was an overall decline in diversity through biotic homogenisation across the summits. Near complete vegetation cover was recorded in 2004 but increased over the 15 years via in-filling and densification, driven by increasing cover of graminoids and shrubs. Consequently, there was also a shift in species composition which was greatest at higher elevations. The results indicate that there has been a shift towards more competitive and thermophilic composition, which may have implications for flammability in a warming and drying climate. Further assessments will be required to more fully explore the effect of climate variation from climate change, and implications for conservation of this and other alpine floras globally.

**Keywords** Climate change biology  $\cdot$  GLORIA  $\cdot$  Vegetation dynamics  $\cdot$  Alpha and beta diversity  $\cdot$  Biotic homogenisation  $\cdot$  Densification

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# Supplementary materials

Refer to the full copy of this paper available from the Springer-Nature website.

# Chapter 5: Landsat-derived alpine vegetation dynamics

## **5.1: Objectives**

The previous chapter assessed climate-induced vegetation dynamics in common alpine plant communities over summits at the scale of hectares along an elevation gradient. It demonstrated that increasing air and soil temperatures were associated with changes in vegetation including some biotic homogenisation via increases in thermophilic and more competitive graminoids at higher elevations and shrubs at lower elevations. Hence, changes in climate over two decades or less have already been associated with localised changes in the dominance of specific types of plants with particular traits seen at the microscale (metres) and mesoscale (hectares) with resulting dynamics in plant communities in the Kosciuszko alpine area.

In this next chapter, I expanded the temporal and spatial scale of my analysis to assess the 455 km<sup>2</sup> continuous Kosciuszko alpine area over the past three decades using remote sensing techniques. While similar remote sensing monitoring approaches are starting to be applied to alpine vegetation in Europe, North America and Asia, this is the first time that such an approach has been applied in the Australian Alps, and is the world-first to incorporate recovery of alpine vegetation from wildfire.

First, dynamics in temperature (1910-2019), precipitation (1900-2019) and snow cover (1954-2021) in the Kosciuszko alpine area were assessed using linear models. These data were then compared to modelling of six broad vegetation types at decadal intervals from 1990 to 2020 based on optimised recursive feature elimination random forest classification of growing season composites using Landsat multispectral data. The LandTrendR disturbance-detection algorithm used to quantify the extent of the 2003 wildfires, and dynamics in the cover and zonation (mean elevation weighted by area) of the six broad vegetation types were assessed with comparisons drawn between unburnt and burnt areas (Figure 1. 9).

# 5.2: Details, author contributions and declaration

This chapter consists of the paper under review that was co-authored with my associate supervisor as well as other academic and industry authors. The details of this paper are:

**Verrall, B.**, Norman, P., Mackey, B., Fisher, S., & Dodd, J. (in review). Decadal alpine vegetation dynamics modelled using Landsat timeseries amidst rapid climate change in Australia.

Author contributions for this paper are as follows:

$\mathbf{BV}$	conceptualisation (lead), project administration (lead), investigation (lead), data
	collection (lead), data analysis (lead), writing (lead), reviewing and editing (lead).

**PN** conceptualisation (supporting), project administration (supporting), investigation (supporting), writing (supporting), reviewing and editing (supporting).

**BM** writing (supporting), reviewing and editing (supporting).

**SF** data collection (supporting), data analysis (supporting), reviewing and editing (supporting).

**JD** data collection (supporting), data analysis (supporting), reviewing and editing (supporting).

10 October 2022

# 5.3: Paper under review

Decadal alpine vegetation dynamics modelled using Landsat timeseries amidst rapid climate change in Australia

### **Abstract**

Alpine ecosystems are characterised by low temperatures and short growing seasons. However, the stability of these ecosystems is threatened by climate change. Climate-induced dynamics in alpine vegetation have been recorded globally with changes in diversity, cover and composition, including in the Australian Alps. However, insights into these dynamics in Australia have been gleaned solely from field studies at fine spatial scales. Here, time series climate data and Landsat imagery were analysed for Australia's highest and most biologically diverse alpine area surrounding Mount Kosciuszko (455 km²). Climatic changes were analysed using gridded climate data (5 x 5 km) for mean annual temperature (1910-2019) and seasonal precipitation (1900-2019), and changes in snow cover were assessed from snow course records (1954-2021). A vegetation cover timeseries (1990, 2000, 2010, 2020) was modelled with an optimised random forest classification using recursive feature selection and tuned model parameters. Over time, increases in mean temperatures (0.1 °C/decade) and summer precipitation (6.5 mm/decade) were observed along with declines in snow cover (12.74 metre-days/decade) and winter precipitation (9.7 mm/decade). Subsequently, there were considerable vegetation cover changes between 1990 and 2020 with the cover of treeline snowgum woodlands increasing (+134.8%) via densification and in-filling at lower elevations with no treeline advance. Treeline subalpine woodlands replaced large tracts of dry alpine heath (36.4 km<sup>2</sup>) and wet alpine heath (38.0 km<sup>2</sup>) while there was less change in cover of grassland vegetation types. The study area experienced a landscape-level wildfire in 2003 (268.4 km<sup>2</sup> burnt or 59%), with the cover of treeline subalpine woodlands increasing at a greater rate in burnt (+1.70 km<sup>2</sup> per annum) verses unburnt (+0.73 km<sup>2</sup> per annum) areas between 2000 and 2020. Evidently, the rate of change in the climate has increased through time and is mirrored by vegetation cover and zonation dynamics with the proliferation of treeline subalpine woodlands (+70.6 km<sup>2</sup>) and advance of dry (+33.5 m) and wet (+12.89 m) heathlands, while in burnt areas there was recession of the treeline (-9.2 m) and dry shrublines (-16.5 m). Warmer temperatures, variable precipitation, especially declining winter rainfall and declining snow cover also increase the frequency and severity of wildfires, which may be amplified by increasing fuel loads and dryness from the proliferation and advance of woody vegetation in alpine areas. In coming decades, alpine vegetation may be impacted by climate change incrementally, through both relatively gradual changes in climatic conditions, and transformatively, through landscape-level disturbance from wildfire.

# Keywords

Remote sensing; LANDSAT 5/7/8; Australian Alps; alpine vegetation cover classification; climateplant interactions; fire ecology

### Introduction

Alpine vegetation occurs above the bioclimatic treeline, and its taxonomic composition and vegetation structure are foremost governed by low temperatures and relatively short growing seasons (Körner, 2003, 2012). However, complex topography, microclimatic heterogeneity, varying substrate and periglacial disturbance regimes result in treeline ecotones transitioning to a mosaic of low growing alpine grasslands, heathlands and fellfields (synonymous with "feldmark") that support high biodiversity and endemism (Elsen & Tingley, 2015; Körner, 2004; Perrigo et al., 2020). Most alpine plants are cryophilic, slow growing and long-lived perennials that are resilient to fluctuations in weather, but respond to both extreme climatic events (Alatalo et al., 2016; De Boeck et al., 2016; Williams et al., 2008) and sustained climatic shifts (De Boeck et al., 2018; de Witte & Stöcklin, 2010; Nagy & Grabherr, 2009). However, anthropogenic climate change has caused rapidly warming temperatures, declining snow cover and lengthening growing seasons (Hock et al., 2019; Huss et al., 2017), and there is evidence of elevation-dependent amplification of these changes in climate (Pepin et al., 2015). Therefore, as the climate continues to warm, alpine ecosystems and vegetation is particularly vulnerable (Grabherr et al., 2010; Guisan et al., 2019; Verrall & Pickering, 2020).

With disproportionate exposure to climate change impacts along with particularly climate-sensitive plants (Dirnböck et al., 2011), climate-induced vegetation dynamics within alpine areas have been broadly reported and are expected to continue with climate change. While there are numerous other factors that may influence alpine vegetation dynamics including the availability of water, nutrients and light as well as biotic interactions, climate change is widely attributed to be the primary factor causing declines in snow cover, variable precipitation regimes, longer growing seasons and warmer temperatures (Hock et al., 2019; Körner, 2003). Treeline dynamics, woody encroachment and increasing competition from thermophilic taxa have been found to occur (Hansson et al., 2021; Lamprecht et al., 2018; Myers-Smith et al., 2015), as the amount of thermal energy available to alpine plants has changed considerably over recent decades (Grabherr et al., 2010). Climate change has also seemingly resulted in the loss of highly specialised, cryophilic vegetation maintained by periglacial process, such as snowpatch communities, via encroachment of thermophilic and generalist alpine species (Carbognani et al., 2014; Pickering et al., 2014; Sandvik & Odland, 2014).

Climate-induced responses of alpine vegetation and subsequent implications on ecosystem processes are well documented, with an array of methods utilised to understand these changes

(Grabherr et al., 2010; Hock et al., 2019; Verrall & Pickering, 2020). Generally, responses of alpine vegetation to climate change are investigated by simulating environmental changes and space-for-time chronosequence approaches (Wieser et al., 2019), as well as investigating historical changes via dendrochronology (Danby et al., 2011) and palynology (Thomas et al., 2022). There has also been an increase in the use of long-term ecological monitoring techniques in alpine areas (Verrall & Pickering, 2020), where permanent vegetation plots are resurveyed through time (Pauli et al., 2012). However, field sampling in large, remote and rugged alpine areas that experience extreme climatic conditions is not always possible, and these logistical barriers may lead to a biased understanding of these changing ecosystems. In response, alongside technological advances over the past few decades, remote sensing techniques have been increasingly used to assess alpine vegetation (Verrall & Pickering, 2020). Remote sensing has a distinct spatial and accessibility advantage, leading to more efficient, effective and comprehensive monitoring of alpine areas (Mienna et al., 2022; Peyre et al., 2021; Zandler et al., 2022), yet most studies focused on the northern hemisphere (Chhetri & Thai, 2019).

The northern hemisphere contains the majority of alpine ecosystems (Testolin et al., 2020) and has received disproportionate research attention (Verrall & Pickering, 2020). However, relatively few studies have focused on the equally socially and ecologically important alpine ecosystems in the southern hemisphere (Körner, 2003; Körner & Ohsawa, 2005), including in the Australian Alps. With relatively small areas high-elevation mountain ranges and bioclimatic treelines only a few hundred meters below the highest peaks, alpine ecosystems are marginal and rare in Australia (Costin et al., 2000), covering less than 0.02% of the continent (Green & Stein, 2015). Yet, they support high species richness and endemism as well as providing crucial ecosystem services including water provisioning to much of south-eastern Australia (Slattery & Worboys, 2020). However, the lack of alpine weather stations and consistent climate data records have resulted in a poor understanding of recent climate changes above the treeline. Therefore, most studies only assess the few decades worth of available data (Verrall et al., 2021), but there is still clear evidence of warming and lengthening growing seasons (Fiddes et al., 2015).

Furthermore, Quaternary climate dynamics in the Australian Alps show that current temperatures are the warmest and snow cover is the lowest in 2000 years (McGowan et al., 2018), and wildfire activity has increased concurrently (Thomas et al., 2022). Generally, pollen-based vegetation reconstructions in the Australian Alps suggest that vegetation dynamics were responsive to past climatic changes, with the decline of alpine taxa coinciding with warming temperatures (Martin, 1986; Thomas et al., 2022). In response to the rapid climate change over recent decades, there has been an array of field-based assessments aiming to understand alpine vegetation dynamics in the Australian Alps (Venn et al., 2017). Generally, there has been an increase in vegetation cover driven by thermophilic graminoids and shrubs (Pickering et al., 2014; Venn et al., 2014; Verrall

et al., 2021) while in burnt areas, most alpine vegetation communities are relatively resilient to a single wildfire event and have been found to recover rapidly (Camac et al., 2013; McDougall et al., 2015; Venn et al., 2016). Nonetheless, wildfire is a strong demographic filter on contemporary treeline dynamics in the Australian Alps (Naccarella et al., 2020), and pastoral burning practices have been linked to stand-densification of the monospecific (*E. niphophila*) treeline (Martin, 1999).

Despite the importance and implications of alpine climate and vegetation dynamics in the Australian Alps, remote sensing has only been used to assess changes in snow cover (Bormann et al., 2012; Rasouli et al., 2022; Thompson, 2016) and growing season phenology (Thompson & Paull, 2017), and has yet to be utilised to model vegetation cover dynamics. Furthermore, given that the risk of wildfire has been found to be increasing in alpine areas around the world (Hock et al., 2019), the Australian Alps also presents an opportunity to assess the impact of landscape-level wildfire on alpine vegetation in the southern hemisphere. Over recent millennia, large wildfires have occurred every few hundred years in the Australian Alps but land-use, fire practices and wildfire regimes changed dramatically post-colonisation (1788) (Dodson et al., 1994; Martin, 1999; Williams et al., 2008). These altered regimes are now amplified by climate change leading to more severe and frequent impacts from wildfires (Clarke et al., 2013; Kirkpatrick & Bridle, 2013; Zylstra, 2018). Alpine vegetation is experiencing warmer temperatures and precipitation variability, and there is also evidence of woody encroachment and densification, which have increase flammability and biomass respectively, forming a positive feedback loop (Camac et al., 2017). Therefore, wildfire may present as a major threat that transforms alpine ecosystems in the future as the climate continues to warm (Fraser et al., 2016; Thomas et al., 2022; Venn et al., 2017; Williams et al., 2008).

By assessing recent climatic and associated vegetation dynamics in the highest alpine area in Australia, this study focused on three primary objectives. The first objective was to test dynamics in relevant climatic factors such as temperature, precipitation and snow cover over the last century, where we hypothesised increasing temperatures and precipitation variability along with declining snow cover. The second objective was to model the response of alpine vegetation over the past 30 years, where we hypothesised densification and in-filling of the treeline subalpine woodlands as well as encroachment of dry alpine heathlands resulting in an advance of the shrubline over time. The third and final objective was to compare burnt and unburnt areas from the 2003 wildfires, where we hypothesised that the dry alpine grasslands and dry alpine heathlands recovered quickly in areas that burned, and there was also treeline and shrubline suppression in burnt areas.

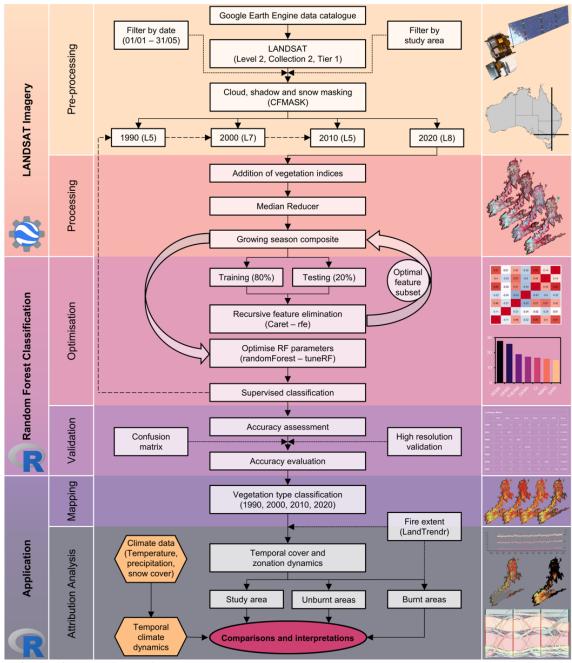
### **Methods**

An overview of the methods used in this study) to assess climatic and vegetation dynamics in a section of the Australian Alps is shown in Figure 1. We used data from the Australian Gridded Climate Data project (Jones et al., 2009), (Jones et al., 2009), snow course records (Snowy Hydro, 2022) and Landsat satellite imagery sourced from the Google Earth Engine data catalogue. By filtering Landsat collections temporally by growing season dates (01/01 - 31/5) and geographically by the study area (091/085), growing season composites were constructed using a median reducer at decadal intervals (1990, 2000, 2010, 2020). The 2020 composite along with geolocated training data were used to optimise a random forest classification model using recursive feature elimination and optimal model parameters to improve classification accuracy. This model with optimised parameters and features was then used to hindcast vegetation cover types from growing season composites for 1990, 2000 and 2010. Temporal dynamics in cover and mean elevation weighted by area (zonation) of vegetation types were then calculated across the study area, as well as in unburnt and burnt areas that were identified using the normalized burn ratio (NBR) through the disturbance detection LandTrendr algorithm. Vegetation type cover and zonation dynamics were then assessed, and attributed to dynamics in relevant climatic metrics including temperature, precipitation, snow cover and burn status.

#### Study area

The largest and most diverse contiguous alpine vegetation complex in Australia is located in the Snowy Mountains section of the Australian Alps, surrounding Mount Kosciuszko/Kunama Namadgi (2,228 m above sea level), which is the highest mountain on the land mass (Costin et al., 2000) (Figure 1). The study area experiences a marginal snowpack that commonly forms in June and becomes discontinuous in September (Bormann et al., 2012; Schwartz, McGowan, Theobald, et al., 2020; Thompson & Paull, 2017), with an annual mean daily temperature of 5.22 °C and an average annual precipitation (rain and snow) of 1,831 mm (Fick & Hijmans, 2017). While wildfire is an agent of disturbance in the study area (Thomas et al., 2022), particularly in periods of extended drought, large and severe wildfires burning over 100 km² of alpine vegetation are rare but were recorded in 1939 and 2003 (Williams et al., 2008). Furthermore, the complex topography, microclimatic heterogeneity and geographic isolation of the study area has given rise to a species rich flora with high endemism (Costin et al., 2000).

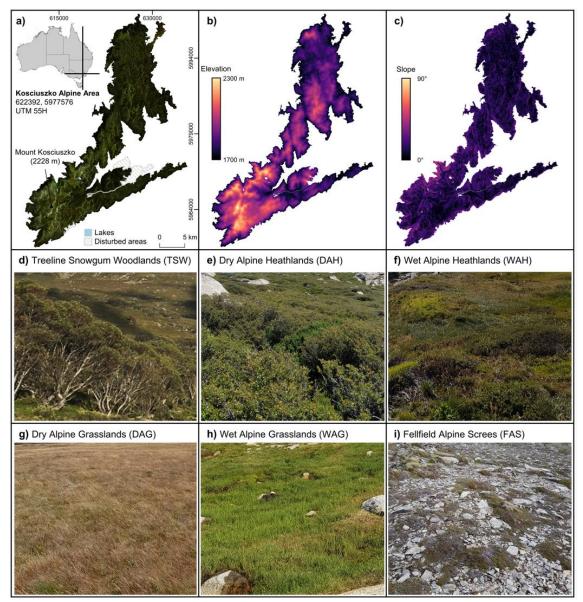
The alpine treeline ecotone is dominated by snowgums (*Eucalyptus niphophila*), forming an irregular and fractured demarcation between the alpine and subalpine zones where it ranges from 1,700 – 1,900 m a.s.l. depending on latitude, aspect, topography and soils (Green, 2009; Green & Venn, 2012). For the purposes of this investigation, the study area covers the continuous ~455 km² above 1,700 m that surrounds Mount Kosciuszko (Kosciuszko Alpine Area), but with



**Figure 1**: Workflow of the methods used to assess climate and vegetation dynamics in the Australian Alps, which can be split into three broad steps with the platform used denoted for each step (Google Earth Engine and R). The first step overviews the Landsat data acquisition and filtering to obtain growing season collections at decadal intervals, and demonstrates how growing season composites were generated. The second step overviews the procedure to obtain an optimised random forest classification model, which was used to classify decadal growing season composites. The third and final step overviews the temporal analysis of dynamics in vegetation types and climate data.

permanent alpine lakes and areas disturbed by human activities (including ski resort infrastructure, cleared ski runs and bitumen roads) masked and excluded from analysis (Figure 2). Previously, there have been several relevant plant community classifications conducted (CSIRO, 1972; Mackey et al., 2015; McDougall & Walsh, 2007). These plant community classifications can further be simplified to broad vegetation types including broad vegetation

types that formed the classification framework for this investigation: Treeline Snowgum Woodlands (TSW): Dry Alpine Heathlands (DAH): Wet Alpine Heathlands (WAH); Dry Alpine Grasslands (DAG); Wet Alpine Grasslands (WAG); Fellfield Alpine Screes (FAS) (Walsh & McDougall, 2004) (Figure 2, Table S1); and one scarcely vegetated landcover type, Alpine Rocky Outcrops (ARO; Figure S1).



**Figure 2**: Location and characteristics vegetation types of the study area with reference photos of vegetation types for the proposed classification.

#### Climate and remote sensing data

Temperature (1910 - 2020) and precipitation (1900 - 2020) data was sourced from the Australian Gridded Climate Data ( $\underline{AGCD\ v1.0.0}$ ) (Jones et al., 2009). Data are downloaded as monthly two-dimensional raster arrays at  $0.05^{\circ}$  ( $\sim 5$  km) spatial resolution, and were clipped to 16 grids ( $\sim 400$  km²) that were located within the study area. Annual mean temperature was calculated by averaging over monthly mean temperatures, while seasonal precipitation was calculated as the

sum of the three-monthly totals for summer (December from previous year, January and February) autumn (March, April and May), winter (June, July and August), and spring (September, October and November). Snow cover (1954 – 2021) data was sourced from the Snowy Hydro Project Spencers Creek Snow Course, which is located at 1,829 m a.s.l. in the south-east of the study area (-36.4257 S, 148.3470 E). To reflect both depth and duration of snow cover, snow-metre days (md<sup>-1</sup>) per year were calculated by summing the snow depth multiplied by the number of days at that depth (Green & Pickering, 2009; Sánchez-Bayo & Green, 2013). To assess temporal dynamics in temperature, precipitation and snow cover, linear regressions were conducted via the base package "Stats" v4.1.3 (R Core Team, 2022).

Imagery data was sourced from the United States Geological Survey (USGS) Landsat Program via the Google Earth Engine data catalogue using atmospherically corrected surface reflectance and land surface temperature collections (Level 2, Collection 2, Tier 1) derived from Landsat 5 Enhanced Thematic Mapper (ETM), Landsat 7 Enhanced Thematic Mapper + (ETM+) and Landsat 8 Operational Land Imager (OLI). Several studies posit that time series extracted from different Landsat sensors can provide an accurate and comparable representation of temporal vegetation dynamics (Banskota et al., 2014; Vogelmann et al., 2016). Thus, Landsat collections (Path: 091, Row: 085) were filtered consistently by date (01/01 to 31/05) to represent the snowfree growing season and the CFMASK algorithm was applied for cloud, cloud shadow and snow masking. Google Earth Engine was then used to generate composite images that were clipped to the extent of the study area at decadal intervals (1990, 2000, 2010, 2020) using a median reducer. Landsat 5 ETM was used to generate growing season composites in 1990 and 2010 (striping present in 2010 composites generated with Landsat 7 imagery due to the scan line corrector malfunction), while Landsat 7 ETM+ and Landsat 8 OLI were used to generate composites for 2000 and 2020, respectively. Digital elevation model (DEM) data at 2 m spatial resolution were downloaded for the study area, and mean elevation, slope and aspect were resampled to 30 m spatial resolution to align with Landsat pixels.

When classifying target objects such as vegetation cover types, raw multispectral data on their own are not always sufficient (Gislason et al., 2006; Guan et al., 2013). Therefore, an array of 69 features, made up of vegetation and geographic indices, were then added to growing season composites (Table S2). Previous classifications of vegetation cover in mountainous regions have highlighted the importance of particular features to improve model performance and classification accuracy, including specific vegetation indices and ancillary geographic data derived from DEM (Lin et al., 2021; McCaffrey & Hopkinson, 2020). Since elevation, slope and aspect are key determinates of alpine vegetation types in the study area (Costin et al., 2000; Mackey et al., 2015; McDougall & Walsh, 2007), they were added as features to growing season composites. Additionally, a range of vegetation indices were calculated and added to growing season

composites, including Vis previously used to classify alpine vegetation (Lin et al., 2021) and sensor-specific VIs (Henrich et al., 2009). Landsat bands were also added as features, with the three visible (Blue, Green and Red), one near-infrared (NIR), two short-wave infrared (SWIR1, SWIR2) bands processed to orthorectified surface reflectance, and one thermal infrared (TIR) band processed to orthorectified surface temperature (Table 1).

**Table 1**: Comparison of the spectral band range of Landsat 5 ETM, Landsat 7 ETM+ and Landsat 8 OLI.

Bands	Spatial resolution	Spectral Range of Sensor (μm)		
		Landsat 5 ETM	Landsat 7 EMT+	Landsat 8 OLI
В	30	0.45-0.52	0.45-0.52	0.452-0.512
G	30	0.52-0.60	0.52-0.60	0.533-0.590
R	30	0.63-0.69	0.63-0.69	0.636-0.673
NIR	30	0.77-0.90	0.77-0.90	0.851-0.879
SWIR1	30	1.55-1.75	1.55-1.75	1.566-1.651
SWIR2	30	2.08-2.35	2.08-2.35	2.107-2.294
TIR	30	10.40-12.50	10.40-12.50	10.60-11.19

### Optimisation of random forest classification

Supervised classification of the study area into the six vegetation cover types (TSW, DAH, WAH, DAG, WAG, FAS) and one landcover type (ARO) was executed using an optimised random forest (RF) algorithm on the 2020 growing season composite. As proposed by Breiman (2001), RF is a nonparametric, tree-based ensemble classifier that generates multiple decision trees using a randomly selected features and training samples. Classification of unlabelled data is then determined by an unweighted voting scheme where each pixel is assigned the class with the majority of votes. RF is also highly effective in generalisation, reducing overfitting as well as handling dimensionality and collinearity bias, and has been shown to be suitable for classifying multispectral data (Belgiu & Drăgut, 2016). It also has been shown to yield greater accuracy in comparison to other classification algorithms, and is capable of dealing with data variability in both training samples and unclassified data (Ma et al., 2017; Talukdar et al., 2020). RF classification has become a popular method to accurately determine vegetation and land cover (Khatami et al., 2016; Ma et al., 2017; Rodriguez-Galiano et al., 2012), including in alpine environments (Filippa et al., 2022; Liu et al., 2021; Meng et al., 2022; Zhang et al., 2019).

For the RF classification of this study area, training data polygons were generated from recent geolocated field surveys (Verrall et al., 2021; Verrall & Pickering, 2019) and high resolution SPOT-7 imagery (1.5 m spatial resolution). As the study area is known to contain varying cover of each vegetation type (Costin et al., 2000; Mackey et al., 2015), training data reflects the *in situ* proportions of data in each class. To improve the accuracy of classification, a minimum of 25 polygons were generated across the study area with a minimum cumulative extent of 15 hectares (0.03% of study area) for each of the six vegetation cover types (TSW, WAH, DAH, WAG, DAG,

FAS), and 5 hectares for the one landcover type (ARO) (Millard & Richardson, 2015). Training data were then randomly cut, with 80% of the dataset used for training and 20% for validation. However, the 2020 growing season composite contained a large set of features (69), which can increase computational complexity and lead to dimensionality problems as features are commonly highly correlated and redundant (Gregorutti et al., 2017).

Deciding which features to select in RF classification is a crucial but difficult, subjective and often error prone task (Belgiu & Drăgut, 2016; Georganos et al., 2018). Hence, classification performance can be greatly improved by optimising feature selection by using Recursive Feature Elimination (RFE) (Lin et al., 2021). This optimised feature selection algorithm is broadly utilised to derive discriminant feature rankings and determine the best performing subset of features. At each iteration, the least useful feature is eliminated, and the model is refit on the reduced feature subset until all features have been evaluated (Georganos et al., 2018; Kuhn et al., 2022). Here, RF-RFE with 10-fold cross-validation repeated 10 times was used to select the optimal feature subset from the 69 contained within the 2020 growing season composite via the "caret" package v6.0-92 (Kuhn et al., 2022) (Figure S2). Features were ranked (Figure S3, S4) and an optimised subset of seven features were selected (Table S3): Digital Elevation Model Elevation (DEME); Digital Elevation Model Slope (DEMS); Thermal Infrared (TIR); Digital Elevation Model Aspect (DEMA); Colouration Index (CI); Normalised Burn Ratio 2 (NBR2); and Green Atmospherically Resistance Index (GARI). Following RFE, the parameters of the RF model were then optimised via the "tuneRF" function in the "randomForest" package v4.7-1.1 (Breiman et al., 2022) (Table S5). These same optimised features and model parameters were then used to classify the growing season composites for 1990, 2000 and 2010.

#### Validation and accuracy assessments of classification

After classification of the 2020 growing season composite, the overall cross-validation accuracy of the optimised RF-RFE model was 97.98%, and the class-specific accuracies were all above 80% (Table S4). To build upon cross-validation and further improve the confidence of classification, manual validation using higher resolution imagery is commonly used (Blatchford et al., 2021; Hansen et al., 2013; Mu et al., 2015). Here, manual validation was conducted using SPOT-7 imagery (1.5 m resolution) captured in 2020 for 500 randomly selected pixels. To avoid bias, pixels that underwent manual validation were independent of training data (Hammond & Verbyla, 1996), and were distributed throughout the diversity of slopes, aspects and elevations present in the study area (Millard & Richardson, 2015; Strahler et al., 2006). Each of the 500 testing pixels was assigned one of the seven cover types based on the dominate vegetation present within the bounds of that pixel and was then compared to the 2020 RF-RFE classification (See Supp. 2). Overall, manual classification accuracy was 88.2%, with a 2% over-estimation of TSW

and WAH being the greatest classification error. Therefore, based on these results, we considered the optimised RF-RFE classifier to have recognised the major vegetation cover types across the study area with sufficient accuracy for the purposes of this study.

### Pixel-based disturbance detection using the LandTrendr algorithm

LandTrendr (Landsat-based detection of trends in disturbance and recovery) is a time series segmentation algorithm to detect disturbance via identifying gradual and abrupt fluctuations in the trajectory of a given spectral index. First, this algorithm calculates the years of change by identifying the beginning and end of each temporal segment in the spectral trajectory, also known as vertices, and second, it calculates the spectral index values at each of the vertices to generate the trajectory of interconnected temporal segments that elucidate to pixel-based disturbance (Kennedy et al., 2007; Kennedy et al., 2010). As the study area is known to have experienced wildfires between 1990 and 2020 (Mackey et al., 2021; Williams et al., 2008), the LandTrendr algorithm was used in Google Earth Engine to quantify the extent of fire-type disturbance using the normalised burn ratio (NBR) spectral index (Kennedy et al., 2018), which has been similarly applied in other mountainous regions (Li et al., 2021; Rodman et al., 2021). The NBR spectral index was selected due to its sensitivity to chlorophyll, charcoal ash and water content in leaves, enhancing the ability to detect fire-type disturbance of vegetation (Kennedy et al., 2010). To obtain the LandTrendr derived extent of burnt areas, the NBR recovery threshold was set at 0.25 and temporal segments in pixels with a magnitude of greater than this threshold in wildfire years (2003 and 2020) were identified as burnt areas.

### Cover and zonation of vegetation types

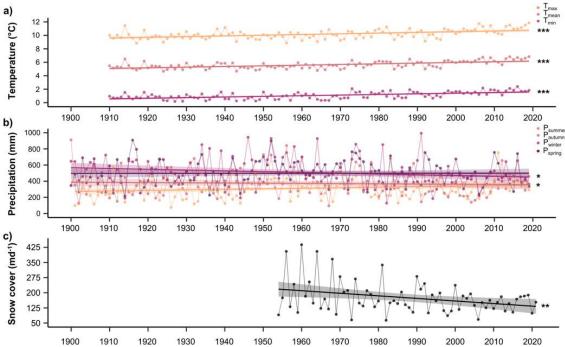
Assessments of the temporal dynamics of vegetation types was pixel-based (Knoflach et al., 2021), with each Landsat pixel covering a planimetric area of 900 m<sup>2</sup> (30 x 30 m resolution) (Knoflach et al., 2021). For each of the 514,214 pixels within the study area, a centroid was generated and was used to spatially join relevant environmental data including mean elevation, slope and aspect. Centroids were also used to sample the modelled vegetation type at each decadal interval so the vegetation dynamics could be assessed for each individual pixel, which permitted temporal network analysis of the cover of vegetation types using Sankey diagrams via the R "networkD3" package v0.4 (Allaire et al., 2017). As there is bioclimatic zonation of different alpine vegetation types in the study area (Costin et al., 2000; Mackey et al., 2015; McDougall & Walsh, 2007), temporal zonation dynamics were assessed using mean elevation weighted by area for each vegetation type at each decadal interval. To improve visual interpretation, the cumulative area of each vegetation type within 10 meter intervals throughout the elevation gradient was then represented using an area plot via the "ggplot2" package v0.4 (Wickham et al., 2022). Changes in cover of vegetation types are represented as percentage and area (km²) change over time. These

analyses were conducted for the entire study area, and then for burnt and unburnt areas to better understand the impacts of wildfire.

### **Results**

#### Climate dynamics

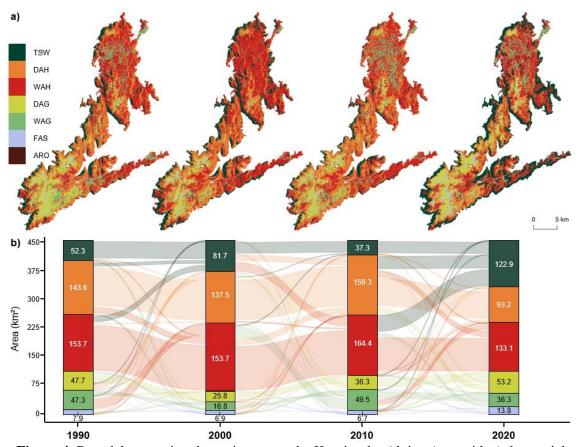
Climatic changes have been observed in the study area over the past century with mean annual temperatures increasing by 0.1 °C per decade ( $R^2 = 0.359$ , p < 0.001) (Table S5), with an overall increase of +0.75 °C since the beginning of the records (1910 – 1939 in comparison to 1990 – 2019; a 30-year period) (Figure 3a). There has also been an increase in minimum ( $R^2 = 0.335$ , p < 0.001) and maximum ( $R^2 = 0.245$ , p < 0.001) annual temperatures, also warming by 0.1 °C per decade. Accumulative annual precipitation in the study area was variable, but there were trends in seasonal precipitation with increasing totals in summer by 6.51 mm per decade ( $R^2 = 0.035$ , p = 0.041) but declining totals in winter by 9.68 mm per decade ( $R^2 = 0.038$ , p = 0.032) (Figure 3b). Snow course records from the only long-term plot (Spencers Creek) in the study area demonstrate declining snow cover by 12.74 md<sup>-1</sup> per decade ( $R^2 = 0.100$ , p = 0.009), which is a reduction of 24.3% since the beginning of records (1954 – 1983 in comparison to 1992 – 2021; 30-year period) (Figure 3c).



**Figure 3**: Climatic dynamics from 1900 to 2020 in the study area for a) mean annual temperature (°C), b) seasonal precipitation (mm) and c) snow cover (metre days<sup>-1</sup>). Asterisks denote significant regressions (\* p - 0.05; \*\*\* p - 0.01; \*\*\*\* p - 0.001).

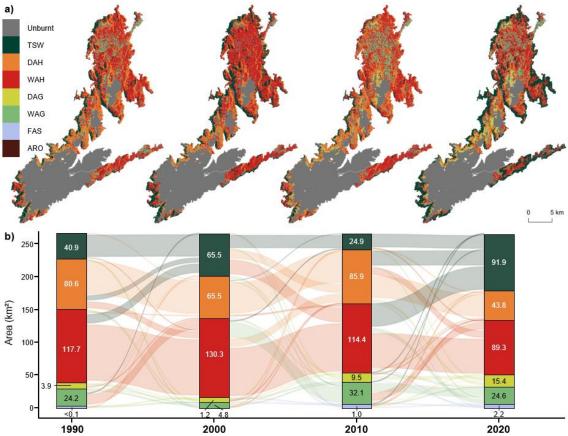
### Vegetation cover dynamics

There were considerable changes in the cover of vegetation types in the four observed growing seasons, with only the cover of ARO having remained relatively constant over time (+0.01 km² p.a.) (Figure 4). The cover of TSW fluctuated through time, with an overall net increase of 70.58 km² (+134.8%; +2.35 km² p.a.) from 1990 to 2020 (Table S6). In 2020, TSW covers an additional 15.5% of the study area compared to 1990, replacing over the last three decades mostly heathlands which had experienced a net loss of 50.45 km² by DAH (-35.1%; -1.68 km² p.a.) and 20.64 km² of WAH (-13.4%; -0.69 km² p.a.). However, there was minimal loss in cover of all three woody vegetation types (-0.52 km²) when grouped together from 1990 to 2020. The cover of grasslands was variable, with a marginal loss in cover over time (5.64 km²; -0.18 km² p.a.) mostly due to the loss of 11.01 km² of WAG (-13.4%; -0.37 km² p.a.). Furthermore, the cover of DAG increased by 1.2% of the study area, expanding from 47.88 km² in 1990 to 53.25 km² in 2020 (+11.2%; +0.18 km² p.a.). Areas of sparse vegetation cover (FAS) including screes, granitic boulder fields and feldmark communities were in decline from 7.97 km² in 1990 to 6.90 km² in 2000 (-13.4%; -0.11 km² p.a.) and then rate of loss slowed, with 6.72 km² present in 2010 (-2.6%; -0.02 km² p.a.). However, the cover of FAS more than doubled to 13.82 km² in 2020.



**Figure 4**: Decadal vegetation dynamics across the Kosciuszko Alpine Area with a) the spatial distribution of vegetation types and b) the flow of area covered by vegetation types through time. Vegetation types include Treeline Snowgum Woodlands (TSW), Dry Alpine Heathlands (DAH), Wet Alpine Heathlands (WAH), Dry Alpine Grasslands (DAG), Wet Alpine Grasslands (WAG), Fellfield Alpine Screes (FAS) and Alpine Rocky Outcrops (ARO).

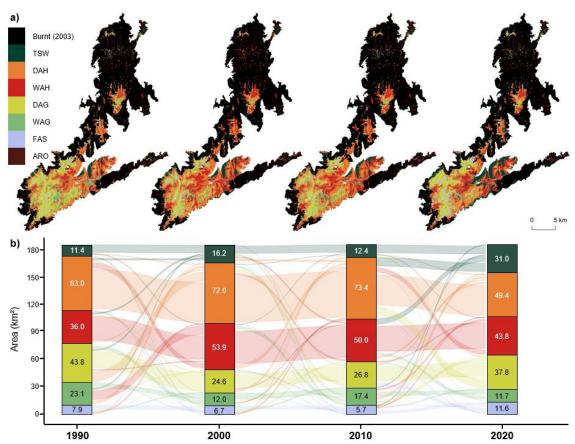
The study area experienced two wildfires between 1990 and 2020, with large tracts of alpine vegetation burnt in 2003 and a smaller area burnt in the 2020 (0.2%; 0.90 km²). In 2003, 58.9% of the study area burnt (267.83 km²) as the wildfire travelled up the steep western escarpment and across the relatively flat and low-elevation northern plateau (see Figure 2). Based on the vegetation types present in 2000, mostly woody vegetation was burnt including 130.31 km² of WAH, 65.84 km² of TSW and 65.63 km² of DAH, with only 6.05 km² of grasslands impacted (Figure 5, Table S6). While the cover of woody vegetation had increased by 22.52 km² (+9.4%; +2.25 km² p.a.) between 1990 and 2000, after the wildfire there was a considerable reduction in the cover of TSW (-62.0%; -40.83 km²) but only 15.93 km² less of WAH (-12.2%) in 2010. However, there was an increase in DAH by 20.39 km² (+31.1%) as well as considerable expansions of WAG by 27.31 km² (+566.6%) and DAG by 8.29 km² (+674.0%), with 1.01 km² of FAS present in 2010. In 2020, the cover of TSW had increased considerably by 66.95 km² (+267.7%) with losses mostly from WAH by 41.09 km² and DAH by 26.47 km². Similarly, the cover of DAG increased by 5.89 km² (+61.9%) from 2010 to 2020, mostly through the loss of 5.93 km² of DAH while 13.87 km² of WAG transitioned to WAH. Overall, when comparing



**Figure 5**: Decadal vegetation dynamics in burnt areas of the Kosciuszko Alpine Area from the 2003 wildfire with a) the spatial distribution of vegetation types and b) the flow of area covered by vegetation types through time. Vegetation types include Treeline Snowgum Woodlands (TSW), Dry Alpine Heathlands (DAH), Wet Alpine Heathlands (WAH), Dry Alpine Grasslands (DAG), Wet Alpine Grasslands (WAG), Fellfield Alpine Screes (FAS) and Alpine Rocky Outcrops (ARO). Burnt and unburnt areas detected using LandTrendr.

vegetation types in 2000 (three years pre-wildfire) and in 2020, those vegetation types that have increased in cover include TSW (+39.7%; +1.31 km<sup>2</sup> p.a.), WAG (+410.4%; +0.99 km<sup>2</sup> p.a.), DAG (+1152.9%; +0.71 km<sup>2</sup> p.a.) and FAS (+0.11 km<sup>2</sup> p.a.). However, vegetation types that have decreased in cover after burning include WAH (-31.5%; -2.05 km<sup>2</sup> p.a.) and DAH (-33.2%; -1.09 km<sup>2</sup> p.a.).

Of the 41.1% of the study area that remained unburnt in 2003, most of this area is centred around the high-elevation southern plateau (Figure 6). Based on the vegetation types present in 2000 in the study area, this unburnt area contained the majority of DAH (52.4%; 72.14 km²), DAG (95.2%; 26.63 km²), WAG (71.3%; 12.00 km²) and FAS (100.0%; 6.90 km²). Similar to burnt areas, the cover of woody vegetation had increased between 1990 and 2000 by 31.64 km², but at 1.4 times the rate (+28.6%; +3.16 km² p.a.) (Table S6). During this decade, woody encroachment was largely driven by an increase in WAH (+48.9%; +1.76 km² p.a.) with smaller increases in TSW (+44.0%; +0.50 km² p.a.) and DAH (+14.3%; +0.90 km² p.a.). From 2000 to 2010, vegetation dynamics were relatively stable but there was a slight expansion of grasslands



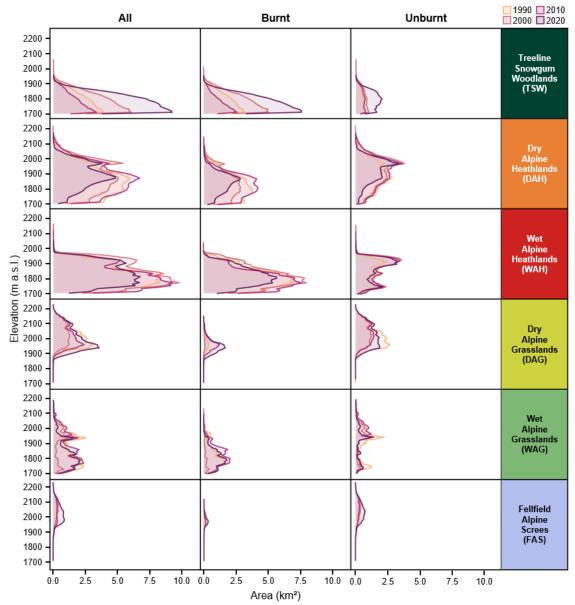
**Figure 6**: Decadal vegetation dynamics in areas of the Kosciuszko Alpine Area that remained unburnt during 2003 wildfire with a) the spatial distribution of vegetation types and b) the flow of area covered by vegetation types through time. Vegetation types include Treeline Snowgum Woodlands (TSW), Dry Alpine Heathlands (DAH), Wet Alpine Heathlands (WAH), Dry Alpine Grasslands (DAG), Wet Alpine Grasslands (WAG), Fellfield Alpine Screes (FAS) and Alpine Rocky Outcrops (ARO). Burnt and unburnt areas detected using LandTrendr.

(+21.1%; 0.77 km² p.a.) and a subsequent reduction in woody vegetation (-4.2%; -0.59 km² p.a.). However, considerable differences emerge when comparing vegetation dynamics in burnt and unburnt areas between 2000 and 2020. While the cover of TSW increased by 14.57 km² (+88.7%; +0.73 km² p.a.) in unburnt areas during these two decades, this is considerably less than the rate of change observed in burnt areas (+39.7%; +1.31 km² p.a.). While the loss of DAH was comparable between unburnt (-31.5%; -1.14 km² p.a.) and burnt (-33.2%; -1.09 km²) areas, the loss of WAH in unburnt areas (-18.3%; -0.49 km²) was considerably less than the rate of change observed in burnt areas (-31.5%; -2.05 km²). As for grasslands, there was a slight loss of WAG in unburnt areas (-2.4%; -0.01 km²) but DAG cover expanded by 13.2 km² (+53.6%; 0.66 km² p.a.), which is less than the rate of change for both WAG (+410.4%; +0.99 km² p.a.) and DAG (+1152.9%; +0.71 km² p.a.) observed in burnt areas.

#### Vegetation zonation dynamics

Vegetation types displayed differences in the extent of cover through the elevation gradient (Figure 7). Across the four observed growing seasons, the mean elevation weighted by area for TSW was 1781.8 m a.s.l. (Table S6), with a consistent decline in area with increasing elevation. Above TSW, there were less consistent elevation to area relationships aside from wet vegetation types covering lower elevations, including WAH at 1819.5 m a.s.l and WAG at 1 862.7 m a.s.l, while dry vegetation types covered higher elevations with DAH at 1869.7 m a.s.l and DAG at 2 017.3 m a.s.l. The vegetation type with the greatest mean elevation weighted by area was FAS at 2037.1 m a.s.l. However, there were also temporal dynamics in the area occupied by each vegetation type throughout the elevation gradient across the study area (Figure 7). While the mean elevation weighted by area for TSW decreased marginally from 1782.1 m in 1990 to 1779.6 m in 2020 (-0.1 m p.a.), there was evidence of treeline advance between 1990 and 2000 (+0.4 m p.a.). There has also been densification of TSW with more cover at lower elevations through time with differences between burnt and unburnt areas. From 2000 to 2020, there was a treeline recession in burnt (-0.4 m p.a.) and unburnt (-0.2 m p.a.) areas through increasing cover and densification at lower elevations. There is also evidence of shrubline advance through time across the study area, with mean elevation weight by area of DAH increasing from 1 851.5 m in 1990 to 1 885.0 m in 2020 (+1.1 m p.a.), with WAH also increasing by 0.4 m p.a. during this period. DAH in burnt areas has advanced through the elevation gradient from 2000 to 2020 at a rate of 0.2 m p.a., whereas this advance has been much faster in unburnt areas at 0.4 m p.a. during the same period. However, WAH in burnt areas has remained relatively stable from 2000 to 2020 (-0.01 m p.a.) while it has advanced in unburnt areas (+0.2 m p.a.). As for grassland vegetation types, the mean elevation weighted by area for DAG (+2.1 m p.a.) and WAG (+5.9 m p.a.) increased between 1990 to 2000. However, there has been a consistent decline in elevation of DAG (-1.81 m p.a.) and WAG (-1.2 m p.a.) in burnt areas from 2000 to 2020 as the cover of these vegetation types

increased at lower elevations after the 2003 wildfire. Similarly, FAS advanced upslope from 1990 to 2000 (+0.8 m p.a.) but there was an overall decline between 1990 and 2020 (-0.5 m p.a.), with greater declines in burnt areas (-2.3 m p.a.) in comparison to unburnt areas (-0.2 m p.a.).



**Figure 7**: Decadal vegetation type cover dynamics of the Kosciuszko Alpine Area throughout the elevation gradient, and the influence of wildfire on the spatiotemporal zonation of vegetation types. Area of each vegetation type was rounded to nearest 10 m interval to reduce noise and improve comprehensibility.

### **Discussion**

Linking past, present and future climate change

Over the past century, the study area has warmed by 1.10° C, which is in line with the broader climatic warming rate in south-eastern Australia of 1.11° C during the same period (BoM, 2022; Jones et al., 2009), and a rate of 1.2° C in the Eastern Italian Alps from 1836 – 2015 (Knoflach et al., 2021). Subsequently, there has been a rapid warming of soil temperatures, which are often

used as a surrogate for the microclimate experience by alpine plants and are correlated to surface air temperatures, in the study area over the past two decades (Verrall et al., 2021). Rapidly increasing temperatures have been reported in numerous alpine areas around the world (Beniston et al., 1997; Hock et al., 2019), and are often compounded by elevation (Pepin et al., 2015). The current rate of warming occurring in the Australian Alps is unprecedented in the past 2 000 years, with temperatures observed from 1970 increasing 2.6 times faster than the previous fastest rate of warming during Medieval Climate Anomaly (950 – 1400 AD) (McGowan et al., 2018). This warming has also coincided with marked decline in snow cover since 1970, which is highlighted in the snow cover records presented in this study, to the lowest during the last 2 000 years (McGowan et al., 2018). As temperatures have increased and snow cover has subsequently declined, growing seasons are becoming longer in the study area (Thompson, 2016; Thompson & Paull, 2017). Globally, similar declines in the snow cover have also been widely reported (Huss et al., 2017; Notarnicola, 2020), with south-eastern Australia identified as a hotspot (Li et al., 2018). Although snow cover is known to be highly variable in the Australian Alps, there has been a marked decline in spring snow cover (Bormann et al., 2012; Nicholls, 2005), and an overall decline in years with above average snow cover since 2000 (Rasouli et al., 2022). The recorded decline in snow cover since 1954 is primarily driven by increasing temperatures and declining winter precipitation, with warmer temperatures accelerating snow melt and light snowfall events, and declining winter precipitation limiting snow accumulation (Fiddes et al., 2015; Pepler et al., 2015). Snow cover is also related to fluctuations in pertinent large-scaled climate drivers especially the El Niño-Southern Oscillation (ENSO), Southern Annular Mode (SAM) and Indian Ocean Dipole (IOD), which considerably influence temperatures and precipitation in the study area (Pepler et al., 2015; Rasouli et al., 2022).

In addition to the observed climate in the study over the past century, these climatic trends are projected to continue into the future (IPCC, 2022). Similarly, alpine areas in the northern hemisphere are projected to experience comparable climatic changes in coming decades (Engler et al., 2011; Ernakovich et al., 2014). As the Australian Alps contain relatively low elevation alpine areas at mid-latitudes and experience a mild, maritime mountain climate, they are likely to be among the most sensitive and vulnerable to changes in climate (Brown & Mote, 2009; Di Luca et al., 2018). Downscaled climate models, as part of the New South Wales and Australian Capital Territory Regional Climate Modelling project (NARCliM), project a further warming of mean annual surface temperatures (ca.  $1.5 - 2^{\circ}$  C) as well as declining winter (ca. 15 - 30 mm) and spring (ca. 45 - 60 mm) precipitation in the Australian Alps by 2070 from present day levels (1990 – 2009) (Olson et al., 2016). Concurrently, NARCliM modelling projects a further warming of mean annual surface temperatures (ca.  $1.7 - 2.1^{\circ}$  C), a 7% decline in annual precipitation and a further decline in snow cover in the Australian Alps by 15% and 60% by 2030 and 2070,

respectively (Di Luca et al., 2018). Most of these projected changes are strongly linked to a strengthening subtropical ridge (Di Luca et al., 2018; Olson et al., 2016), in addition to a positive trend in SAM under high emission scenarios, leading to drier conditions in winter (Lim et al., 2016). These climatic changes are in line with global patterns, as snow, glaciers and permafrost are expected to decline in most regions throughout the 21st century (Hock et al., 2019). Furthermore, climate change is likely to result in increasing frequency, severity and magnitude of extreme climatic event such as heatwaves and dangerous wildfire weather conditions (IPCC, 2021). In the Australian Alps, there has been considerable increases in in the forest fire danger index in recent decades (Dowdy, 2018), and wildfire regimes are predicted to intensify in coming decades (Clarke & Evans, 2019). In the coming decades there is also to be an increase in the frequency of pyrocumulonimbus wildfires within the mountainous areas of south eastern Australia, increasing the risk of wildfires within the Australian Alps (Di Virgilio et al., 2019). As winter and spring precipitation, and consequently, snow cover declines and the growing seasons lengthen with warming temperatures, there is a clear trend toward increasing vegetation flammability and increasingly dangerous wildfire conditions during spring and summer in addition to an earlier start to the wildfire season in the Australian Alps (Clarke et al., 2013; Dowdy, 2018; Zylstra, 2018).

### Climate- and fire-induced vegetation dynamics

Over the past 30 years, it is evident that alpine plants are on the move alongside the rapid climate change that is occurring in the study area. The observed dynamics in cover and zonation of vegetation types correlated with wildfire impacts, particularly for the alpine treeline ecotone, with varying responses when comparing burnt and unburnt areas from the 2003 wildfire. As the risk and incident of wildfire in high elevation areas have increased with climate change, there has been growing interest in how wildfire may impact alpine treelines globally (Bader et al., 2008; Cansler et al., 2016, 2018; Stine & Butler, 2015; Wang et al., 2019), and in Australia (Green, 2009; Naccarella et al., 2020). In the study area, there has been a considerable expansion of Treeline Subalpine Woodlands (TSW) over the study period, with TSW cover expanding at almost three times the rate in burnt areas. While there was little change in the zonation of the treeline in the study area, with an overall decline of -0.08 m per year, a single wildfire has apparently caused a considerable decline in treeline by a factor of 7.5 when compared to unburnt treeline dynamics. As the alpine treeline ecotone is primarily governed by thermal growth limitation (Körner, 2012), it is widely accepted that climate change has caused the observed widespread advance in treelines globally (Hansson et al., 2021; Harsch et al., 2009). However, treeline dynamics are also dependant on seedling establishment and microclimatic factors dictated by snow cover as well as solar and wind exposure that limit seedling survival above the current treeline (Hansson et al.,

2021; Harsch & Bader, 2011; Smith et al., 2009), which change dramatically in a post-wildfire landscape.

In the Australian Alps, treeline stasis amidst recent climate change has been attributed to the lack of a seed dispersal mechanism for the dominant E. niphophila, which relies primary on gravity and less commonly on windblow branches containing viable seed (Green, 2009; Green & Venn, 2012; Naccarella et al., 2020). In contrast, most treelines around the world are dominated by wind dispersed species that permit the establishment of seedlings above the current treeline, if climatic conditions permit (Körner, 2012). However, a single wildfire seems to promote the establishment of E. niphophila seedlings at or below the treeline following the removal of competition from understory plants and loss of canopy (Green, 2009; Green & Venn, 2012; Naccarella et al., 2020). Furthermore, wildfire causes an abrupt change in microclimatic conditions that lead to accelerated snowmelt (Schwartz et al., 2021; Schwartz, McGowan, & Callow, 2020), which may further promote seedling establishment (Green & Venn, 2012). Although the 2003 wildfire caused the widespread loss of E. niphophila canopy, over 95% of trees survived and resprouted from lignotubers leading to lower-growing trees with a mallee form (Pickering & Barry, 2005). Ultimately, a single wildfire has resulted in increasing TSW cover via densification and in-filling, as E. niphophila establish as the dominant vegetation over smaller stature vegetation types, with grasslands and shrublands cover faster to recover following fire (Camac et al., 2017; Camac et al., 2013; McDougall et al., 2015). Wildfire has also effectively resulted in treeline recession, as E. niphophila regenerate from lignotubers to form mallee stands and seedlings germinate at higher rates following wildfire but lacks effective dispersal mechanisms to establish above the current treeline, even if climatic, abiotic and biotic conditions are favourable in a post-wildfire landscape (Green & Venn, 2012).

There were also important dynamics of heathlands and grasslands in burnt areas. Generally, there was a reduction in cover of both dry and wet alpine heathlands in areas that burnt in 2003. Dry alpine heathlands recovered swiftly following wildfire at lower elevations, as shrublands in the Australian Alps are resilient to infrequent wildfire (Camac et al., 2013; McDougall et al., 2015), and it can promote increased seedling establishment of a dominant alpine shrub *Grevillea australis* (Camac et al., 2017). Surprisingly, the cover of Fellfield Alpine Screes (FAS) increased over time but may be attributed to the small tracts that burnt in the 2020 wildfires that left soils exposed. Furthermore, increasing cover of FAS could also be the result of drought impacts on dry grasslands including amplified senescence and dieback from phytophagous moth larvae (McDougall et al., 2018; Scherrer & Pickering, 2005). The decline of wet alpine heathlands may be attributed to their well-established vulnerability to wildfire, with considerable losses of important and defining structural species following the 2003 wildfire, as underlying peat burnt down to mineral soils (McDougall et al., 2015). However, large tracts of heathlands were replaced

by grasslands in burnt areas at higher elevations in the study area, causing the suppression of shrubline advance by a factor of approximately 2.5 when compared to unburnt areas. Following the 2003 wildfire, vegetative cover in dry and wet grasslands were the first to recover (McDougall et al., 2015), and were dominated by competitive, tussock-forming graminoids. Concurrently, the relatively high flammability of shrublands led to high temperature burns and subsequently, recovered much slower than surrounding grasslands (McDougall et al., 2015). Similarly, in high elevation paramo grasslands of South America, fire has been shown to suppress shrub advance and encroachment (Matson & Bart, 2013; Zomer & Ramsay, 2021). However, most research in the Australian Alps suggests the encroachment of dry shrublands on grasslands following wildfire (Camac et al., 2015; Camac et al., 2017; Camac et al., 2013), but these studies were mostly conducted at lower elevations below or at treeline (~1 750 m a.s.l.) and focus on less than a decade of recovery. Overall, alpine vegetation in the Australian Alps is resilient to large, infrequent wildfires (Kirkpatrick & Bridle, 2013; Venn et al., 2016; Williams et al., 2008), apart from cryophilic periglacial communities (Verrall, 2018), but frequent wildfires may negate this resilience (Fairman et al., 2017; Naccarella et al., 2020).

Contrastingly, attribution of climate-induced dynamics without the influence of wildfire can be assessed in the unburnt areas. Over the study period, there was an increase in the cover TSW by 0.65 km<sup>2</sup> per year with treeline stasis. As the climate warms and growing seasons lengthen, the densification and infilling processes at the alpine treeline ecotone without treeline advancement have been widely observed across the world (Shi et al., 2022). Globally, climate change has promoted treeline densification via increased seed germination, seedling establishment and tree growth (Körner, 2012; Lett & Dorrepaal, 2018). In the Australian Alps, there is some evidence of treeline densification in unburnt areas (Green, 2009; Green & Venn, 2012), with stands not recruitment-limited as there are several established saplings and young trees relative to older trees (Naccarella et al., 2020). There was also an advance of the DAH shrubline by 1.24 m per year in unburnt areas over the study period. While increasing shrub cover and densification has been reported in many alpine regions with climate change (Brandt et al., 2013; Myers-Smith et al., 2015; Verrall et al., 2021; Wilson & Nilsson, 2009), there are a growing number of regions where shrubline advance has also been recorded (Dial et al., 2016; Hallinger et al., 2010; Myers-Smith & Hik, 2018; Wang et al., 2021), however all from the northern hemisphere. Overall, the expansion of woody vegetation types in unburnt areas ultimately occurred as they encroached on dry and wet alpine grasslands. Furthermore, the phenomena of woody encroachment and increasing competition from thermophilic growth forms occurring in the study area are in line with climate-induced responses of alpine vegetation in the northern hemisphere (Erschbamer et al., 2011; Lamprecht et al., 2018; Malfasi & Cannone, 2020; Scharnagl et al., 2019). While alpine plants are on the move in response to climate change in the Australian Alps (Auld et al., 2022;

Verrall et al., 2021), there may be dispersal lags and growing extinction debt for long-lived perennials that are unlikely to keep pace with the rapid rate of warming (Alexander et al., 2018; Zimmer et al., 2018).

### Implications, benefits, limitations and future research

Globally, climate change has resulted in increasing vegetation biomass in alpine areas via densification of treelines and woody encroachment of grasslands. These responses in vegetation are a reflection of warming temperatures, declining snow cover and increased precipitation variability. The combination of these changing biotic and abiotic factors (especially decreasing winter rainfall and increasing spring temperatures) ultimately results in more dangerous wildfire weather conditions and increased landscape flammability (Zylstra, 2013; Zylstra, 2018), which has considerable implications in the Australian Alps and other fire-prone high elevation areas as wildfire may become a more frequent and influential agent of change (Hock et al., 2019; Thomas et al., 2022). Before 2003, the last landscape-level wildfire in the study area occurred 64 years prior in 1939 (Williams et al., 2008), but there was potential for the 2020 black summer wildfires to cause widespread burning of alpine vegetation in the Australian Alps, shortening the interval between burns to just 17 years. Furthermore, global warming has the potential to strengthen positive feedback loops between wildfire and woody encroachment (Camac et al., 2017). Postwildfire landscapes have been shown to alter microclimate by amplifying soil and vegetation temperatures, leading to accelerated snowmelt, runoff and erosion (Schwartz et al., 2021; Schwartz, McGowan, & Callow, 2020), which is likely to impact the establishment and recovery of alpine vegetation following wildfire into the future. Altered hydrology in alpine catchments because of increasing frequency, severity and magnitude of wildfires may have considerable ecological and socioeconomic consequences as climate trends continue (Gallucci et al., 2011; IPCC, 2021). Increasing dangerous wildfire weather conditions and the flammability of alpine ecosystem vegetation poses an immediate threat to cryophilic and periglacial communities and species that are vulnerable to wildfire (Venn et al., 2017; Verrall, 2018), but increases in the frequency and intensity of wildfire regimes may result in changes in the resilience of previouslythought fire-tolerant vegetation leading to ecosystem transition or collapse (Fairman et al., 2017; Lindenmayer & Taylor, 2020; Naccarella et al., 2020).

Limitations of this study include that analysis were focussed on broad vegetation types and not the composite individual species which can vary in their life history traits and responses to changes in climate conditions and wildfire regimes (McDougall et al., 2015). Although this study used the most sophisticated climate products available for this study area, the establishment and maintenance of multiple weather stations and snow courses in Australia's largest alpine area is vitally important to understanding the impacts climate change into the future (Fiddes et al., 2015). While this study was the first to use remotely sensed times series data to study alpine vegetation

dynamics in Australia and high classification accuracy was achieved, future research would benefit from complementary field data measurements, none withstanding the logistical difficulties this presents. Furthermore, the 30-year period where vegetation dynamics were assessed spanned considerable year-to-year and decadal variability in climatic conditions including drought preceding the 2003 wildfire. Thus, further research is needed on the impacts of this intra-decadal climatic variability on vegetation dynamics. More details studies are also warranted on TSW mortality and establishment through surveying burnt and unburnt alpine areas along with comparisons of soil seedbanks and soil properties (Naccarella et al., 2020; Pickering & Barry, 2005). Given the rapid rate of change, there is a need for continued monitoring of shifts in the extent, density and zonation of the major alpine vegetation types in Australia.

### **Conclusion**

Considering recent changes in temperature, precipitation, and snow cover over the past century alongside climate-induced alpine vegetation dynamics that were modelled using optimised random forest classification of Landsat timeseries, provided novel insights into how the major vegetation types in the highest and most diverse alpine area in Australia are responding to climate change. Furthermore, this study applied a robust and cost-effective methodology that makes uses of widely available remotely sensed and ancillary data and which could be readily applied to monitor similar climate-induced changes in other alpine areas globally including trends in treeline densification, woody encroachment and advancement. Evidently, alpine ecosystems are particularly sensitive to warming temperatures, varying precipitation regimes and declining snow cover, demonstrating relatively incremental vegetation responses in addition to transformative changes that occur after large fire-type disturbance events. The interaction and feedbacks between climate change, densification woody encroachment, and landscape flammability may present as a crucial aspect in understanding the responses of alpine vegetation globally to climate change.

## **Supplementary materials**

Refer to Appendix B.

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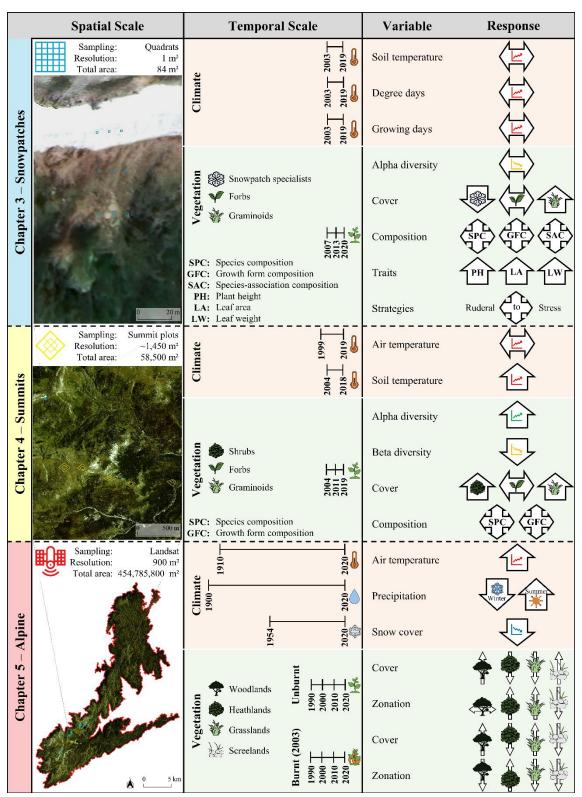
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# **Chapter 6: Discussion**

### **6.1: Introduction**

Alpine ecosystems are primarily governed by low temperatures and short growing seasons, and often have high plant endemism as they act as refugia for cryophilic plant species and communities (Körner, 2003; Nagy & Grabherr, 2009). These climate sensitive ecosystems act as sentinels of climate change as they are among the most vulnerable to warming temperatures, declining snow cover and lengthening growing seasons (Grabherr et al., 2010; Seddon et al., 2016), and are experiencing disproportionate warming (Pepin et al., 2015; Pepin et al., 2022). The alpine ecosystems of the Australian Alps are particularly vulnerable, as they cover less than 0.02% of the continent, experience a marginal alpine climate and the bioclimatic treeline is only a few hundred metres below the highest summits (Bergstrom et al., 2021; Green & Stein, 2015; Laurance et al., 2011). Furthermore, the Australian Alps are surrounded by some of the most wildfire prone ecosystems in the world (Collins et al., 2021; Fletcher et al., 2021). As the rate and impacts of climate change have intensified (IPCC, 2021), there is an increasing focus on monitoring climate-induced responses of alpine vegetation, particularly over the last few decades (Chapter 2). However, the response and future of unique alpine vegetation in the Australian Alps remains unclear (Camac et al., 2021).

This thesis addresses knowledge gaps surrounding the response of alpine vegetation to climate change, with a specific focus on climate and vegetation dynamics across the Kosciuszko alpine area in the Australian Alps. Over recent decades, climate and vegetation dynamics were assessed at different spatiotemporal scales using field-based repeat vegetation surveys harnessing existing LTEM protocols, as well as a new LTEM for this alpine area using remote sensing. A range of response variables were assessed including temperature, precipitation, snow cover, alpha diversity, beta diversity, vegetation cover, composition, community-weighted traits and strategies, with temporal dynamics determined using a range of statistical and analytical techniques including linear modelling, linear mixed modelling, generalised linear modelling, beta regression, beta dissimilarity indexes, analysis of similarity, principal components analysis, nonmetric dimensional scaling, ternary analysis and random forest classification. This thesis demonstrates extensive changes in climate and vegetation in the Kosciuszko alpine area over recent decades, with divergent dynamics along environmental gradients and across spatiotemporal sampling scales. Specifically, there were significant changes in macroclimate and microclimate including increasing temperatures, declining snow cover and variable precipitation regimes. Concurrently, there were changes in vegetation cover and composition of species, growth forms and vegetation types generally resulting in an increase in thermophilic vegetation and subsequent decline cryophilic vegetation but few changes in diversity (Figure 6. 1).



**Figure 6. 1:** Overview of methods, resolution, total areas sampled, spatiotemporal scale, vegetation types assessed, response variables and key results from each chapter. Location of sampling sites from Chapter 3 (blue) and Chapter 4 (yellow) shown within the sampling area of Chapter 5 (red). Thick arrows indicate significant differences over time with trends indicated by encapsulated icons: up is equivalent to a significant increase, down is equivalent to a significant decrease, quad-ended arrows indicate a significant shift in similarity, and double-ended arrows indicate no significant difference. Thin arrows indicate trends (no statistical tests performed) using the denotation system above.

All results chapters are either published (Chapters 2, 3 and 4) or in review (Chapter 5), and include their own abstracts, introductions, methods, results, discussions and reference lists. Here in this last chapter, I summarise and contextualise key results within and across chapters in relation to the overall thesis aims (Section 1.7). Then, this research is discussed in relation to local and global contributions to knowledge, and implications of climate change for the alpine ecosystems of the Australian Alps, and future research directions for monitoring alpine vegetation dynamics as climate change continues.

## 6.2: Aim 1 – What is the current state of research on alpine vegetation in the context of climate change?

Alpine vegetation has attracted the focus of researchers for hundreds of years, with the earliest scientific description of bioclimatic zonation of vegetation along an elevation gradient from the Swiss Alps published in 1554 (Körner, 2003). Over the centuries, there has been increasing research on alpine vegetation (Grabherr, 1997), and as of August 2022 there were ~ 14,300 publications on alpine plants in the Web of Science database, including 435 reviews. Much of this research focused on plant physiology and functional ecology to explore how alpine vegetation survive the specific environmental conditions characteristic of the alpine ecosystems (Körner, 2003). As the impacts and knowledge of climate change strengthened at the end of the 20<sup>th</sup> century (IPCC, 2001) alongside further research demonstrating how alpine vegetation is primarily governed by low temperatures and short growing seasons (Körner, 2003, 2012), the importance of research and monitoring that assesses how climate change affects alpine vegetation has been increasingly recognised (Pauli et al., 1996; Theurillat & Guisan, 2001). As of August 2022, there were ~ 3,700 publications in the Web of Science that focus on climate change and alpine vegetation including over 150 reviews. Many of the reviews had specific topic or geographical foci (Buytaert et al., 2011; Kullman, 2010; Wipf & Rixen, 2010), with some meta-analyses and systematic reviews of research from multiple countries (Sumner & Venn, 2021; Vazquez-Ramirez & Venn, 2021). In contrast, there had not been a bibliometric literature review that assessed all global research on alpine vegetation in the context of climate change prior to the research in this thesis (Chapter 2), which evaluated current research and future directions highlighting again the responsiveness and vulnerability of alpine vegetation as climates continue to warm (Hock et al., 2019).

The review of the literature in this thesis provided important insights including highlighting how there has been very specific geographical and vegetation type focus, and important temporal changes in research themes and topics about alpine vegetation in the context of climate change (Chapter 2). Across the 3,143 publications assessed dating back to 1978, there has been an exponential increase in the number of publications, and an expanding geographical range to the

research, particularly in China, reflecting growing recognition of the importance of this topic and the range of authors conducting such research. Historically, most research was published by authors based in Europe, echoing alpine research more broadly (Grabherr, 1997; Körner, 2009; Pauli et al., 1996; Theurillat & Guisan, 2001). However, more recently there was a rapid increase in research by authors in China and about the Qinghai-Tibetan Plateau, particularly since 2010. Overall, there has been disproportionate research allocation (publications vs alpine area) to some regions with research deficits for South America and Asia (Chapter 2). Vegetation types such as grasslands and forests have been broadly studied and account for ~ 75% of research in contrast to periglacial and cryophilic types which have received less than 3% of research (Chapter 2) although they are among the most responsive to climate change (Galen & Stanton, 1995; Kudo et al., 2010; Schöb et al., 2009). Research themes and topics have diversified, reflecting the increasing volume of research but also changes in the methods used. This includes how traditional ecological monitoring approaches such as LTEM are starting to be supplemented by remote sensing methods with technological advances and accumulation of data over several decades (Chapter 2).

#### 6.3: Aim 2 – How is climate changing in the Kosciuszko alpine area?

The chemical, biological and ecological processes of alpine vegetation are particularly sensitive to climatic conditions such as temperature, precipitation, snow cover and duration of growing seasons (Körner, 2003; Lütz, 2013; Nagy & Grabherr, 2009). Although showing some resilience to shorter-term climatic oscillations, alpine vegetation is particularly vulnerable to sustained climatic changes (Guisan et al., 2019; Körner, 2003; Lütz, 2013), and this vulnerability has been amplified by elevation-dependant warming (Pepin et al., 2015). While changes in atmospheric conditions and macroclimate are important, alpine plants are generally low-growing and the microclimate they experience can be at least in part decoupled from atmospheric conditions (Körner, 2003), with microclimatic heterogeneity providing at least some potential buffer against climatic warming (Körner & Hiltbrunner, 2021; Scherrer & Körner, 2011). Therefore, soil temperatures are often used as surrogates for microclimates in alpine ecosystems, and are strongly linked to ecosystem processes and function (Björk & Molau, 2007), in addition to providing information on the duration of snow cover at finer spatial scale scales (Bürli et al., 2021; Körner & Paulsen, 2004). Thus, monitoring deterministic macroclimatic and microclimatic factors in alpine areas is important to understanding vegetation dynamics and inferring causal drivers of change (Grabherr et al., 2010), including in the Kosciuszko alpine area (Green & Pickering, 2009; Pickering & Green, 2009).

The dearth of long-term climatic data for the Australian Alps and particularly the Kosciuszko alpine area has been a major challenge for research (Di Luca et al., 2018; Fiddes et al., 2015).

There is just a single active weather station in the Kosciuszko alpine area (Thredbo AWS 071032), with long-term records for the region inconsistent and spatiotemporally limited (Bureau of BoM, 2022; Verrall, 2018; Chapter 4; Chapter 5). In this thesis, the available range of climate metrics and data sources were used to better understand climatic dynamics including assessing data at the macroclimatic scale (Chapter 4; Chapter 5) but also using soil temperature monitoring to assess changes at the microclimatic scale (Chapter 3; Chapter 4). These sources spanned differing temporal scales but often showed similar patterns (Table 6. 1). Over the past century, the macroclimate in the Kosciuszko alpine area has become warmer, snow cover has declined, and precipitation regimes have changed resulting in drier winters and wetter summers (Chapter 5). These trends are congruent with changes over the past 2000 years, with the warmest temperatures and lowest snow cover occurring in recent years in the Australian Alps (McGowan et al., 2018). Such climatic changes are predicted to continue, with temperatures projected to increase by a further  $1.5^{\circ}$  C  $-2^{\circ}$  C and precipitation predicted to decline by a further 60-90 mm over winter and spring in the Australian Alps by 2070 (Olson et al., 2016), in addition to snow cover projected to decline by a further 57% (Di Luca et al., 2018).

In addition to broader changes in macroclimate, as demonstrated in this thesis, there are both temporal-, elevational- and snowmelt-dependant changes in microclimates. By comparing the mean decadal change in temperature across the differing spatiotemporal scales in the chapters, warming over the past 15 years (+0.55 °C/decade) has occurred at a rate 5.5 times greater than the last century (+0.10 °C/decade) (Chapter 4; Chapter 5) (Table 6. 1). Although soil and air temperatures can be decoupled, they both increased through time and were correlated (Chapter 4). Furthermore, the varying rate of increasing temperatures recorded on summits along an elevation gradient are in line with elevation-dependant warming recorded globally (Chapter 4), with climatic warming amplified at higher elevations (Pepin et al., 2015). Similarly, there were snowmelt-dependant changes in temperature, growing season length and growing degree days with greater changes occurring where snow persisted the longest in the Kosciuszko alpine area (Chapter 3). While microclimatic heterogeneity within alpine ecosystems may provide some buffering against climatic warming (Körner & Hiltbrunner, 2021; Scherrer & Körner, 2011), this thesis provides evidence that such microclimatic refugia and buffer zones (higher elevations and where snow persists the longest) are undergoing the largest changes in microclimate in the Kosciuszko alpine area (Chapter 3; Chapter 4).

**Table 6. 1**: Summary of climatic changes along environmental gradients measured in this thesis expressed as difference per decade with significant regressions in bold. T = Temperature (°C); GSL = Growing Season Length (1 °C); GDD = Growing Degree Days (1 °C); P = Precipitation (mm); SMD = Snow Metre-Days (md-1)

	Gradient	Start	End	$ m T_{mean}$	CSL	GDD	$\mathbf{P}_{\mathrm{sum}}$	Paut	$\mathbf{P}_{\mathrm{win}}$	$P_{\rm spr}$	SMD
V	All zones	2003	2019	+0.49	+10.8	+146.35					
Τ	Late	2003	2019	+0.72	+21.56	+254.02					
4	Mid	2003	2019	+0.53	+10.45	+180.84					
Н	Early	2003	2019	+0.20	+0.47	+42.00					
4	Air	1999	2019	+0.69							
7	All summits	2004	2018	+0.55							
_	CL1	2004	2018	+0.70							
_	CL2	2004	2018	+0.65							
_	CL3	2004	2018	+0.51							
_	CL4	2004	2018	+0.49							
Ŭ	CL5	2004	2018	+0.43							
`	All KAA	1900	2020	+0.10			+6.51	-2.54	89.6-	+0.26	-12.74

## 6.4: Aim 3 – Are there differing responses of vegetation along environmental gradients in the Kosciuszko alpine area?

There are steep environmental gradients in alpine areas, including often declining temperatures and growing season but increasing snow cover and precipitation along elevation gradients (Grabherr et al., 2010; Rangwala & Miller, 2012). However, alpine areas often contain complex topography where the influence of increasing elevation may be buffered or amplified by microclimatic heterogeneity within the landscape (Körner & Hiltbrunner, 2021; Scherrer & Körner, 2011). Ultimately, these factors contribute to the bioclimatic distribution and zonation of alpine vegetation (Grabherr et al., 2010). The most conspicuous transition along environmental gradients is often the realised niche of the treeline ecotone, which forms at the physiological growth and seedling establishment limit of tree species and demarcates the lower elevational boundary of alpine vegetation (Körner, 2012; Körner & Paulsen, 2004). However, with the alpine ecotone there are often less obvious transitions in vegetation caused by other environment gradients such as the impact of wind on snow cover in snowpatch and fellfield vegetation, water availability in transitions from wet to dry grasslands and heathlands as well as the potentially important role of fire in some alpine areas (Bader et al., 2007; Costin et al., 2000; Körner, 2003; Zomer & Ramsay, 2021). As the distribution and zonation of alpine vegetation is generally determined by abiotic conditions, climate-induced responses are likely to vary along environmental gradients (Camac et al., 2021; Lamprecht et al., 2018; Rumpf et al., 2018; Rumpf et al., 2019; Schöb et al., 2009; Steinbauer et al., 2018). This is reflected the elevation- and snowdependant changes in microclimate recorded in the Kosciuszko alpine area in the thesis (Chapter 3; Chapter 4).

In regard to vegetation dynamics along environmental gradients in the Kosciuszko alpine area (Table 6. 2), changes in graminoid and forb cover varied. Across the small distances but strong snowmelt gradients in snowpatches, there were increases in graminoid cover in snowpatches where snow persists the longest, likely via the colonisation of bare ground (Chapter 3). Graminoid cover dynamics were less obvious and consistent among summits that already had near complete vegetation cover in the first survey in 2004. However, an elevation-dependant trend in relative percentage increase of graminoids was evident among summits, with the greatest increases occurring at lower elevations (Chapter 4). Here, increasing cover of graminoids seems to be a result of densification via competitive graminoids recruiting within shrub canopies, detected by sampling overlapping vegetation cover. Similar densification processes have been recorded elsewhere in the Australian Alps (Jarrad et al., 2008; Williams & Ashton, 1988). Increasing graminoid cover has also been recorded in high elevations areas of the Italian Alps, largely through the colonisation of bare ground (Cannone & Pignatti, 2014), and may be comparable to grassification processes occurring in snowpatches (Chapter 3) and fellfields (Verrall, 2018) of the

Kosciuszko alpine area. Paralleling the increase of graminoid cover in snowpatches was the loss of forb cover that was most evident where snow persisted the longest, with losses mainly consisting of snowpatch specialists (Chapter 3). There was some increases in forb cover on lower elevation summits but gains were marginal and dominated by generalist species (Chapter 4). The rate of declining forb cover has been linked to snow cover in Norway (Sandvik & Odland, 2014) but in lieu of assessing forb cover, most studies focus on the loss of cryophilic specialists (Carbognani et al., 2014; Lamprecht et al., 2018), which can vary in growth form from region to region. Across the whole Kosciuszko alpine area there has been a decline in the cover of alpine grasslands. However, wildfire seems to promote the expansion and persistence of grasslands, where grasslands replaced dry heathlands at higher elevations and wet heathlands at lower elevations (Chapter 5).

**Table 6. 2**: Summary of responses of alpine vegetation along environmental gradients measured in this thesis as decadal difference with significant changes in bold. SR = Species Richness;  $\alpha_{diversity} = alpha diversity (diversity profile area); <math>G_{cover} = Graminoid cover$ ;  $F_{cover} = Forb cover$ ;  $S_{cover} = Shrub cover$ ;  $T_{cover} = Tree cov$ 

Ch.	_	Gradient	Diver	sity	Ov	erlapping	g Cover (	%)
CII.		Graulent	SR	adiversity	$G_{cover}$	Fcover	Scover	Tcover
hes		All zones	+0.29	-7.54	+11.32	-6.45	+0.02	
patc]	melt	Late	+0.12	+5.38	+12.58	-10.63		
Snowpatches	Snowmelt	Mid	+0.43	-13.62	+18.32	-9.56		
3: S	S	Early	+0.38	-1.08	+4.68	-0.88	+0.06	
	Elevation	All summits	+5.83	+0.09	+24.92	+1.14	+10.42	
ts.		CL1 (2114 m)	+5.17	-1.65	+18.77	-1.60	+4.71	
nmi		CL2 (2079 m)	+7.33	+3.60	+25.27	+1.80	+10.66	
4: Summits	Elev	CL3 (1992 m)	+6.00	-1.16	+26.23	-2.59	+5.17	
4		CL4 (1948 m)	+7.67	+0.43	+23.05	+4.01	+17.51	
		CL5 (1813 m)	+3.00	+1.19	+31.27	+1.14	+14.05	
Ch.		Gradient	Met	ric	AG		AH	TSW
5: Alpine	Wildfire	All alpine area	Top Cover (%) (±difference/decade)		-1.24		-5.23	+5.19
		Unburnt area			-3.87		-0.44	+1.44
		Burnt area			+2.63		-4.79	+3.75
5: A		All alpine zonation			-2.58		3.41	-0.19
4,		Unburnt zonation	Mean eleva (±difference		-0.39		3.9	-0.11
		Burnt zonation	(_difference	c, accade)	-2.43		1.6	-0.67

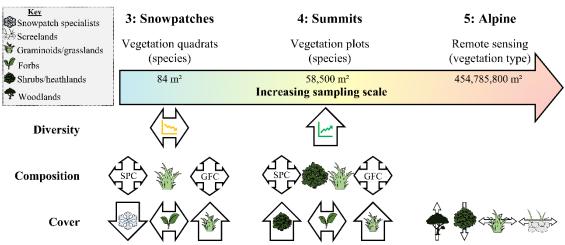
In regards to dynamics in the cover woody growth forms (shrubs and trees) in the Kosciuszko alpine area, responses also varied along environmental gradients (Table 6. 2). Elevation-dependant increases in shrub cover varied but relative increase was greatest at the three highest

summits (Chapter 4), and this is supported by evidence of the shrublines rapidly moving upslope (Chapter 5). Furthermore, the first shrubs were recorded in 2020 in the early melt zone of snowpatches (Chapter 3), where persistent snow cover has historically excluded shrubs (Pickering et al., 2014). Climate-induced shrubification (Brandt et al., 2013; Myers-Smith et al., 2015; Wilson & Nilsson, 2009), upslope advance of shrublines (Dial et al., 2016; Hallinger et al., 2010; Myers-Smith & Hik, 2018) and shrub encroachment into snowpatches (Kullman, 2002; Sandvik & Odland, 2014) have also been recorded across many alpine areas in the northern hemisphere. Alongside elevation- and snow-dependant responses, fire seems to play an important role in the cover and zonation dynamics of different vegetation types in the Kosciuszko alpine area (Chapter 5). Wildfire is also important and seems to be linked to treeline recession via densification at lower elevations with treeline canopy and seedlings recovering more slowly than grasslands and heathlands (McDougall et al., 2015). Wildfire was also linked to slower rates of advancing shrublines, as grasslands established and persisted in high elevation areas that burnt (Chapter 5). These insights are in line with other literature regarding the impacts of fire on vegetation in the Australian Alps (Dodson et al., 1994; Fairman et al., 2017; Kirkpatrick & Bridle, 2013; Williams et al., 2008), particularly for the concept of fire-regulated treeline stasis (Martin, 1999; Naccarella et al., 2020), divergent rates of recovery among alpine plant communities (Venn et al., 2016; Verrall, 2018) and implications for shrub dynamics (Camac et al., 2017; Camac et al., 2013).

# 6.4: Aim 4 – Are there differing responses of vegetation at different sampling scales in the Kosciuszko alpine area?

As responses of alpine vegetation vary along environmental gradients over time (Carbognani et al., 2014; Erschbamer et al., 2009; Steinbauer et al., 2020; Steinbauer et al., 2018), and some species and plant communities have limited distributions, the ability to detect changes is affected by the spatiotemporal sampling design and scale (Gitzen et al., 2012). Repeat surveys of permanent vegetation plots over time can provide fine-scale assessments of species cover and composition dynamics in alpine areas (Kullman, 2010; Pauli et al., 2012; Steinbauer et al., 2018). However, there can be limitations to such approaches including small spatiotemporal scales and focusing on particular environmental gradient such as elevation (Gottfried et al., 2012) or snow cover (Carbognani et al., 2014). Conversely, the spatiotemporal limitations of field-based LTEM are less of a problem with remote sensing techniques, as there are only temporal limitations due to data availability. However, analysis of vegetation dynamics is dependent on data availability and limited by sampling resolution (Lawley et al., 2016). Thus, dynamics occurring on smaller spatial sampling scales may be masked by broader dynamics (Gitzen et al., 2012), so the integration of repeat surveys of vegetation plots and remote sensing monitoring can provide greater insights across spatial scales, as presented in this thesis.

Differing responses of vegetation in the Kosciuszko alpine area were in part affected by the type of data collected at specific sampling scales with vegetation recorded to species level via repeat sampling of permanent vegetation plots in snowpatches (Chapter 3) and on summits (Chapter 4), but only to vegetation type with remote sensing across the whole alpine area (Chapter 5). Therefore, it was only possible to deduce dynamics in diversity, composition, overlapping cover, plant traits and strategies with the species level data (Chapter 3; Chapter 4), while top cover dynamics and zonation of broader vegetation types were assessed across the whole alpine area (Chapter 5) (Figure 6. 2).



**Figure 6. 2**: Overview of differing responses of alpine vegetation over time at different sampling scales in this thesis, highlighting the level of taxonomic resolution and related analyses. Thick arrows indicate significant differences over time with trends are indicated by encapsulated icons: up is equivalent to a significant increase, down is equivalent to a significant decrease, quad-ended arrows indicate a significant shift in similarity, and double-ended arrows indicate no significant difference. Thin arrows indicate trends (no means testing performed) using the denotation system above.

Generally, remote sensing is used to monitor broad-scale, long-term vegetation cover dynamics (Chaves et al., 2020; Gomez et al., 2016), and has recently started to be applied to modelling cover dynamics in alpine areas (Bolton et al., 2018; Dinca et al., 2017; Knoflach et al., 2021). Modelling some types of species-level dynamics and plant communities with small and irregular distributions using multispectral sensors with larger resolutions (e.g. MODIS or Landsat) is challenging and often error prone (Fassnacht et al., 2016). Therefore, remote sensing monitoring in alpine areas should be supplemented with repeat sampling of vegetation plots to determine compositional dynamics over time (Gitzen et al., 2012; Lawley et al., 2016). Additionally, the comparative scale of repeat sampling of permanent vegetation plots may also mask some climate-induced vegetation responses. Species-area relationships are well established (Hill et al., 1994), and could explain why changes in diversity were detected on summits where a total of ~ 50,000 m² was assessed each survey (Chapter 4) but not in snowpatches where only 84 m² was assessed each survey (Chapter 3). To adequately assess the often heterogenous composition of alpine

vegetation, the size of vegetation plots must consider the size of individual plants and speciesarea relationships (Otypková & Chytry, 2006). Furthermore, the greater diversity of
microclimates and habitats on summits is likely to account for the greater absolute species
richness (Elsen & Tingley, 2015; Körner, 2003, 2004; Scherrer & Körner, 2011), with 91 species
recorded across all three surveys in comparison to only 67 species recorded in snowpatches.
However, species enrichment and turnover attributed marginally to compositional change in
snowpatches and on summits, as the difference in mean overlapping cover of appearing and
disappearing species between the first and last surveys was less than 1% (Chapter 3; Chapter 4).
As the climate continues to change, however, there may be a growing extinction debt among
alpine plants as most alpine species are long-lived perennials (Alexander et al., 2018; Dullinger
et al., 2012).

In contrast to species richness, dynamics in species and growth form cover were important drivers of compositional change across the varying sampling scales used in snowpatches and on summits. Most of these changes were associated with the increasing cover of tall, tussock-forming Poaceae over time (Chapter 3; Chapter 4). However, there were other species contributing to compositional change including increasing cover of tall shrubs (Nematolepis ovatifolium and Kunzea muelleri) on summits (Chapter 4) and declining cover of a snowpatch specialist forb (Neopaxia australasica) in snowpatches (Chapter 3). Similar patterns of increasing cover of generalist, thermophilic graminoids and shrubs driving compositional changes amidst climate change have been reported across varying scales in northern hemisphere alpine areas (Ababneh & Woolfenden, 2010; Björk & Molau, 2007; Cannone et al., 2007; Gao et al., 2016; Lamprecht et al., 2018). However, these differential responses in compositional dynamics are likely to be the result of the varying abiotic factors between snowpatches and summits. Increasing cover of shrubs on summits but not in snowpatches is unlikely to be a factor of sampling scale, as persistent snow cover has historically excluded shrubs from snowpatches (Costin et al., 2000; Pickering et al., 2014). However, some dynamics may be more influenced by sampling scale. Macroscale monitoring of the whole alpine area detected the densification of the treeline as woodlands replaced grasslands and heathlands at lower elevations. These compositional dynamics were only apparent as the sampling scale was broad enough to capture the realised niche of the alpine treeline. There were also some divergent cover responses across sampling scales. These could be partially attributed to different measurements of cover, with snowpatches (Chapter 3) and summits (Chapter 4) quantified as overlapping cover while only top cover could be quantified across the whole alpine area (Chapter 5). Therefore, increasing overlapping cover of graminoids and shrubs is also likely to be occurring across this alpine area, in line with dynamics in snowpatches (Chapter 3) and on summits (Chapter 4), via in-filling and densification.

## 6.5: Aim 5 – What vegetation is increasing and decreasing in response to climate change in the Kosciuszko alpine area?

While alpine vegetation is broadly considered as vulnerable to climate change, there are particular species, growth forms and broad vegetation types that are more susceptible to warmer temperatures and longer growing seasons (Camac et al., 2021; Gritsch et al., 2016; Kobiv, 2018). Climate change in alpine areas is limiting suitable habitat for specialised, cryophilic species such as those found in snowpatches and fellfields but suitable habitat for generalist, thermophilic and drought-tolerant species has often increased (Kullman, 2010; Lamprecht et al., 2018; Petriccione & Bricca, 2019; Rosbakh et al., 2014; Rosbakh et al., 2017; Rumpf et al., 2018; Verrall, 2018). Decreasing alpha diversity and convergence of once distinct alpine plant communities has also been broadly recorded, providing important insights on the response of alpine vegetation compositions to climate change (Amagai et al., 2018; Britton et al., 2009; Danby et al., 2011; Porro et al., 2022; Porro et al., 2019).

In the Kosciuszko alpine area, the influence of species turnover on vegetation dynamics and changing compositions appears minimal. For instance, between the first and last sampling of snowpatches (2007-2020) there were 17 new species recorded and nine disappearances, but appearances (<0.2%) and disappearances (<0.6%) were marginal (Chapter 3) (Table 6. 3). Similarly, there were 15 new species on summits but only one species disappeared (2004-2019), and all appearances (<0.6%) and disappearances (<0.1%) were marginal (Chapter 4). Instead, changing composition appears to be primarily driven by an increasing cover of a few competitive, generalist and thermophilic graminoids and shrubs and the subsequent decline in cryophilic, specialist graminoids and forbs (Table 6. 4). This echoes patterns of decreasing alpha diversity and converging alpine plant communities in Europe (e.g. Porro et al., 2022), North America (e.g. Danby et al., 2011) and Asia (e.g. Amagai et al., 2018).

It appears that there is a general trend for increasing cover of tall, tussock forming graminoids *P. costiniana* and *P. fawcettiae* in the Kosciuszko alpine area. These two graminoids are found in many alpine plant communities and broad vegetation types (Costin et al., 2000; Walsh & McDougall, 2004). They appear to be responding to climate change by encroaching on mid and late melt zones of snowpatches that were previously dominated by snowpatch specialists (Chapter 3), increasing in cover and recruiting within shrub canopies causing densification (Chapter 4), and establishing or resprouting rapidly following fire (Chapter 5). As the climate changes, shrub cover has also increased in many alpine areas (Brandt et al., 2013; Myers-Smith et al., 2015; Wilson & Nilsson, 2009), but shrub dynamics in the Kosciuszko alpine area are mixed. While the cover of the tall shrub *Kunzea muelleri* did increase on summits through time (Chapter 4), top cover of heathlands declined across the whole Kosciuszko alpine area (Chapter 5). Heathlands

were mostly replaced by woodlands at lower elevations, but shrubs may be persisting below the canopy of trees. Over time, there was also a marginal increase in the cover of screelands across the whole alpine area, but this was mostly driven by the drought impacts and small areas that burnt during the 2020 wildfires (Chapter 5).

Table 6. 3: Species appearances and disappearances from the first and last surveys from

snowpatches (Chapter 3) and summits (Chapter 4).

snowpatches (Chapter 3) and summits (		C 4 E	CI 2	CI 4
Species	Family	Growth Form	Ch. 3	Ch. 4
Appearances				
Aciphylla glacialis	Apiaceae	Forb	✓	
Argyrotegium fordianum	Asteraceae	Forb		✓
Argyrotegium mackayi	Asteraceae	Forb		✓
Astelia psychrocharis	Asteliaceae	Forb		$\checkmark$
Australopyrum velutinum	Poaceae	Graminoid	✓	✓
Blechnum penna-marina subsp. alpina	Blechnaceae	Fern	$\checkmark$	
Coronidium scorpioides	Asteraceae	Forb		✓
Craspedia costiniana	Asteraceae	Forb	$\checkmark$	
Deyeuxia crassiuscula	Poaceae	Graminoid		$\checkmark$
Epilobium gunnianum	Onagraceae	Forb	$\checkmark$	$\checkmark$
Epilobium tasmanicum	Onagraceae	Forb		$\checkmark$
Geranium potentilloides	Geraniaceae	Forb		$\checkmark$
Grevillea australis	Proteaceae	Shrub	$\checkmark$	
Kelleria dieffenbachii	Thymelaeaceae	Shrub	✓	
Luzula alpestris	Juncaceae	Graminoid	$\checkmark$	
Microseris lanceolata	Asteraceae	Forb	$\checkmark$	
Olearia algida	Asteraceae	Shrub		$\checkmark$
Oreomyrrhis brevipes	Apiaceae	Forb	$\checkmark$	$\checkmark$
Orites lancifolia	Proteaceae	Shrub		$\checkmark$
Podocarpus lawrencei	Podocarpaceae	Shrub		$\checkmark$
Polystichum proliferum	Dryopteridaceae	Fern	$\checkmark$	
Prasophyllum alpestre	Orchidaceae	Forb	$\checkmark$	
Prasophyllum tadgellianum	Orchidaceae	Forb	$\checkmark$	
Psychrophila introloba	Ranunculaceae	Forb	✓	
Ranunculus granticola	Ranunculaceae	Forb	$\checkmark$	
Ranunculus muelleri	Ranunculaceae	Forb	$\checkmark$	
Stylidium graminifolium	Stylidiaceae	Forb		$\checkmark$
Viola bentonicifolia	Violaceae	Forb	✓	
Wahlenbergia ceracea	Campanulaceae	Forb		$\checkmark$
Disappearances	•			
Brachyscome spathulata	Asteraceae	Forb	✓	
Carex breviculmis	Cyperaceae	Graminoid	✓	
Cotula alpina	Asteraceae	Forb	✓	
Erigeron bellidioides	Asteraceae	Forb	✓	
Erigeron nitidus	Asteraceae	Forb	✓	
Gonocarpus montanus	Haloragaceae	Forb	✓	
Isolepis subtilissima	Cyperaceae	Graminoid	✓	
Leptorhynchos squamatus	Asteraceae	Forb	✓	
			✓	
Ranunculus gunnianus	Ranunculaceae	Forb		$\checkmark$
Ranunculus acrophilus Ranunculus gunnianus	Ranunculaceae Ranunculaceae	Forb Forb	✓	✓

 Table 6. 4: Decadal cover dynamics of species (Chapter 3 and 4) and vegetation type (Chapter

5) between the first and last sampling for each chapter in this thesis.

Ch		Species/vegetation type	Family	Growth Form	Cover (±%/decade)
		Poa costiniana	Poaceae	Graminoid	+16.77
	3g	Poa fawcettiae	Poaceae	Graminoid	+2.09
	Increasing	Carex hypandra	Cyperaceae	Graminoid	+2.11
sei	Inc	Psychrophila introloba	Ranunculaceae	Forb	+0.19
3: Snowpatches		Senecio pinnatifolius var. alpinus	Asteraceae	Forb	+0.16
Snow		Neopaxia australasica	Montiaceae	Forb	-6.14
33.	gu	Rytidosperma nudiflorum	Poaceae	Graminoid	-5.22
	Decreasing	Luzula acutifolia	Juncaceae	Graminoid	-1.76
	De	Celmisia costiniana	Asteraceae	Forb	-0.59
		Polytrichum juniperinum	Polytrichaceae	Bryophyte	-0.57
		Poa fawcettiae	Poaceae	Graminoid	+17.54
	gu	Epacris gunnii	Epacridaceae	Shrub	+5.08
	Increasing	Kunzea muelleri	Myrtaceae	Shrub	+4.42
70	Inc	Empodisma minus	Restionaceae	Graminoid	+3.21
4: Summits		Trisetum spicatum subsp. australiense	Poaceae	Graminoid	+2.53
4: Su		Craspedia adenophora	Asteraceae	Forb	-0.62
,	ing	Grevillea australis	Proteaceae	Shrub	-0.35
	Decreasi	Craspedia maxgrayii	Asteraceae	Forb	-0.19
	De	Ranunculus acrophilus	Ranunculaceae	Forb	-0.18
		Ewartia nubigena	Asteraceae	Shrub	-0.14
5: Alpine	ng	Treeline Subalpine Woodlands			+5.19
	Increasing	Fellfield Alpine Screes			+0.43
	Iπ	Dry Alpine Grasslands			+0.39
5: A	ing	Dry Alpine Heathlands			-3.71
	Decreasing	Wet Alpine Heathlands			-1.52
	Dec	Wet Alpine Grasslands			-0.81

## 6.6: Aim 6 – What are the benefits, limitations and implications of LTEM when assessing vegetation dynamics?

As the climate continues to rapidly change, its impacts may begin to outpace the resistance and resilience of many ecosystems (Bergstrom et al., 2021). Thus, LTEM is an important tool that aggregates ecological records over time and allows researchers to detect ecosystem instability via major fluctuations in key biotic and abiotic factors (Müller et al., 2010). Since alpine vegetation experiences relatively low anthropogenic land-use impacts, low temperatures and short growing seasons (Körner, 2003; Nagy & Grabherr, 2009), it is possible to use LTEM to explore long-term processes and changes that can be mostly attributed to climate change (Grabherr et al., 2010; Pauli et al., 2015). However, there are benefits and limitations to LTEM (Burns et al., 2014; Gitzen et al., 2012; Lindenmayer et al., 2012; Müller et al., 2010), including in relation to the research presented in this thesis (Table 6. 5).

**Table 6. 5**: Common benefits and limitations of Long-Term Ecological Monitoring (LTEM) (Burns et al., 2014; Gitzen et al., 2012; Lindenmayer et al., 2012; Müller et al., 2010), and where they were seen in the research presented in the thesis.

	Factor	LTEM	Ch. 3	Ch. 4	Ch. 5
	Quantifies ecological responses to long-term drivers of change that act over decades to centuries.	✓	✓	✓	✓
	Improves understanding of complex, long-term ecosystem processes.	✓	✓	✓	✓
Benefits	Delivers scale-relevant insights for evidence- based conservation policy and management.	✓	✓	✓	✓
	Delivers scale-relevant insights for evidence- based conservation policy and management.	✓	✓	✓	✓
	Promotes scientific collaboration and multidisciplinary research across nations, institutions and generations.	✓	✓	✓	✓
	Inadequate spatiotemporal design that provides data that mismatches with objectives and goals, and difficulty to detangle cause and effect.	✓	✓	✓	
S	Confined to the parameters of the original monitoring design and data collected.	✓	✓	✓	
Limitations	Requires sustained dedication and determination at multiple levels including scientific, political and financial.	✓	✓	✓	
	Ongoing maintenance of monitoring infrastructure including field equipment and data repositories.	✓	✓	✓	
	Most LTEM projects are developed from the bottom-up, with a disconnect between science and policy.	✓	✓	✓	✓

Obvious benefits of LTEM include the ability to capture and quantify ecological responses to long-term drivers of change, filtering out some of the noise from annual and interannual variability (Gitzen et al., 2012; Lindenmayer et al., 2012; Müller et al., 2010). This is particularly relevant when assessing climate-induced alpine vegetation dynamics, as most alpine plants are slow growing and long-lived perennials that are resilient to short-term climatic fluctuations but are susceptible to sustained climatic changes (de Witte & Stöcklin, 2010; Körner, 2003; Lütz, 2013). However, LTEM require large levels of commitment and resources, and often as a result, there are spatiotemporal sampling constraints that can lead to less effective monitoring. This can result in mismatches in sampling frequency and scale in relation to interannual variability and climatic oscillations (Gitzen et al., 2012; Müller et al., 2010). Existing LTEM are also often developed to address specific issues, and hence, the designs may misalign with those required for current and future conservation priorities (Burns et al., 2014; Lindenmayer & Likens, 2010; Lindenmayer et al., 2012). Another issue with LTEM arises from the difficulty to detangle cause and effect. Due to the complex nature and temporal variability of ecosystems, inferring drivers of ecosystem responses over time is often challenging and somewhat ambiguous (Burns et al., 2014). Thus, long-term and sustained scientific, financial and political support is required for successful LTEM (Burns et al., 2014), but is difficult to secure. Despite some of the limitations listed here, LTEM provides important insights and must be continued as the climate changes.

Some of these challenges are exemplified in this thesis in relation to the LTEM of snowpatches (Chapter 3) and summits (Chapter 4). Despite the valuable data, evidence-base and insights they have provided, the future of these LTEM projects is insecure. Both of these LTEM rely on paid and volunteer labour, student research projects, a string of unrelated funding from various sources, and the active collaboration of universities and government agencies (Pickering et al., 2014; Venn et al., 2014). Inherently, there has been turnovers in personnel, with the continuity and integrity of these LTEM projects hinging on a few key researchers (i.e. Professor Catherine Pickering and Professor Ken Green). Another common challenge experienced here with LTEM is maintaining monitoring infrastructure (Burns et al., 2014). There were relocating sites, as alpine soils undergo mass wasting, frost creep, solifluction and cryoturbation. This resulted in damaged soil temperature loggers and plot markers, particularly in snowpatches (Chapter 3; Chapter 4). However, the continued and effective LTEM in this thesis was permitted by careful design, project management, detailed field notes and the involvement of the founding members of each project (Chapter 3; Chapter 4). This enabled the resurveying of vegetation plots and the relatively continuous soil temperature monitoring, but will remain an ongoing challenge (Burns et al., 2014). Therefore, effective and sustained LTEM also requires successional planning to ensure project knowledge is translated to upcoming project leaders and participants (Burns et al., 2014).

Other challenges of LTEM include the inherent inflexibility such as inadequate spatiotemporal design and being confined to the parameters of the original monitoring. This can render LTEM projects less effective at providing objectives and insights as they struggle to deal with changing issues (Burns et al., 2014). For example, this thesis posits that vegetation dynamics are primarily driven by rapidly warming conditions but may also be influenced by recovery from the millennium drought (2001 – 2009) (Chapter 3; Chapter 4). There are a few other LTEM in the Kosciuszko alpine area in addition to those assessed in this thesis. This includes LTEM examining the impacts of grazing by introduced ungulates (mainly cows and sheep) but that have also been used to look at the effects of drought, fire and climate change (Scherrer & Pickering, 2005; Venn et al., 2016; Wimbush & Costin, 1979). Separating out the cause and effect among these different factors can be difficult, and LTEM in this alpine area may not adequately address other threats that have arisen such as plant pathogens (Green, 2016b; Rigg et al., 2018), introduced plants (Hill & Pickering, 2006; Schroder et al., 2015), increasing pressures from native (McDougall et al., 2018; Parida et al., 2015) and introduced animals (Driscoll et al., 2019; Worboys, 2018) as well as recreational use (Ballantyne et al., 2014; Pickering & Buckley, 2003). In some cases, monitoring using remote sensing techniques can be used to complement and expand the temporal and spatial scale of field-based LTEM, and help monitor for a range of factors as was done here for climate and wildfire (Chapter 5).

### 6.7: Thesis contributions to knowledge

As the climate changes, there is increasing research on the responses of alpine vegetation including a greater diversity in geographic and methodological approaches (Chapter 2), although, important gaps remain and these shaped the research aims for the thesis. The research presented here has contributed to knowledge regarding the response of alpine vegetation to climate change by drawing on insights afforded using a diversity of LTEM methods including field-based and remote sensing approaches at varying spatiotemporal scales. These contributions are grouped into three overarching insights summarised below (Table 6. 6). In this thesis, two existing LTEM protocols plus a newly developed remote sensing monitoring have highlighted diverse responses of alpine vegetation climate change including warmer temperatures, lengthening growing seasons, declining snow cover, variable precipitation and wildfire. Firstly, this thesis highlighted the importance of LTEM as the climate continues to change. Secondly, this thesis provided evidence that the impacts of climate change are not uniform across the entire alpine ecotone, and there is apparent elevation, snowmelt- and wildfire-dependent responses of alpine vegetation in the Kosciuszko alpine area. Lastly, this thesis suggests that compositional dynamics have been driven largely by cover with increasing dominance, but not diversity, of thermophilic graminoids, shrubs and trees and subsequent decline in cryophilic taxa.

**Table 6. 6**: Specific contributions to knowledge from the results chapters included in this thesis.

Contribution	Ch. 2	Ch. 3	Ch. 4	Ch. 5
1. LTEM provides important insights into climate-induced resp	onses o	f alpine	vegetati	on
1.1 The application of LTEM is increasing and diversifying	$\checkmark$			
<b>1.2</b> Integrated, multiscale and mixed-method approaches can assess a range of responses of alpine vegetation	✓	✓	✓	✓
<b>1.3</b> LTEM have benefits but also limitations, but are useful methods for assesses climate-induced dynamics	✓	✓	✓	✓
2. Changes in microclimate and vegetation linked to environm	ental gr	adients		
<b>2.1</b> Microclimatic changes are greater at higher elevations		$\checkmark$	$\checkmark$	
<b>2.2</b> Microclimatic changes are greater in areas where snow persists the longest		✓	✓	
<b>2.3</b> Composition changes are most pronounced in microclimatic refugia at higher elevations and where snow persists longest		✓	✓	
<b>2.4</b> Vegetation cover changes are most pronounced at lower elevations			✓	✓
<b>2.5</b> Wildfire results in range of changes including treeline recession and suppression of advancing shrublines but promotes densification of woody vegetation at lower elevations and grassification at higher elevations				✓
3. Taxa-specific responses in cover and dominance drive comp	osition	change		
<b>3.1</b> Increasing cover of tall, tussock-forming graminoids		$\checkmark$	$\checkmark$	✓
<b>3.2</b> Increasing cover of woody growth forms			✓	✓
3.3 Declining cover of cryophilic taxa		$\checkmark$	$\checkmark$	
<b>3.4</b> Increasing diversity			✓	
<b>3.5</b> Stable diversity		✓		
<b>3.6</b> Species and/or growth-form specific responses to climate change		✓	✓	✓
<b>3.7</b> Biotic homogenisation and convergence of plant composition		✓	✓	✓

#### 6.8: Future changes in the Kosciuszko alpine area

Past drivers of vegetation dynamics

Understanding how the vegetation in the Kosciuszko alpine area might change in the future can be informed by assessing past vegetation dynamics and identifying relevant drivers of such changes. Pollen-based ecological reconstructions of vegetation in the Australian Alps have highlighted the responsiveness of alpine vegetation to past climatic fluctuations (Dodson et al., 1994; McKenzie, 1997; Thomas et al., 2022). Specifically, following glacial retreat in the Kosciuszko alpine area approximately 15,000 years ago, deglaciated areas were colonised and dominated by cryophilic communities similar to present-day fellfields until 10,000 years ago when the encroachment of dry alpine grasslands began (Martin, 1986). Over the next 7,000 years, there was an increase in sedges and subsequent decline in forbs, and then a slow rise of the

broadleaved evergreen tree E. niphophila, which is the present-day treeline species, as it colonised higher elevations (Martin, 1986). Since deglaciation, successional vegetation dynamics in the Kosciuszko alpine area are attributed to climate change where warmer temperatures are linked into increasing dominance and encroachment of E. niphophila, but shifts from graminoid and forb dominated compositions to woodland taxa also coincide with increasing wildfire frequency over the past millennia (Dodson et al., 1994; Martin, 1986; Thomas et al., 2022). Thus, the alpine vegetation dynamics presented in this thesis are primarily attributed to the rapidly changing climate of the Kosciuszko alpine area over recent decades. Alongside climate-induced responses, there may be several other contributing factors including legacy effects of past droughts and anthropogenic land-use impacts in the Kosciuszko alpine area (Costin, 1954; Dodson et al., 1994; Good & Johnston, 2019; Scherrer & Pickering, 2005). This alpine area has experienced at least four broad periods of anthropogenic land-use beginning with thousands of years of Indigenous custodianship (Flood, 1973; Slattery & Worboys, 2020). This was dismantled by colonisation, which led to a period of pastoralism (~1830-1958). In response to widespread impacts from pastoralism, there was a partly overlapping period of western scientific inquiry and active rehabilitation (1944-1972), which paved the way for a more contemporary conservation management era and continued scientific inquiry (Slattery & Worboys, 2020).

As highlighted in Chapter 1, the Kosciuszko alpine area is significant to Indigenous cultures as a place of spirituality, corrobboree, ceremony and trade in addition to providing abundant, if seasonally intermittent, food and water resources (Flood, 1973; Slattery & Worboys, 2020). However, Indigenous custodianship does not appear to have led to any discernible vegetation dynamics in this alpine area, with increasing wildfire activity more likely attributed to warmer temperatures and snow cover decline over recent millennia rather than Indigenous cultural burning practices (Dodson et al., 1994; Martin, 1986; McGowan et al., 2018; Slattery & Worboys, 2020; Thomas et al., 2022; Zylstra, 2006). Although Indigenous cultural burning was widespread and methodical in much of Australia (Fletcher et al., 2021; Gammage, 2011; Pascoe, 2014), there was little motivation to burn vegetation in the Kosciuszko alpine area and surrounding treeline woodlands as there were few large marsupials to hunt (Costin et al., 2000). Therefore, during this long period of Indigenous custodianship the vegetation of the Kosciuszko alpine area experienced infrequent (~ 140 years at treeline) fire-intervals (Williams et al., 2008), little to no grazing pressure from large mammals (Costin, 1954), and no permanent occupation or discernible anthropogenic land-use impacts (Martin, 1999; Slattery & Worboys, 2020).

However, colonisation ushered in a period of pastoralism that caused extensive ecological impacts, with the forced the removal of Indigenous peoples and custodianship from the broader region (Slattery & Worboys, 2020). Pastoralism in the Kosciuszko alpine area may have begun as early as 1830 (Costin et al., 2000), but was formalised in 1862 with the granting of the Excelsion

Run with sheep and cattle grazing across ~ 100 km<sup>2</sup> of the Kosciuszko alpine area (Worboys & Pickering, 2002). In addition to grazing and trampling pressures from large, hard-hooved ungulates (mainly cattle), which this alpine area had never experienced in the past, pastoralists also introduced burning practices commonly used in Europe to promote the growth of palatable species (Good & Johnston, 2019). The Kosciuszko alpine area also experienced a landscape-level wildfire in 1939, but the severity, impacts and recovery from this disturbance event are unclear (Williams et al., 2008). However, haphazard pastoral burning practices were linked to numerous, widespread and severe fires in the surrounding subalpine area, leading to the densification of subalpine woodlands (Martin, 1999). The ecological impacts of pastoralism, which were first recorded in the 1890s, also included soil erosion, altered hydrology, silting of Sphagnum bogs and degradation of vegetation (Helms, 1893). These destructive pastoral practices continued until the 1950s resulting in the complete loss of large tracts of vegetation due to sheet erosion, with at least 1.2 million tonnes of soil lost (Good & Johnston, 2019). Pastoralism also impacted alpine vegetation through the introduction of invasive plants and selective grazing of native palatable species, leaving openings in the vegetation cover that led to drying soils and the deleterious effects of frost heave (Costin, 1954). Selective pastoral grazing almost caused the localised extinction of native plants including the forbs Aciphylla. glacialis and Aciphylla. simplicifolia in addition to decimating the Kosciuszko alpine endemic graminoid Chionochloa. frigida and forb Ranunculus. anemoneus (Costin et al., 2000; Good & Johnston, 2019). A further 30 species, including five more Kosciuszko alpine endemics, are currently listed as rare and threatened plants due in part to past grazing impacts (Good & Johnston, 2019). Overall, vegetation dynamics during this era were driven by the widespread destructive practices of pastoralism, but inspired at a period of western scientific inquiry, rehabilitation and contemporary conservation (Slattery & Worboys, 2020).

During the decades of rehabilitation beginning in the 1950s, vegetation dynamics in degraded areas were influenced by rehabilitation and revegetation efforts by the New South Wales Soil Conservation Service (Costin, 1954; Good & Johnston, 2019). However, the initial rehabilitation efforts were challenging and thwarted by mistakes. These included the spread of introduced plants and disturbance of sensitive nutrient regimes from rehabilitation materials leaching zinc that caused the localised dieback of surrounding vegetation, with some impacts still occurring (Good & Johnston, 2019). Until 1970, degraded but stabilised areas were mostly covered with introduced graminoids and forbs from Europe (e.g. *Agrostis capillaris*, *Lolium perenne*, *Poa pratensis*, *Festuca rubra* subsp. *commutata* and *Phleum pratense*). After stabilising soils, rehabilitation moved towards the propagation and planting of 35 native species of graminoids, forbs and shrubs that had been affected by pastoralism (Good & Johnston, 2019). Furthermore, the establishment of Kosciuszko National Park in 1967 afforded protected area status to the alpine area and marked the beginning of contemporary conservation (Slattery & Worboys, 2020). While the ongoing

conservation and management of the Kosciuszko alpine area has led to widespread ecological recovery (Good & Johnston, 2019), there are select areas and plant communities where legacy effects of pastoralism persist. These include trampled wet heathlands and wet grasslands (bogs and fens) where hydrological function has been degraded as well as severely eroded dry grasslands that now exist as an erosion fellfield with skeletal soils and limited vegetation cover (Good & Johnston, 2019; Wimbush & Costin, 1979). Ultimately, rehabilitation has stabilised and revegetated most degraded areas but also contributed to vegetation dynamics with the creation of novel mosaic of vegetation in some areas that diverges from pre-pastoral vegetation (Good & Johnston, 2019).

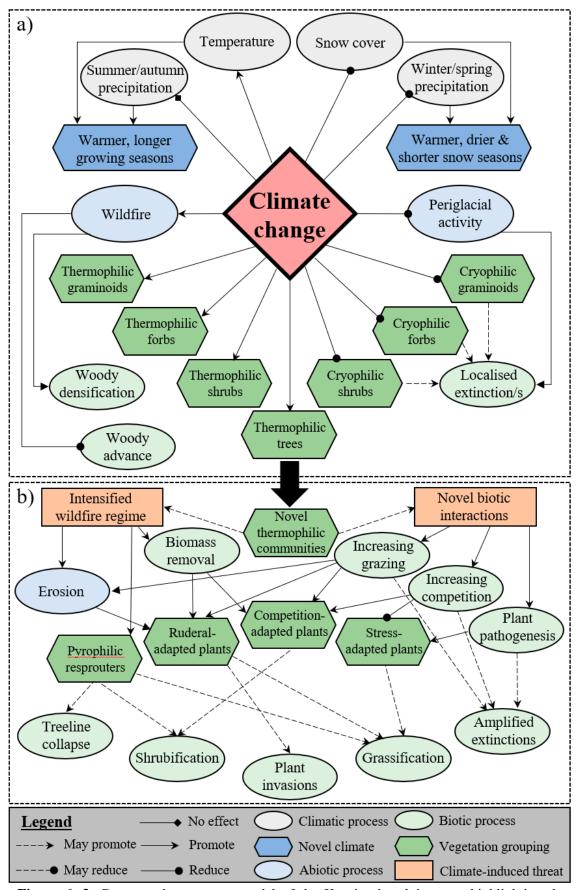
There has been varying success in removing historical drivers of vegetation dynamics during the contemporary conservation era, as well as dealing with novel and amplified threats. In some areas, these include impacts from increasing abundance and distribution of introduced ungulates (Driscoll et al., 2019; Worboys, 2018), invasive plants and plant pathogens (Costin et al., 2000; Rigg et al., 2018; Scherrer & Pickering, 2006; Schroder et al., 2015) in addition to impacts related to recreation, tourism and associated infrastructure (Ballantyne et al., 2014; Hill & Pickering, 2006; Martin, 1999; Normyle & Pittock, 2020; Pickering & Buckley, 2003; Pickering & Growcock, 2009; Wilson et al., 2022). However, responses of vegetation in the Kosciuszko alpine area are largely attributed to the rapidly changing climate (Auld et al., 2022; Pickering et al., 2014; Scherrer & Pickering, 2005; Schroder et al., 2015; Sritharan et al., 2021; Venn et al., 2017; Venn et al., 2014). Similar to quaternary vegetation dynamics in this alpine area (Dodson et al., 1994; Martin, 1986; Thomas et al., 2022), changing compositions over recent decades are often linked to increasing temperatures (Auld et al., 2022; Scherrer & Pickering, 2005; Sritharan et al., 2021; Venn et al., 2017; Venn et al., 2014), wildfires (Venn et al., 2016) and snow cover decline (Pickering et al., 2014). While climate-induced vegetation dynamics were more gradual over past millennia, the current rate of climate change over recent decades is considerably faster (McGowan et al., 2018), and has likely prompted more rapid responses of vegetation in the Kosciuszko alpine area. This thesis addresses some knowledge gaps and hence provides some additional insights into recent climate-induced vegetation dynamics. However, future dynamics in coming decades are likely to be complex, but some predictions can be made based on current knowledge.

#### Possible changes in the vegetation of the Kosciuszko alpine area by 2070

If the current rate of emissions continues, the climate of the Australian Alps is predicted to be considerably different by 2070, with climatic conditions in alpine areas likely to resemble those of present-day subalpine areas. Downscaled climate modelling is projects further warming of 1.7 – 2.1 °C, a 57% decline in snow cover area and 40% reduction in the duration of snow cover compared to recent conditions (1990–2009) across the Australian Alps (Di Luca et al., 2018). Furthermore, projected increasing temperatures are likely to be amplified by elevation, in line

with elevation-dependant warming theorem (Pepin et al., 2022), which is consistent with results presented in the thesis (Chapter 4). However, projected changes in precipitation are less clear with mean annual declines of 7% across the Australian Alps (Di Luca et al., 2018), with declining winter and spring precipitation by 60 – 90 mm (Olson et al., 2016). With increasing temperatures as well as declining precipitation and snow cover, fire conditions could increase by ~25% in the woodlands surrounding the Kosciuszko alpine area, resulting in more frequent and severe wildfires (Clarke & Evans, 2019). These changes in climate will have a range of direct and indirect impacts for the vegetation in the present-day geographical extent of the Kosciuszko alpine area including irreversible changes in ecosystem structure, function and composition (Bergstrom et al., 2021; IPCC, 2021, 2022; Laurance et al., 2011; Venn et al., 2017; Williams et al., 2008; Williams et al., 2015). Vegetation dynamics in response to climate-induced impacts are also likely to be non-linear, as novel climatic and environmental conditions as well as biotic interactions may eclipse the resilience of certain species and vegetation communities (Alexander et al., 2018; Alexander et al., 2015). Therefore, predicting future dynamics in the Kosciuszko alpine area is complicated by the numerous synergistic impacts of climate change and other threats.

Potential features, interactions, processes and threats that may drive vegetation dynamics in the Kosciuszko alpine area in the coming decades are presented in a conceptual model (Figure 6. 3). Climate change has, and will continue to, cause warmer, drier and shorter snow seasons with increasingly warmer and longer growing seasons (Di Luca et al., 2018; Thompson, 2016; Thompson & Paull, 2017; Chapter 3; Chapter 4; Chapter 5). In response, increasing cover of thermophilic species and growth forms has occurred (Pickering et al., 2014; Venn et al., 2014; Chapter 3; Chapter 4; Chapter 5), often at the expense of cryophilic taxa. Furthermore, climate change is likely to reduce periglacial activity that maintains fellfields, with warming temperatures limiting the extent and duration of cryoturbation and solifluction in this alpine area (Barrow et al., 1968; Green & Pickering, 2009; Venn et al., 2017; Williams et al., 2015). Thus, an ongoing decline of cryophiles may result in localised extinctions as climatic and environmental conditions eclipse the resilience of species and growth-forms dependent on periglacial processes (Bergstrom et al., 2021; Camac et al., 2021; Verrall, 2018). Wildfire is exacerbated by climate change (Williams et al., 2008), and promotes woody densification (Camac et al., 2015; Camac et al., 2017; Martin, 1999), but supresses woody advance (Chapter 5). These direct and indirect impacts of climate change are predicted to culminate in novel thermophilic communities Figure 6. 3a), with fellfields replaced by grasslands, and grasslands replaced by woodlands and heathlands in some areas (Camac et al., 2021). However, climate change is likely to amplify other threats as well as causing novel threats, such as an intensifying wildfire regime and novel biotic interactions (Figure 6. 3b).



**Figure 6. 3**: Conceptual ecosystem model of the Kosciuszko alpine area highlighting the impacts of climate change on vegetation over a) recent decades, as highlighted in this thesis, and b) coming decades.

Novel thermophilic communities are likely to be competition-adapted and dominated by taller and more competitive graminoids, forbs, shrubs and trees, with climate change driving densification of vegetation. However, climate change is likely to amplify and disrupt current disturbance regimes, which may lead to a shift towards ruderal-adapted communities. With wildfire conditions increasing with climate change (Clarke & Evans, 2019), there is the potential of a positive feedback loop between increasing biomass, woody densification and landscape flammability (Camac et al., 2021; Camac et al., 2015; Camac et al., 2017; Zylstra, 2013; Zylstra, 2018). This intensified wildfire regime may be the greatest threat to vegetation of the Kosciuszko alpine area, with wildfires likely to occur at greater frequency and severity than the regenerative capacity of the treeline species E. niphophila by 2070 (IPCC, 2022). Such intensification of the wildfire regime might result in treeline collapse as the resilience of this monospecific treeline is eclipsed, and subsequent shrubification and replacement by a low-diversity shrubline dominated by pyrophilic resprouters. However, alpine grasslands are currently the most resilient vegetation to wildfire in the Kosciuszko alpine area (McDougall et al., 2015; Venn et al., 2016; Verrall, 2018). If wildfire frequency and severity outpace the resilience of resprouting shrubs by limiting the epicormic resource accumulation period, there may be subsequent grassification and replacement by ruderal-adapted graminoids and forbs. Furthermore, wildfires result in the loss of biomass and removal of competition, which may promote the spread of ruderal-adapted species including invasive plants (McDougall et al., 2015; Schroder et al., 2015). Intensifying wildfire regimes would likely also likely result in soil erosion with a mosaic of burn scars at different stages of recovery. Ultimately, composition and dominant species and growth-forms are likely to be influenced by the severity and frequency of wildfires, as well as other disturbance events that are amplified by climate change.

Climate change is also likely to create or amplify novel biotic interactions, including plant-plant and plant-animal interactions as well as plant pathogenesis. Warmer conditions are known to increase plant pathogenesis (Garrett et al., 2021) and similarly impact alpine soil microbial communities (Broadbent et al., 2021; D'Alò et al., 2021). Recently, some shrub species have experienced dieback in the Kosciuszko alpine area due to pathogenic water moulds including *Phytophthora* species (Green, 2016b; McDougall et al., 2018; Rigg et al., 2018), but most impacts were below the treeline. However, if shrubification of the Kosciuszko alpine area occurs with climate change, there is the potential for plant pathogens to regulate shrub expansion, resulting in subsequent grassification. Perhaps more influential and immediate pressures may be caused by plant-plant competition for resources with the densification of vegetation and novel thermophilic communities (Alexander et al., 2018; Alexander et al., 2015; Choler et al., 2001; De Boeck et al., 2018; Margreiter et al., 2021). With warmer and longer growing seasons, communities are likely to shift from stress-tolerant towards competition- and ruderal-tolerant compositions as abiotic

factors become less important in lieu of novel biotic interactions (Alexander et al., 2015; Callaway et al., 2002; Vandvik et al., 2020). Novel or amplified competitive interactions are likely to reduce the cover of stress-adapted plants in favour of competition-adapted plants, which may lead to shrubification where there is increasing dominance of tall shrub species that are more prominent at lower elevations, or might result in the replacement of forbs by taller snow grasses (Jarrad et al., 2012; Verrall et al., 2021). Ultimately, warmer temperatures and longer growing seasons in themselves (i.e., in areas not burnt by wildfire) are likely to incrementally result in biotic homogenisation via the loss of cryophiles and replacement by thermophilic generalists, leading to novel communities that are better adapted to the contemporary climate of the surrounding subalpine area.

With climate change, grazing pressures are also likely to change including increasing impacts of phytophagous native arthropods. Populations of *Lomera caespitosae* increase during dry periods, with larvae grazing on native snowgrasses (Poa spp.) resulting in discrete patches of dead grass (Costin, 1954; Green & Osborne, 2012). Another common arthropod grazer is Oncopera alpina, which also causes episodic mortality of patches of the dominant *Poa* snowgrasses, facilitating the establishment of ruderal-adapted plants including forbs (McDougall et al., 2018). Both of these grazing arthropods may benefit from longer growing seasons over the coming decade, but climate change is predicted to greatly reduce these species' distribution and associated impacts on vegetation dynamics by 2070 (Parida et al., 2015). Climate change seems to be increasing the impacts of other native arthropods, including a native wood borer (*Phoracantha* sp. – longicorn beetle). This wood-borer may also contribute to treeline collapse and shrubification, as it can cause dieback of E. niphophila as a result of ring-barking (Green & Osborne, 2012; McDougall et al., 2018; Naccarella et al., 2020). Drought- and fire-stressed trees seem to be more susceptible, and hence climate change may exacerbate the effect of the longicorn beetle, with research on this phenomenon ongoing. Climate change may also bring about increasing marsupial grazing pressure, where *Macropus rufogriseus* and *Macropus giganteus* move up from subalpine areas as a result of declining snow cover and longer growing seasons (Green, 2016a; Green & Osborne, 2012). If there are sufficient lags in woody advance and localised extinctions of alpine grassland species, there is the potential for native marsupial grazing pressure to transform vegetation to marsupial lawns, akin to the process currently seen in the alpine ecosystems of Tasmania in Australia that experience less consistent snow cover during colder months (Roberts, 2009).

Additionally, there may be several other contributing pressures that determine the vegetation in the Kosciuszko alpine area by 2070, such as invasive species and new infrastructure. Similar to the climate-induced threat of increasing marsupial grazing pressure, widespread grazing and trampling pressure from introduced ungulates (e.g. horses, deer and pigs) could potentially occur if populations are not managed effectively (Driscoll et al., 2019). This may result in similar

impacts as seen in the past under pastoralism where there was widespread erosion, loss of palatable native forbs and destructive trampling of wet grasslands and heathlands (Good et al., 2019). Furthermore, there may also be further pressure on vegetation from last-chance tourism and related infrastructure development as the most persistent snowpack in Australia rapidly declines (Fiddes et al., 2015; Morrison & Pickering, 2013; Pickering, 2011). Already there is increasing pressure for prolonged and diversified snow-free recreation including more intensive hiking and mountain biking in the Kosciuszko alpine area with new walking tracks and other facilities (Pickering, 2011; Pickering & Buckley, 2003; Pickering & Growcock, 2009; Pickering et al., 2021). There are likely to also be proposals for more intensive winter tourism in what will be one of the last areas in Australia with a consistent snow cover (NSW Government, 2022). Concomitantly, climate change and related disturbances may result in increasing cover and diversity of invasive plants in the Kosciuszko alpine area (Hill & Pickering, 2006; Scherrer & Pickering, 2006; Schroder et al., 2015). Increasing disturbance from wildfires, grazing and trampling, tourism and associated infrastructure development all favour ruderal-adapted plants including many introduced plants. All aspects considered, the impacts of climate change and related pressures on vegetation in the Kosciuszko alpine area by 2070 will be considerable, but the exact trajectory and composition is complex as it is will be both threat- and process-dependent (Camac et al., 2021).

#### Potential management implications for the Kosciuszko alpine area

The foremost threat to the Kosciuszko alpine area is climate change, with important impacts already demonstrated in this thesis, with further impacts predicted for the future. Without timely and effective climate action that limits further warming, the persistence of some alpine species and communities is unlikely in the Kosciuszko alpine area. However, there are direct on-ground management actions that could help increase the resilience of alpine vegetation (Worboys & Pickering, 2002), as well as important associated research activities. However, the plausibility and extent of the management actions and research activities may be limited by logistical, financial and societal pressures (Slattery & Worboys, 2020; Worboys, 2018; Worboys & Pickering, 2002). Ultimately, there needs to be increased opportunities for on-going collaborations among government, researchers and other stakeholders. This will help ensure that research aligns with conservation goals and provides further insights that guide conservation practices.

The most important management actions include the effective sterilisation, removal and exclusion of introduced ungulates to limit the threat of exacerbated trampling and grazing pressures on vegetation. There has been varying success in such actions in the past, particularly for horses as some people have deeply-held colonial attachments to this species (Pickering & Norman, 2020; Worboys, 2018). Fervent opposition to removing feral horses led to the introduction and passing

of the *Kosciuszko Wild Horse Heritage Act 2018* (NSW), which was the first law in Australia to prioritise the protection of an introduced species above native species (Driscoll et al., 2019; Hagis & Gillespie, 2021). Nevertheless, the widespread and diverse impacts of introduced ungulates and resulting selective grazing are well documented (Costin, 1954; Good & Johnston, 2019), and hence monitoring populations, impacts and the effectiveness of control measures remain important research priorities (Driscoll et al., 2019; Worboys, 2018).

Other threats include those from introduced plants and plant pathogens, with future management actions required to minimise the spread of these organisms. This includes evaluating risks associated with specific species prior to being planted in and close to the Kosciuszko alpine area, as gardens and rehabilitation plantings have been the source of many introduced plants (McDougall et al., 2005; Pickering et al., 2007). Similarly, careful hygiene programs to minimise the spread of seeds and pathogen spores are required and have been implemented with varying success including wash down facilities for vehicles, bikes and footwear (Gill et al., 2018; Pickering, 2022; Rigg et al., 2018). Care is also required with the introduction materials such as soil, hay and gravel that may be contaminated. Furthermore, disturbance associated with recreation and tourism should also be minimised and mitigated where they contribute to the establishment of introduced plants and plant pathogens (Barros et al., 2020; Haider et al., 2022; Hill & Pickering, 2006; Lembrechts et al., 2016; Pickering et al., 2007; Scherrer & Pickering, 2006).

While dedicated programs to minimise the spread of some introduced plants continue, including the Hawkweed Eradication Program (Hamilton et al., 2015), such approaches need to be extended to include other species. This includes focusing on colonisation by introduced plants in the most vulnerable alpine communities. For instance, as fellfields are governed by relatively intensive periglacial disturbance regimes and have skeletal soils, they are likely to be particularly susceptible to encroachment by introduced plants (Costin, 1954; Verrall, 2018). Therefore, systematic monitoring of these and other alpine plant communities could incorporate methods currently being trailed for automated hawkweed detection in the region (Ajamian et al., 2021; Hung & Sukkarieh, 2015), where remotely piloted drones and machine learning could be used to identify introduced plant dynamics. Additionally, existing field-based LTEM must continue for alpine communities with climate change, as it has provided important insights into fellfield communities and contributed to their listings as critically endangered (Duretto, 2019a, 2019b; Eldridge, 2015; Verrall, 2018). Such monitoring could also serve broader conservation and research priorities by examining how other alpine communities are respond to climate change.

Perhaps the most difficult threat to mitigate is wildfire. However, wildfire may also be the most important threat to manage for the Kosciuszko alpine area, as it is associated with others including

erosion and post-fire colonisation of introduced plants. While climate change is predicted to intensify wildfire regimes in the regions surrounding the Kosciuszko alpine area (Clarke & Evans, 2019; Di Virgilio et al., 2019; Dowdy, 2018; Dowdy, 2020), it is more than a climate problem (Fletcher et al., 2021; Zylstra, 2013; Zylstra, 2018). Colonisation caused the decimation of Indigenous custodianship and cultural burning practices, which once managed the structure and biomass of montane and other lower elevation forests in South Eastern Australia that surround the Kosciuszko alpine area (Fletcher et al., 2021; Zylstra, 2006). However, there is no evidence for cultural burning or frequent wildfires in the Kosciuszko alpine area under Indigenous custodianship over recent millennia, and cultural burning was used sparingly in surrounding subalpine woodlands (Dodson et al., 1994; Martin, 1986, 1999; Zylstra, 2006). The removal of Indigenous fire management of montane and lower elevation forests has led to unprecedent periods of densification and biomass accumulation, where highly flammable and pyrophilic species formed contiguous fuel connectivity from ground to canopy. Climate change has then exacerbated the threat of catastrophic wildfire in these lower elevation forests in South Eastern Australia with warmer and drier conditions as well as an increase in dry lightning strikes (Collins et al., 2021; Di Virgilio et al., 2019). Both the 2003 and 2020 landscape-level wildfires in the Kosciuszko alpine area spread from lower elevation forests several kilometres away (Collins et al., 2021; Worboys, 2003). Recent western wildfire management strategies, including localised prescribed burning, have actively attempted to limit wildfire spreading to subalpine and alpine vegetation but also prioritises asset and infrastructure protection. These contemporary and less integrative wildfire mitigation strategies have resulted in mixed outcomes with fire regimes intensifying with climate change (NSW Government, 2008). Therefore, integrated and holistic management of the surrounding landscapes including montane and lower elevation forests is required to manage the threat and impacts of wildfires for subalpine woodlands as well as the Kosciuszko alpine area (Zylstra, 2013; Zylstra, 2018). Ultimately, there is the potential for the reintroduction of Indigenous fire management and cultural burning protocols to manage the threat of wildfire in much of South Eastern Australia as the climate continues to warm (Fletcher et al., 2021).

#### Research priorities for the Kosciuszko alpine area

There remain important knowledge gaps regarding the responses of vegetation in the Kosciuszko alpine area to climate change including over coming decades, as highlighted in the thesis. Thus, future research and monitoring priorities must address these gaps to better inform conservation and management. Clearly it is important to continue existing LTEM to further understand how alpine vegetation continue to respond to climate change and other threats. This includes the two field-based LTEM projects in the thesis (Chapter 3; Chapter 4), as well as other LTEM established after pastoralism (Wimbush & Costin, 1979) and wildfires (Venn et al., 2016; Verrall, 2018).

New LTEM projects that focus on other vegetation types or communities should be established, and where possible incorporate multiple spatial and environmental gradients to better delineate spatiotemporal dynamics and taxa-specific responses to climate change. What is clear from the research in this thesis, is how remote sensing provides opportunities for enhanced monitoring in the Kosciuszko alpine area (Chapter 5). Future remote sensing could capture high resolution data from orthophotography or remotely piloted drones, with the potential to automate the assessment of vegetation dynamics using machine learning and object-based image analysis for even more effective LTEM (King et al., 2020; Niederheiser et al., 2021). Such applications would be important for vegetation susceptible to trampling as well as with small and irregular distributions (e.g., fellfields and wet heathlands).

The research in the thesis again highlighted the dearth of weather stations and climate data for the Kosciuszko alpine area, which is an issue for monitoring climate change and also applies over much of the Australian Alps (Di Luca et al., 2018; Fiddes et al., 2015). Therefore, the establishment and maintenance of a network of weather stations to collect general climatic data (e.g., air temperature and precipitation) as well as more sophisticated apparatus capable of measuring microclimatic soil temperatures, nutrients and moisture content would provide valuable insights in the Kosciuszko alpine area as well as the Australian Alps. Furthermore, snow observation stations at a variety of elevations and aspects to measure snow depth, duration, temperature, liquid water content and snow water equivalent are important (Schwartz et al., 2021; Schwartz et al., 2020). Such additional climatic data will provide insights about climate change which can then be used alongside monitoring changes in vegetation and other ecological processes to better understand dynamics in this alpine area.

There are also other opportunities for further research that improves our understanding of climate change and impacts for the Kosciuszko alpine area. While there has been relatively extensive research in the past on soils (Costin, 1954; Wilson et al., 2022), there remains limited information on soil microbial communities and how they might be impacted by climate change. There is also a scarcity of research on the ecology of aquatic ecosystems in the Kosciuszko alpine area including periglacial lakes, alpine streams and pools (Benzie, 1984; Clements et al., 2016; Hancock et al., 2000). Hence, there is the potential to establish LTEM protocols to provide insights into the response of these ecosystems and processes in relation to climate change (Green, 2012), particularly with the increasing threat of wildfire and associated erosion. Monitoring arthropods in the Kosciuszko alpine area is another important research priority, as they are the primary grazers and pollinators and climate change has already caused phenological mismatches and changing plant-animal interactions (Green, 2010; Green & Green, 2022; Green & Slatyer, 2020; McDougall et al., 2018).

There are few studies on seedbanks and seed persistence of alpine species in the face of climate change (Venn et al., 2011), which is likely to be important for the future conservation of plant communities such as the critically endangered fellfields as well as threatened species (Chapter 3). Future species-specific research should focus on keystone plant species as well Kosciuszko alpine endemics and should include investigating plasticity and distribution modelling under climate change (Briceno et al., 2014; Kirchhoff, 2020; Notarnicola et al., 2021; Sritharan et al., 2021). There is also important opportunities to study biotic interactions among alpine plants (Ballantyne & Pickering, 2015; Jarrad et al., 2012; McDougall et al., 2018), and how novel interactions may contribute to future compositions as the climate changes (Alexander et al., 2015). In particular, this includes how climate change may lead to changing disturbance regimes with increasing wildfires and grazing pressure, and how these events may impact biotic interactions among alpine species (Camac et al., 2017; Camac et al., 2013; Fraser et al., 2016; Verrall, 2018).

#### 6.9: Conclusion

Climate change has caused widespread impacts on the biosphere, including in alpine ecosystems which are among the most responsive and vulnerable to warming temperatures. Climate-induced threats are amplified in the marginal alpine ecosystems of the Australian Alps, particularly in the Kosciuszko alpine area. This thesis highlights the growing importance of understanding alpine vegetation in the context of climate change globally, as well as identifying key methodologies such as LTEM. Furthermore, this thesis demonstrates the response of vegetation in the Kosciuszko alpine area to climate change in recent decades using LTEM across varying spatiotemporal scales. While there were divergent responses across the different spatiotemporal scales, some generalised trends were identified. These include the rapidly warming temperatures of the Kosciuszko alpine area as well as increasing growing season length, declining snow cover and more variable seasonal precipitation. Furthermore, elevation-, and snowmelt-dependant changes in microclimate and vegetation were identified, as well as linking vegetation dynamics to wildfire. Generally, there has been an increase in thermophilic vegetation and subsequent decline of cryophilic vegetation in response to climate change in the Kosciuszko alpine area. There was also a general trend of woody densification following wildfire, likely resulting in increased biomass and landscape flammability. These dynamics highlight the susceptibility of the vegetation to further climate changes, with predictions made regarding possible outcomes for the Kosciuszko alpine area in the coming decades. As climate change continues, the loss of distinct alpine microclimates and vegetation communities seems imminent with future compositions likely dictated by novel climates, biotic interactions, disturbances and wildfire regimes. Alongside effective climate action, there are other threats that need to be better managed to increase the resilience of alpine vegetation as temperatures warm, growing seasons increase and snow cover declines.

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# **Appendix A -** Griffith University policy for inclusion of papers within the thesis





Home > Research > Griffith Graduate Research School > Preparing your thesis > Inclusion of papers within the thesis



**Please note:** Candidates enrolled in the PhD by Prior Publication should refer to the degree finder for program-specific thesis formatting information.

HDR candidates may include one or more papers within the body of their thesis if the papers have been produced under supervision and during the period of candidature;

and where the quality is appropriate to Doctoral or Masters (Research) level research. A thesis prepared in this way is a different thesis format, it is not a different degree. There are several advantages to organising a thesis in this way:

- Preparing papers for publication saves time when preparing the thesis for examination as papers may make up one or several chapters within the thesis
- It is to your advantage to publish work from your thesis as a means of disseminating your research and developing your writing skills
- It may improve the quality of your thesis as part of your thesis has already been subjected to peer review
- Examiners may have more confidence in your thesis if they can see that you have already published your research and you will have already met one of the criteria of examination, with the thesis suitable for publication.

As a candidature requirement, all doctoral candidates are expected to have at least one peer reviewed output accepted for <u>publication during candidature</u>. Candidates are encouraged to include this publication in the body of the thesis.

Requirement for inclusion of papers within the thesis  $\checkmark$ 

# REQUIREMENT FOR INCLUSION OF PAPERS WITHIN THE THESIS

Inclusion of papers within a thesis is not a suitable thesis format for all research projects (e.g. collaborative projects where there may be several coauthors for each paper which may make it difficult for the examiner to establish the independence of the candidates work; where primary data is not collected or results obtained until late in the candidature; or where the research will not produce a logical sequence of papers that are able to be presented as an integrated whole).

Candidates should also consider whether this thesis format is an accepted practice within their discipline and likely to be received well by the thesis examiners (refer also to the examination requirements below). Candidates are required to consult with their supervisor(s) early in their candidature to determine if this thesis format is appropriate. It is expected that candidates will identify as part of the confirmation of candidature milestone if their thesis

is to be prepared in this format. Candidates should consult their Group specific guidelines in addition to the requirements detailed below. Candidates are also encouraged to attend the workshop: 'Inclusion of papers within a thesis' offered by the Griffith Graduate Research School.

Refer also to the Griffith University code for the Responsible Conduct of Research (PDF, 202k), specifically the sections pertaining to publication ethics and the dissemination of research findings, and authorship.

### Status of papers

A thesis may include papers that have been submitted, accepted for publication, or published. Some disciplines may specify a variation to the status of papers requirement, refer to your Group specific guidelines.

### Type of papers

For the purpose of this requirement, papers are defined as a journal article, conference publication, book or book chapter. Papers which have been rejected by a publisher must not be included unless they have been substantially rewritten to address the reviewers' comments or have since been accepted for publication. Some disciplines may specify a variation to the type of papers requirement, refer to your Group specific guidelines.

### Number of papers

A thesis may be entirely or partly comprised of papers. A paper maybe included as a single chapter if the paper contributes to the argument of the thesis, or several papers may form the core chapters of the theses where they present a cohesive argument. Where a thesis is entirely comprised of papers, there is no minimum requirement for the number of papers that must be included (except as noted below) and is a matter of professional judgment for the supervisor and the candidate. Overall, the material presented for examination needs to reflect the research thesis standard required for the award of the degree.

Where a thesis is entirely comprised of papers, some disciplines may specify a minimum number of papers to be included, refer to your Group specific quidelines.

### Authorship

The candidate should normally be principal author (that is, responsible for the intellectual content and the majority of writing) of any work included in the body of the thesis. Where a paper has been co-authored, the candidate is required to have made a substantial contribution to the intellectual content and writing. Co-authored work in which the candidate was a minor author can only be used and referenced in the way common to any other research publication cited in the thesis. A signature from the corresponding author is required in order to include co- authored material in the body of the thesis, refer to the declarations section below.

For co-authored papers, the attribution of authorship must be in accordance with the Griffith University code for the Responsible Conduct of Research (
PDF, 202k), which specifies that authorship must be based on substantial contributions in one or more of:

- Conception and design of the research project
- Analysis and interpretation of research data
- Drafting or making significant parts of the creative or scholarly work or critically revising it so as to contribute significantly to the final output.

Some disciplines may specify a variation to the authorship requirement, refer to your Group specific guidelines.

### Quality of papers

Candidates should endeavour to publish their research in high-quality, peer-reviewed publications. Papers to be included in the body of the thesis should be published (or submitted for publication) in reputable outlets that are held in high regard in the relevant field of research. Candidates can consult their supervisor(s) for advice on suitable publications specific to their research discipline. Some disciplines may specify quality standards that must be met for papers to be included, please see below for Group-specific quidelines.

The library provides detailed support and advice to candidates on choosing journals in which to publish. Candidates should take care to avoid 'predatory' journals and publishers.

- Scholarly publishing strategies
- Open research: Make your research visible

### Copyright

As copyright in an article is normally assigned to a publisher, the publisher must give permission to reproduce the work in the thesis and put a digital copy on the institutional repository. Information on how to seek permission is available at: Copyright and Articles in thesis. If permission cannot be obtained, students may still include the publication in the body of the thesis, however following examination the relevant chapter(s) will be redacted from the digital copy to be held by the Griffith University Library so that the copyright material is not made publicly available in the institutional repository. Students are required to advise the copyright status of each publication included in the thesis via a declaration to be inserted in the thesis, as detailed below.

Students requiring further advice regarding copyright issues can contact the Information Policy Officer on (07) 3735 5695 or copyright@griffith.edu.au.

### Group and discipline requirements

Some groups or elements may specify additional requirements for including papers within a thesis, refer below:

- · Arts, Education and Law
- Griffith Business School (PDF, 214k)
- · Griffith Health
- Griffith Sciences (PDF, 271k)

Presentation of theses when including papers V

# PRESENTATION OF THESES WHEN INCLUDING PAPERS

### General

Consult the thesis preparation and formatting guidelines for general information about the requirements for formatting the thesis. Some disciplines may specify a variation to the thesis format requirements below, refer to your Group specific guidelines.

Structure of thesis and linking chapters

The structure of the thesis will vary depending on whether the thesis is partly or entirely comprised of papers. Whatever the format, the thesis must present as a coherent and integrated body of work in which the research objectives, relationship to other scholarly work, methodology and strategies employed, and the results obtained are identified, analysed and evaluated.

A thesis should include a general introduction and general discussion to frame the internal chapters. The introduction should outline the scope of the research covered by the thesis and include an explanation of the organisation and structure of the thesis. The general discussion should draw together the main findings of the thesis and establish the significance of the work as a whole and should not just restate the discussion points of each paper.

It is important that candidates explicitly argue the coherence of the work and establish links between the various papers/chapters throughout the thesis. Linking text should be added to introduce each new paper or chapter, with a foreword which introduces the research and establishes its links to previous papers/chapters.

Depending on the content of the paper(s) and nature of research, a research methods chapter may also be necessary to ensure that any work that is not included in the paper(s), but is integral to the research, is appropriately covered. Any data omitted from a paper may also be included as an addendum to the thesis.

For further information on the thesis structure, refer to the following examples of acceptable ways to format the thesis when including papers.

• See Examples of Table of Contents (PDF, 39k)

### Format of papers

The papers may be rewritten for the thesis according to the general formatting guidelines; or they can be inserted in their published format, subject to copyright approval as detailed above.

### **Pagination**

Candidates may repaginate the papers to be consistent with the thesis. However, this is at the discretion of the candidate.

### Declarations

All theses that include papers must include declarations which specify the publication status of the paper(s), your contribution to the paper(s), and the copyright status of the paper(s). The declarations must be signed by the corresponding author (where applicable). If you are the sole author, this still needs to be specified. The declaration will need to be inserted at the beginning of the thesis, and for any co-authored papers, additional declarations will need to be inserted at the beginning of each relevant chapter. You may wish to consult the declaration requirements for inclusion of papers under Thesis Structure to ensure that you insert the correct declaration(s) within the thesis. Please note that completion of the declaration(s) does not negate the need to comply with any other University requirement relating to co-authored works as outlined in the Griffith University code for the Responsible Conduct of Research (PDF, 202k).

Examination requirements >

## **EXAMINATION REQUIREMENTS**

### Assessment by examiners

Candidates who wish to include papers within their thesis, and who have determined that this thesis format is appropriate to the research project, should also consider whether this thesis format will be well received by the thesis examiners. The inclusion of papers may negatively impact on the thesis upon assessment by the examiners where: the thesis format is not a common or accepted practice within the candidates discipline area; where the inclusion of co-authored papers makes it difficult for the examiner to establish the independence and originality of the candidates work; where the thesis does not present to the examiner as an integrated whole; or where there is too much repetition in the thesis which an examiner may view as a weakness.

Theses that include papers are subject to the same examination criteria as theses submitted in the traditional format. It should also be noted that the inclusion of published papers within the thesis does not prevent an examiner from requesting amendments to that material.

Candidates should discuss the suitability of this thesis format for examination with their supervisor(s).

### Nomination of examiners

It is the responsibility of the principal supervisor to <u>nominate thesis examiners</u>, and the process dictates that the principal supervisor must approach all nominees to determine their willingness to examine. Where a candidate's thesis is formatted to include papers, the principal supervisor must also ensure that the examiners are familiar with and/or accepting of, this thesis format.

Upon dispatch of a candidate's thesis to an examiner, the examiner will be reminded that the thesis has been formatted to include papers. The examiner will also be provided with the relevant information and regulations regarding this thesis format.

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# **Appendix B** – Supplementary materials (Chapter 5)

Treeline Stowygum Woodlands are dominated Stabupine woodlands are dominated stable by Eucatypus paracuftors or E. miphophila, and Woodlands are the inject treed trees in the Antalian Woodlands are the inject treed trees in the Antalian Apps They are wideopened, occurring the Berkens 1700 m. It is feathlands benthaled benthaliand and problem to stopes and rocky exposed areas a considerable benthaliand or stablew soils.    MA	Character	Code	Landcover Category Description	Australian Alps Classes (Mackey et al.,	Treeless Ve (McDougal	Treeless Vegetation Group & Community (McDougall & Walsh, 2007)	Kosciuszko Alpine Flora (Costin et al., 2000)
are the highest treed areas in the Australian are and the 2000 m. DAH Day Alpine Heathlands are tall closed areas found high on slopes and rocky exposed areas a found high on slopes and rocky exposed areas and the arthlands are tall closed.  WAH Wet Alpine Heathlands are low, closed Alpine Bogs, a large and along margins on waterways.  DAG DAY the for Creaslands occurring in broad Yalleys and a seepage corner on slopes with low relief and along margins on waterways and in seasonal the high tree less plans to the grassy herbfields are from extensive thick grassy swards on the high tree less plans to the grassy herbfields are low, clocury water are bare. low, open filled by snow much and precipitation.  WAG Wet Alpine Grasslands occur above 1700 m. Alpine Fens, a lapine heathland are low-velocity waterways and in seasonally while characteristic and precipitation.  FAS Fellfield Alpine Screes are bare. low, open flaw alpine heathland and herbfields growing construction grassland coccur above 1700 m. Alpine Fens, and are underlain with a large and bridge and herbfields growing on saled summits, and leeward hollows where late than the procurative solis that are alpine heathlands and herbfields growing on saled along the peathlands and herbfields growing construction and precipitation.  They occur above 1700 m. Alpine Fens, and are underlain by water-retentive solis that are alpine heathland and herbfields growing constructions are bare. low, open selected and than alpine heathlands and herbfields growing constructions are bare and the late of the steps of	Treeline	TSW	Treeline Snowgum Woodlands are dominated	2015) Subalpine		N/A	Subalpine woodland (Eucalyptus
DAH Dry Alpine Heathlands are tall closed heathland curron shows lost solves and rocky exposed areas on shallow soils.  WAH Wet Alpine Heathlands cocurring above 1700 m. It is found high on slopes and rocky exposed areas on shallow soils.  WAH Wet Alpine Heathlands cocurring in broad valleys and heathland along margins on waterways.  DAG Where a provided a long margins on waterways.  WAG Wet Alpine Grasslands occurration to the grassy heathfields of the steep or concave high elevation slopes.  WAG Wet Alpine Grasslands occurration on the high treeless plains to the grassy heathfields of the steep or concave high elevation slopes.  WAG Wet Alpine Grasslands occurration and needed with elevation slopes.  WAG Wet Alpine Grasslands occurration on valerways and needed along margins on waterways.  WAG Wet Alpine Grasslands occurration solpes.  WAG wet Alpine Grasslands occurration solpes.  WAG wet Alpine Grasslands occurration solpes with interest proving season.  They occurrate the proving season.  They occurrate alpine heathland and herefields growing season.  They occurration of elevations on the high treeless plains to the grassy herefields and precipitation.  They occurrate the growing season.  They occurrate the growing season of elevations.	Snowgum		by Eucalyptus pauciflora or E. niphophila, and are the highest treed areas in the Australian Alps. They are widespread, occurring generally between 1200 m and up to 2000 m.	Woodlands & Low Open Forests			mphophila)
WAH         Wet Alpine Heathlands are low, closed         Alpine Bogs, heathland         1-2 by acris moist heathland         Richea - Carpha - Sphagmum wet heathland           DAG         Dry Alpine Grasslands occurring in broad valleys and along margins on vaterways.         Alpine Heathland         TVII.53         Podocarpus - Epacris open heathland           DAG         Dry Alpine Grasslands occur above 1700 m vaterways and in seasonally along the high treeless plains to the grassy herbfields of the steep or concave high elevation slopes.         Herbfields VII.22         Poa - Celmicia grassland valleys, and are low-velocity waterways and in seasonally along vater-retentive soils that are filled by snow melt and precipitation.         Alpine Grasslands         1.5         Alpine herbfield           FAS         Fellfield Alpine Screes are bare, low, open skeletal soils of windswept ridges and summits, and leeward hollows where late individual grass and skeletal soils of windswept ridges and summits, and leeward hollows where late individual grass and skeletal soils of windswept ridges and summits, and leeward hollows where late individual grass and skeletal soils of windswept ridges and summits, and leeward hollows where late individual grass and skeletal soils of windswept ridges and summits, and leeward hollows where late individual grass and skeletal soils of windswept ridges and summits, and leeward hollows where late individual grass and skeletal soils of windswept ridges and summits, and leeward hollows where late individual grass and summits, and leeward hollows where late	Dry Alpine Heathlands	DAH	Dry Alpine Heathlands are tall closed heathlands occurring above 1700 m. It is found high on slopes and rocky exposed areas on shallow soils.	Alpine Heathland	VII-23 X-39 XIV-46 XVI-51	Grevillea – Nematolepis open heathland Epacris – Kunzea open heathland Nematolepis – Prostanthera closed heathland Austrodanthonia – Grevillea open heathland	Heath (Oxylobium — Podocarpus — Kunzea)
DAG Dry Alpine Grasslands occur above 1700 m  where snow cover is more prolonged. They aring a from extensive thick grassy swards on the high treeless plains to the grassy herbfields of the step or concave high elevation slopes.  WAG Wet Alpine Grasslands occur above 1700 m  They occur above 1700 m  Alpine Fens, III-10  Alpine Fens, III-10  Alpine valley grassland  VI-13  Poa - Chonizia grassland  VI-13  Poa - Euphrasia grassland  VI-19  Chionochloa grassland  VI-19  Chionochloa grassland  VI-19  Chionochloa grassland  VI-19  Chionochloa grassland  Alpine Fens, III-10  Short alpine herbfield  Fen  III-10  Short alpine herbfield  Snowpatch  skelelat solis of windswept ridges and summits, and leeward hollows where late thawing snow truncates the growing season. They occur above 1700 m.  ARO  Rocky Outcrops are open rocky areas range of elevations.	Wet Alpine Heathlands	WAH	Wet Alpine Heathlands are low, closed heathlands occurring in broad valleys and seepage zones on slopes with low relief and along margins on waterways.	Alpine Bogs, Alpine Heathland	I-2 I-4 XVIII-53	Richea – Carpha – Sphagnum wet heathland Epacris moist heathland Podocarpus – Epacris open heathland	Heath ( <i>Epacris</i> ) Raised bog ( <i>Epacris</i> – Sphagnum)
the high treeless plains to the grassy herbfields of the steep or concave high elevation slopes.  WAG Wet Alpine Grasslands occur above 1700 m are a low-velocity water-verentive soils that are underlain by water-retentive soils that are filled by snow melt and precipitation.  FAS Fellfield Alpine Screes are bare, low, open alpine hearthlands and herbfields growing on skeletal soils of windswept ridges and summits, and leeward hollows where late thawing snow truncates the growing season.  They occur above 1700 m.  ARO Rocky Outcrops are open rocky areas including screes slopes, with little or sparse outcrops are open rocky areas a range of elevations.	Dry Alpine Grasslands	DAG	Dry Alpine Grasslands occur above 1700 m where snow cover is more prolonged. They range from extensive thick grassy swards on	Alpine Grasslands & Herbfields	VI-17 VI-18 VII-22	Poa – Celmisia snowpatch grassland Poa – Uncinia grassland Poa – Euphrasia grassland	Tall alpine herbfield a (Celmisia – Poa)
WAG Wet Alpine Grasslands occur above 1700 m  NAG Wet Alpine Grasslands occur above 1700 m  near low-velocity waterways and in seasonally and near low-velocity waterways and in seasonally and precipitation.  Imundated depressions and valleys, and are underlain by water-retentive soils that are filled by snow melt and precipitation.  ARS Fellfield Alpine Screes are bare, low, open skeletal soils of windswept ridges and summits, and leeward hollows where late thawing snow truncates the growing season.  They occur above 1700 m.  ARO Rocky Outcrops are open rocky areas including scree slopes, with little or sparse vegetation, occurring on steep slopes at a range of elevations.			the high treeless plains to the grassy herbfields of the steep or concave high elevation slopes.		VI-19	Chionochloa grassland	Tall alpine herbfield b (Brachyscome – Austrodanthonia)
underlain by water-retentive soils that are filled by snow melt and precipitation.  d FAS Fellfield Alpine Screes are bare, low, open skeletal soils of windswept ridges and summits, and leeward hollows where late thawing snow truncates the growing season.  They occur above 1700 m.  ARO Rocky Outcrops are open rocky areas including scree slopes, with little or sparse vegetation, occurring on steep slopes at a range of elevations.	Wet Alpine Grasslands	WAG		Alpine Fens, Alpine Grasslands & Herbfields	I-6	Alpine valley grassland Fen	Sod tussock grassland Valley bog (Carex – Sphagnum) Fen (Carex gauidchaudiana)
d FAS Fellfield Alpine Screes are bare, low, open alpine heathlands and herbfields growing on skeletal soils of windswept ridges and summits, and leeward hollows where late thawing snow truncates the growing season.  ARO Rocky Outcrops are open rocky areas including scree slopes, with little or sparse vegetation, occurring on steep slopes at a range of elevations.			underlain by water-retentive soils that are filled by snow melt and precipitation.		III-10 VII-20	Short alpine herbfield Short turf snowpatch grassland	Short alpine herbfield (Plantago - Neopaxia)
thawing snow truncates the growing season.  They occur above 1700 m.  ARO Rocky Outcrops are open rocky areas including scree slopes, with little or sparse vegetation, occurring on steep slopes at a range of elevations.	Fellfield Alpine Screes	FAS	Felifield Alpine Screes are bare, low, open alpine heathlands and herbfields growing on skeletal soils of windswept ridges and summits, and leeward hollows where late	Feldmark & Snowpatch	X-40	Epacris – Veronica feldmark	Feldmark a ( <i>Epacris – Veronica</i> )
ARO Rocky Outcrops are open rocky areas Open Rocky including scree slopes, with little or sparse outcrops vegetation, occurring on steep slopes at a range of elevations.			thawing snow truncates the growing season. They occur above 1700 m.		IV-12	Coprosma – Colobanthus snowpatch feldmark	Feldmark b (Coprosma – Colobanthus)
	Alpine Rocky Outcrops	ARO	Rocky Outcrops are open rocky areas including scree slopes, with little or sparse vegetation, occurring on steep slopes at a range of elevations.	Open Rocky outcrops		N/A	

Lin et al (2021) Lin et al (2021) Lin et al (2021) Reference Landsat Fable S2. Multi-dimensional features ingested by recursive feature elimination, with the seven selected features used to classify growing season composites in bold. N/A N/A N/A  $MSAVI = \frac{(2 \times NIR + 1) - \sqrt{(2 \times NIR + 1)^2 - 8(NIR - R)}}{(2 \times NIR + 1)^2 - 8(NIR - R)}$  $EVI = 2.5 \left( \underbrace{NIR + 6 \times R - 7.5 \times B + 1}_{VIR} \right)$ ST\_B6 (L5, L7); ST\_B10 (L8) SR\_B5 (L5, L7); SR\_B6 (L8) SR\_B2 (L5, L7); SR\_B3 (L8) SR\_B3 (L5, L7); SR\_B4 (L8) SR\_B4 (L5, L7); SR\_B5 (L8) SR B7 (L5, L7); SR B7 (L8) SR B1 (L5, L7); SR B2 (L8)  $GARI = \frac{1}{NIR + (1.7 \times (B - R))}$  $NIR - (1.7 \times (B - R))$ NIR - RDerived from 2 m LiDAR Derived from 2 m LiDAR Derived from 2 m LiDAR  $NIR - (2 \times R - B)$  $ARVI = \underbrace{NIR + (2 \times R - B)}_{}$  $NBR = \frac{MIR + SWIR2}{NIR + SWIR2}$   $NBR2 = \frac{SWIR1}{NIR - SWIR1}$  $NDVI = \overline{NIR + R}$  NIR - R $SAVI = 1.5 \left( \overline{NIR + R + 0.5} \right)$  $NDMI = \frac{NIR + SWIR1}{NIR - R}$ NIR - SWIR2 DVI = NIR - RAtmospherically Resistant Vegetation Index Digital Elevation Model-derived Elevation Modified Soil Adjusted Vegetation Index Normalised Difference Vegetation Index Digital Elevation Model-derived Aspect Green Atmospherically Resistant Index Normalised Difference Moisture Index Digital Elevation Model-derived Slope Soil Adjusted Vegetation Index Difference Vegetation Index Enhanced Vegetation Index Normalised Burn Ratio 2 Normalised Burn Ratio Shortwave Infrared 2 Shortwave Infrared 1 Near Infrared Band/Index Description Thermal Green Red MSAVI DEME DEMA SWIR2 DEMS SWIR1 NBR2 NDMI NDVI GARI ARVI SAVI NBR DVI TIR EVI Ö

Lin et al (2021)

5DVI = NIR - G

Green Difference Vegetation Index

GDVI

Band/Index	Description	Formula	Reference
GEMI	Global Environmental Monitoring Index	$GEMI = \frac{2(NIR \times NIR) + (1.5 \times NIR) + (0.5 \times R)}{NIR + R + 0.5} \times \left(0.75 \left(\frac{2((NIR \times NIR) - (R \times R)) + ((1.5 \times NIR) + (0.5 \times R))}{NIR + R + 0.5}\right)\right) - \left(\frac{R - 0.125}{1} - R\right)$	Lin et al (2021)
GNDVI	Green Normalised Difference Vegetation Index	$GNDVI = \frac{(NIR - G)}{(NIR + G)}$	Lin et al (2021)
GRVI	Green Ratio Vegetation Index	$GRVI = \frac{NIR}{G}$	Lin et al (2021)
GVI	Green Vegetation Index	$GVI = (-0.2848 \times B) + (-0.2435 \times B) + (-0.5436 \times R) + (0.7243 \times NIR) + (0.0840 \times SWIR1) + (-0.18 \times SWIR2)$	Lin et al (2021)
IPVI	Infrared Percentage Vegetation Index	$IPVI = \frac{NIR + R}{2} \times \left(\frac{R - G}{R + G} + 1\right)$	Lin et al (2021)
LAI	Leaf Area Index	$LAI = \left(3.618 \left(2.5 \left(\frac{NIR - R}{NIR + 6 \times R - 7.5 \times B + 1}\right)\right)\right) - 0.118$	Lin et al (2021)
MSR	Modified Simple Ratio	$MSR = \frac{NIR - 1}{\frac{R}{R} + 1}$	Lin et al (2021)
NLI	Non-Linear Index	$NLI = \frac{NIR^2 - R}{NIR^2 + R}$	Lin et al (2021)
OSAVI	Optimised Soil Adjusted Vegetation Index	$OSAVI = \frac{1.5(NIR - R)}{NIR + R + 0.16}$	Lin et al (2021)
RDVI	Renormalised Difference Vegetation Index	$RDVI = \frac{NIR - R}{\sqrt{NIR + R}}$	Lin et al (2021)
SR	Simple Ratio	$SR = \frac{NIR}{R}$	Lin et al (2021)
TDVI	Transformed Difference Vegetation Index	$TDVI = \sqrt{0.5 + \frac{NIR - R}{NIR + R}}$	Lin et al (2021)
VARI	Visible Atmospherically Resistant Index	$VARI = \frac{G - R}{G + R - B}$	Lin et al (2021)
ATSAVI	Adjusted Transformed Soil Adjusted Vegetation Index	$ATSAVI = 1.22 \left( \frac{NIR - 1.22 \times R - 0.03}{1.22 \times NIR + R - 1.22 \times 0.03 + 0.08(1 + 1.22^2)} \right)$	Henrich et al. (2012)

Band/Index	Description	Formula	Reference
BWDRVI	Blue-Wide Dynamic Range Vegetation Index	$BWDRVI = \frac{(0.1 \times NIR) - B}{(0.1 \times NIR) + B}$	Henrich et al. (2012)
GCVI	Green Chlorophyll VI	$GCVI = {NIR \choose \overline{G}} - 1$	Henrich et al. (2012)
CVI	Chlorophyll VI	$CVI = NIR \times \left(\frac{R}{G \times G}\right)$	Henrich et al. (2012)
CI	Coloration Index	$CI = \frac{R - B}{R}$	Henrich et al. (2012)
CTVI	Corrected Transformed VI	$CTVI = \left(\frac{R - G}{R + G} + 0.5 \right) \times \sqrt{\frac{R - G}{ R + G  + 0.5 }}$	Henrich et al. (2012)
GVMI	Global Vegetation Moisture Index	$GVMI = \frac{(NIR + 0.1) - (SWIR2 + 0.02)}{(NIR + 0.1) + (SWIR2 + 0.02)}$	Henrich et al. (2012)
GLI	Green Leaf Index	$GLI = \frac{(2 \times G) - R - B}{(2 \times G) + R + B}$	Henrich et al. (2012)
GOSAVI	Green Optimised Soil Adjusted VI	$GOSAVI = \frac{NIR - G}{NIR + G + 0.16}$	Henrich et al. (2012)
GSAVI	Green Soil Adjusted VI	$GSAVI = \frac{NIR - G}{NIR + G + 0.5} \times 1.5$	Henrich et al. (2012)
GBNDVI	Green-Blue NDVI	$GBNDVI = \frac{NIR - (G+B)}{NIR + (G+B)}$	Henrich et al. (2012)
GRNDVI	Green-Red NDVI	$GRNDVI = \frac{NIR - (G + R)}{NIR + (G + R)}$	Henrich et al. (2012)
INI	Intensity	$INT = \frac{1}{30.5} \times (R + G + B)$	Henrich et al. (2012)
MIDIRVI	Mid Infra-red VI	$MIDIRVI = \frac{NIR}{SWIR1}$	Henrich et al. (2012)

Band/Index	Description	Formula	Reference
NORMG	Normalised Green	$NORMG = \frac{G}{NIR + R + G}$	Henrich et al.
NORMIR	Normalised Infrared		Henrich et al. (2012)
NORMR	Normalised Red		Henrich et al. (2012)
NDBaI	Normalised Difference Bareness Index	RM RM	Henrich et al. (2012)
NDBSI	Normalised Difference Bare Soil Index	VIR - B) $VIR + B$ )	Henrich et al. (2012)
NDGRI	Normalised Difference Green – Red Index	$NDGRI = \frac{G - R}{G + R}$	Henrich et al. (2012)
NDNIRBI	Normalised Difference NIR – Blue Index	<u>- B</u> + B	Henrich et al. (2012)
NDNIRGI	Normalised Difference NIR – Green Index		Henrich et al. (2012)
NDMNI	Normalised Difference Modified NIR Index/Normalised Burn Ratio	R2 R2	Henrich et al. (2012)
NDRBVI	Normalised Difference Red – Blue VI	+ B) + B)	Henrich et al. (2012)
NDRGRI	Normalised Difference Red – Green Redness Index		Henrich et al. (2012)
NDRI	Normalised Difference Rock Index	$NDRI = \frac{SWIR1 - R}{SWIR1 + R}$	Henrich et al. (2012)
NDWI	Normalised Difference Water Index		Henrich et al. (2012)
PNDVI	PAN NDVI	G+R+B) $G+R+B$ )	Henrich et al. (2012)
R54	Band Ratio 54		Henrich et al. (2012)
R35	Band Ratio 35		Henrich et al. (2012)
SRDI	Simple Ratio Drought Index		Henrich et al. (2012)

Band/Index	Band/Index Description	Formula	Reference
SRGI	Simple Ratio Green Index	$SRGI = \frac{SWIR2}{G}$	Henrich et al. (2012)
SRRI	Simple Ratio Red Index	$SRRI = \frac{SWIR2}{R}$	Henrich et al. (2012)
SLAVI	Specific Leaf Area VI	$SLAVI = \frac{NIR}{R + SWIR2}$	Henrich et al. (2012)
TCV	Tasselled Cap Vegetation	$TCV = (-0.2848 \times B) - (0.2435 \times G) - (0.5436 \times R) + (0.7243 \times NIR) + (0.084 \times SWIR1) - (0.18 \times SWIR2)$	Henrich et al. (2012)
TCW	Tasselled Cap Wetness	$TCW = (0.1509 \times B) + (0.1973 \times G) + (0.3279 \times R) + (0.3406 \times NIR) - (0.7112 \times SWIR1) - (0.4572 \times SWIR2)$	Henrich et al. (2012)
TVI	Transformed VI	$TVI = \sqrt{\frac{R - G}{R + G} + 0.5}$	Henrich et al. (2012)

**Table S3.** Selected features from Recursive Feature Elimination using 10-fold cross-validation repeated five times via the means of "Caret" package in R.

Number of	Accura	icy	Kappa Selecter		
features	%	SD	Value	SD	Selected
1	0.8465	0.0158	0.7842	0.0218	
2	0.8883	0.0103	0.8416	0.0147	
3	0.9347	0.0085	0.9077	0.0120	
4	0.9593	0.0070	0.9426	0.0100	
5	0.9648	0.0080	0.9503	0.0114	
6	0.9744	0.0058	0.9640	0.0082	
7	0.9761	0.0047	0.9664	0.0066	:
8	0.9758	0.0051	0.9659	0.0073	
9	0.9725	0.0057	0.9613	0.0081	
10	0.9715	0.0057	0.9599	0.0081	
11	0.9708	0.0053	0.9589	0.0074	
12	0.9711	0.0055	0.9593	0.0078	
13	0.9703	0.0059	0.9582	0.0083	
14	0.9704	0.0060	0.9583	0.0084	
15	0.9708	0.0058	0.9590	0.0082	
16	0.9709	0.0055	0.9590	0.0077	
17	0.9703	0.0058	0.9582	0.0081	
18	0.9703	0.0057	0.9582	0.0080	
19	0.9694	0.0069	0.9569	0.0097	
20	0.9697	0.0061	0.9573	0.0086	
21	0.9693	0.0060	0.9567	0.0084	
22	0.9698	0.0059	0.9574	0.0084	
23	0.9699	0.0058	0.9576	0.0082	
24	0.9694	0.0057	0.9568	0.0080	
25	0.9706	0.0056	0.9586	0.0079	
26	0.9707	0.0062	0.9587	0.0088	
27	0.9708	0.0060	0.9588	0.0085	
28	0.9699	0.0060	0.9576	0.0085	
29	0.9704	0.0061	0.9583	0.0086	
30	0.9705	0.0063	0.9584	0.0089	
31	0.9703	0.0059	0.9582	0.0084	
32	0.9703	0.0063	0.9581	0.0089	
33	0.9697	0.0059	0.9573	0.0084	
34	0.9696	0.0060	0.9572	0.0084	
35	0.9692	0.0060	0.9566	0.0086	
36	0.9697	0.0063	0.9574	0.0089	
37	0.9699	0.0059	0.9576	0.0083	
38	0.9696	0.0064	0.9572	0.0090	
39	0.9697	0.0064	0.9573	0.0091	
40	0.9697	0.0062	0.9573	0.0087	
41	0.9693	0.0066	0.9568	0.0093	
	-				

Number of	Accura	cy	Карра				
features	%	SD	Value	SD	Selected		
43	0.9690	0.0061	0.9564	0.0087			
44	0.9690	0.0067	0.9563	0.0094			
45	0.9686	0.0062	0.9558	0.0087			
46	0.9686	0.0062	0.9558	0.0088			
47	0.9682	0.0061	0.9552	0.0086			
48	0.9685	0.0065	0.9557	0.0092			
49	0.9688	0.0060	0.9560	0.0085			
50	0.9691	0.0061	0.9564	0.0086			
51	0.9686	0.0067	0.9558	0.0094			
52	0.9679	0.0063	0.9548	0.0089			
53	0.9684	0.0063	0.9554	0.0089			
54	0.9679	0.0062	0.9548	0.0087			
55	0.9681	0.0066	0.9551	0.0093			
56	0.9683	0.0064	0.9553	0.0091			
57	0.9681	0.0064	0.9550	0.0090			
58	0.9679	0.0064	0.9548	0.0090			
59	0.9676	0.0061	0.9544	0.0086			
60	0.9677	0.0063	0.9544	0.0089			
61	0.9680	0.0060	0.9549	0.0084			
62	0.9676	0.0060	0.9543	0.0085			
63	0.9675	0.0061	0.9541	0.0086			
64	0.9682	0.0062	0.9552	0.0088			
65	0.9680	0.0060	0.9549	0.0086			
66	0.9678	0.0061	0.9546	0.0086			
67	0.9681	0.0061	0.9551	0.0086			
68	0.9678	0.0064	0.9547	0.0090			
69	0.9678	0.0061	0.9547	0.0086			

**Table S4.**: Optimised Random Forest model (p = 7; ntree = 500; mtry = 2; Validation accuracy = 97.98%; OOBerr = 2.02%) confusion matrix and variable importance.

<b>Confusion M</b>	<b>Iatrix</b>							
	TSW	DAH	WAH	DAG	WAG	FAS	ARO	Error
TSW	3963	3	0	0	0	0	0	0.000756
DAH	11	951	7	10	1	2	0	0.031568
WAH	6	19	680	1	3	0	0	0.040903
DAG	0	4	0	2238	1	5	1	0.004891
WAG	0	17	5	21	177	1	0	0.199095
FAS	0	4	0	44	0	658	1	0.069307
ARO	2	0	0	9	0	2	68	0.160494
Variable im	portance p	er landcov	er class					
DEME	91.92	73.81	84.36	74.23	54.16	37.02	29.53	
DEMS	40.29	68.57	123.40	57.87	70.90	39.09	38.09	
TIR	31.18	44.95	53.13	50.34	32.54	50.99	30.07	
DEMA	33.48	49.56	39.85	60.25	36.17	44.79	21.15	
CI	25.30	50.34	41.25	63.10	37.89	38.30	31.64	
NBR2	51.65	84.38	41.14	74.89	38.94	29.08	46.07	
GARI	23.88	46.27	43.75	59.95	31.18	45.57	16.17	

**Table S5.** Linear regression between Year and climatic variables from Australian Gridded Climate Data (AGCDv1 -  $T_{min}$ ,  $T_{mean}$ ,  $T_{max}$ ,  $P_{annual}$ ,  $P_{summer}$ ,  $P_{autumn}$ ,  $P_{winter}$ ,  $P_{spring}$ ) and Snowy Hydro Spencers Creek Snow Course (Snow Cover Metre-days).

Doto	Data Variable By ANOVA		OVA	Regression						
Data	variable	$\mathbb{R}^2$	df	F	Model	Estimate	SE	T	p	
	т	0.225	1-109	54.310	Intercept	0.438	0.095	4.628	< 0.001	***
	$T_{\min}$	0.335	1-109	34.310	Slope	0.010	0.001	7.370	< 0.001	***
	$T_{mean}$	0.359	1-109	60.515	Intercept	4.965	0.094	53.016	< 0.001	***
	1 mean	0.557 1-107 00.515	00.515	Slope	0.010	0.001	7.779	< 0.001	***	
	$T_{\text{max}}$	0.245	1-109	35.006	Intercept	9.493	0.128	73.930	< 0.001	***
	1 max	0.243	1-109	33.000	Slope	0.010	0.002	5.917	< 0.001	***
v.1	Pannual	0.003	1-119	0.344	Intercept	1721.140	66.729	25.793	< 0.001	***
Á	<b>r</b> annual	0.003	1-119	0.344	Slope	-0.561	0.957	-0.586	0.559	
AGCD v1	P <sub>summer</sub>	0.035	1-118	4.292	Intercept	272.686	22.012	12.388	< 0.001	***
Ā	<b>□</b> summer	0.033	1-110	4.292	Slope	0.651	0.314	2.072	0.041	*
	D	0.003	1-119	0.375	Intercept	388.169	28.942	13.412	< 0.001	***
	$P_{autumn}$	0.003	1-119	0.575	Slope	-0.254	0.415	-0.613	0.541	
	<b>D</b> .	0.038	1-119	4.684	Intercept	567.780	31.165	18.219	< 0.001	***
	$\mathbf{P}_{\mathrm{winter}}$	0.038	1-119	4.004	Slope	-0.968	0.447	-2.164	0.032	*
	<b>D</b> .	0.001	1-119	0.004	Intercept	495.788	28.485	17.405	< 0.001	***
	P <sub>spring</sub>	0.001	1-119	0.004	Slope	0.026	0.409	0.065	0.948	
Snow	Snow	0.100	1-67	7.339	Intercept	288.169	42.637	6.759	< 0.001	***
S	cover				Slope	-1.274	0.470	-2.709	0.009	**

**Table S6**: Decadal area and mean elevation weighted by area for each vegetation type with annual rate of change ( $\_B = Burnt$  in 2003;  $\_UB = Unburnt$  in 2003).

	Vegetation	3					nge			
	type	1990	2000	2010	2020	90-00	00-10	10-20	90-20	00-20
	TSW	52.36	82.26	37.58	122.94	2.99	-4.47	8.54	2.35	2.03
	TSW_UB	11.40	16.42	12.57	30.99	0.50	-0.39	1.84	0.65	0.73
	TSW_B	40.96	65.84	25.01	91.96	2.49	-4.08	6.69	1.70	1.31
	DAH	143.69	137.77	159.69	93.23	-0.59	2.19	-6.65	-1.68	-2.23
	DAH_UB	63.12	72.14	73.68	49.40	0.90	0.15	-2.43	-0.46	-1.14
	DAH_B	80.58	65.63	86.02	43.83	-1.49	2.04	-4.22	-1.22	-1.09
	WAH	153.73	183.92	164.40	133.09	3.02	-1.95	-3.13	-0.69	-2.54
(2)	WAH_UB	36.01	53.61	50.02	43.81	1.76	-0.36	-0.62	0.26	-0.49
Area (km²)	WAH_B	117.72	130.31	114.38	89.28	1.26	-1.59	-2.51	-0.95	-2.05
vrea	DAG	47.88	25.87	36.53	53.25	-2.20	1.07	1.67	0.18	1.37
₹	DAG_UB	44.00	24.63	27.00	37.84	-1.94	0.24	1.08	-0.21	0.66
	DAG_B	3.88	1.23	9.52	15.41	-0.26	0.83	0.59	0.38	0.71
	WAG	47.32	16.82	49.50	36.31	-3.05	3.27	-1.32	-0.37	0.97
	WAG_UB	23.11	12.00	17.37	11.71	-1.11	0.54	-0.57	-0.38	-0.01
	WAG_B	24.21	4.82	32.13	24.60	-1.94	2.73	-0.75	0.01	0.99
	FAS	7.97	6.90	6.72	13.82	-0.11	-0.02	0.71	0.20	0.35
	FAS_UB	7.94	6.90	5.72	11.61	-0.10	-0.12	0.59	0.12	0.24
	FAS_B	0.03	0.00	1.01	2.21	< 0.01	0.10	0.12	0.07	0.11
	TSW	1782.11	1786.03	1779.60	1779.57	0.39	-0.64	0	-0.08	-0.32
	TSW_UB	1793.49	1796.78	1795.32	1792.05	0.34	-0.16	-0.32	-0.04	-0.24
	TSW_B	1779.59	1778.71	1766.50	1770.42	-0.08	-1.22	0.39	-0.3	-0.41
	DAH	1851.48	1878.64	1863.59	1885.01	2.71	-1.5	2.14	1.11	0.32
s.L.)	DAH_UB	1885.45	1915.29	1907.38	1922.94	2.98	-0.79	1.55	1.24	0.38
m a	DAH_B	1825.79	1838.36	1826.09	1842.27	1.25	-1.22	1.61	0.54	0.20
by area (m a.s.l.)	WAH	1814.64	1824.49	1811.28	1827.53	0.98	-1.32	1.62	0.42	0.15
by a	WAH_UB	1845.26	1856.50	1852.17	1860.80	1.12	-0.43	0.86	0.51	0.21
	WAH_B	1805.94	1811.32	1793.39	1811.21	0.53	-1.79	1.78	0.17	-0.01
eigh	DAG	2013.69	2034.73	2019.71	2000.94	2.1	-1.5	-1.87	-0.42	-1.69
on w	DAG_UB	2017.85	2037.18	2039.76	2021.79	1.93	0.25	-1.79	0.13	-0.77
vati	DAG_B	1973.15	1985.93	1962.85	1949.75	1.27	-2.3	-1.3	-0.77	-1.81
n ele	WAG	1851.45	1910.35	1860.00	1829.05	5.89	-5.03	-3.09	-0.74	-4.07
Mean elevation weighted	WAG_UB	1893.42	1944.25	1936.36	1884.20	5.08	-0.78	-5.21	-0.3	-3.00
F	WAG_B	1812.50	1825.95	1818.72	1802.81	1.34	-0.72	-1.59	-0.32	-1.16
	FAS	2040.90	2049.33	2033.42	2024.77	0.84	-1.59	-0.86	-0.53	-1.23
	FAS_UB	2041.62	2049.32	2044.57	2034.37	0.77	-0.47	-1.02	-0.24	-0.75
	FAS_B	2044.55	20 17.32	1970.03	1975.25	0.77	0.77	0.52	-2.3	98.76



Figure S1: Scarcely vegetated Alpine Rocky Outcrop (ARO) in the study area.

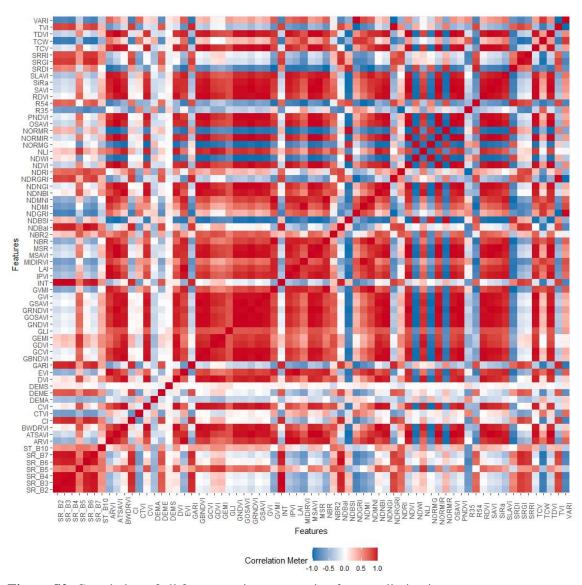
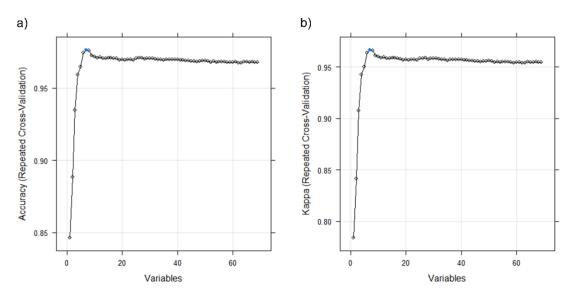


Figure S2: Correlation of all features prior to recursive feature elimination.



**Figure S3**: Most important variables (7) based on the least a) Accuracy and b) Kappa for five times repeated, 10-fold cross-validation for LANDSAT 8 composite data for 2020 growing season (01/01/2020 - 30/05/2020).

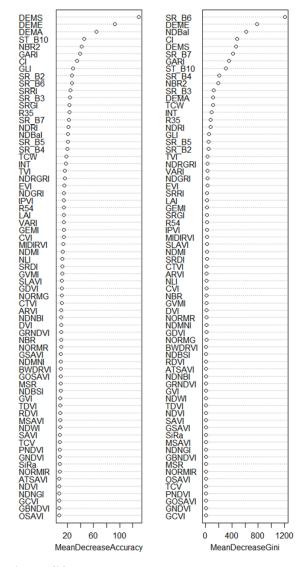
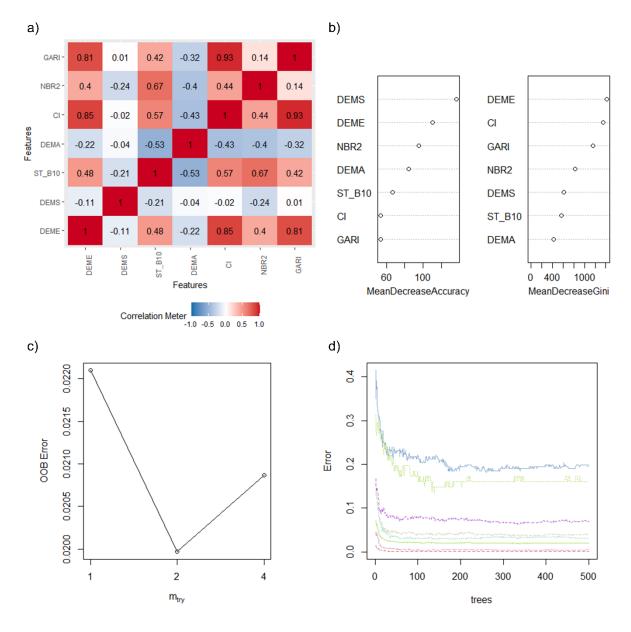


Figure S4: Feature importance ranked by mean percentage decrease in Accuracy and Gini Index



**Figure S5**: Optimised Random Forest model parameters after recursive feature elimination showing a) feature correlation, b) feature importance ranked by mean percentage decrease in Accuracy and Gini Index, c) optimised *mtry* based and d) optimal *ntree* for each feature.

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