

Climate change and trajectories of vegetation change in an alpine heathland

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Abstract

Global warming is predicted to have substantial effects on vegetation dynamics in mountainous and high latitude ecosystems worldwide. In order to predict plausible trajectories of future vegetation change, we must first determine how temperature influences rates and directions of potential changes. Furthermore, we must quantify how these rates are influenced by disturbance and biotic interactions and how these may interact with climate. We also require detailed knowledge about how these interactive effects are likely to influence the establishment, growth and survival of seedlings; a life stage to which vegetation dynamics are sensitive and one which is highly vulnerable to changes in climate, disturbance and biotic interactions.

In this thesis, I examine these issues in open heathland on the Bogong High Plains, Victoria, Australia. Using data derived from a combination of long-term monitoring, field and experimental studies I (1) demonstrate how one may model rates of vegetation change; (2) show how higher temperatures interact with climate-mediated disturbance, and biotic conditions to influence these rates; (3) determine how these effects are likely to influence vegetation change in alpine heathland under future climate and burned and unburned conditions. I then focused on examining how shrub dynamics may change under global warming. Specifically I determine: (1) How fire, elevation, adult density and topographic wetness influence shrub seedling establishment; (2) whether warmer post-fire conditions influence rates of seedling growth and mortality; (3) whether experimental growth responses are validated along by field surveys; (4) whether the proximity to *Poa hiemata* (the dominant grassland species) influences shrub seedling growth and mortality rates; and (5) whether *Poa* effects are altered by warmer conditions. I then synthesise all this information to examine whether global warming is likely to strengthen an existing feedback loop between shrubs and fire.

I found that warming affected rates of life form cover change by altering post-fire regeneration and by reducing negative effects of competing life forms. In terms of shrubs, I found that fire increased shrub seedling establishment by more than 20-fold. Experimental warming of 1.2°C doubled seedling growth rates and increased survival. Warming also changed tussock grass interactions from facilitative to competitive. The consequences of these changes suggest that global warming will strengthen an existing feedback loop leading to changes in vegetation and fire regimes.

Declaration

This is to certify that:

- i) the thesis comprises only my original work towards the PhD except where indicated in the Preface,
- ii) due acknowledgement has been made in the text to all other material used,
- iii) the thesis is fewer than 100,000 words in length, exclusive of tables, maps, bibliographies and appendices.



James S. Camac

March 2014

Preface

In order to articulate a coherent and comprehensive narrative I have structured the thesis into two high impact publishable units. These chapters are currently in review as indicated below. Furthermore, appended to this thesis are published papers I authored (1) or co-authored (4; including a book chapter) while undertaking my PhD that are related to this thesis, but do not themselves form part of it. The contribution of each author to each thesis chapter and published papers is described below.

Chapter 2.

Chapter 2 uses data derived from a medium-term warming experiment to develop statistical models that examine how rates of life form cover change are influenced by warming, fire and life form interactions. This chapter is currently in review at *Oecologia*.

Camac, J.S., Williams, R.J., Wahren, C-H., Jarrad, F.C., Hoffmann, A.A., Vesk, P.A. (in review) Modeling rates of life form cover change in burned and unburned alpine heathland subject to experimental warming. *Oecologia*.

Camac, J.S. (PhD Candidate)

Collected data, conducted analysis and wrote manuscript.

Williams, R.J.

Supervised development of work and edited manuscript.

Wahren, C-H.

Collected data, supervised development of work and edited manuscript.

Jarrad, F.C.

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Hoffmann, A.A.

Supervised development of work and edited manuscript.

Vesk, P.A.

Supervised development of work, aided with data analysis and edited manuscript.

Chapter 3.

Chapter 3 uses data derived from warming experiments and an extensive field survey to examine five critical questions related to shrub dynamics. It then synthesizes this information into a conceptual model that determines whether global warming is likely to strengthen an existing feedback loop between shrubs and fire. This chapter is currently in review at Nature Climate Change. Note: as this chapter was written for Nature Climate Change the introduction, results and discussion are all integrated into a single section.

Camac, J.S., Williams, R.J., Wahren, C-H., Hoffmann, A.A., Vesk, P.A. (**in review**)
Climatic warming strengthens a positive feedback between alpine shrubs and fire.
Nature Climate Change.

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Designed experiments, obtained funding and permits, collected data, conducted analysis and wrote manuscript.

Williams, R.J.

Supervised development of work, collected data and edited manuscript.

Wahren, C-H.

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Hoffmann, A.A.

Supervised development of work, provided funding and edited manuscript.

Vesk, P.A.

Supervised development of work, aided with data analysis, provided funding and edited manuscript.

Primary authored published papers:

Camac, J.S., Williams, R.J., Wahren, C-H., Morris, W.K., Morgan, J.W. 2013. Post-fire regeneration in alpine heathland: does fire severity matter? – Austral Ecol, 38:199-207.

In this paper I compare three models of different functional forms (linear, humped shape or no effect) to determine how vegetation attributes of alpine heathland respond to varying fire severity. This question was formed during my PhD, but uses data I collected as part of my BSc (Honours) degree. I analysed and wrote this manuscript during my PhD. I did not include this as a chapter of my thesis because it builds on the work I conducted as an honours student.

Camac, J.S. (PhD Candidate)

Designed study, obtained permits, collected data, conducted analysis and wrote manuscript.

Williams, R.J.

Supervised development of work and edited manuscript.

Wahren, C-H.

Supervised development of work and edited manuscript.

Morris, W.K.

Aided in analysis and edited manuscript.

Morgan, J.W.

Supervised development of work and edited manuscript.

Co-authored published papers:

Williams, R.J., Papst, W.A., McDougall, K.L., Mansergh, I.M., Heinze, D., Camac, J.S., Nash, M.A., Morgan, J.W., Hoffmann, A.A. 2014. – In: Alpine Ecosystems. In: *Biodiversity and Environmental Change: Monitoring, Challenges and Directions*. (Eds: Lindenmayer, D, Burns, E., Thurgate, N., Lowe, A.) CSIRO Publishing, pp. 167-212.

In this book chapter we summarize the major discoveries obtained from both experimental and long-term monitoring studies conducted in the Australian Alps. In addition to this we outline how these discoveries have been used to better inform land management and what knowledge gaps remain. My contribution to this work included supplying data and editing the manuscript.

Wahren, C-H., Camac, J.S., Jarrad, F.C., Williams, R.J., Papst, W.A., Hoffmann, A.A. 2013. Experimental warming and long-term vegetation dynamics in sub-alpine open-heathland. - Aust J Bot. 61:36-51.

In this paper we use general linear models and hierarchical partitioning parameterized using data from long-term monitoring sites as well as a warming experiment to determine which climatic variables influence the composition, structure and diversity of Australian alpine heathlands. My contribution to this work included collecting data and editing the manuscript.

Williams, R.J., Wahren, C-H., Shannon, J.M., Papst, W.A., Heinze, D.A., Camac, J.S. 2012. Fire regimes and biodiversity in Victoria's alpine ecosystems. - Proc Tran Roy Soc Vic. 124:101-109.

In this review paper we summarize how fire has influenced both fauna and flora in the Victorian alps. My contribution to this work included supplying data and editing the manuscript.

Hoffmann, A.A., Camac, J.S., Williams, R.J., Papst, W.A., Jarrad, F.C., Wahren C-H. 2010. Phenological changes in six Australian sub-alpine plants in response to experimental warming and year-to-year variation. J Ecol, 98:927-937.

In this paper we assess how experimental warming has influenced the flowering and seed maturation of six sub-alpine plants. My contribution to this work included: analyses and cowriting the manuscript with Ary Hoffmann.

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Chapter 1:

General Introduction

1.1 Overview: climate change and vegetation change

Climate change has the potential to radically reshape the ecosystems around us. Mean global temperatures have increased by 0.85°C since 1880 and are predicted to rise by as much as 4.8°C by the end of the 21st century (IPCC 2013a). This unprecedented rate of warming, coupled with altered hydrological cycles is expected to have profound long-term effects on species (Parmesan and Yohe 2003), communities (Walker et al. 2006) and ecosystems (Field et al. 2007) worldwide. Plants are expected to be particularly vulnerable to climate change because they are sessile organisms. As such, the persistence of plant species is dependent on their ability to adapt to a changing climate, and whether their propagules can disperse far enough to match spatial shifts in suitable habitat. Because vegetation plays an integral role in many ecosystem services (Chapin et al. 2008, Richardson et al. 2013) and can influence the frequency and severity of stochastic events such as fire (Bradstock 2010, Bradstock et al. 2014), it is imperative to understand how it will respond to changing climatic conditions.

In this thesis I explore the potential impacts of climate change on the dynamics of alpine vegetation. Globally, high altitude and high latitude ecosystems are vulnerable to climate change (Grabherr et al. 1994). However, the effects of warming are likely to be contingent on other factors, such as disturbance and the interactions between biota. These interacting factors are rarely studied in combination, even though their combined effects may potentially exacerbate or mitigate climate-induced changes in vegetation dynamics. For this reason, I use multiple datasets to investigate how warming, disturbance and biotic interactions affect alpine vegetation, and use conceptual and statistical models to make projections of trajectories and rates of vegetation change as a consequence of climate change in an alpine environment.

In the following sections of this chapter I summarise commonly used approaches that examine how climate impacts vegetation. I also briefly review what these studies have found and how researchers are currently attempting to forecast future climate induced changes in vegetation. Following this I highlight why these models should also incorporate disturbances and biotic interactions and why I should examine seedling responses and model rates of change as opposed to differences. I then present the aims and context of my thesis.

1.2 How have vegetation responses to climate change been observed?

Global change researchers have used observations in time, observations in space and experimental studies to determine how various aspects of climate change may impact terrestrial vegetation dynamics. The utility of these approaches in examining climatic effects on vegetation is reviewed briefly below and the strengths and limitations of each are summarized in Table 1.1.

1.2.1 Observations in time

Historical records have been widely used to determine responses of both individual species and communities to past climate on the assumption that they provide insights into how future vegetation change may change (Willis and MacDonald 2011). Sources include historical records of phenological events (Menzel et al. 2006, Primack et al. 2009) and the systematic collection of occurrence, abundance and composition data from repeatedly sampled long-term monitoring sites (Hudson and Henry 2010, Elmendorf et al. 2012b, Wahren et al. 2013). In regions containing few such data, researchers have used alternative sources such as herbarium records (Primack and Miller-Rushing 2009, Gallagher et al. 2009) and historical photography (Sturm et al. 2001, McDougall 2003, Tape et al. 2006, Tng et al. 2011). Most datasets span several decades, with very few extending beyond a century (Lunt 2002, Rustad 2008). The longest known dataset of historical observations is of peak flowering dates of Japanese

cherry trees, which goes back to the 9th century (Primack et al. 2009). Others have attempted to examine past vegetation change over much longer temporal scales by using palaeoecological approaches such as palynology (Davis 1967, Willis and MacDonald 2011) and dendrochronology (Briffa 2000). The advantages of these approaches is that past climate-vegetation relationships can be reconstructed over millennia, providing information on how vegetation has responded to millennial-scale changes in climate. More importantly, it provides researchers with the ability to hind cast their models in order to determine their accuracy in predicting past vegetation distributions (Prentice et al. 1996).

Although historical and palaeoecological studies have provided some of the most compelling evidence of vegetation responses to both short-term and long-term climatic changes, their applicability in forecasting future responses is limited for three reasons. First, unlike the past, current distributions of species and plant communities have been highly modified and fragmented by human activities (Hobbs et al. 2009, Cabral et al. 2012). Second, global temperatures are currently increasing at a rate unprecedented in millennia (IPCC 2013a). And third, most historical datasets are restricted to particular sites, with the majority in Europe and North America (Menzel et al. 2006, Primack and Miller-Rushing 2009). However, attempts have been made to increase the number of sites and regions sampled through the establishment of global monitoring networks such as the Global Observation Research Initiative in Alpine Environments (GLORIA; Pauli et al. 2004) and the International Phenological Gardens Project (IPG; Primack and Miller-Rushing 2009).

1.2.2 Observations in space

Existing geographical and topographical gradients of temperature and precipitation have also been used to provide information on potential climate change impacts on vegetation. The primary assumption here is that changes in space may be used as proxies for changes in time (Dunne et al. 2004). Such ‘space-for-future-climate’ studies have been widely used to determine changes in plant establishment (Munier et al. 2010), growth (Prior and Bowman 2014), phenology (Crimmins et al. 2010), nutritional

status (Körner 1989), biotic interactions (Callaway et al. 2002, Roux et al. 2012) and species diversity (Kreft and Jetz 2007). Species adaptive and persistence capabilities have also been assessed by transplanting plants along (Byars et al. 2007, Bennington et al. 2012) and beyond the geographical and topographical climatic gradients in which they occur (e.g. tree lines; Munier et al. 2010). Predictions based on species distribution models (SDMs) also fall into this category as they implicitly sample climatic gradients by correlating the climatic space with the spatial occurrence and abundance of species (Elith and Leathwick 2009).

Space-for-future-climate studies have several practical advantages over longitudinal studies: 1) they can identify plant-climate relationships at both regional and global spatial scales (Dunne et al. 2004); 2) they can encompass a range of potential climatic conditions (Rustad 2008); and 3) they are not limited by the amount of historical data available (Dunne et al. 2004). However, space-for-future-climate studies assume vegetation will track temporal shifts in climate the same way they track it over space (Dunne et al. 2004); an assumption currently not verified. Another limitation of climatic gradients is that spatial shifts in climate are typically confounded by other factors such as long-term local adaption (and dispersal), fine-scale environmental heterogeneity, and co-varying abiotic and biotic factors; all of which make disentangling climatic effects on vegetation difficult (Dunne et al. 2004, Rustad 2008).

1.2.3 Manipulative experiments

Researchers have also experimentally manipulated temperature, plant available water and CO₂ concentrations in order to explicitly determine their impacts on vegetation. These experiments have been conducted in highly controlled laboratory and glasshouse conditions (Griffin and Hoffmann 2012, Hoyle et al. 2013), and in the field, so that vegetation responses can be assessed in more natural conditions (Henry and Molau 1997, Saavedra et al. 2003). Several approaches have been used to manipulate climatic variables in the field. Temperatures have been increased actively via infrared lamps (Wada et al. 2002) and cables (Moser et al. 2011) or passively via a variety of methods such as open top chambers (Marion et al. 1997), windshield nets (Takahashi 2005) and

reflective curtains (Prieto et al. 2009b). Plant available water has been manipulated by using multiple watering treatments (Piper et al. 2013) or by reducing precipitation via 'rain out shelters' (Fay et al. 2000). And local CO₂ concentrations have been elevated in the field via various CO₂ emitting devices (Ainsworth and Long 2005).

The strength of manipulative experiments is that they are the only tools available that can determine casual relationships, and thus are essential to improving my mechanistic understanding of the processes by which climate influences vegetation (Dunne et al. 2004, Rustad 2008). However, the generality of experimental findings is often limited in space and time. Manipulative experiments are expensive, both financially and logistically, and therefore typically involve low replication (at both site and plot levels), small plots (e.g. 1 m²) and few treatments (Dunne et al. 2004, Rustad 2008). They are also rarely maintained for more than a decade (Rustad 2008). As a consequence, experimental effects may be transitory and not reflective of longer-term changes (Arft et al. 1999, Rustad 2008). They are also difficult to extrapolate in space as they do not encapsulate larger scale processes such as herbivory and disturbance. Researchers have attempted to address some of these limitations by establishing global experimental networks that use standardized methodology and meta-analyses to assess climate-plant relationships. Examples of such networks include the Free-Air Carbon Dioxide Enrichment Experiment (FACE; Ainsworth and Long 2005) and the International Tundra Experiment (ITEX; Henry and Molau 1997).

Table 1.1. The strengths and limitations associated with three commonly used approaches to examine climate change impacts on vegetation.

Approach	Strengths	Limitations
Observation in time (human contemporary observations)	Provide strong evidence of current and past responses to climate.	Rarely go back more than 100 years; past responses do not necessarily equate to future responses; often restricted to particular sites or regions.
(Paleoecology)	Long time intervals; provides opportunity to test models by hind casting vegetation responses.	Low taxonomical and spatial resolution; past responses do not necessarily equate to future responses.
Observations in space	Can identify plant-climate relationships at multiple scales; can be used at a range of potential climatic conditions; are not limited by the amount of historical data available.	Assumes changes in space equate to changes in time; gradients are confounded by other biotic and abiotic factors; difficult to disentangle climatic effects.
Manipulative	Can evaluate causal relationships; provide new insights and validate models.	Financially and logistically expensive; generality of experimental findings are often limited in time and space.

1.3 What have these studies shown?

Observations in space and time together with manipulative experiments have revealed a variety of climate change impacts on vegetation. Temperature increases, which affect virtually all chemical and biological processes, have been shown to affect individuals, populations and communities. Warming has affected individuals by altering: timing of phenological events (Hoffmann et al. 2010); leaf morphology (Hudson et al. 2011); and growth rates (Arft et al. 1999). At the population level warming has been correlated with pole ward and elevation shifts in species distributions (Chen et al. 2011, Gottfried et al. 2012, Pauli et al. 2012), accelerated extinction rates (Dullinger et al. 2012) and changes in genetic structure (Byars et al. 2009, Jay et al. 2012). While plant communities have responded to warming through changes in plant-plant (Callaway et al. 2002, Kikvidze et al. 2005) and plant-herbivore (O'Connor 2009, Lemoine et al. 2013) interactions and the expansion of woody species (Walker et al. 2006, Myers-Smith et al. 2011). Elevated CO₂ concentrations and changes to plant available water have also been shown to influence vegetation. In both agricultural and non-agricultural

systems, elevated CO₂ has increased water-use-efficiency and rates of photosynthesis resulting in increased plant productivity (Ainsworth and Long 2005) and has the potential to result in abrupt vegetation shifts (Higgins and Scheiter 2012). By contrast, declines in plant available water have been associated with reductions in plant establishment, growth and survival (Prieto et al. 2009a, Barbeta et al. 2013). A common trend observed across observational and experimental studies is that species respond idiosyncratically to climatic change, that is, some species show strong immediate responses, some exhibit lagged responses, some show contradictory responses and others show no response (Arft et al. 1999, Dormann and Woodin 2002).

1.4 Forecasting impacts of climate change on vegetation

Researchers predict vegetation dynamics under climate change using four primary approaches: conceptual models, correlative species distribution models (SDMs), process-based models and hybrid models. I review the utility of these techniques for forecasting vegetation change below with strengths and limitations summarized in Table 1.2.

1.4.1 Conceptual models

Conceptual models are visual representations of how systems work. In ecology and global change biology they have been used to summarize modeling approaches (e.g. Clark and Gelfand 2006, Vesk et al. 2010) and complex relationships between factors that lead to a change in state. For example, conceptual diagrams have been used to summarize carbon (e.g. Reichstein et al. 2014) and hydrological cycles (e.g. Oki 2006), mechanisms of succession (Connell and Slatyer 1977), food webs (e.g. Paine 1966) and drivers of vegetation state (e.g. Westoby et al. 1989). Moreover, they have been used to highlight feedback loops between climate change and vegetation (Chapin et al. 2005), shrub expansion (Myers-Smith et al. 2011) and disturbance regimes (Bradstock 2010). Although these models are qualitative in that they visually describe the direction of various effects, relationships are typically quantified through detailed observational and experimental studies. The advantage of conceptual models is that they are easily built

and can use multiple sources of evidence. Moreover, they can convey a complex story via a simple diagram, making them highly accessible. As such, conceptual models often provide the theoretical foundations upon which more complex quantitative models are built. However, although conceptual models may provide an indication of the direction in which a system may be heading, they rarely make explicit predictions of magnitude and do not incorporate uncertainty. Furthermore, these models are difficult (although not impossible) to formalize as mathematical functions and can become unwieldy with increasing numbers of states, effects and/or interactions.

1.4.2 Correlative species distribution models

Correlative species distribution models (SDMs), also referred to as ‘ecological niche models’, ‘habitat suitability models’ or ‘bioclimatic envelope models’ are ubiquitous for forecasting the effects of climate change on species (Elith and Leathwick 2009). The use of SDMs in this context is based on the fundamental theoretical assumption that species’ distributions are influenced by climate (Elith and Leathwick 2009). These models function by identifying relationships between spatial environmental data (climatic and non-climatic) and patterns of species occurrence or abundance across geographic space (Guisan and Thuiller 2005, Elith and Leathwick 2009). In effect, correlative SDMs estimate Hutchinson’s (1957) ‘realized niche’ – the environmental space within which a species can survive and reproduce in the presence of biotic interactions – which can subsequently be mapped onto a landscape of interest to illustrate the geographic distribution of suitable habitat. Correlative SDMs are parameterized using a variety of approaches ranging from linear regression methods such as generalized linear models (GLMs) and generalized additive models (GAMs), to the increasingly popular methods employing machine learning such as Maxent (Phillips et al. 2006) and Boosted Regression Trees (Elith et al. 2008). The estimated relationships between species distribution patterns and environmental predictors allude to important variables limiting species’ distributions and provide a means for predicting potential impacts of a changed environment (e.g. due to climate change).

Correlative SDMs are less computationally intensive than process-based or hybrid models (see below), and can accurately estimate habitat suitability using only distributional (i.e. occurrence or abundance data) and readily available bioclimatic data at both regional and global scales (Franklin and Miller 2010). As such, these models have been applied to a large suite of species in order to predict the impacts of climate change. For example, Thomas *et al.* (2004) fit correlative SDMs for a thousand species to examine potential changes in suitable habitat caused by climate change. That study concluded that 15-37% of species were ‘committed to extinction’ due to projected declines in suitable habitat.

The limitation of correlative SDMs is that they rely on assumptions that might prove untenable in many situations, and their applicability to project change as a consequence of potentially novel future climatic conditions may be limited (Elith and Leathwick 2009). Chief amongst the criticisms of correlative SDMs is that the environmental space occupied at known occurrence localities may not reflect the species’ realized niche (Franklin and Miller 2010). This may be because the species’ distribution is not in equilibrium with the environment (e.g. due to lagged responses to environmental change, or because environmentally suitable regions are unreachable due to an inhospitable matrix) (Franklin and Miller 2010); or because the occurrence sample is environmentally biased (e.g. towards easily accessible areas or human habitation) (Elith and Leathwick 2009, Yackulic *et al.* 2012). Secondly, correlative SDMs rarely incorporate biotic interactions explicitly (Araújo and Luoto 2007), instead assuming that they are captured in the relationships between the abiotic environment and the species’ pattern of occurrence (Davis *et al.* 1998, Elith and Leathwick 2009). Third, when models are projected under scenarios of environmental change, these implicit interspecies relationships, and the fitted relationships between species and environmental gradients, are assumed to be constant. This is tenuous, since it requires extrapolation of these relationships to novel environmental conditions and fails to acknowledge that interactions may be altered by future climatic conditions (Davis *et al.* 1998). Finally, correlative SDMs do not consider population dynamics, and yield only limited insight into the mechanisms by which climate influences species’ distributions (Kearney *et al.* 2010, Fordham *et al.* 2013b).

1.4.3 Process-based models

Climate change impacts on vegetation have also been examined using ‘process-based’, ‘mechanistic’, ‘physiological’ or ‘population’ models. These are mathematical functions that describe causal relationships between aspects of climate and physiological traits (e.g. resource uptake and allocation, thermal/moisture tolerances) influencing the viability and fitness of a species, functional group, or population (Buckley et al. 2010, Higgins et al. 2012). In contrast to correlative SDMs, process-based models (1) require detailed knowledge of the mechanistic links between a species’ environment and measures of performance; (2) are parameterized without calibration to distributional data; and (3) typically (unless biotic variables are considered) define Hutchinson’s (1957) potential niche – the environmental space in which a species can survive and reproduce in the absence of biotic interactions (Kearney and Porter 2009). A variety of process-based models have been developed for predicting vegetation dynamics under changing climatic conditions, including: population viability analysis (e.g. Maschinski et al. 2006), growth models (e.g. Hackett and Vanclay 1998), phenological models (e.g. Chuine and Beaubien 2001), niche models (Higgins et al. 2012 based abiotic effects on carbon and nutrient uptake and its influence on growth) and biogeographic models based on plant functional types (e.g. trees, shrubs, grasses, evergreen, deciduous) such as BIOME (Prentice et al. 1992) and dynamic global vegetation models (Cramer et al. 2001). Primary advantages of process-based models over correlative SDMs include that: (1) they can incorporate biotic interactions and stochastic events such as disturbances, (2) with the exception of BIOME (which is an biogeographic equilibrium model), can theoretically be applied to non-equilibrium and novel conditions (Kearney and Porter 2009); and (3) they utilize independent datasets such as experimental and observational studies, rather than relying on distributional data, which are often geographically or environmentally biased (Yackulic et al. 2012). However, despite the deeper understanding that these models yield, they are rare in practice (Dormann et al. 2012) because they require seldom-available detailed mechanistic knowledge of climate-trait relationships, are difficult to scale up from individuals to ecosystems (Higgins et al. 2012) and pose computational challenges associated with making them spatially explicit (Higgins et al. 2012).

1.4.4 Hybrid models

More recently, correlative SDMs have been linked to process-based models in an attempt to translate spatial predictions of habitat suitability to measures of population viability more relevant to conservation management (e.g. Keith et al. 2008, Anderson et al. 2009, Fordham et al. 2012). These ‘hybrid’ models (Thuiller et al. 2008) function by relating factors governing demographic rates (e.g. population carrying capacity) to climate dependent habitat suitability derived from correlative SDMs (Keith et al. 2008). As such, these models are considered to be a compromise between the realistic but complex process-based models and the accurate but simple correlative SDMs (Thuiller et al. 2008). The advantage of hybrid models is that they can directly estimate the impacts of environmental change on population dynamics and extinction risk. They can also incorporate other processes such as biotic interactions (Fordham et al. 2013a), dispersal (Midgley et al. 2006) and disturbances (Keith et al. 2008). However, hybrid models suffer from some of the limitations associated with process-based models and correlative SDMs, including the need for detailed knowledge of species’ life histories, the assumption that species are equilibrium with their environment and problems associated with biased distributional data. Due to their complexity, they are difficult to parameterize, and are likely to model greater uncertainty than other approaches already discussed (Fordham et al. 2013b). Hybrid models also contain additional assumptions in order to link correlative SDMs to population models. For example, Keith *et al.* (2008) linked correlative SDMs to population dynamic models by assuming population carrying capacity was linearly related to habitat suitability predicted by SDMs, despite the functional form underlying this relationship being unknown.

Table 1.2. The strengths and limitations associated with four common modeling approaches used to forecast climate change impacts on vegetation.

Model type	Strengths	Limitations
Conceptual	Simplify complex interactions; are highly accessible; and provide foundations for more complex models.	Qualitative and difficult to formalize as mathematical functions, not spatially explicit, can quickly become unwieldy.
Correlative SDMs	Can accurately predict current distributions; only require occurrence data; and readily available climate layers and can be applied to most species.	Assume species are in equilibrium with the environment; not amenable to explicitly incorporating biotic interactions; and occurrence records are often environmentally biased.
Process-based	Can incorporate causal processes, utilize experimental and observational findings, do not rely on biased occurrence records.	Requires seldom available mechanistic knowledge of climate-trait relationships, computationally intensive, difficult to extrapolate to large scales
Hybrid	Spatially explicit; directly estimate extinction risk and changes to population dynamics; and can incorporate processes such as disturbance and dispersal.	Difficult to parameterize; higher model uncertainty; require detailed knowledge of species' life history; affected by biased distributional data; assumes species are in equilibrium with environment; contains additional assumptions (e.g. a linear relationship between predicted habitat suitability and carrying capacity).

1.5 Forecasting vegetation change: the importance of seedling responses, disturbances, biotic interactions and modeling rates of change

As reviewed above, most models that forecast climate change effects on vegetation dynamics are based on implicit climate-species relationships, and more recently, causal links between climate and traits associated with physiological, morphological and population dynamics (e.g. process-based and hybrid models). Although researchers using these approaches have begun to incorporate the effects of disturbance and biotic interactions on vegetation dynamics, most assume their effects on vegetation are not altered by climate change. This assumption is contradicted by many experimental (Lutze et al. 1998, O'Connor 2009) and observational studies (Callaway et al. 2002). In order to develop models that accurately predict trajectories of future vegetation change

we must: (1) quantify the interactive effects of climate on biotic interactions and disturbance; (2) require an understanding of how these interactive effects influence seedlings (a critical life stage in terms of persistence and migration; Leck et al. 2008) and (3) model these interactive effects on rates of vegetation change. Below I briefly justify the importance of these points. I then conduct a literature review to examine the number of experimental papers published that have attempted to address these points.

1.5.1 Disturbances

Disturbances can modify survivorship, biotic interactions, microclimatic conditions and recruitment opportunities (Pickett and White 1985). As such, disturbance plays a major role in the distribution of species, and consequently, the composition and structure of plant communities and biomes worldwide (e.g. Bond et al. 2005). Hence, disturbances may intensify or mitigate how vegetation responds to climate change (Overpeck et al. 1990). For example, in tundra vegetation climatic warming has increase shrub cover, and the rate of this increase is exacerbated in highly disturbed landscapes (e.g. burned; Lantz et al. 2013). Species responses to disturbance can also be modified by climate change. For example, Rixen *et al.* (2011) showed that increases in both CO₂ and temperature resulted in lower frost tolerance in multiple alpine and subalpine plants. Lastly, climate can indirectly influence vegetation dynamics by altering natural disturbance regimes (Bradstock et al. 2014). In fact, such disturbance regimes have already begun to shift as a consequence of climate change. In some parts of south-east Australia for example, the frequency of extreme fire weather days may double by 2050 (Williams et al. 2009). This may lead to fires that are more frequent and/or severe; a trend observed in many other parts of the world (Westerling et al. 2006, Turetsky et al. 2011).

1.5.2 Biotic interactions

Interactions among species are also known to affect vegetation dynamics (Connell and Slatyer 1977, Crawley and Ross 1990). These effects can range from the complete exclusion of a species from a particular area or niche (i.e. competitive exclusion; Grime 1973) through to species facilitating each other to persist in otherwise inhospitable environments (Callaway et al. 2008). Bertness & Callaway (1994) proposed that the strength and direction of these interactions are strongly linked to abiotic conditions. For example, they hypothesized that in arctic and alpine environments, low temperatures would limit plant growth. Under these conditions the benefit gained from neighbouring plants ameliorating stressful conditions (e.g. via sheltering) would be greater than the cost associated with sharing resources such as light, nutrients and water. If this hypothesis is broadly valid, then climate change is likely to have significant effects on biotic interactions and consequently vegetation dynamics. Numerous studies have shown that changes in climatic conditions can: strengthen plant-herbivore interactions (O'Connor 2009); and shift plant-plant interactions from facilitative to competitive, or vice versa (Callaway et al. 2002, Klanderud 2005). As with shifts in disturbance regimes, changes in biotic interactions also have the capacity to exacerbate or mitigate the direct effects of climate on vegetation. For example, Post *et al.* (2008) documented that experimental warming increased plant community biomass and the cover of woody species; however, these effects were negated by herbivory.

1.5.3 Seedlings

All plants are sessile organisms, and most rely on the dispersal, establishment and survival of seedlings in order to expand their ranges, persist and track spatial changes in environmental conditions (Leck et al. 2008). The vital rates of seedlings are highly vulnerable to changes in climate, biotic interactions, disturbances and their interactive effects (Walck et al. 2011). Seedlings are therefore likely to respond to environmental changes more rapidly than mature vegetation, which is more resilient and therefore less likely to exhibit an immediate response to shifts in climate (Davis 1989). Seedlings are therefore likely to be highly predictive of climate-induced changes to both population dynamics and species extent (Walck et al. 2011).

1.5.4 Modeling rates of change

Quantifying how climate and other abiotic and biotic factors influence rates of vegetation growth or cover change is critical for developing accurate models of future change. As opposed to tests of differences (e.g. via ANOVA) between experimental treatments, modeling climatic effects explicitly on rates of change provides information on not only the direction of change but also the speed at which change may occur (Paine et al. 2011). This information is critical to predicting height or cover changes through time and under multiple environmental conditions. In other words, without information on rates we will be unable to determine when a change (e.g. state change from grassland to heathland) will occur.

1.6 A proposed way forward

Most forecasting models are based on implicit climate-species relationships (e.g. correlative SDMs; Elith and Leathwick 2009), and as such rarely incorporate mechanisms identified by experiments (Thuiller et al. 2008). However, researchers are becoming increasingly aware that mechanistic processes will be required for accurate predictions of extinction risk and future vegetation change (Keith et al. 2008). As such, experimental data and their associated findings will play an increasingly important role in both parameterizing and validating models. For this reason, and the reasons stated above, I propose that future experiments should model how climate, disturbance and biotic interactions interact to influence rates of change. I also propose that experiments should focus on the seedlings because they are likely to be the most vulnerable to changes in climate, disturbance and biotic interactions (Walck et al. 2011).

To determine the current state of knowledge on how climate interacts with disturbance and biotic relationships to influence rates of vegetation change I conducted a formal literature review. Using Google Scholar and the search terms [“climate change” OR “global warming”], [“vegetation” OR “plant”] and “experiment” I collated field experimental papers that simulated climate change impacts (e.g. manipulations of temperature, CO₂, water or nutrients) on vegetation composition, abundance and/or growth. I focused on studies published between 2000 and 2013 that contained a

minimum of two years of experimental data. In total, 54 papers met these requirements. Following this I then determined the number of experimental papers that: (1) explicitly estimated the effects of treatments on rates of change in either abundance or growth; (2) assessed seedling responses; (3) incorporated the effect of a disturbance (or was conducted on disturbed vegetation); and (4) incorporated an effect of a biotic interaction. I found few experiments that addressed any of these factors (Fig. 1.1), and none that examined the effects of experimental treatment on rates of compositional change or vegetation growth (the full list of papers is given in Appendix 1.1).

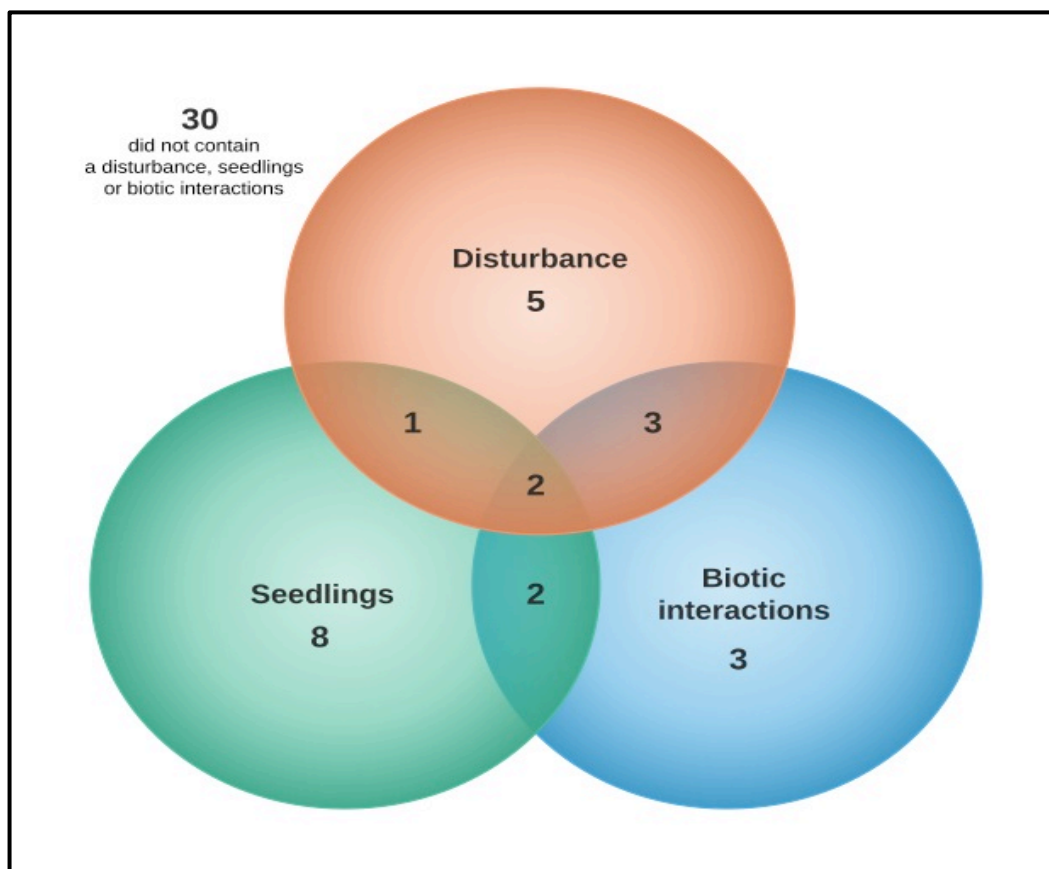


Figure 1.1. Venn diagram of the number of climate change experimental papers published between 2000 and 2013 that examined seedling responses (green) or incorporated a disturbance (orange) or biotic interaction (blue) when examining changes in vegetation cover or growth.

The majority of the 54 papers focused on estimating differences among treatments (e.g. repeated measures ANOVA). However, two papers (Takahashi 2005, Piper et al. 2013) that examined plant growth did attempt to estimate incremental growth rates (GR) for each treatment by using the post-hoc equation: $\frac{\Delta height}{\Delta time}$. Although this approach provides an estimate of growth rate, it suffers from several shortcomings: (1) it does not explicitly estimate treatment effect on rate of growth; (2) it contains no measure of the uncertainty of treatment effect; (3) unless incorporated into a non-linear growth rate model, it assumes that changes are constant through time (i.e. linear) and does not contain a asymptote (e.g. carrying capacity or limits for cover and heights). The implications of these shortcomings include over predicting changes and obtaining impossibilities such negative or infinite plant height or cover estimates outside the percentage bounds (0, 100) (see Fig.1.2. for an illustrated example).

Twenty-four papers included at least one of the following: seedling responses (13 papers), disturbances (12 papers) or biotic interactions (10 papers). Eight of these papers considered at least two of the factors when examining climate change impacts on vegetation, while only two (Tercero-Bucardo et al. 2007, Munier et al. 2010) attempted to incorporated all three; although neither papers quantify both two-way climate-disturbance or climate-biotic interactions.

In this thesis I attempt to address this information gap by developing models that explicitly estimate the effects of climate, disturbance and biotic interactions on rates of compositional change and vegetative growth. I parameterize these models from data derived from experimental and observational studies conducted in alpine heathland on the Bogong High Plains of Victoria, Australia.

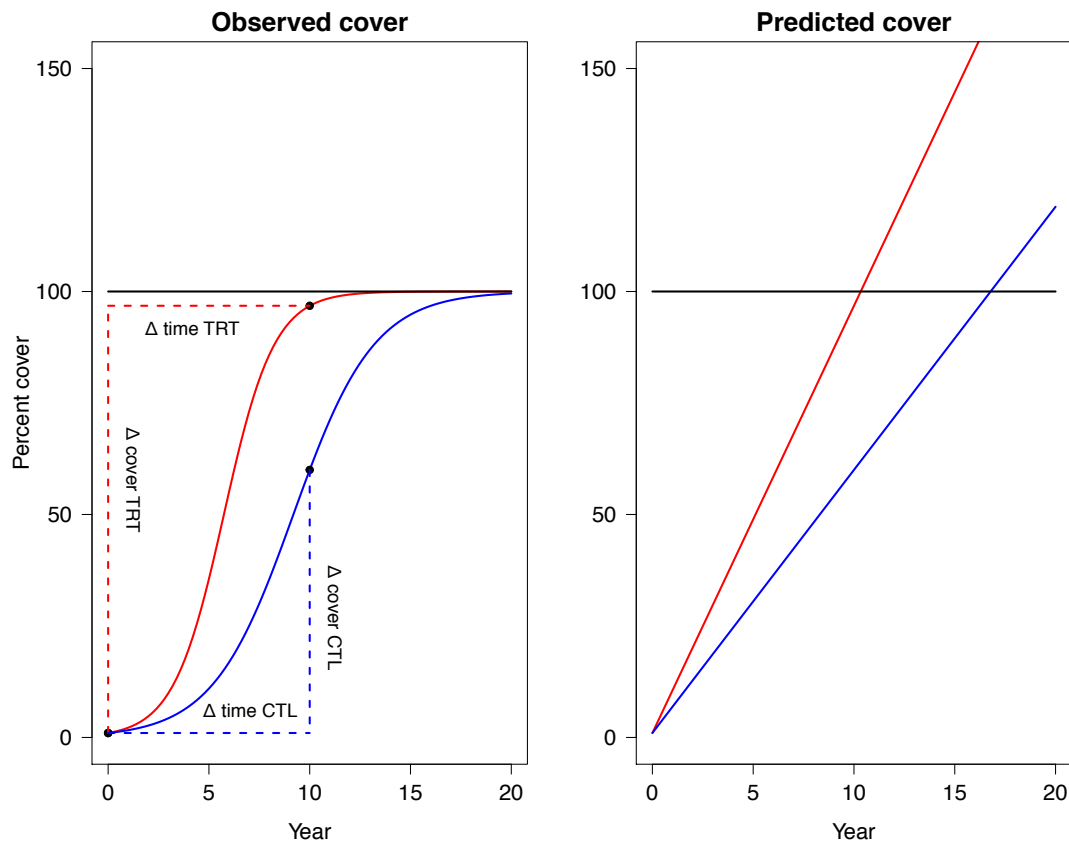


Figure 1.2. Consequences of estimating rates of change post-hoc. Left panel: observed shrub cover increase over a 20-year period for two hypothetical plots; red solid line: plot with growth rate stimulated by treatment; blue line = control plot; black line: asymptotic limit (100%); dashed lines: the difference in cover or years between two sampling periods. Right panel; predicted population growth for same period using post-hoc RGR multiplied by time. Note: this approach does not incorporate non-linear growth or asymptotes, and therefore, overestimates true population size. It also does not directly estimate treatment effect on rate and thus does not measure its uncertainty.

1.7 The Australian Alps: changing climate and fire regimes and its implications for alpine vegetation

Like many other alpine and tundra ecosystems (Grabherr et al. 1994), the Australian Alps is considered highly vulnerable to climate change (Williams et al. 2014). This is because it is extremely restricted, occupying less than 0.15% of the continent and the alpine ‘treeless’ zone occurs in a narrow altitudinal band (ca. 1800 - 2200 m) with no nival zone (i.e. no zone of permanent snow) (Körner 2003). Consequently, no higher

altitudinal refuges are available to alpine species to colonize under a warmer climate. The Australian Alps are also experiencing shifts in climate. Since 1979, mean growing season temperatures have risen by approximately 0.4°C, and annual precipitation has fallen by 6% (Wahren et al. 2013) with a consequent decline in the snow pack (Sánchez-Bayo and Green 2013). This change in climate has been accompanied by a 25% decline in graminoids and a 20% and 9% increase in shrubs and forbs, respectively (Wahren et al. 2013). A trend also observed in aerial photography between 1936 and 1980 (McDougall 2003), which documented increases in shrub cover through the conversion of grassland to open heathland. This change in climate coupled with extreme drought has also resulted in recent increases in fire frequency (Williams et al. 2008, 2014), particularly in the Bogong High Plains, which has experienced fires in 2003, 2006 and 2013 (Fig. 1.3).

The Bogong High Plains, located within the Australian Alps network of national parks, are a series of alpine and high subalpine plateaux, situated approximately 250 km northeast of Melbourne. The undulating terrain ranges in altitude from ca. 1400–1900 m a.s.l and contains a well-developed mantle of soil. Mean annual temperature is approximately 6°C, with persistent snow cover from June to September. Annual precipitation is 1200 mm, yet droughts occur at roughly decadal intervals (Wahren et al. 2013). The vegetation is a mosaic of Eucalyptus woodland and treeless vegetation, with the latter largely consisting of heathlands and tussock grasslands, but also herbfields and wetlands (McDougall and Walsh 2007). The treeline is irregular (due to cold air drainage), occurring at altitudes ranging from 1600 to 1700 m a.s.l. The Bogong High Plains also contain many long-term monitoring sites (Williams et al. 2014) and the only International Tundra Experiment (ITEX; Henry and Molau 1997) sites located in the southern hemisphere (Jarrad et al. 2008, Hoffmann et al. 2010). It also occasionally burns (Williams et al. 2006, Camac et al. 2013), with large wildfires typically occurring once or twice per century; generally during periods of extended regional drought coupled with severe fire weather and multiple ignitions in the surrounding montane forests (Williams et al. 2008).



Figure 1.3. Approximately 400,000 of the Victorian alpine national park was burned by the wildfires in 2003. Heathlands were the primary vegetation type burned, with very few grasslands burned (**Williams et al. 2006**). Photo courtesy of Carl-Henrik Wahren.

In summary, the Bogong High Plains have experienced shifts in climate, fire regimes and vegetation (i.e. increases in shrubs, decreases in graminoids) over the past few decades. It also contains strong environmental gradients (i.e. elevation, wetness and fire severity gradients), long-term monitoring sites and experimental warming sites. As such, the Bogong High Plains contains all the features necessary to examine how disturbance and plant-plant relationships interact with climate to influence rates of vegetation growth and cover change.

1.8 Thesis aims

In this thesis, I take advantage of long-term monitoring and experimental warming sites, natural environmental gradients and recent fires to examine two primary questions for alpine environments: (1) how does warming, fire and interactions among life forms interact to influence the rate and trajectory of shrub, graminoid and forb

cover changes? And (2) how are shrubs likely to expand their range in a warmer, potentially more flammable alpine environment?

These two broad questions were examined in open heathland (Fig. 1.4). I used open heathland as my model community for three reasons. First, open heathland is an ecotone community between dense heathland and tussock grassland that occupies approximately 25% of the Australian alpine landscape (McDougall and Walsh 2007). Second, it has the potential to act as an ‘invasion front’ for future shrub encroachment into grass-dominated plant communities and is itself susceptible to shrub thickening from closed heathland species (McDougall 2003). And third, it contains shrubs which are both highly flammable (Williams et al. 2006) and expected to respond positively to warming (Myers and Harms 2011), thereby potentially providing valuable insights into changes in flammable fuel dynamics and consequently future fire regimes.

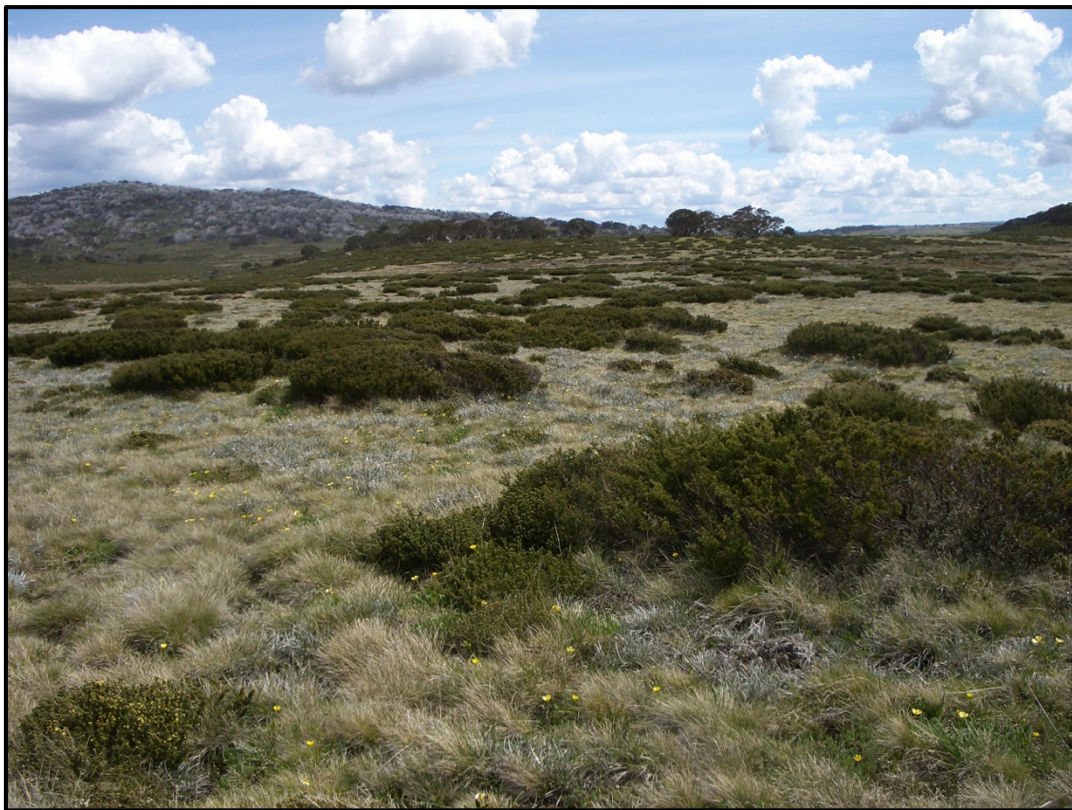


Figure 1.4. *Grevillea australis*-dominated open heathland on the Bogong High Plains of Victoria, Australia.

1.9 Thesis outline

Chapter two of this thesis illustrates a way of explicitly modeling abiotic and biotic factors on rates of cover change in three dominant life forms. The models are parameterized using data from a 7-year warming experiment and later validated using burned and unburned long-term monitoring sites. This chapter addresses three questions: (1) does warming, and associated drying, influence rates and trajectories of cover change in alpine shrubs, graminoids and forbs? (2) how do warmer and drier conditions alter rates of cover change by influencing life form interactions and their responses to disturbance? (3) how are these interactive effects likely to influence life form composition in alpine heathland under future climate and burned and unburned conditions?

Chapter three uses data derived from an extensive field survey and two studies nested within one warming experiment. It addresses five critical questions related to shrub seedling dynamics (Fig. 1.5). Specifically, it determines: (1) what factors influence shrub seedling establishment; (2) whether warmer post-fire conditions influence rates of seedling growth and mortality; (3) whether experimental growth responses are validated along by field surveys; (4) whether the proximity to *Poa hiemata* (the dominant grassland species) influences shrub seedling growth and mortality rates; and (5) whether *Poa* effects are altered by warmer conditions. I then synthesise this information to examine whether global warming is likely to strengthen an existing feedback loop between shrubs and fire (Fig. 1.6); the effects of which have the capacity to rapid change the composition and structure of alpine vegetation. Note, all questions related to shrub dynamics are addressed in this chapter in order to articulate a complete and coherent narrative of shrub dynamics under warming.

Chapter four provides a brief discussion of the significance of the findings and their implications for management of the Australian Alps. It also provides details about potential future directions of research.

Appendices contain the JAGS (Plummer 2011) code for all models used in this thesis and a table of experimental papers reviewed in this chapter. Also included is a supplementary figures for chapter three and published papers I authored or co-authored while undertaking this PhD that are related to this thesis but do not form part of it.

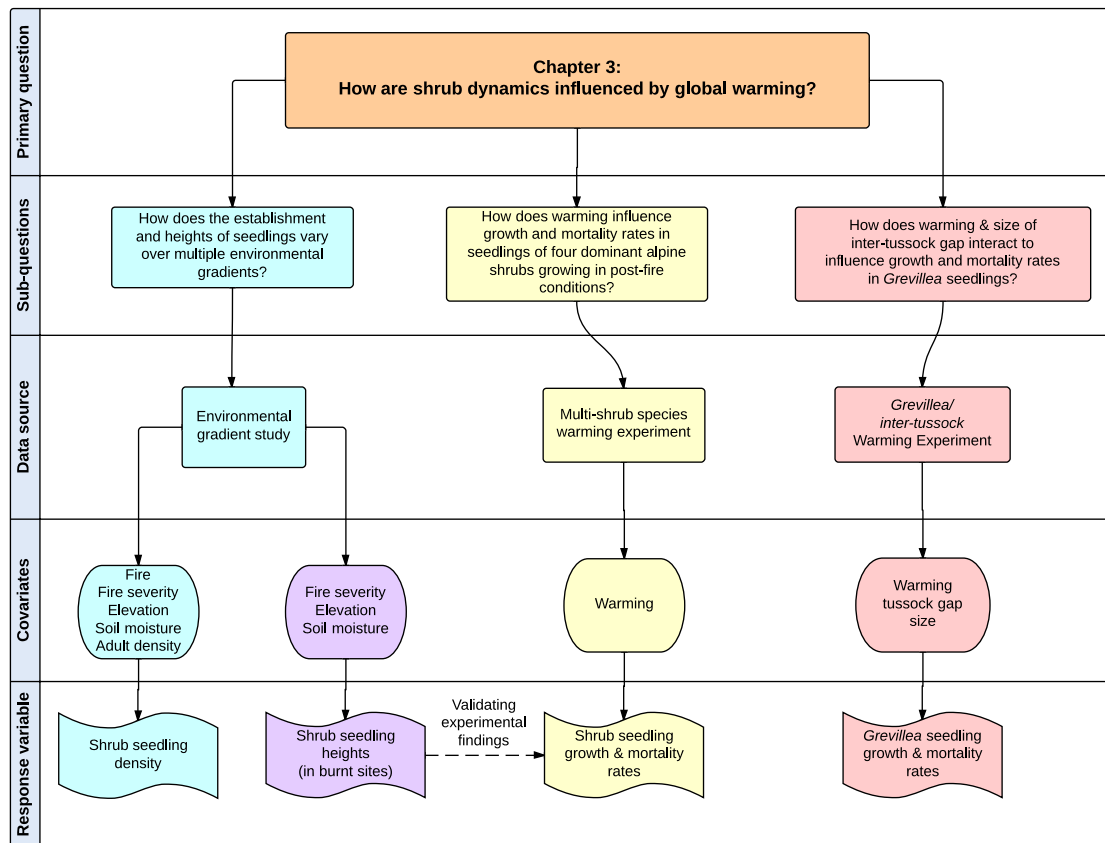


Figure 1.5. Questions and data sources included in chapter 3

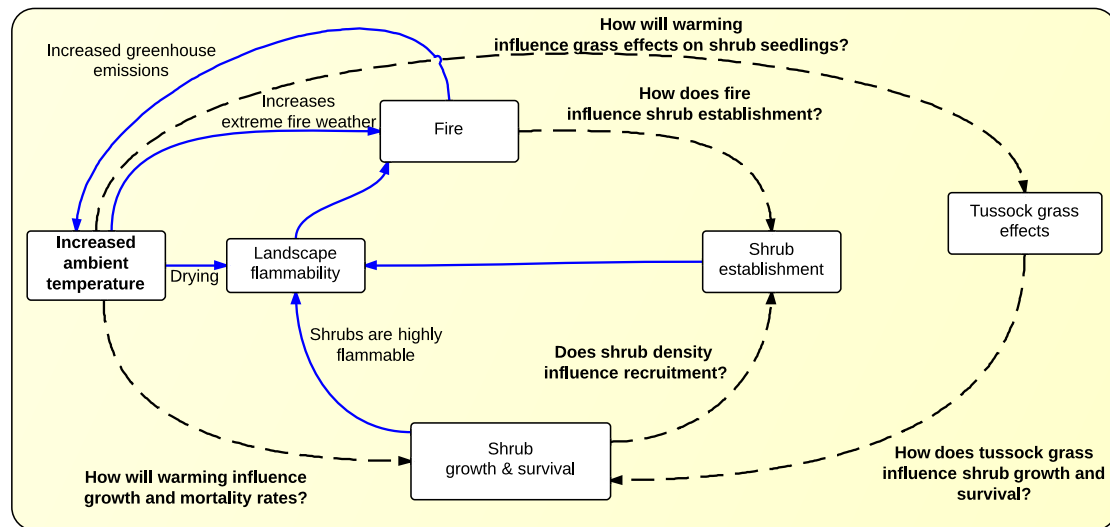


Figure 1.6. Potential feedback loop between elevated temperature, shrubs and fire. Blue solid lines: known positive effects; black dashed lines illustrate the questions addressed in chapter 3.



Chapter 2:

**Modeling rates of life form cover change
in burned and unburned alpine heathland
subject to experimental warming**

2.1 Abstract

Elevated global temperatures are expected to alter vegetation dynamics by interacting with physiological processes, biotic relationships and disturbance regimes. However, few studies have explicitly modeled these interactions on rates of vegetation change, despite such information being critical to forecasting temporal patterns of vegetation. In this study, I build and parameterize rate-change models for three dominant alpine life forms using a 7-year warming experiment. These models allowed me to examine how the interactive effects of experimental warming and the abundance of bare ground and neighboring life forms affect rates of change, and thus trajectories, of cover in shrubs, graminoids and forbs. I show that experimental warming altered rates of life form cover change by reducing negative effects associated with other life form abundance and positive effects associated with bare ground. Furthermore, I show that these models can broadly predict both the direction and rate of past life form cover trajectories at burned and unburned alpine heathland sites not used to train the models. Model simulations revealed that warming in unburned vegetation would result in rates that decrease graminoid cover but increase forb and shrub cover. By contrast, in burned vegetation, warming is expected to slow post-fire regeneration in both graminoids and forbs while allowing for rapid expansion in shrub cover. These findings highlight the applicability of modeling rates of vegetation change from experimental data and the need to account for both the abundance of other life forms and disturbance when examining and predicting vegetation dynamics under climatic change.

2.2 Introduction

Manipulative warming experiments provide an opportunity to establish causality and develop process-based understanding of how and why elevated temperatures are expected to affect ecological systems at the individual, population and community levels. In high mountain and latitude ecosystems, warming experiments have linked elevated temperatures to changes in plant phenology (Hoffmann et al. 2010), leaf morphology (Hudson et al. 2011), growth (Arft et al. 1999) and genetics (Jay et al. 2012). The results of these experiments may then be related to recent shifts in species ranges (Pauli et al. 2007, Gottfried et al. 2012), local extinctions (Dullinger et al. 2012) and changes in community composition and structure (Myers-Smith et al. 2011).

Although manipulative experiments have provided invaluable information on the broad direction and magnitude of warming effects, to date they have all done so by using differences or ratios of state variables for control and manipulated groups observed at some time(s). Most studies (e.g. Hoffmann et al. 2010, Elmendorf et al. 2012a, Wahren et al. 2013) have use repeated measures analysis or GLMs with random effects to account for time. Yet such analysis do not provide estimates of rates, rather they account for the non-independence of observations through time by computation of appropriate F-ratios (Sokal and Rohlf 1995, Gelman and Hill 2007). As far as I am aware, there has been no experimental study that explicitly models rates of change as a consequence of climate change.

All biological systems are subject to change in state over time. A large body of ecological theory has focused on the dynamics of individual (e.g. Richards 1959), populations (e.g. Volterra 1926, Levins 1969, Hanski 1999) and community growth (e.g. Tilman 1988, Chesson 1994). The state observations that researchers make are snapshots in time from dynamic systems, resulting from multiple processes (e.g. growth and decay, birth and death, immigration, colonization, extinction and emigration, predation, competition). Regardless of the focus or complexity of such theoretical models, they all concern rates of change, described with difference or differential equations for discrete and continuous representation of time, respectively.

In a meta-analysis of the difference between warmed and control plots in tundra and alpine warming experiments, Elemendorf *et al.* (2012a) highlighted the importance of time. Nearly all models they fit showed that time affected the magnitude of observed warming effects. Importantly, in those models, time commonly interacted with other covariates or displayed nonlinear effects. This leads to the conclusion that warming effects on vegetation play out over time in complex ways. Because of this, a focus on temporal dynamics is important, especially for predicting future changes in vegetation. This requires a model of temporal change that has as its core a rate parameter, to predict the state of the system at some future time step based on a set of initial values. In other words, a model that tests the effects of warming on *rates* of vegetation change, as opposed to testing for (or estimating) treatment differences.

To accurately estimate rates of vegetation change under climatic warming, other processes such as disturbance and biotic interactions must also be considered. Both are well known to play a major role in structuring ecological communities (Grime 1977, Pickett and White 1985, Brooker and Kikvidze 2008). But importantly, the effects of both processes are likely to change as a consequence of global warming (Tylianakis *et al.* 2008, Lantz *et al.* 2009).

In this study I illustrate how to build and parameterize rate-of-change models by using an existing 7-year warming experiment established in Australian alpine heathland. Using these models I examine how the interactive effects of warming and the abundance of bare ground and neighboring life forms affect rates, and thus temporal trajectories, of cover in three dominant life forms - shrubs, graminoids and forbs. I then examine whether these rate models can predict historical life form cover trajectories observed in burned and unburned alpine heathland sites and how these trajectories may change under climatic warming.

2.3 Methods

2.3.1 Study site

To parameterize our rate models I used four Australian International Tundra Experimental (ITEX; Molau and Mølgaard 1996) sites situated on the Bogong High Plains, in Australia's south-eastern highlands (Fig. 2.1). These sites are unique in that they are the only ITEX sites established in the southern hemisphere and also the only ITEX node that incorporates fire into the experimental design (Jarrad et al. 2008).

The Australian Alps have high conservation significance; they occupy less than 0.15% of the continent and contain high levels of invertebrate, vertebrate and plant endemism (Williams et al. 2014). They also occur over a narrow altitudinal range (1600 – 2200 m a.s.l) and contain no nival zone (i.e. no zone of permanent snow) to which species can migrate. Consequently the ecosystem is considered highly vulnerable to climate change (Williams et al. 2014). Since 1979, mean growing season temperatures in the Australian Alps have risen by approximately 0.4°C, and annual precipitation has fallen by 6% (Wahren et al. 2013) with a consequent decline in the snow pack (Sánchez-Bayo and Green 2013). They have also been subject to recent drought (Griffin and Hoffmann 2012), and parts, such as the Bogong High Plains, have been extensively burned by wildfires (Camac et al. 2013).

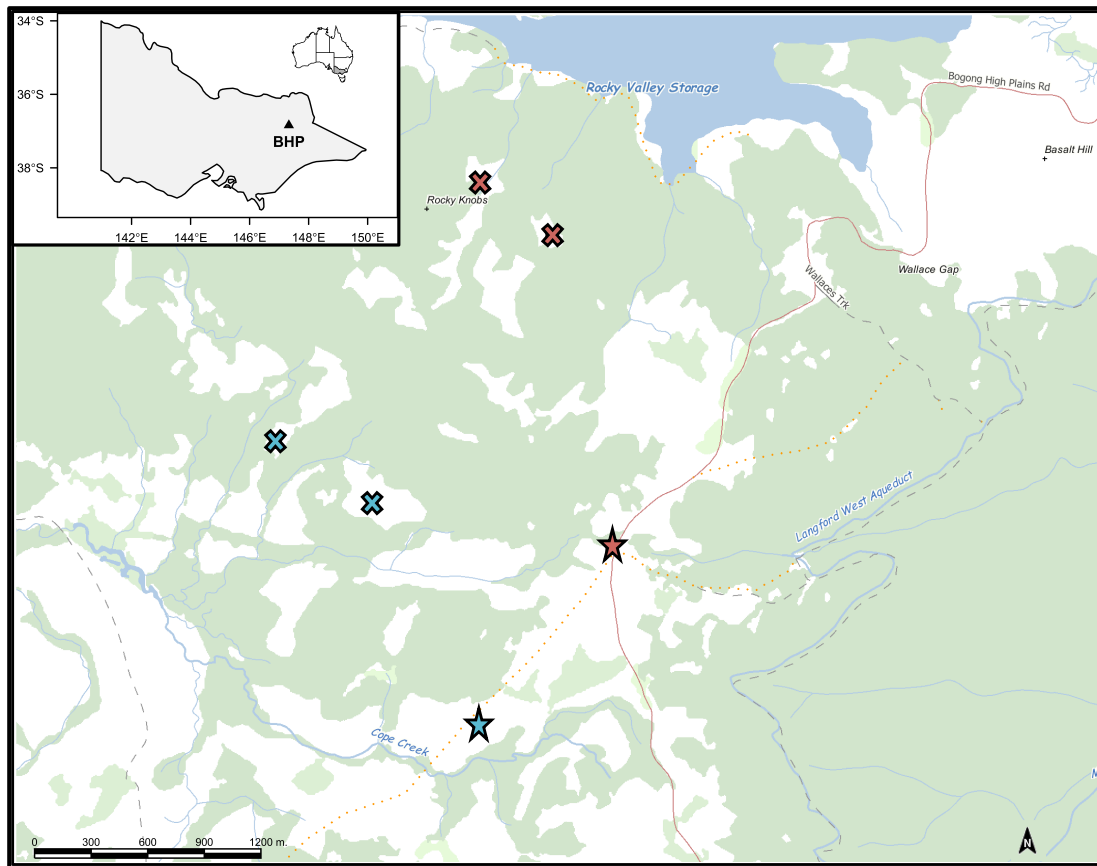


Figure 2.1. Map of Bogong high plains ITEX (crosses) and long-term monitoring (stars) sites used in this study. Red: burned by 2003 fires; blue: unburned. White areas signify alpine ‘treeless’ vegetation.

2.3.2 Experimental design

Like at other ITEX sites, Open Top Chambers (OTCs; Molau and Mølgaard 1996) were used to simulate warmer conditions. In late 2003, at approximately 1750 m a.s.l, OTCs were established at four sites (Jarrad et al. 2008). Two sites were located in relatively undisturbed, intact vegetation, and two others were in vegetation burned by the fires of January 2003. All sites were a minimum of 500 m apart and burned sites were approximately 2 km away from unburned sites. In total 80 1 m² plots were established. Each unburned site had 26 experimental plots (13 OTC; 13 control) and each burned site had 14 plots (7 OTC; 7 control). Plots were randomly located along permanent transects 10 m apart, they were then randomly allocated as either a control or OTC (see Jarrad et al. 2008). All sites were floristically open-grassy-heathland (McDougall and Walsh 2007), a species-rich (~20 species/ 8 m² quadrats) plant

community dominated by non-clonal graminoids (e.g. *Poa hiemata*, *Carex breviculmis*), dense patches of rhizomatous and rosette forbs (e.g. *Celmisia pugioniformis* & *Erigeron bellidioides*) and evergreen shrubs (e.g. *Grevillea australis*, *Asterolasia trymalioides*). Plots contained very low abundances of tall ($>1\text{ m}^2$ or $>0.5\text{ m}$ high) shrub species such as *Grevillea australis* because they exceeded the scale of investigation (i.e. they were larger than the 1 m^2 plot). Instead, the dominant shrubs within plots were small prostrate evergreen shrubs such as *Asterolasia trymalioides* (Rutaceae) and *Pimelea alpina* (Thymelaeaceae). Note: the effect of warming on larger alpine shrub species is addressed in chapter 3. Cattle grazing ceased in 2003, prior to the establishment of the experimental sites. Instead invertebrates were the dominant herbivores present at the sites (Nash et al. 2013, Williams et al. 2014).

OTCs were hexagonal, 58 cm tall with an open-top diameter of 110 cm and base diameter of 168 cm (Fig. 2.2 and 2.3). OTCs were placed over plots each year at the start of the snow-free period (October), where they remained until snowfall (early June). Temperature in both control and OTC plots were measured using Onset 4-channel temperature loggers (Onset Computer Corporation, Bourne, MA, USA). Loggers were randomly installed into four control and four OTC plots at each unburned site and two control and two OTC plots at each burned site. Each logger measured ambient (5 cm above ground) and soil surface (1-2 cm below ground) temperature at hourly intervals from 2004 - 2010. In 2010, following the data collection used in this study, eight Onset Micro Stations were randomly installed into four control and four OTC plots at one of the unburned sites. These Micro Stations measured volumetric soil moisture between 3 and 10 cm below ground at hourly intervals from 2010 to 2013. To ensure OTC treatment soil moisture differences were in the same direction and of similar magnitude across all sites, a Theta probe (Type ML2x, Delta-T Devices Ltd., UK) was used to take five replicate measurements of volumetric soil moisture from each plot in all four sites in November and May from 2010 to 2012. Over the duration of the experiment OTCs simulated the lower end of IPCC predictions (IPCC 2013b) by passively raising daily mean growing season ambient and soil surface temperatures by 1.2°C (± 0.1 ; 95% CI), and minimum and maximum ambient temperatures by 2°C (± 0.2 ; 95% CI). Daily soil moisture in OTC plots was also consistently 4% (± 0.1 ; 95%

CI), lower than controls between 2010 and 2013, a decrease that was consistent across all sites, regardless of whether or not the site had been burned. As such experimental warming here refers to both warmer and drier conditions.

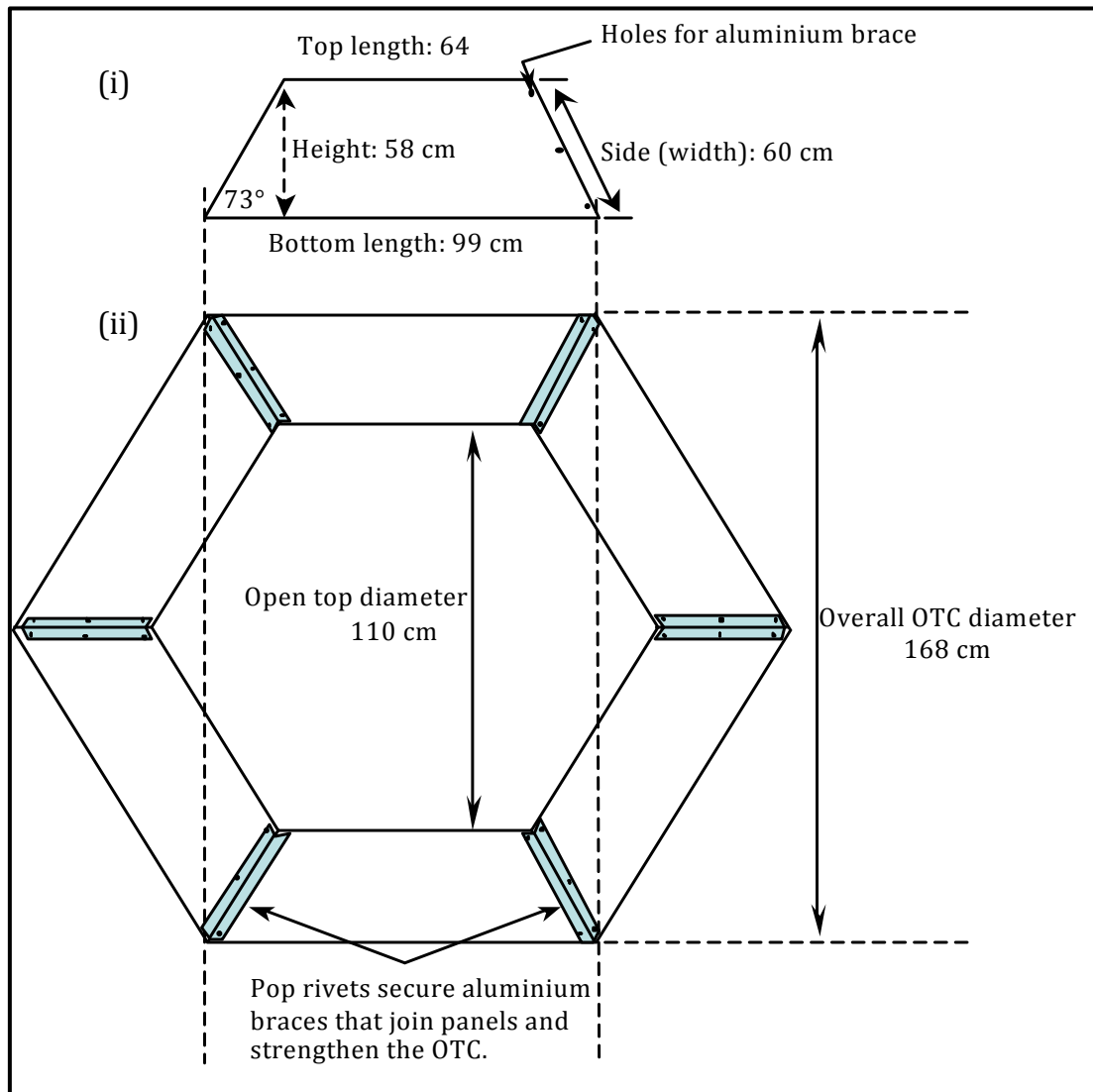


Figure 2.2. Dimensions of an open-top chamber (OTC). (i): side view of one panel; (ii): OTC dimensions, viewed from above. Design as per (Marion et al. 1997).



Figure 2.3. Open Top Chamber (OTC) at one of the unburned sites. Photo courtesy of Carl-Henrik Wahren.

2.3.3 Vegetation and ground cover measurements

Foliage projective cover of all species in each plot was estimated biennially in January from 2004 to 2010 using a 1 m² point-frame with 100 points in a 10 x 10 grid with 10 cm spacing (Fig 2.4; Molau and Mølgaard 1996). At each point, the presence of all species and the amount of bare ground was recorded. Because our central focus was on modeling rates of life form cover changes, and because the model would become unwieldy at the species level, I assigned each species to one of three dominant life forms (shrub, graminoid or forb) and calculated the number of unique hits per life form and ground cover type for each plot. These three life forms were used for four reasons: 1) both experimental and natural observation studies indicate they can summarize and predict broad community trajectories under global change (Chapin and Shaver 1996, Elmendorf et al. 2012a); 2) increasing the number of functional groups resulted in

groupings that contained too few species to accurately estimate their responses to treatments; 3) they are well understood by both land managers and the broader scientific community; and 4) adding additional groups would greatly increase both the number of models to be fitted but also the number of parameters each model would contain (i.e. via the inclusion of each groups neighborhood effect – see below).



Figure 2.4. ITEX point quadrat frame over a plot containing a variety of graminoids, shrubs and forbs.

2.3.4 Data analysis

I used hierarchical generalized linear models to estimate rates of temporal life form cover change as a function of experimental warming, the abundance of neighboring life forms, and the abundance of bare ground - a measure of both disturbance and recruitment opportunity (Williams 1992). Hierarchical models, also known as multi-level models, are well suited to datasets that have a hierarchical structure (e.g. plots

within sites) because they can account for observation error and partition both explained and unexplained variation at multiple levels of a dataset (Gelman and Hill 2007). In our models, experimentally manipulated (i.e. OTC treatment) and unmanipulated variables (i.e. the abundance of neighboring life forms and bare ground) were all treated as covariates affecting rates of cover change (Fig. 2.5).

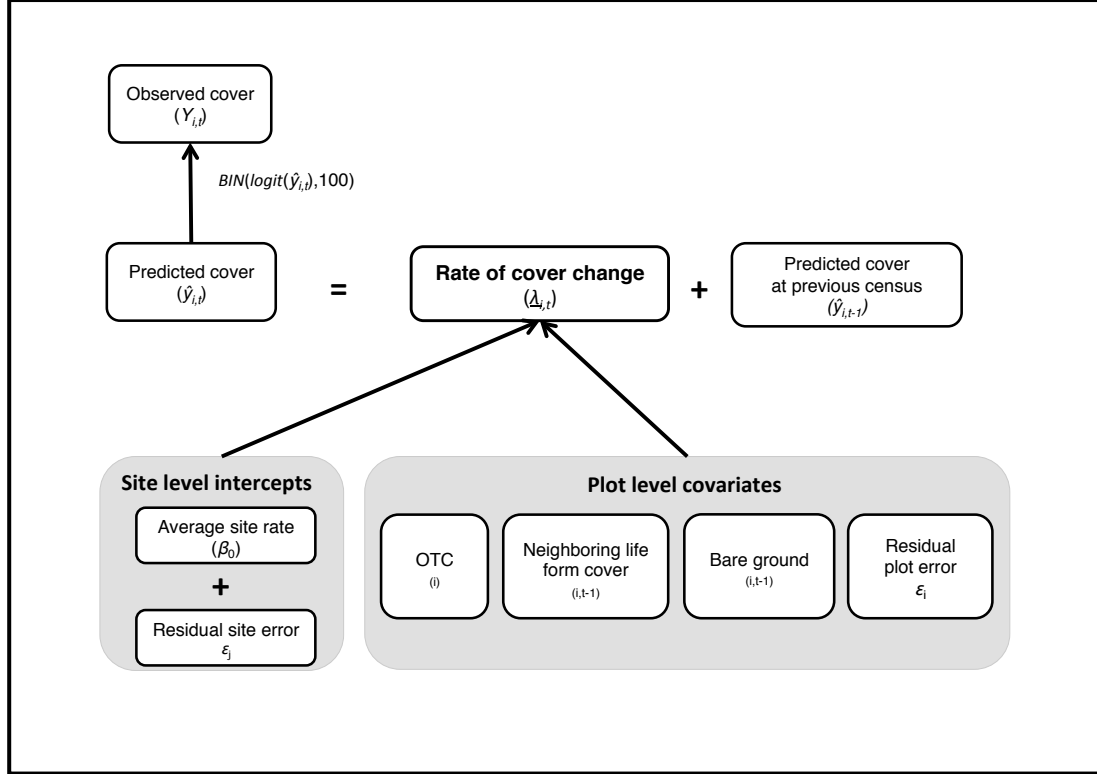


Figure 2.5. Diagram summarizing structure of rate model. Subscripts i, j and t refer to plots, sites and sampling census, respectively.

Because I was interested in rates of cover change but our observations were of number of hits for each life form (an estimate of cover), Y , in each plot i and census t , I first modeled the data as a random realization from a binomial distribution:

$$Y_{i,t} \sim \text{Binomial}(\text{logit}(\hat{y}_{i,t}), 100), \quad (2.1)$$

where $\hat{y}_{i,t}$ is the predicted probability that a life form occupies a given point for each plot-census combination and 100 equals the number of sample trials per plot. From

here on, I refer to $\hat{y}$ as the predicted cover. Using a logit-link, $\hat{y}_{i,t}$ was modeled as the sum of the mean rate of cover change, $\lambda_{i,t}$, and $\hat{y}_{i,t-1}$, the predicted cover in a plot in the previous sampling period:

$$\hat{y}_{i,t} = \lambda_{i,t} + \hat{y}_{i,t-1} \quad (2.2)$$

I used a logit-link because the underlying observations (i.e. presence of a life form at a point) were binary, but also because it implicitly allows the model to account for density dependence at both low and high abundance (i.e. via a sigmoidal curve). That is, at low cover, rates of cover change are reduced due to low recruitment potential (few occupied points), whereas at high cover, rates of change are constrained because of limited space (few unoccupied points).

The rate of cover change, $\lambda_{i,t}$ was modeled as a function of covariates at two spatial scales (site and plot):

$$\lambda_{i,t} = \alpha_{i[j]} + \beta \cdot X_{i,t} + \varepsilon_i, \quad (2.3)$$

where, $\alpha_{i[j]}$ is the varying intercept for each site j to which plot i belongs (interpreted as the mean rate of cover change for each site), $\beta \cdot X_{i,t}$ is a matrix of linear predictors and their coefficients for plot i at time t and ε_i is the residual plot level variation. Varying site intercepts, α_j , were drawn from a normal distribution:

$$\alpha_j \sim N(\beta_0, \sigma_{site}), \quad (2.4)$$

where β_0 is the mean rate across all sites and σ_{site} is the associated standard deviation (estimated from uninformative priors; see Bayesian implementation). Residual plot level variation, ε_i , was estimated from a normal distribution centered on zero and σ_{plot} (estimated from uninformative priors; see Bayesian implementation):

$$\varepsilon_i \sim N(0, \sigma_{plot}). \quad (2.5)$$

Parameters

Plot-level covariates used to estimate rates of cover change included experimental treatment (i.e. OTC or control) as well the cover of bare ground and the cover of other life forms within the same plot (hereafter referred to as ‘neighboring life forms’) at the previous census, $t-1$. I used the cover of neighboring life forms at $t-1$ as a measure of life form interaction because it varied over time and between plots and sites and provides a measure of how life forms influence each other. Bare ground was also included as a time dependent plot level covariate because 1) it too varied between years, plots and sites, 2) it is correlated with the occurrence and severity of fire and other disturbances (e.g. frost heave and herbivory) (Camac et al. 2013, Wahren et al. 2013), 3) it is a determinant of colonization opportunity (Williams 1992, Lantz et al. 2009), and 4) it is a continuous variable that is directly measurable at the plot level. I did not fit a binary fire effect at the site level for two reasons. First, preliminary analyses showed that the level of replication ($N = 2$) was insufficient to estimate a burning effect. Second, and more importantly, fitting a binary (burned/unburned) parameter to a rate-change model, or analyzing burned and unburned sites separately produce biologically unrealistic models because they assume that the magnitude of burning-effects remains constant over time (i.e. a burned site never recovers to an unburned state). Instead, the effect of fire on rates of life form cover change was implicitly examined via changes in bare ground and neighboring life form abundance; both of which I assume is a measure of fire severity and temporal recovery.

I was unable to include soil moisture as a covariate within our models because it was not measured at the same time as the abundance data and thus its effect on rates of change could not be assessed. However, treatment differences in soil moisture are implicitly incorporated into the OTC modeled parameter because, compared with the control treatment, the OTCs resulted in both warmer and drier conditions (see *Experimental design*). Other climate variables, such as annual rainfall and mean growing season temperature, were not included as modeled parameters because the number of censuses ($N = 4$) was insufficient to adequately estimate such effect on rates of change. However, with continued sampling I envisage that these variables will

eventually be included and will further improve models by explaining inter-annual variation.

Cover-estimates of neighboring life forms and bare ground were logit transformed so that I could accurately estimate means and standard deviations needed for centering and scaling (see below). However, because some cover values were 0 or 100% (and thus could not be logit transformed), I first multiplied estimates by 0.995 and then added a small constant (0.004). Each covariate was then centered on zero (by subtracting the mean) and standardized by two standard deviations (Appendix 2.1) (Gelman and Hill 2007). Centering coefficients allows them to be interpreted more easily, with intercepts interpreted as average responses and slope terms as partial dependencies conditional on other continuous variables at their mean. Furthermore, standardizing by two standard deviations allows the magnitude of effects to be compared between binary (i.e. OTC treatment) and continuous variables (i.e. the cover of bare ground and neighboring life forms) (Gelman and Hill 2007). Because I was interested in whether experimental warming could alter the effects of neighboring life form and bare ground abundance, I included associated two-way interactions with the OTC treatment. The statistical significance was determined using ‘inference by eye’ (Cumming and Finch 2005). In the case of parameter estimates, if the estimated 95% credible intervals overlapped zero they were considered not significant at $P = 0.05$. The advantage of this approach over reporting p-values is that the inference by eye approach highlights both the effect size and its associated uncertainty, allowing the reader to make his/her own decision on whether the effect is ‘biologically significant’. To further aid in interpretation I also included 80% credible intervals to allow the reader to determine with confidence whether the effect was estimated to be primarily positive or negative.

Bayesian implementation and prior distributions of parameters

I used Bayesian inference and therefore needed to specify prior distributions for all model parameters. The response (probability of being at a point in a plot) was binary, so I used weakly informative Cauchy priors as recommended by Gelman et al (2008). For each life form the mean rate across site, β_0 (i.e. the mean hyper-parameter used to estimate the varying site intercepts) was drawn from a Cauchy distribution with prior mean 0 and prior scale 10. The regression coefficients, which model variation in rate of

cover change for each life form (see eq. 3), were drawn from Cauchy distributions with prior mean 0 and prior scale 2.5. Site and plot-level variation σ_{site} , σ_{plot} respectively, were drawn from positive half Cauchy distributions truncated at 0, with prior mean 0 and prior scale 10. Models were fitted using Markov chain Monte Carlo (MCMC) sampling in R 2.15.1 using package R2jags version 0.03-08 (Su and Yajima 2012) as an interface to JAGS 3.3.0 (Plummer 2011). I used three chains to ensure convergence. I assessed convergence through visual inspection of chains and reference to the Brooks-Gelman-Rubin convergence diagnostic (Brooks and Gelman 1998). For all models, posterior distributions of each parameter always converged within 50,000 iterations. After discarding the first 50,000 iterations as burn-in, a further 50,000 iterations were taken from the joint posterior and thinned to every 50th sample. Sample JAGS code for the model is provided in Appendix 2.2.

Model checks, hind casting & simulating vegetation change

The residuals of each model were checked graphically against predicted cover and none showed any systematic pattern or severe heteroscedasticity. To ensure all parameters were identifiable we selectively removed each covariate and visually inspected whether the direction and magnitude of effects were severely altered; none were. Overall predictive fit of each life form model was examined by calculating the R-square between experimental observations and model fit without random effects.

To assess the transferability of our models beyond the four experimental sites and at a larger spatial scale (approximately 1 ha), I hind-casted temporal changes in life form cover at two nearby (within 5 km of experimental sites) alpine heathland sites; one burned by the 2003 fires and the other unburned. I then compared model predictions to biennial observations from 2003 to 2013. The sites were floristically similar to the experimental sites, were approximately 1 ha in area and yielded a decade (2004 – 2013) of life form and bare ground cover estimates measured from point quadrats along permanent reference transects (Fig. 2.6; Wahren et al. 2013).

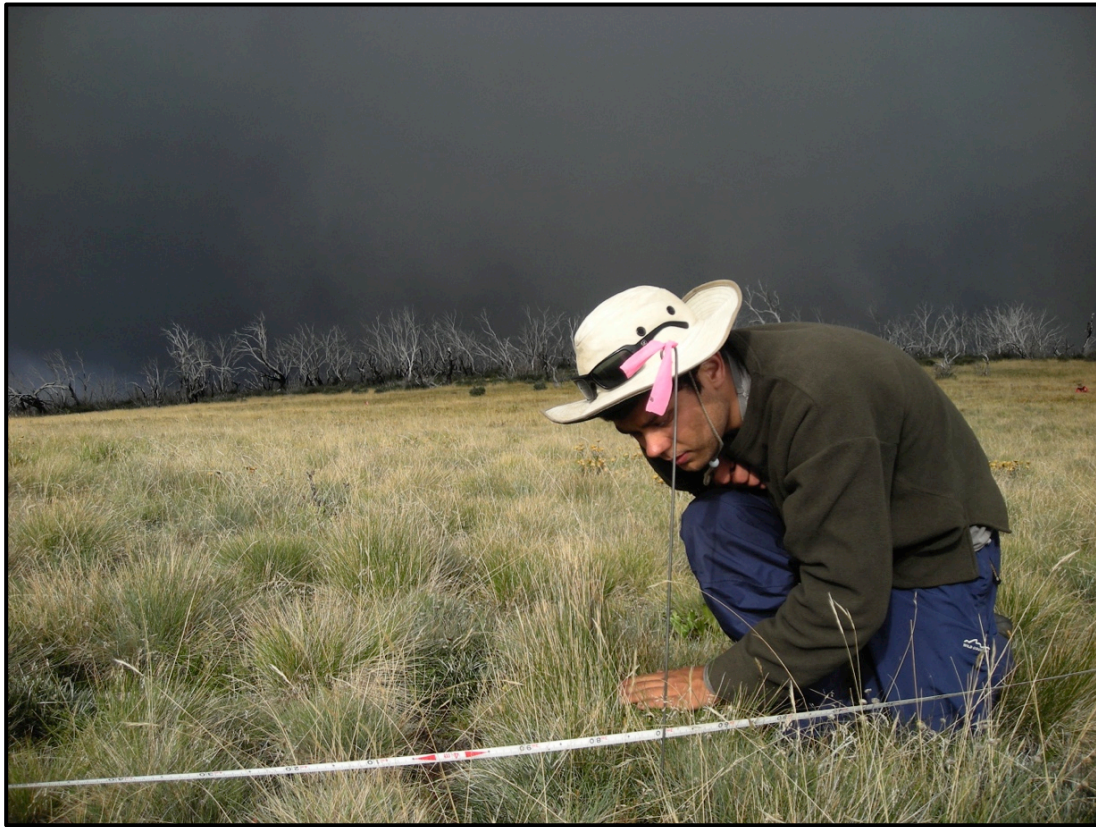


Figure 2.6. Sampling a grassland long-term monitoring site using pointing pin and line transects.

In order to hind-cast community level changes, I merged the three life form models into a single model that used posterior parameter distributions of β_0 , the mean cover across all sites, and other covariates from the three models related to unwarmed conditions (i.e. not including OTC parameters). This allowed for the model to simultaneously estimate the abundance of each life form in each year based on the cover of bare ground (supplied – see below) and the predicted cover of neighboring life forms. To initialize the model, I used 2003 observed life form covers. Because I did not have a model to predict temporal changes in bare ground, I supplied observed estimates of its cover for all years. These initial conditions were then logit transformed and centered and standardized based on experimental means and standard deviations (Appendix 2.1). I then simulated the model 3000 times for each year to produce a reliable estimate of the mean cover for each life form. I then plotted these predictions against observations. Lastly, to assess potential compositional shifts in life form abundances I simulated

warmed and unwarmed conditions for burned and unburned alpine heathland using the initial conditions obtained from the long-term monitoring sites.

2.4 Results

2.4.1 Observed cover changes in experimental plots

Pooling across plots and sites (i.e. ignoring plot variation in bare ground or life form covers) indicated that experimental warming had negligible effects on the average cover of shrubs, graminoids and forbs (Fig. 2.7). Instead, whether vegetation was burned or unburned appeared to have the strongest effect on cover, with shrubs marginally increasing in unburned sites but remaining low in burned sites. By contrast, cover of graminoids decreased by 20% from 2004 to 2010 in unburned sites but increased by approximately 40% in burned sites over the same period. Forb cover increased regardless of burning. At the first census, approximately 10 months post-fire, bare ground cover was on average 2% higher and three times as variable at burned sites compared unburned sites (range: 0-33% & 0-10%, respectively; Fig. 2.7); a difference maintained over the duration of this study. Experimental warming did not influence the temporal pattern of bare ground cover in either burned or unburned vegetation in any year.

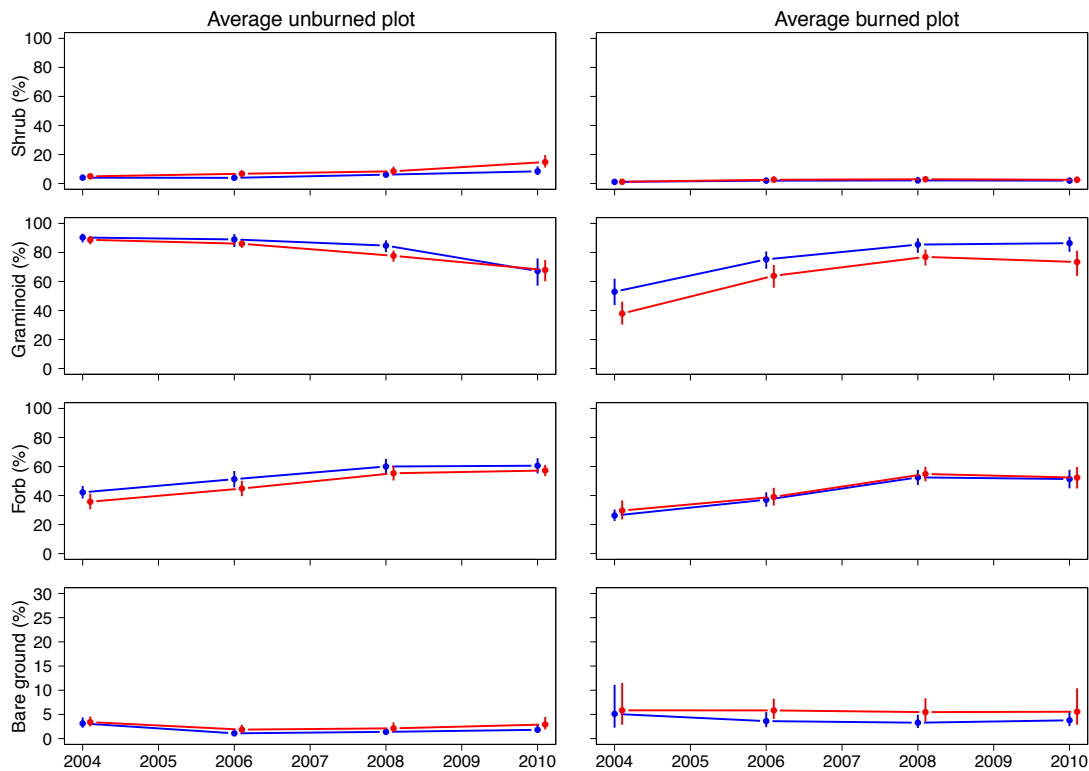


Figure 2.7. Observed foliage projective cover (means $\pm$ 95% confidence intervals) in experimental plots burned and unburned by the 2003 wildfires. Solid line: OTC treatment; Dashed line: Control. Note: this figure shows treatment effects at the broadest level (i.e. burned and unburned) and therefore mean and uncertainty estimates do not account for either site or plot variation in bare ground or neighboring or how these may interact with OTC treatment.

2.4.2 Model fit to experimental data

Model fit (i.e. model fit without random effects) to experimental data was high for forbs ($R^2 = 77\%$), moderate for shrubs ($R^2 = 58\%$) and low for graminoids ($R^2 = 13\%$). Rates of cover change varied among sites and plots, with the amount of unexplained variation at each level dependent on life form (Table 2.1). In graminoids, the weaker predictive fit was largely due to much unexplained variation between sites, with a standard deviation nearly three times that of the standard deviation among plots (Table 2.1). By contrast, the magnitude of unexplained variation for shrubs and forbs was less compared to graminoids and the variation was evenly split between site and plot level.

Table 2.1. Estimated residual variation at both site and plot levels for each life form (median point estimate and 95% credible intervals).

Model	Data level	Standard Deviation (95% CI)
Shrub	Site	0.33 (0.03 , 1.24)
	Plot	0.30 (0.21 , 0.41)
Graminoid	Site	1.16 (0.37 , 4.11)
	Plot	0.39 (0.31 , 0.48)
Forb	Site	0.18 (0.01 , 0.72)
	Plot	0.15 (0.12 , 0.19)

2.4.3 Effects of experimental warming

Experimental warming effects on rates of cover change were small and 95% credible intervals overlapped zero for all three life forms (Fig. 2.8). Instead, rates were strongly influenced by the abundance of other neighboring life forms. The effects of neighboring life forms were predominately negative: rates of graminoid cover change decreased with increasing forb abundance, while rates of forb and shrub cover change decreased with increasing graminoid abundance. Shrub abundance did not affect graminoids or forbs with small estimated effects and credible intervals overlapping zero. Thus, the abundance of neighboring life forms tended to reduce the rates of cover expansion, and in some sites (e.g. graminoid cover in site 2; Fig. 2.8) exacerbated declines. The predicted effect of bare ground, an indicator of both disturbance and recruitment opportunity, was predominately negative (90% of credible interval is negative) on rates of shrub cover change, but had predominately positive effects on rates of cover change in both graminoids and forbs (98% of credible interval is positive for both life forms).

2.4.4 Experimental warming and the effects of bare ground and life form interactions

Experimental warming did affect rates of life form cover by reducing the negative effects of both neighboring life forms and the positive effects of bare ground via two-way interactions (Fig. 2.8). Forbs growing in OTCs exhibited higher rates of cover change compared to those growing in control plots because the positive warming-

graminoid interaction negated the negative direct effect of graminoid abundance (Fig. 2.8). In graminoids, experimental warming negated the positive effect of bare ground, but not the negative effect of forb abundance.

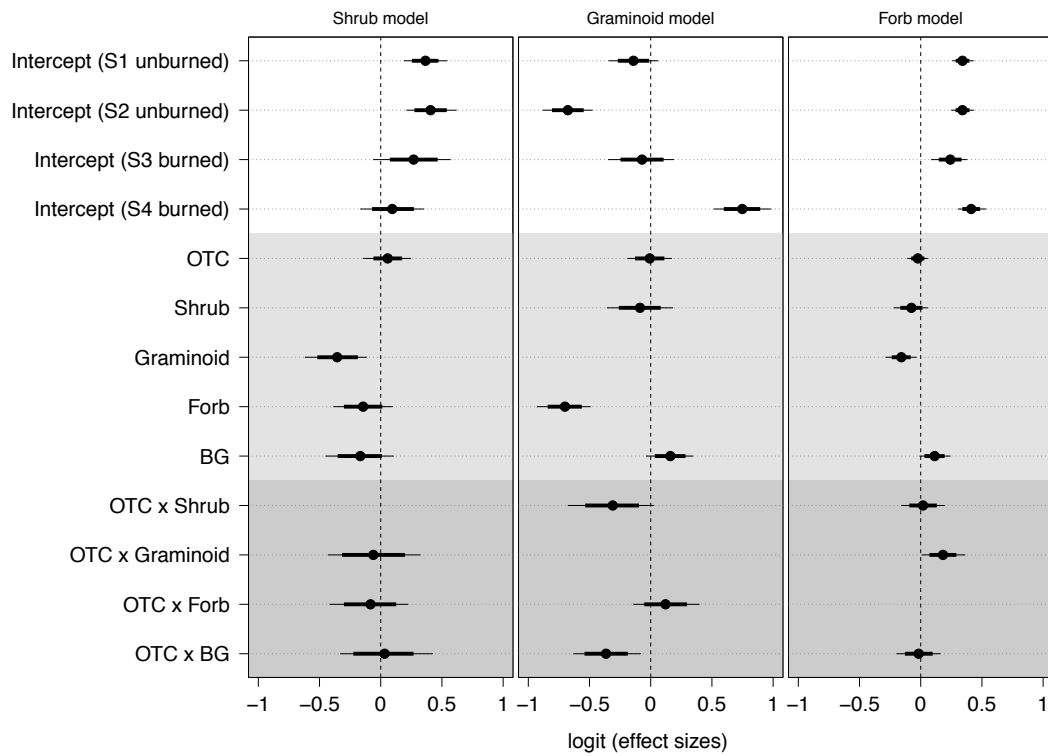


Figure 2.8. Mean (logit) coefficients $\pm$ 95 (thin line) and 80% (thick line) credible intervals from each life form model. White sections: site intercepts (S1 to S4) interpreted as the mean rate of cover change for a control plot when all other covariates are at their mean; Light grey sections: plot level covariate effects; Dark grey sections: two-way experimental warming interactions. In logit space, these models are additive, thus to determine the expected rate of change in control plots, add the relevant intercept from the white section and covariate effects from the light grey section, respectively. To determine the expected rates of cover change for OTC plots, add the relevant intercepts, covariate effects, and two-way interactions in the white, light grey and dark grey sections, respectively. BG = bare ground; OTC = Open-Top-Chamber.

2.4.5 Hind casting – comparing model predictions against long-term monitoring observations

Our rate change models predicted the overall historical trajectory of life form cover change in both burned and unburned long-term heathland monitoring sites, though not in detail (Fig. 2.9). Specifically, the model was predictive of the lack of shrub cover change in both burned and unburned vegetation with mean predictions falling between the 2.5th and 95th observed percentile for all years. The model was also predictive of graminoid post-fire regeneration, but failed to account for the sharp decline in graminoid cover during the severe drought between 2007 and 2009 and its subsequent rapid regeneration. Forb predictions captured general trajectories but slightly overestimated forb cover in unburned vegetation and underestimated cover in burned vegetation (Fig. 2.9).

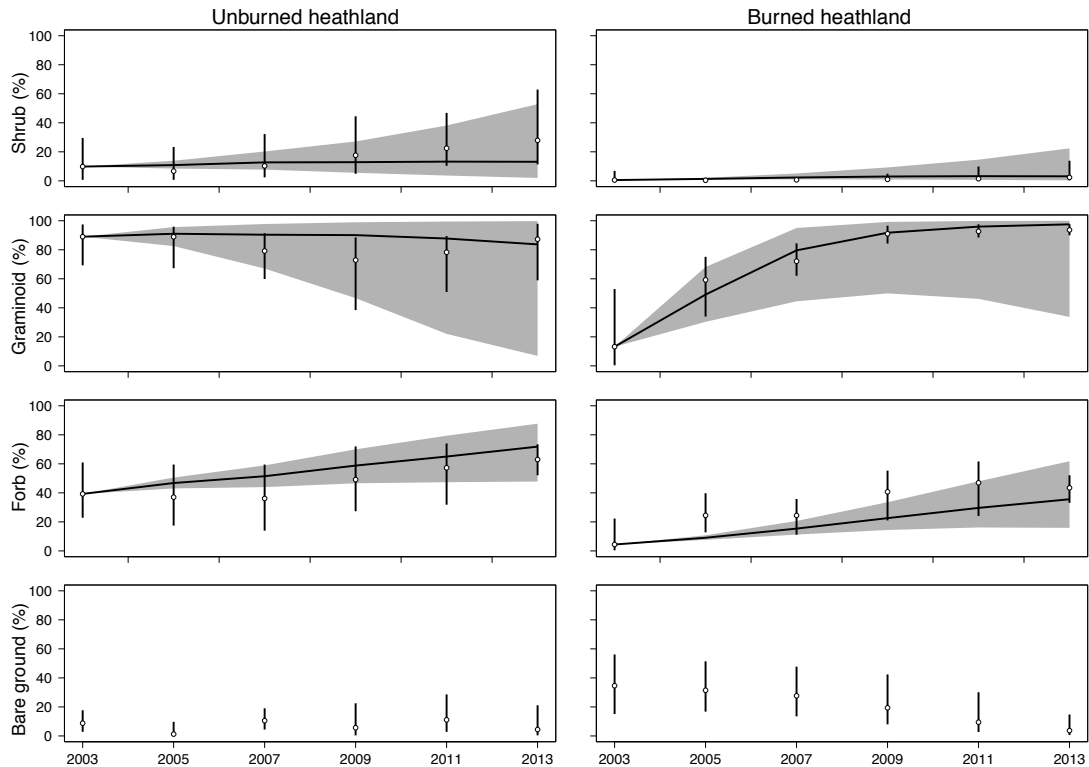


Figure 2.9. Comparison between ambient climate hind-cast predictions of temporal changes in life form cover with observations in long-term alpine heathland monitoring sites that were burned and unburned by the 2003 wildfires. Open circles: observed mean cover estimates (with vertical lines representing the observed interval between the 2.5th and 97.5th quantiles); Solid lines with grey shading: predicted mean (+/- 95% credible intervals) cover. Model simulations were initialized using mean observed covers in 2003. Bare ground was supplied to the models as a known entity for all years and was not explicitly modeled (bottom two panels).

2.4.6 Simulating warming effects in burned and unburned alpine heathland

Simulated changes in life form composition for an average unburned alpine heathland suggested that cover of shrubs and forbs was expected to increase at a faster rate under warmer conditions (Fig. 2.10). By contrast, graminoid cover was expected to substantially decrease under warmer conditions. Warming was also predicted to influence the trajectory and rate of post-fire regeneration by reducing the rate of regeneration in both graminoids and forbs but increasing the recovery rates in shrubs (Fig. 2.10).

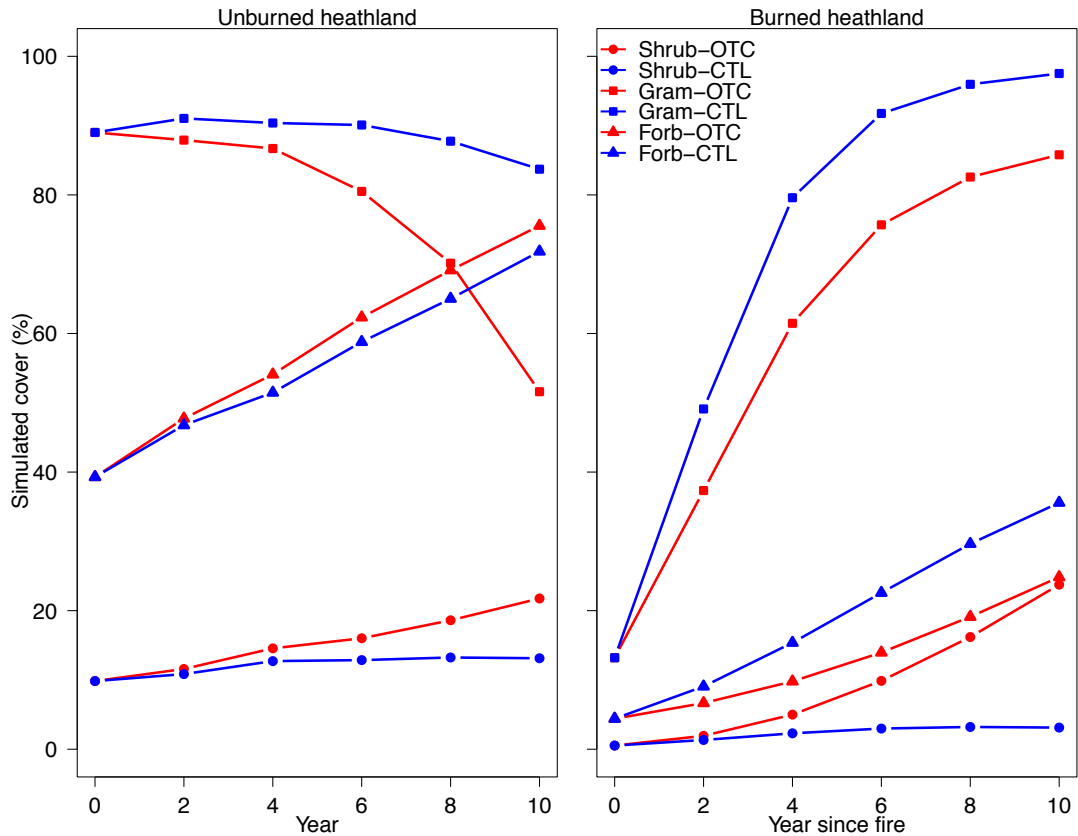


Figure 2.10. Simulated changes in life form cover over a decade for a recently burned and long-unburned open heathland site under ambient and warmed conditions. The model was initialized with 2003 life form covers observed in alpine heathland long-term monitoring sites burned and unburned by the 2003 wildfires. Bare ground was supplied to the models as a known entity for all years (based on observations in figure 2.9). Red line: OTC condition; blue line: current (control) conditions; Circles: shrubs, Squares: graminoids, Triangles: forbs.

2.5 Discussion

In this study, I built and parameterized rate change models using a 7-year warming experiment. These models allowed us to examine how experimental warming and the abundance of bare ground and neighboring life forms interact to affect rates, and thus trajectories, of cover change in three dominant life forms - shrubs, graminoids and forbs. I show that experimental warming altered rates of life form cover change by reducing negative effects associated with contrasting life form abundance and positive effects of bare ground. These models predicted broad directions and rates of past life form cover trajectories at burned and unburned alpine heathland sites. Furthermore, model simulations suggest that warming in unburned vegetation would decrease

graminoid cover and increase the rates of forb and shrub cover growth. By contrast, in burned vegetation, warming is expected to slow post-fire regeneration in both graminoids and forbs while allowing for the rapid expansion in shrub cover.

2.5.1 The lack of direct experimental warming effect

The muted direct effect of experimental warming on rates of cover change in all three life forms may be due to idiosyncratic responses of species within life forms (Dormann and Woodin 2002). However, in all cases the uncertainty around the OTC parameter was small, indicating that this is unlikely to be the case. Instead the muted effect of OTCs may be a consequence of physiological processes that influence growth (and thus cover), such as photosynthesis and respiration, not being significantly altered by a 1.2°C temperature rise during the growing season (the period when the OTCs are actually on the plots). Chapin (1983) and Körner (2003) suggested that, for alpine and polar plants, a negligible growth response to warmer spring and summer months may be due to photosynthesis not being limited by growing season temperatures. This is because many cold-adapted plants require lower temperatures (~15°C) for optimum rates of photosynthesis compared to temperate species (~25°C). Moreover, alpine and arctic plants have wide temperature response curves, allowing substantial rates of photosynthesis even at 0°C (Chapin 1983, Körner 2003). Microclimate data collected from our plots suggest mean growing season temperatures experienced at the plant level (9-12°C at 10 cm above ground) are already close to those needed for optimum rates of photosynthesis in alpine plants. Thus, increasing temperatures by 1.2°C during the growing season is unlikely to elicit a strong physiological response that is ultimately expressed in rates of cover change of the major life forms.

2.5.2 Life-form interactions and experimental warming

Bertness & Callaway (1994) proposed that low temperatures in alpine and arctic ecosystems ‘stress’ plants and allow positive instead of negative plant-plant interactions to predominate. If broadly valid, warming should reduce this low temperature stress and generate stronger competitive effects. Such responses have been observed in several experimental warming studies (e.g. Klanderud 2005, Olsen and Klanderud 2013). Yet, contrary to these expectations, I found that life form interactions were predominately negative and experimental warming decreased these negative effects. One possible explanation for this could be that OTCs increased plant stress by reducing soil moisture during a period when plant available water was limited. Water availability is known to be a major determinant of vegetation change in alpine and arctic environments (le Roux et al. 2013) and can alter the magnitude of experimental warming effects (Elmendorf et al. 2012a).

Data used to parameterize these rate models was collected during part of the driest 13-year period (1996 – 2009) on record for south-eastern Australia since the late 1880s (Wahren et al. 2013). On the Bogong High Plains, this drought has been correlated with a 25% reduction in alpine grass cover at long-term monitoring sites (Wahren et al. 2013) and significant mortality in both shrubs (Morgan 2004) and grasses (Griffin and Hoffmann 2012). Microclimate data suggests that from 2003 to 2010 OTCs were likely to have on average 4% less soil moisture than control plots (see *Experimental design*). In arid and semi-arid vegetation, studies have shown that lower water availability increases the importance of positive plant-plant interactions (Pugnaire et al. 2009). However, in alpine and arctic ecosystems, water is often considered not limiting (Körner 2003) and hence few studies have assessed whether it influences alpine plant-plant interactions (e.g. Cavieres et al. 2006). I suggest that the shift from negative to neutral neighboring life form interactions may reflect the drier conditions experienced within OTCs. Here a decrease in soil moisture, particularly during drought, may shift the net effect of neighboring plants from negative to neutral as neighbor protection from both drying winds and high temperature extremes becomes more important. However, to describe this relationship, further experimental studies are required that can partition temperature and soil moisture effects.

2.5.3 Effects of bare ground

Disturbance at varying temporal and spatial scales affects vegetation dynamics in all plant communities (Pickett and White 1985, Turner 2010). In the Australian Alps, like many other alpine and tundra environments, vegetation cover is high (> 95%) and the total area suitable for seedling colonization is low (Williams et al. 2014). However, disturbances such as frost heave, herbivory and fire can rapidly increase the area suitable for colonization by creating bare ground and reducing competition from surrounding vegetation (Williams 1992). In the present study, bare ground had a positive effect on graminoid rates of cover change. However, this effect was negated in warmed plots by a negative bare ground-OTC interaction (Fig. 2.8). This could be due experimental warming increasing the frequency and duration of lethal temperatures experienced in bare ground patches, thereby inhibiting the ability of non-clonal graminoids (e.g. *Poa hiemata*) to colonize and survive. In the Australian Alps bare ground patches have been observed to reach temperatures of up to 80°C during the growing season (Williams 1985).

2.5.4 Simulating temporal changes in life form abundance in burned and unburned heathland

Fire activity is projected to increase in many ecosystems worldwide as a consequence of climate change (Westerling et al. 2011, Turetsky et al. 2011). In south-eastern Australia, the severity of fire weather has increased in recent decades (Clarke et al. 2013) resulting in increased fire activity in the Australian Alps bioregion (Bradstock et al. 2014). Future warming and drying is likely to further exacerbate this increased fire activity. Thus, in order to accurately forecast rates and trajectories of vegetation change it is crucial to understand how climate affects vegetation dynamics in both burned and unburned conditions. Model simulations predict that, in unburned open heathland, graminoid cover will decrease at a faster rate under warmer conditions. By contrast, shrub and forb cover will increase as a consequence of warming, with increases in the latter likely to further exacerbate grass decline. This prediction is entirely consistent with long-term monitoring observations across the unburned sections of the Bogong High Plains, with temperatures increases (0.4°C) and precipitation declines (6%) since 1979 being correlated with a 25% decline in graminoids and a 20% and 9% increase in shrubs and forbs, respectively (Wahren et al. 2013). The simulations also suggest that warmer conditions will reduce post-fire regeneration in both graminoids and forbs and allow shrubs to rapidly increase in cover, potentially exposing the landscape to elevated risk of soil erosion (Williams et al. 2014).

The findings of this study highlight that models of vegetation change need to account for both direct and indirect effects of warming. I suggest that current and future experimental warming studies focus on modeling rates of change, as opposed to differences or ratios of state variables for control and manipulated groups observed at some time. By doing this, the utility of experimental work will be greatly extended, particularly for predicting vegetation dynamics under climatic change.



Chapter 3:

**Climatic warming strengthens a positive
feedback between alpine shrubs and fire**

3.1 Abstract

Climate change is increasing fire frequency and severity worldwide, but it is not clear how the interaction between increases in temperatures and fire will affect threatened ecosystems. Here I examine alpine shrub growth and survival at the critical seedling establishment stage using manipulative and natural experiments. Fire increased shrub seedling post-fire establishment by more than 20-fold. Experimental warming of 1.2°C doubled seedling growth rates and increased survival. Warming also had the capacity to change the effect of tussock grass on shrub seedling survival from positive to negative. However, this effect was highly uncertain and likely to be of diminishing importance in areas with high levels of bare ground (e.g. following fire). These changes will increase shrub cover and consequently fire frequency and severity, which further exacerbate shrub expansion. Global warming therefore strengthens an existing feedback loop leading to changes in vegetation and fire regimes.

3.2 Introduction, results and discussion

Forecasting the effects of warming on vegetation change requires an understanding of mechanisms by which climate and vegetation interact. Most forecasting models include the direct effects of changing climatic conditions, but ignore biotic interactions and the type, frequency and severity of disturbances that are also likely to change (Guisan and Thuiller 2005, Tucker et al. 2012, Giannini et al. 2013). Because disturbance influences the composition and structure of plant communities and biomes worldwide (Dale et al. 2001, Bond et al. 2005, Bowman et al. 2009, Turner 2010) it can either exacerbate or diminish the effects of climate change. By altering the strength of biotic relationships and recruitment opportunities, the interaction between climate change and disturbance is expected to strongly influence how vegetation regenerates after disturbance (Lantz et al. 2009, Landhausser et al. 2010, Munier et al. 2010). Seedlings are the most sensitive life stage for vegetation dynamics because their establishment, growth and survival rates are highly susceptible to changes in climate, disturbance and biotic interactions, hence they are unlikely to exhibit a lagged response to climate change (Lloret et al. 2004, Leck et al. 2008, Walck et al. 2011). Changes in seedling establishment, growth and survival are therefore expected to be highly predictive as to whether a species distribution will expand or contract under changing climate and disturbance regimes.

Manipulative experiments have been widely used to investigate the potential effects of climate change on plant communities. These experiments have provided invaluable information on how climate change directly influences plant phenology (Hoffmann et al. 2010), reproduction (Klady et al. 2011), morphology (Hudson and Henry 2009), growth (Hollister et al. 2005a), floristic composition (Elmendorf et al. 2012a, Sistla et al. 2013) and biotic interactions (Klanderud 2005). However, because disturbances vary both spatially and temporally, they are inherently difficult to incorporate into an experimental design. As such, few climate change experiments have been conducted on vegetation growing in post-disturbance conditions (Jarrad et al. 2008, Munier et al. 2010, Classen et al. 2010, Graae et al. 2010). Consequently, little is known about how climate change influences vegetation in post-disturbance conditions.

In alpine and arctic vegetation worldwide, warming experiments and long-term monitoring have documented significant increases in the growth and cover of woody species (Sturm et al. 2001, McDougall 2003, Walker et al. 2006, Myers-Smith et al. 2011, Elmendorf et al. 2012a). The frequency and extent of wildfires have also increased in these environments over recent decades, a trend expected to continue (Flannigan et al. 2009, Qiu 2009, Westerling et al. 2011). Yet, warming experiments have not assessed how vegetation, particularly highly flammable woody vegetation, is likely to change under warmer potentially more flammable conditions. A likely consequence of more frequent and severe fires is to increase recruitment opportunities for woody species (Myers-Smith et al. 2011). When coupled with higher growth and survival rates caused by rising temperatures, such a trend would spur shrub expansion and increase the likelihood of more frequent and severe fires (Higuera et al. 2008, Lantz et al. 2009, Myers-Smith et al. 2011). In effect, warming is likely to strengthen an existing feedback loop that not only has the potential to cause rapid changes in the composition and structure of vegetation, but also have serious social, biodiversity and carbon sequestration consequences (Mack et al. 2011).

I explored several components of this feedback loop in the Victorian Alpine National Park, Australia. Australian alpine ‘treeless’ vegetation is highly vulnerable to climate change because it is extremely restricted, occupying less than 0.15% of the continent and occurs in a narrow altitudinal band (ca. 1800 - 2200 m) with no nival zone (Körner 2003). Consequently, there are no higher altitudinal refuges available for Australian alpine species. As with tundra ecosystems (Hinzman et al. 2005) the Australian Alps has experienced rapid changes in climate. Since 1979, mean growing season temperatures have risen by approximately 0.4°C and annual precipitation has fallen by 6% (Wahren et al. 2013), with a consequent decline in snow pack (Sánchez-Bayo and Green 2013). These climatic changes have been correlated with increases in forb and shrub cover by 9% and 20%, respectively, and a 25% decline in graminoids (Wahren et al. 2013). The landscape has also recently been burned by multiple wildfires in 2003, 2006 and 2013. The largest of these occurred in 2003 and burned more than 400,000 ha (~50%) of the Victorian Alpine National Park, Australia (Williams et al. 2008).

I took advantage of areas burned by either the 2003 and 2006 fires and focused on alpine open heathland (McDougall and Walsh 2007) a plant community that occupies ca. 25% of the Australian alpine landscape, and is an ecotone between dense heathland and tussock grassland. Under global warming this plant community is likely to change substantially in shrub cover because it acts as the ‘invasion front’ for future shrub encroachment into grass-dominated plant communities and is itself susceptible to shrub thickening (McDougall 2003). To determine how warmer and drier post-fire conditions affects shrub cover, I combined field observations with a warming experiment that used seedlings of four dominant alpine shrubs - *Grevillea australis*, *Asterolasia trymalioides*, *Prostanthera cuneata* and *Phebalium squamulosum*. This approach allowed us to address three questions. (1) How does fire, elevation, adult density and topographic wetness (an estimate of a site’s plant-available water – see methods) influence shrub seedling establishment? (2) Do warmer post-fire conditions influence rates of seedling growth and mortality? (3) Does the size of inter-tussock gaps influence growth and mortality rates, and if so, does the effect change under warmer conditions?

I first investigated how altitude, topographic wetness, adult density, fire, and fire severity (estimated from post-fire twig diameters – see methods) influenced the density of *Grevillea* and *Asterolasia* seedlings. In 2010-11, I estimated seedling density for both species across 40 alpine sites (see methods). I found that the abundance of *Grevillea* and *Asterolasia* seedlings were strongly influenced by the occurrence and severity of fire (Fig 3.1a,b,c & Fig 3.2a,b,c, respectively), but not by elevation or topographic wetness (Fig 3.1e,f & Fig 3.2d,e, respectively). Sites burned by the 2003 fires had seedling densities between twenty and forty times higher than unburned sites. In *Grevillea*, mean densities were 1.4 and 0.03 seedlings/m² at burned and unburned sites, respectively (Fig 3.1b). *Asterolasia* had similar densities: 1.7 and 0.08 seedlings/m² at burned and unburned sites, respectively (Fig 3.2b). Fire severity also positively influenced seedling density of both species, with more seedlings at severely burned sites compared to lightly burned sites (Fig 3.1c & Fig 3.2c). Seedling density was also positively correlated with adult density (Fig 3.1d).

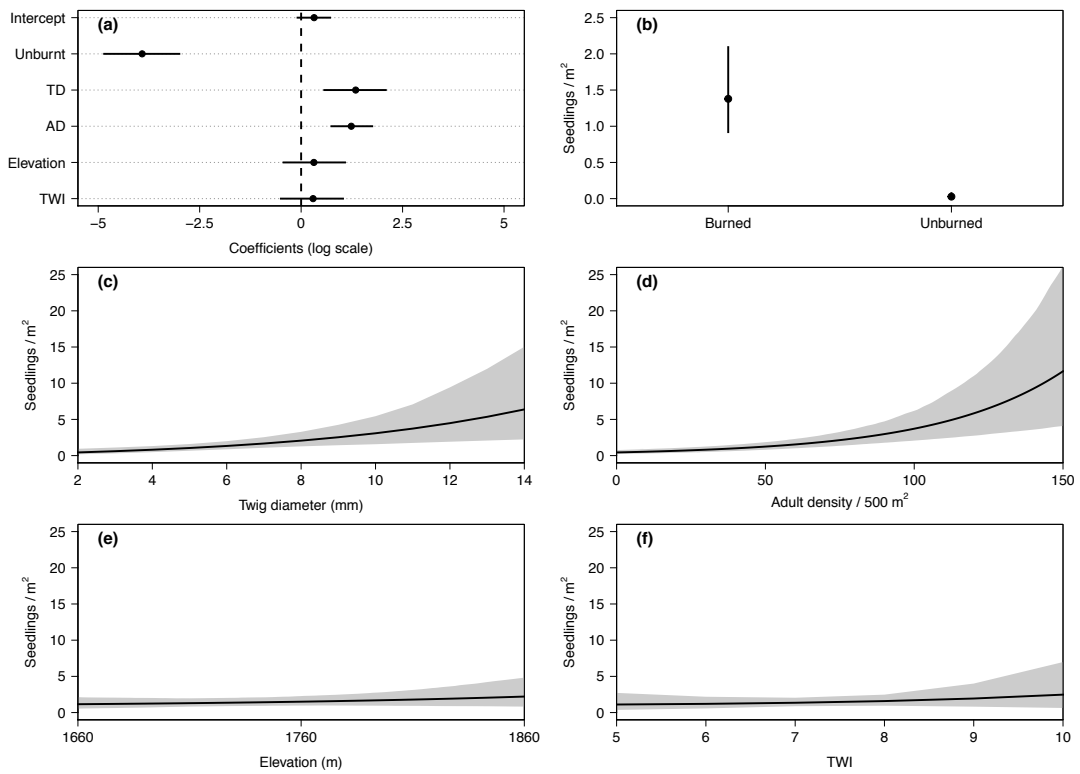


Figure 3.1. Mean *Grevillea australis* seedling density along burning, fire severity (TD; estimated from post-fire twig diameters), adult density (AD), elevation and topographic wetness index (TWI; an estimate of a site's plant available water) gradients. a) centered and standardized model coefficients (log scale). Here, the intercept is interpreted as the average seedling density at a burned site assuming TD, AD, Elevation and TWI are at their mean; b) the effect of burning on average seedling densities; c-f) partial dependence plots illustrating how seedling density varies along observed severity, adult density, elevation and topographic wetness gradients in areas burned by the 2003 fires. All error bars are 95% credible intervals.

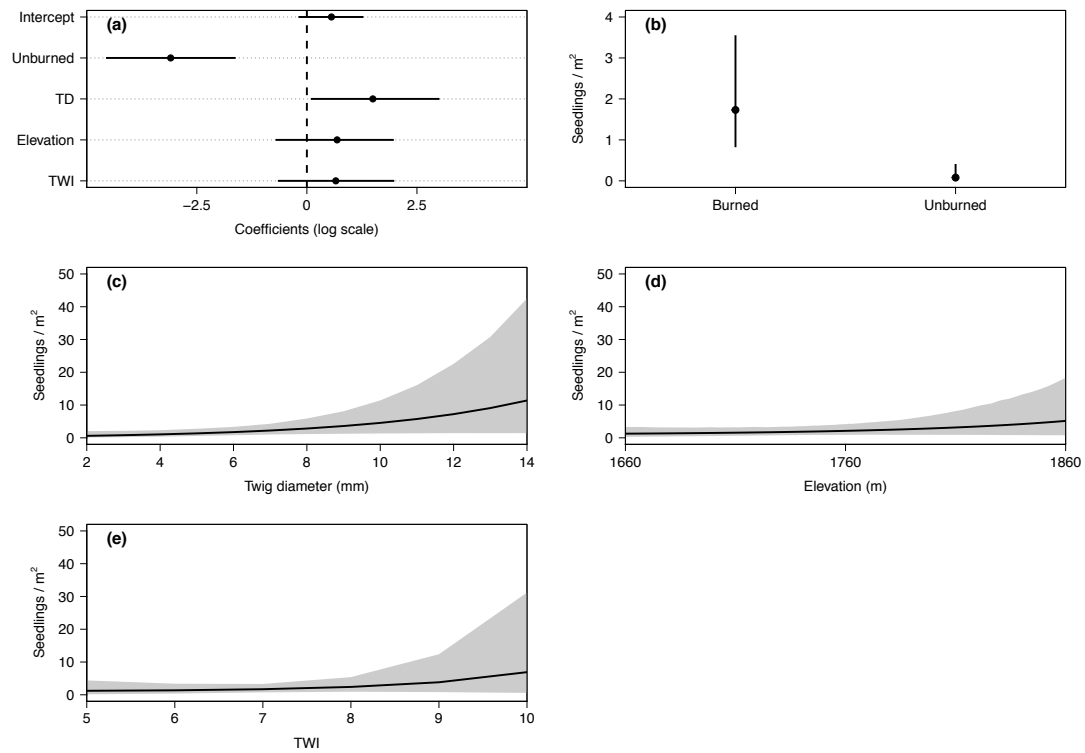


Figure 3.2. Mean *Asterolasia trymalioides* seedling density along burning, fire severity (TD; estimated from post-fire twig diameters), elevation and topographic wetness index (TWI; an estimate of a site's plant-available water) gradients. a) centered and standardized model coefficients (log scale). Here, the intercept is interpreted as the average seedling density at a burned site assuming TD, Elevation and TWI are at their mean; b) the effect of burning on average seedling densities; c-e) partial dependence plots illustrating how seedling density varies along observed severity, elevation and topographic wetness gradients in areas burned by the 2003 fires. All error bars are 95% credible intervals. Note this species did not have a measure for adult density.

I then investigated whether warmer post-fire conditions influenced seedling growth and mortality rates. Seedlings of *Grevillea*, *Asterolasia*, *Prostanthera* and *Phebalium* emerging after a wildfire were transplanted into experimentally burned plots that were passively warmed by 1.2°C using open top chambers (OTCs) and controls (Marion et al. 1997). In each year, in both warmed and control plots, seedling heights in the four shrub species increased during the spring and summer months and remained unchanged over winter (Fig. 3.3). After 1064 days (of which 611 were growing season days where OTC treatment was applied), mean seedling heights of *Grevillea*, *Prostanthera* and *Phebalium* were taller in warmed plots by 5.8, 8.9 and 2.7 cm respectively (Fig. 3.3). Warming increased heights of both *Grevillea* and *Prostanthera* seedlings in all years, while *Phebalium* did not respond to warming treatment until the second growing season. *Asterolasia* seedlings showed no difference in growth rate between warmed and control plots. Mean predicted daily growth rates of *Grevillea*, *Prostanthera* and *Phebalium* were 2.2, 1.8 and 1.4 times that observed in control plots, respectively (Appendix 3.1). These differences equate to a mean 6 cm tall seedling (the mean initial size used in this experiment) predicted to reach mature size in 26 (20 vs. 46) fewer years for *Grevillea* and 11 fewer years for both *Prostanthera* (15 vs. 26) and *Phebalium* (28 vs. 39) (Fig. 3.3). *Asterolasia* was predicted to reach a mature height 1 year earlier in control plots (18 vs. 17), however this effect was not significant. These experimental warming effects were also representative of treatment effects on basal growth (Appendix 3.2).

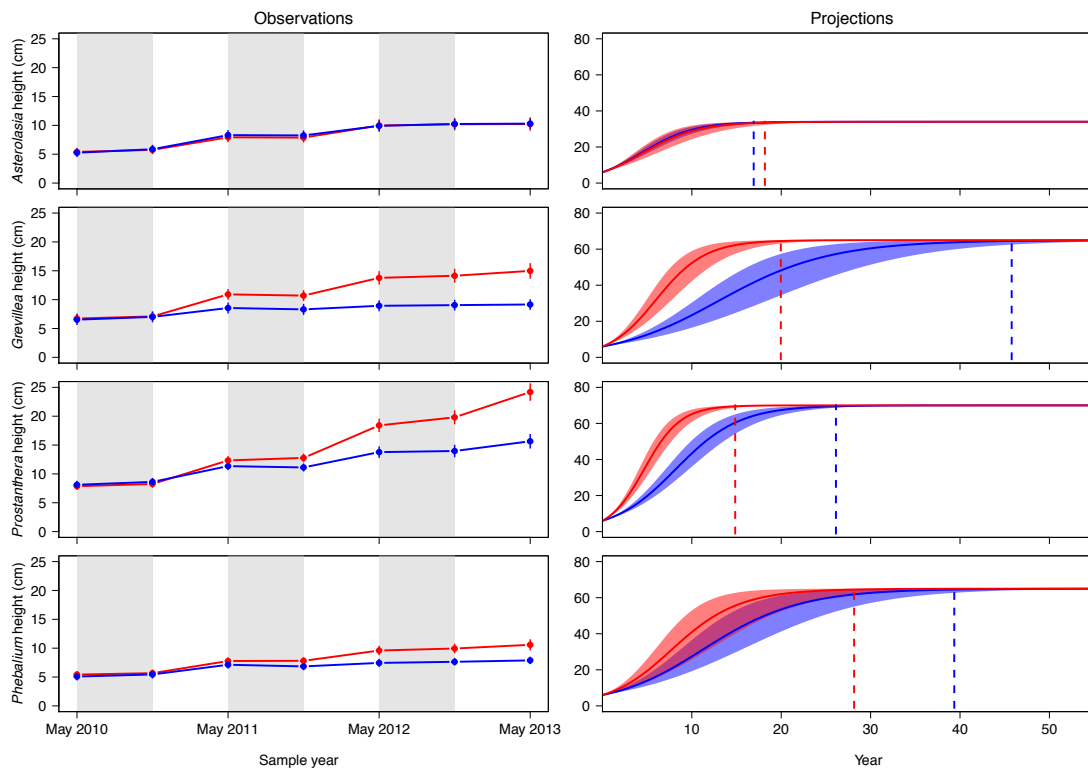


Figure 3.3. Observed and projected height growth trajectories of seedlings from four dominant alpine shrubs. Left panels: mean ($\pm$ 95% confidence intervals) observed heights during the 1064-day experiment. Shaded areas are the winter snow periods when warming treatment was not applied to plots. Right panels: mean ($\pm$ 95% credible intervals) projected height growth for each species over 55 years. Red lines: seedlings growing in warmed (OTC) conditions; blue lines: seedlings growing in current (control) conditions. Projections were based on an initial seedling size of 6 cm (the mean initial seedling height used in this experiment) and mean maximum heights observed in long-unburned sites (i.e. 34, 65, 70 and 65 cm for *Asterolasia*, *Grevillea*, *Prostanthera* and *Phebalium*, respectively). Dashed lines: indicate year when maximum height was reached.

Experimental warming also reduced seedling mortality (Fig. 3.4). After three years and across all plots, 22% (115 out of 512) of all seedlings growing in burned bare ground patches had died. Most deaths occurred in *Phebalium* (43) followed by *Asterolasia* (38), *Grevillea* (21) and *Prostanthera* (13). *Prostanthera* showed the largest treatment effect, with mean predicted seedling death 20% lower in warmed plots compared to control plots (0 vs. 13 deaths, respectively). Warming also reduced mean seedling mortality in *Grevillea* and *Phebalium*; however, for both species, the effect was uncertain (i.e. confidence intervals overlap; however large proportion of intervals suggest reduction). Seedling mortality in *Asterolasia* was not affected by warming treatment. This increase in survival is a likely consequence of OTCs reducing the severity of spring frosts by rising minimum ambient and soil temperatures by 1°C (see section 3.3: Methods).

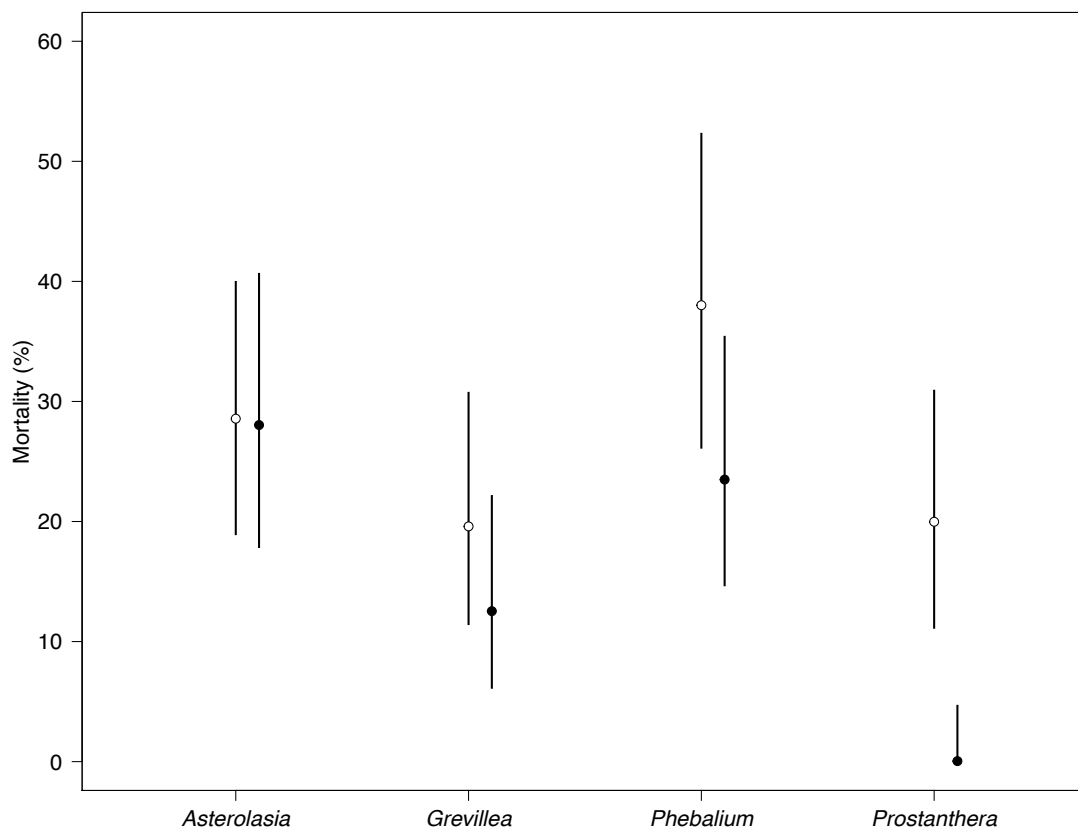


Figure 3.4. Mean ($\pm$ 95% credible interval) probability of seedling mortality for each species in control (open circle) and warmed (solid circle) conditions.

I validated the *Grevillea* and *Asterolasia* growth responses observed in experimentally warmed plots by using an elevation gradient and maximum height data for 2003 post-fire recruits (i.e. suspected 9 year old seedlings). Here, a 200 m altitudinal range is equivalent to an ambient temperature difference of approximately 1.5°C (Brown and Millner 1989), which is comparable to that observed between experimental warmed and control plots (1.2°C). In response to shifts in temperature, maximum heights of *Grevillea* post-fire recruits were expected to vary with elevation, whereas *Asterolasia* seedlings were not expected to show this pattern. The experimental predictions were verified (Fig. 3.5). Mean maximum heights of *Grevillea* seedlings in burned open heathland were 7.9 cm (19.4 cm vs 11.5 cm; a difference comparable to experimental findings) taller at 1660 m a.s.l compared to seedlings at 1860 m a.s.l (Fig 3.5a,e). In contrast, mean maximum heights of *Asterolasia* seedlings did not vary significantly with elevation (Fig 3.5a,f). Fire severity (Fig 3.5a,b,c,d) and Topographic Wetness Index (Fig 3.5a,b,g,h) had no detectable influence on maximum seedling heights in either species.

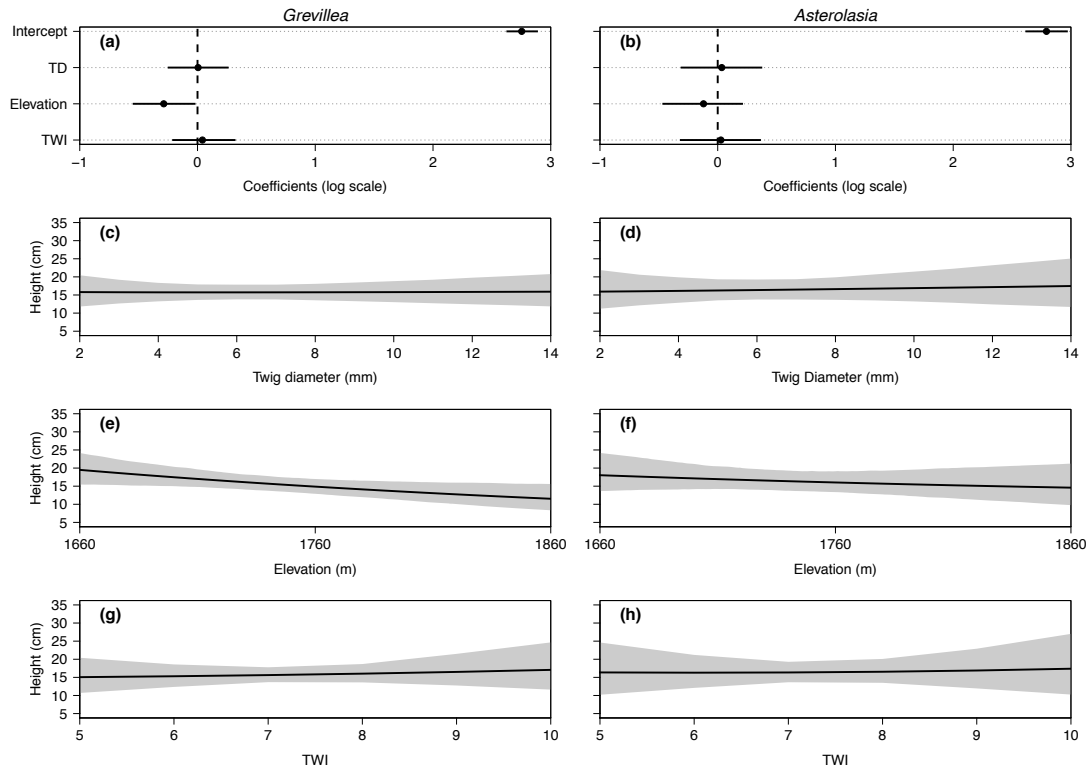


Figure 3.5. Mean maximum seedling height along fire severity (TD; as estimated from post-fire twig diameters), elevation and topographic wetness index (TWI; an estimate of a site's plant-available water) gradients in areas burned by the 2003 wildfires. Left panels: *Grevillea australis*; Right panels: *Asterolasia trymalioides*. a-b) centered and standardized model coefficients (log scale). Here, the intercept is interpreted as the mean maximum seedling height at a burned site assuming TD, Elevation and TWI are at their mean; c-h) partial dependence plots illustrating how seedling maximum height varies along observed severity, elevation and topographic wetness gradients in areas burned by the 2003 fires. All error bars are 95% credible intervals.

Climate change is expected to alter biotic interactions because their strength and direction depend strongly on climatic conditions, particularly in alpine and arctic ecosystems (Callaway et al. 2002, Klanderud 2005). Here, I assess the interactive effects of warming and inter-tussock gap size (i.e. proximity to grass tussock) on the growth and survival of *Grevillea* seedlings. In warmed plots, the size of gaps affected seedling mortality but not growth rates (Fig. 3.6). In control plots tussock grass facilitated seedling survival, with mean survival increasing with decreasing gap size. By contrast, tussock grass tended to have competitive effects in warmed plots, with mean seedling survival declining in smaller gaps. Although this change from facilitative to competitive was highly uncertain, it is consistent with the abiotic stress hypothesis (Callaway et al. 2002), indicating that warming alleviates the cause of seedling death (i.e. low spring temperatures) and therefore diminish the benefit-cost (i.e. shelter vs. competition) associated with growing near a tussock. Regardless of inter-tussock gap size, seedlings growing in warmed plots were still on average 6.7 cm (14.7 cm vs. 7.5 cm) taller and had growth rates 4.2 times that of seedlings in control plots.

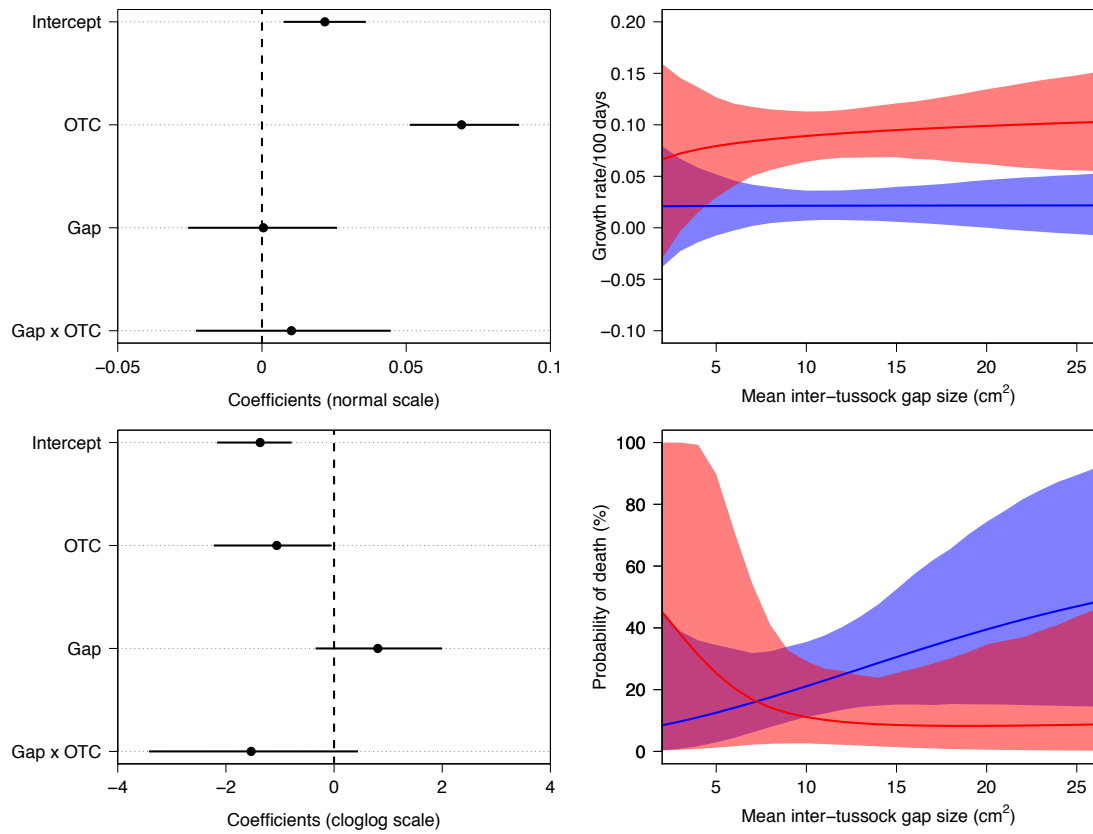


Figure 3.6. Effects of experimental warming and tussock grass proximity on height growth and mortality in *Grevillea* seedlings growing in natural inter-tussock gaps. First row: Effects on height growth rate; second row: Effects on mortality. Left panels are centered and standardized model coefficients. Intercepts are interpreted as the average height growth or mortality in control plots at mean inter-tussock gap size. Right panels are the predicted growth and mortality rates along an inter-tussock gap size gradient in warmed (red) and control (blue) conditions. All error bars are 95% credible intervals.

These results support the general finding that the extent and severity of disturbances such as fire are critical for providing recruitment opportunities necessary for shrub expansion (Racine et al. 2004, Lantz et al. 2013, Frost and Epstein 2014). The results also highlight that a 1.2°C temperature rise can double shrub seedling growth rates (Arft et al. 1999, Myers-Smith et al. 2011, Elmendorf et al. 2012b) and increase their survival. Furthermore, experimental warming had the capacity to shift tussock grass interactions from facilitative to competitive (Olsen and Klanderud 2013). Here I use these quantified interactions between fire, shrub-grass relationships and climate to build a conceptual model of alpine shrub dynamics under climate change (Fig 3.7).

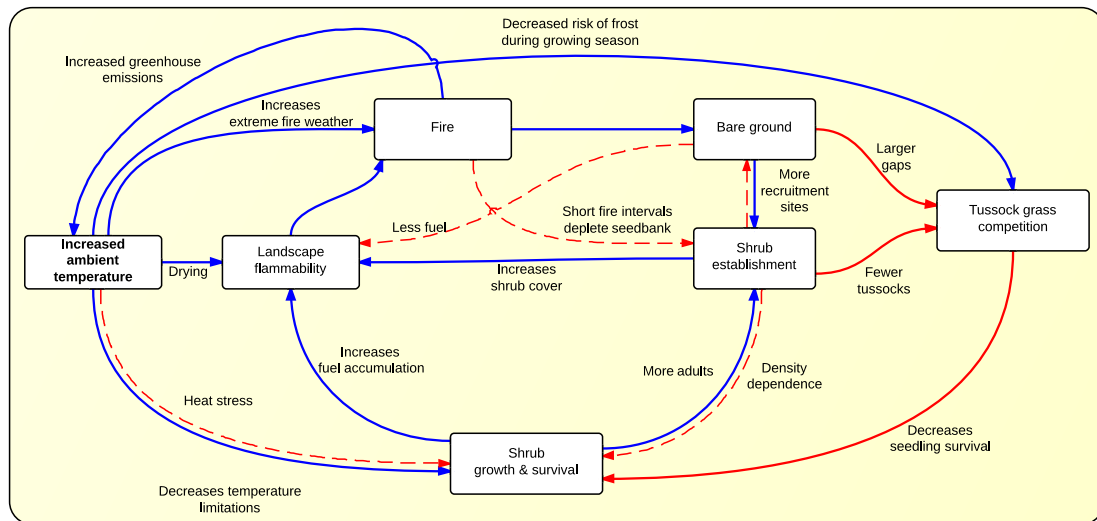


Figure 3.7. Conceptual diagram illustrating fire-warming feedback loop. Blue arrows: positive effects; red arrows: negative effects. Solid lines: quantified by this study or other literature; dashed lines: potential limiting effects that require further research

Figure 3.7 illustrates how these interactions produce a feedback loop that can rapidly increase shrub cover in alpine and tundra ecosystems. The combination of rising temperatures and more frequent and severe fire creates conditions that allow shrub seedlings to establish in greater densities, double their growth rates, and potentially increase their survival. This thickening and expansion of shrub cover provides the fuel necessary for more frequent and severe fires that in turn creates additional recruitment opportunities for shrubs. Other than the unlikely scenario of long-term fire intervals becoming short enough to prevent adults reaching reproductive age (approximately 10-

15 years in the Australian Alps; Williams et al. 2008) and exhausting the seedbank, the only interaction I detected in this study that may slow this feedback loop is where warmer conditions change the shrub-grass interaction from facilitative to competitive. However, this effect was highly uncertain, of lower magnitude compared to direct effects on shrub growth. Moreover the impact of this biotic interaction is likely to diminish as fire creates more bare ground. Decreasing albedo as a result of increased shrub cover may also enhance this feedback loop (Chapin et al. 2005). However, other factors may reduce the strength of this feedback loop, such as: heat stress (Körner 2003), soil moisture (Morgan 2004) and herbivory (Post and Pedersen 2008, O'Connor 2009). These all require further research because they are likely to be altered by the interactive effects of climate and disturbance in less predictable ways (Myers-Smith et al. 2011).

These findings shed light on the mechanisms governing rapid shrub expansion in burned or highly disturbed landscapes (Lantz et al. 2013). Based on current IPCC observations and predictions, average global temperature has already increased by 0.85°C since 1880 and is expected to rise by as much as 4.8°C by 2100 (IPCC 2013a). In alpine and tundra environments, temperatures (Post et al. 2009, Wahren et al. 2013), shrub cover (Myers-Smith et al. 2011) and the frequency and severity (Turetsky et al. 2011) have all increased in the last few decades. These changes mean that the fire-warming feedback identified here has already strengthened, causing grasslands and other non-woody communities to transition to an alternative state of more shrubs and more fire (Lantz et al. 2013, Pearson 2013).

3.3 Methods

3.3.1 Study site

Research sites were on the Bogong High Plains, a series of alpine and high subalpine plateaux in the Alpine National Park, approximately 250 km northeast of Melbourne, Australia. The undulating terrain ranges in altitude from 1400 – 2000 m a.s.l and contains a well-developed mantle of soil. Mean annual temperature is approximately 6°C, with persistent snow cover from June to September. Annual precipitation is 1200 mm, yet droughts occur at roughly decadal intervals (Wahren et al. 2013). The vegetation is a mosaic of Eucalypt-woodland and treeless vegetation, with the latter largely consisting of heathlands and tussock grasslands, but also herbfields and wetlands (McDougall and Walsh 2007). The treeline is irregular (due to cold air drainage), occurring at altitudes ranging from 1600 to 1700 m a.s.l. Approximately 50% of the alpine ‘treeless’ landscape consists of heathlands, most of which were extensively burned by a 400,000 ha wildfire in 2003 (Williams et al. 2006, Camac et al. 2013). Large wildfires in Australian alpine landscapes have occurred once or twice per century and typically occur during periods of extended regional drought coupled with severe fire weather and multiple ignitions in the surrounding montane forests (Williams et al. 2008).

I investigated shrub dynamics in open heathland because it is a common and highly flammable plant community in the Australian Alps above 1600 m a.s.l (Fig.3.8; Williams et al. 2006). It is also an ecotone between closed heathland (>70% shrub cover) and tussock grassland consisting of *Grevillea australis* shrubs interspersed among a sward of *Poa hiemata*. Under climate change, this plant community is likely to change substantially, acting as an ‘invasion front’ of shrub expansion into grassland, while the community itself may become susceptible to shrub thickening by closed heathland dominants such as *Prostanthera cuneata*.



Figure 3.8. Shrubs are the most flammable component in Australian alpine 'treeless' vegetation (Williams et al. 2006). Burned patches were shrubs. Note that grasses between the shrubs were only lightly scorched. Photo courtesy of Carl-Henrik Wahren.

3.3.2 Open top chamber experiment

I used an experimental warming study to address two questions: (1) do warmer post-fire conditions influence rates of seedling growth and mortality? And (2) if the size of inter-tussock gaps affects growth and mortality rates, does this effect change when conditions after fire are warmer?

Alpine and tundra shrub seedlings typically establish and grow in bare ground created by disturbance (Williams and Ashton 1987a, Batllori et al. 2009, Frost et al. 2013). Here, I used fire to create bare ground because (1) Australian alpine shrub seedlings occur in greatest abundance after fire (see seedling density results) and (2) in many parts of the world, including Australia, wildfires are predicted to increase in frequency and severity (Flannigan et al. 2009, Westerling et al. 2011). Thus, to forecast likely changes in shrub abundance I need to know how warming affects growth and mortality

rates of shrub seedlings growing in burned plots. In March 2010, at approximately 1750 m a.s.l, I assessed warming effects in burned sites by burning 32 randomly selected mature (~ 60 cm tall & $\sim 1.5\text{m}^2$) *Grevillea australis* shrubs with a drip torch in open heathland. This created 32 burned patches of bare ground approximately 0.7 m^2 ; a common size in open heathland burned by wildfire (Fig. 3.9).



Figure 3.9. Setting up experimental plots. Top left: unburned *Grevillea australis*; Top right: *Grevillea* after being burned; Bottom left: *Grevillea* remains removed leaving burned bare ground patch. Transplant holes were then created using Hamilton planter (note: photo does not show holes for inter-tussock seedlings; Bottom right: all seedlings planted within 1 m^2 .

After creating the bare ground patches I collected seedlings of dominant alpine shrub species from a nearby (< 2 km) site of similar altitude burned by a late 2006 wildfire. This allowed us to collect sufficient seedling numbers from species occurring in both open and closed heathland. I collected shrub seedlings of two dominant open heathland species, *Grevillea australis* (Proteaceae; a tall shrub) and *Asterolasia trymalioides* (Rutaceae; a prostrate shrub); a closed heathland species, *Prostanthera cuneata*

(Lamiaceae; a tall shrub); and a species that commonly occurs in both open and closed heathland, *Phebalium squamulosum* (Rutaceae; a tall shrub) (Fig. 3.10). All four species are: obligate seeders post-fire (i.e. fire killed), common in the Australian Alps, and under global warming, likely candidates to invade non-shrubby plant communities such as alpine grasslands and herbfields. For each species, I collected a range of seedling heights (2 – 12 cm) using a forestry planter (12.5 cm deep by 5.5 cm wide). The size of the planter was selected to minimize root damage across the range of seedling sizes and to allow for the extraction of a constant volume (378 cm³) of intact soil and roots. The planter also minimized soil disturbance during seedling extraction and replanting.



Figure 3.10. Alpine shrub species used in warming experiment. Top left: *Asterolasia trymalioides*; Top right: *Grevillea australis*; Bottom left: *Prostanthera cuneata*; Bottom right: *Phebalium squamulosum*.

I collected a total of 640 seedlings: 256 *Grevillea* (half used in *Poa* inter-tussock experiment – see below) and 128 for each of *Asterolasia*, *Prostanthera* and *Phebalium*. Four seedlings from each species were then randomly selected (using random number generator while ensuring height range was sampled) and transplanted into a 4 x 4

square grid located in the center of each burned bare ground patch. This grid ensured 14 cm between all individuals and the edge of the patch, which was dominated by the tussock grass, *Poa hiemata*. Four additional *Grevillea australis* seedlings were also randomly transplanted into various sized, naturally occurring, *Poa hiemata* inter-tussock gaps that immediately surrounded the bare ground patch. Only *Grevillea* seedlings were transplanted into inter-tussock gaps because it is the dominant open heathland shrub species (i.e. occurs closest to the shrub/grassland boundary) and is therefore the most likely to invade grasslands. This combination of seedlings growing in bare ground and inter-tussock gaps (a total of 20 seedlings per 1 m²) formed plots (Fig. 3.11). However, the two sets of seedlings were treated separately because they were spatially confounded (e.g. center vs. edge of the 1m² opening) and addressed different questions. Seedlings in bare ground patches (i.e. the center of the plot) were used to assess whether warmer post-fire conditions altered growth and mortality rates in four dominant alpine shrub species. By comparison, *Grevillea* seedlings growing in inter-tussock gaps were used to determine whether inter-tussock gap size altered growth and mortality rates, and whether such effects were modified by warmer conditions.

To simulate near-term warmer conditions predicted under IPCC (2013a), I used Open Top Chambers (OTCs; Molau and Mølgaard 1996). OTCs (Fig. 3.12) were randomly assigned to half (16) the plots, with the remainder treated as controls. OTCs were hexagonal, 58 cm tall with an open-top diameter of 110 cm and base diameter of 168 cm. The chambers were constructed following the International Tundra Experiment (ITEX) protocols (Molau and Mølgaard 1996) using sun-lite: a lightweight shatter-resistant fiberglass with high light transmittance (86%) and low infrared transmittance (< 5%; Solar Components Corporation, USA). OTCs were placed over plots, ensuring all seedlings occurred within the 1.1 m² open top (thereby minimising edge effects), at the start of the growing season (October) where they remained until snowfall (early June). Treatment was first applied in October 2010 and maintained for three growing seasons: 2010-11, 2011-12 and 2012-13.

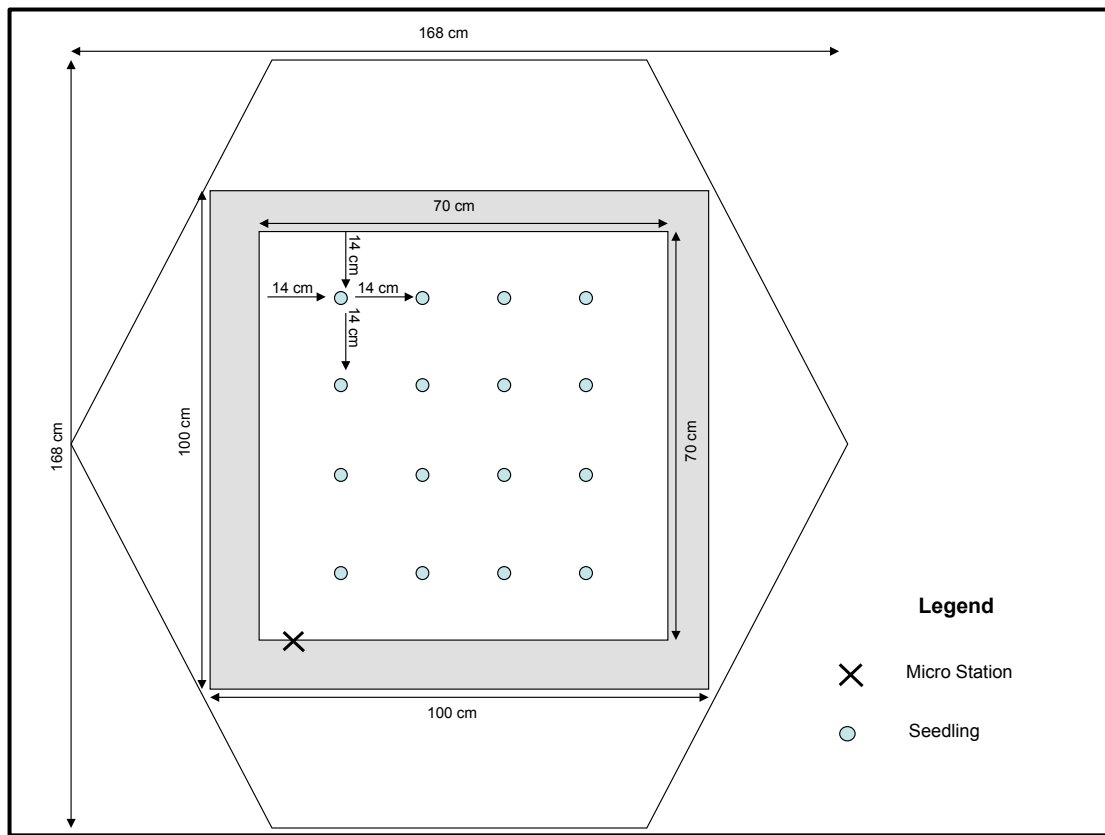


Figure 3.11. Schematic outlining positions of transplanted seedlings in an OTC plot. Inner white square: the burned bare ground patch used to assess heights of four dominant alpine shrubs. Grey area: *Grevillea australis* seedlings randomly transplanted into burned inter-tussock gaps. The area beyond the grey section was subject to OTC panel sheltering (i.e. it is outside the 110 cm opening of the chamber) and therefore was not used in this experiment.

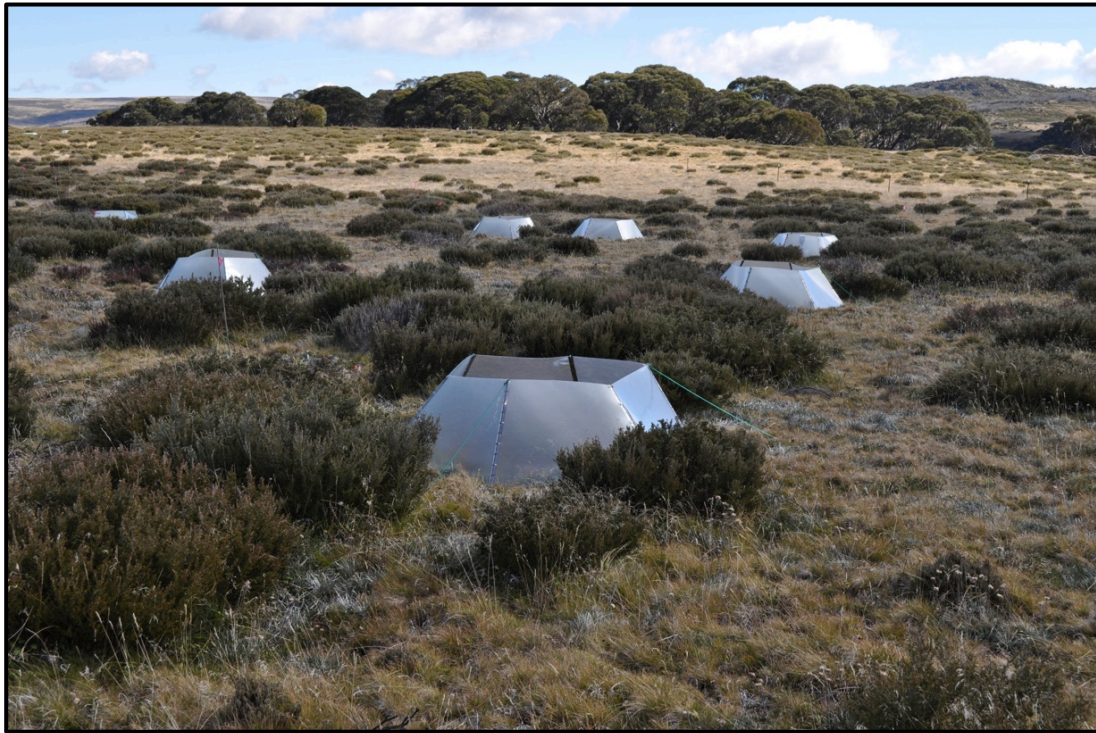


Figure 3.12. Experimental site with OTC chambers on plots.

I measured changes in microclimate using Onset Micro Stations (Onset Computer Corporation, Bourne, MA, USA) randomly installed into four control plots and four OTC plots. Each Micro Station measured ambient temperature, relative humidity (both at 10 cm above ground), soil temperature (3 cm below ground) and volumetric soil moisture (between 3 and 10 cm) at hourly intervals for the entire duration of the experiment. Across three growing seasons (611 days), OTCs simulated warmer and drier conditions at the lower end of IPCC predictions (IPCC 2013a). OTCs passively raised mean daily ambient and soil temperatures by 1.2°C (± 0.08 & 0.05 95% CI, respectively) and marginally lowered both soil moisture ($-0.80\% \pm 0.002$) and relative humidity ($-2.3\% \pm 0.002$) (Fig. 3.13). OTCs also increased minimum daily ambient and soil temperatures by 0.95°C (± 0.06 95% CI) and 0.93 (± 0.04 95% CI) respectively (Fig. 3.13). Maximum temperatures were also strongly influenced by OTCs with ambient and soil maximum temperatures increasing by 2.9°C (± 0.21 95% CI) and 2°C (± 0.17 95% CI). Because OTCs strongly increase temperatures relative to other measures, throughout I refer to it as a ‘warming treatment’.

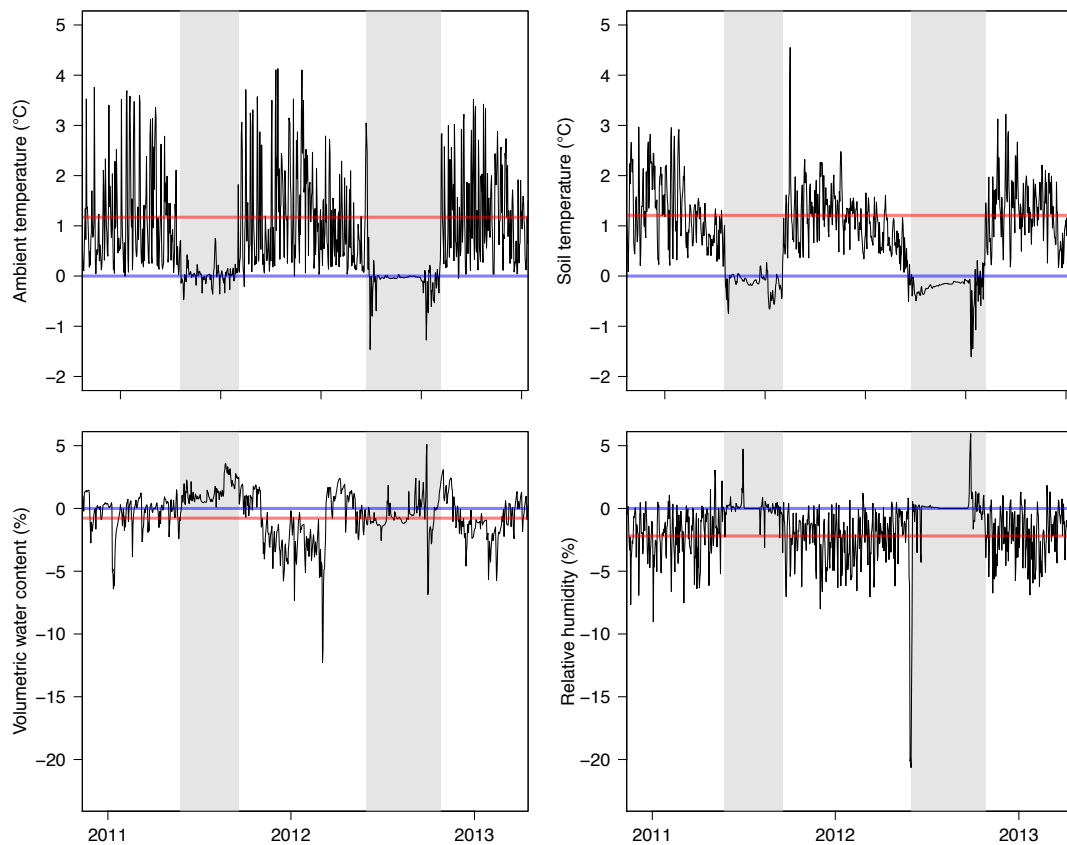


Figure 3.13. Mean daily difference (OTC - Control) for ambient temperature (10 cm above ground), soil temperature (3 cm below ground), volumetric water content (3 to 10 cm below ground) and relative humidity (10 cm above ground). Red lines: mean difference across all growing seasons (when chambers were applied); blue lines: no difference between OTCs and controls (zero line); shaded areas: winter snow periods when chambers were not over plots.

In May 2010, a month after transplanting and prior to OTC application, the status (alive or dead) basal diameter and maximum height (measured to the nearest millimeter using Vernier calipers) of all individual shrub seedlings in each plot were recorded. The proximity of the nearest tussock in each of four cardinal directions was also measured for each seedling growing in an inter-tussock gap. These measurements were repeated in October 2010 and thereafter in May and October of each year. Seven censuses were taken between May 2010 and May 2013. For the analysis I focused on height growth as opposed to basal growth for three reasons: 1) heights were measured with less observer error (presumably because some seedlings had diameters ~ 1 mm); 2) I had estimates of maximum height for all species, and thereby had an estimate of when growth should become asymptotic; and 3) it is a commonly measured trait that incorporates multiple

trade-offs associated with demographic rates (Westoby et al. 2002). Note: the effects of experimental warming on height growth was also representative of basal growth (Appendix 3.2). I did not assess shrub seedling height growth responses to warming in unburned conditions. This was because such a treatment would be a biologically unrealistic as shrub seedlings almost always occur in bare ground and are exceptionally rare in unburned vegetation (see seedling density results of this chapter and Williams and Ashton 1988).

3.3.3 Seedling survey

I measured seedling density and maximum heights in open heathland across the Bogong High Plains. The primary aim of this study was to evaluate how variables such as altitude, Topographic wetness index (a measure of plant available water), adult density, fire, and fire severity influence the density of *Asterolasia* and *Grevillea* seedlings in open heathland. A secondary aim was to validate growth rates observed in the OTC experiment by assessing maximum seedling heights of *Asterolasia* and *Grevillea* along altitude, soil moisture and fire severity gradients in areas burned by the 2003 wildfires.

The study used 40 open heathland sites (Camac et al. 2013) established immediately post-2003 fires. Thirty sites were burned, while the remaining ten were unburned, likely for more than 70 years (Camac et al. 2013). These sites encompassed most of the Bogong High Plains (120 km²) and ranged in altitudinal from 1660 m to 1860 m a.s.l (Fig. 3.14). Sites were at least 0.25 ha and more than 500 m apart. In the summer of 2012-13, 9 years post-fire, seedling density in each site was estimated using 40 1 m² quadrats, evenly distributed in groups of 10 along four 50 m transects. Transects were positioned in the center of each site and were parallel to each other with exactly 10 m between transect lines. This effectively created a grid of 40 plots (10 plots x 4 transects) per site, subsampling an area of 2000 m².

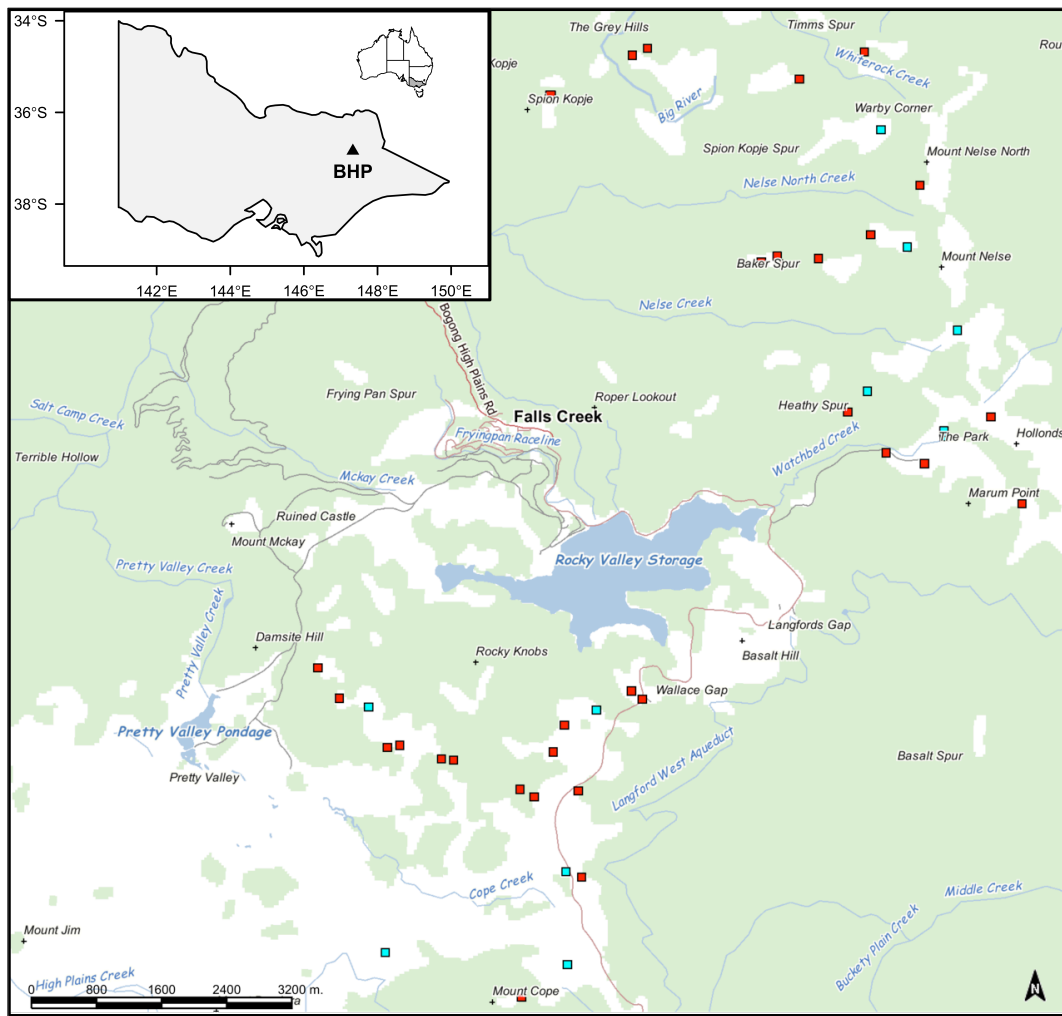


Figure 3.14. Distribution of open heathland sites across the Bogong high plains. Red: sites burned by the 2003 wildfires; blue: unburned sites. Sites were originally established by Williams et al (2006) immediately following the fire, and were later surveyed by Camac et al (2013). Sampling intensity was higher for burned sites for two reasons: 1) they varied in burn severity and 2) exhibited higher variation in seedling densities compared to unburned sites. White areas signify alpine ‘treeless’ vegetation.

Different variables were recorded at the three sampling levels (site, transect and plot). Within plots I recorded the number and maximum height of *Grevillea* and *Asterolasia* seedlings. Along each transect I estimated the density of mature *Grevillea* shrubs ($> 0.5 \text{ m}^2$), and at each site I recorded altitude, Topographic Wetness Index (TWI), whether the site was burned, and, if so, burn severity. I estimated the density of mature *Grevillea* by counting the number of individuals (alive or dead) within 5 m either side of the transect. In burned sites, mature *Grevillea* densities were estimated by counting the number of woody skeletons, which persist even after severe fire (Fig. 3.15). By contrast, *Asterolasia* adult density could not be estimated because this species' woody skeleton rapidly degrades after fire.



Figure 3.15. Example of a 1m^2 plot used to estimate seedling density. Also an example of a burned *Grevillea australis* skeleton.

For each site, altitude and TWI were derived from a 30 m resolution digital elevation model of the Bogong High Plains. TWI, which approximates the relative plant-available water based on a site's position in the landscape (Moore et al. 1993), was derived for each site using $TWI = \ln\left(\frac{A}{\tan \theta}\right)$, where, A is the upslope catchment area per unit width orthogonal to the flow direction and θ is the slope (in degrees). Across the 40 sites, TWI varied twofold (5 – 10 units). Altitude ranged by 200 m (from 1660 to 1860 m a.s.l), or by approximately 1.5°C from the lowest to the highest (based on a lapse-rate of 0.77°C/100 m elevation; Brown and Millner 1989). This altitudinal temperature range is comparable to that observed in the OTC experiment (1.5°C vs. 1.2°C, respectively).

The occurrence and severity of fire was initially determined by Williams et al. (2006) immediately after the 2003 fire. The severity of the fires in each burned site was estimated using twig diameters, a proxy measure of fire severity (Whight and Bradstock 1999). These twig diameters were recorded between 1 and 10 months post-fire from 10 replicate *Grevillea australis* individuals. Across the 30 burned sites, the average twig diameter ranged from 2 to 13 mm, with smaller diameters assumed to have experienced lower fire intensity. This encompassed the full range of fire severity from lightly scorched sites containing shrubs with only the tips of the outer branches burned, to severely burned sites where the majority of large shrub branches were consumed (Fig. 3.16).



Figure 3.16. Example of an area severely burned by the 2003 wildfires. Photo courtesy of Carl-Henrik Wahren.

3.3.4 Data analysis

I used hierarchical generalized linear models to assess factors influencing shrub seedling density, growth and mortality. These models are well suited to datasets that have a hierarchical structure (e.g. plots within sites) because they can account for observation error and partition both explained and unexplained variation at multiple levels of a dataset (Gelman and Hill 2007, Kéry and Schaub 2012). For each model I used Bayesian inference and fitted models to data using Markov chain Monte Carlo (MCMC) sampling in R 3.0.2 using package R2jags version 0.03-11 (Su and Yajima 2012) as an interface to JAGS 3.3.0 (Plummer 2011). For each model, three independent chains were executed. In all cases modeled parameters converged within 50000 iterations. Convergence was assessed through both visual inspection of chains and reference to the Brooks-Gelman-Rubin convergence diagnostic (Gelman and Rubin 1992, Brooks and Gelman 1998). After discarding the first 50000 iterations as ‘burn in’, a further 50000 iterations were taken from the joint posterior and thinned to

every 50th sample. Below I describe the model structure, parameters and priors used to assess factors influencing growth, mortality and density of alpine shrub seedlings. The residuals of all models were checked graphically against predictions with none showing any systematic pattern or severe heteroscedasticity. To ensure all parameters were identifiable I selectively removed each covariate and visually inspected whether the direction and magnitude of effects were severely altered; none were. JAGS codes for all models are provided in Appendices 3.3 to 3.8.

Experimental warming - growth

For the purpose of modeling seedling average annual growth rates I used heights measured in May of each year from seedlings that survived throughout the passive warming experiment. This meant that my observations were of maximum height for each individual i at each May census t . I modeled these heights, $height_{it}$, as a random realization from a normal distribution:

$$height_{it} \sim Normal(\widehat{height}_{it}, \sigma_{obs}), \quad (3.1)$$

where $\widehat{height}_{it}$ is the model fitted maximum height for each individual i at each May census t and σ_{obs} is the standard deviation of the observation error. The parameter $\widehat{height}_{it}$ was estimated using a logistic parameterization of the unified Richards equation (Tjørve and Tjørve 2010):

$$\widehat{height}_{it} = \frac{H_{j[i]}^{max}}{\left(1 + \left(\frac{H_{j[i]}^{max}}{H_i^{init}} - 1\right)e^{-R_i \frac{Days_t}{100}}\right)}. \quad (3.2)$$

I used a logistic equation because it can simulate sigmoidal growth. That is, a curve whereby initial seedling growth is slow before increasing in speed and finally levelling off when adult height is reached. I used this particular parameterization because it accounts for seedling size at the beginning of an experiment and contained biologically interpretable parameters. Here $H_{j[i]}^{max}$ is the asymptotic height: the average mature height an individual i belonging to species j achieves. Based on maximum height data

from 5 to 22 sites (depending on the species) I estimated the average mature height to be approximately 34, 65, 65 and 70 cm for *Asterolasia*, *Grevillea*, *Phebalium* and *Prostanthera*, respectively. H_i^{init} is the height of individual i at the start of the experiment (i.e. the first May measurement). $Days_t$ is the number of days from the beginning of the experiment to each May census t . The experiment ran for a total of 1064 days. I divide the number of days at each census by 100 in order to improve model sampling. The parameter of interest, R_i , is the mean growth rate per 100 days for each individual i . I modeled R_i separately for seedlings growing in bare ground (eqn. 3.3.1) compared to those growing in inter-tussock gaps (eqn. 3.3.2).

For individual seedlings of the four shrub species growing in the bare ground patch located in the centre of each plot I modeled R_i using a varying intercept linear model:

$$\begin{aligned}
R_i &= \alpha_{j[i]} + \beta_{1j[i]} \times OTC_{k[i]} + \varepsilon_{plot_{k[i]}} + \varepsilon_i \\
\alpha_j &\sim Normal(\mu_{spp.}^{CTL}, \sigma_{spp.}^{CTL}) \\
\beta_{1j} &\sim Normal(\mu_{spp.}^{OTC}, \sigma_{spp.}^{OTC}) \\
\varepsilon_{plot_{k[i]}} &\sim Normal(0, \sigma_{plot}) \\
\varepsilon_i &\sim Normal(0, \sigma_{ind})
\end{aligned} \tag{3.3.1}$$

Here, the intercept term, $\alpha_{j[i]}$, represents the expected control plot growth rate of species j to which individual i belongs. It is estimated from a normal distribution centred on $\mu_{spp.}^{CTL}$ (the expected control plot growth rate for an average hypothetical species) with a standard deviation, $\sigma_{spp.}^{CTL}$, which defines the variation between species' growth rates at control plots. The parameter $\beta_{1j[i]}$ is the OTC effect for each species j to which individual i belongs. β_{1j} is also estimated from a normal distribution, but unlike α_j , it is centred on $\mu_{spp.}^{OTC}$, (the expected OTC growth rate for an average hypothetical species) with a standard deviation, $\sigma_{spp.}^{OTC}$, which defines the variation between species' growth rates at OTCs. The terms $\varepsilon_{plot_{k[i]}}$ and ε_i represent residual variation at the plot level (for each plot, k , within which individual i is located), and the individual level (for

each individual i), respectively. Both error terms were drawn from normal distributions centred on zero with standard deviations that defined the variation amongst plots, σ_{plot} , or amongst individuals, σ_{ind} , respectively.

In contrast, R_i for *Grevillea australis* seedlings growing in inter-tussock gaps was modeled using a fixed intercept linear model:

$$\begin{aligned}
R_i &= \alpha + \beta_1 \times OTC_{k[i]} + \beta_2 \times Gap_i + \beta_3 \times (OTC_{k[i]} \times Gap_i) \\
&\quad + \varepsilon_{plot_{k[i]}} + \varepsilon_i \\
\varepsilon_{plot_k} &\sim Normal(0, \sigma_{plot}) \\
\varepsilon_i &\sim Normal(0, \sigma_{ind})
\end{aligned} \tag{3.3.2}$$

The structure and parameter definitions differ slightly to that in eqn 3.3.1. Here, the model has two additional parameters, β_2 and β_3 . The parameter β_2 is the effect of average inter-tussock gap size, while β_3 is the interactive effect of OTC and inter-tussock gap size. The inclusion of these parameters alters the definition of the intercept, α , which now represents the mean control plot growth rate at the average inter-tussock gap size. The parameter β_1 is the OTC effect and ε_{plot_k} and ε_i are residual errors at the plot and individual level, respectively.

Experimental warming - mortality

I was interested in whether the probability that a seedling would die varied amongst shrub species, OTC treatment and inter-tussock gap size. As such, my observations, Y_i , were binary (0 = alive or 1 = dead) for each individual i at the end of the 1064-day experiment. I modeled these observations as a random realization from a Bernoulli distribution based on the model-fitted probability that individual i would die, $\hat{p}_i$:

$$Y_i \sim \text{bernoulli}(\hat{p}_i), \tag{3.4}$$

As with growth rates, I modeled each individual's probability of dying, $\hat{p}_i$, separately for seedlings growing in bare ground patches to those in inter-tussock gaps. In both

cases, the model structure of $\hat{p}_i$ is largely identical to that of R_i in equations 3.3.1 & 3.3.2. However, here I model $\hat{p}_i$ on the complementary log-log scale, $\log_e(-\log_e(1 - p))$; which makes a regression model equivalent to a standard survival analysis (Allison 1982).

For individual seedlings of the four shrub species located in the bare ground patch of each plot, I modeled $\hat{p}_i$ using a varying intercept model:

$$\begin{aligned} \text{cloglog}(\Pr(\hat{p}_i = 1)) &= \alpha_{j[i]} + \beta_{1j[i]} \times \text{OTC}_{k[i]} + \varepsilon_{\text{plot}_{k[i]}} \\ \alpha_j &\sim \text{Normal}(\mu_{spp}^{CTL}, \sigma_{spp}^{CTL}) \\ \beta_{1j} &\sim \text{Normal}(\mu_{spp}^{OTC}, \sigma_{spp}^{OTC}) \\ \varepsilon_{\text{plot}_k} &\sim \text{Normal}(0, \sigma_{\text{plot}}) \end{aligned} \tag{3.4.1}$$

Here, the intercept term, $\alpha_{j[i]}$, represents the expected probability of death in a control plot for species j within which individual i belongs. It is estimated from a normal distribution centred on μ_{spp}^{CTL} (the control plot expected probability of death for the average hypothetical species) with a standard deviation, σ_{spp}^{CTL} , which defines the variation between species' death probabilities at control plots. The parameter $\beta_{1j[i]}$ is the OTC effect for each species j to which individual i belongs. β_{1j} is also estimated from a normal distribution, but unlike α_j , it is centred on μ_{spp}^{OTC} , (the OTC expected probability of death for the average hypothetical species) with a standard deviation, σ_{spp}^{OTC} , which defines the variation between species' death probabilities at OTCs. The term $\varepsilon_{\text{plot}_{k[i]}}$ represent residual variation at the plot level (for each plot, k , within which individual i is located), it is drawn from a normal distribution centred on zero with a standard deviation that defines the variation amongst plots, σ_{plot} .

In contrast, $\hat{p}_i$ for *Grevillea* seedlings growing in inter-tussock gaps was modeled using a fixed intercept linear model:

$$\begin{aligned} \text{cloglog}(\Pr(\hat{p}_i = 1)) &= \alpha + \beta_1 \times OTC_{k[i]} + \beta_2 \times Gap_i \\ &+ \beta_3 \times (OTC_{k[i]} \times Gap_i) + \varepsilon_{plot_{k[i]}} \\ \varepsilon_{plot_k} &\sim \text{Normal}(0, \sigma_{plot}) \end{aligned} \quad (3.4.2)$$

Here, the structure and parameter definitions are similar to eqn 3.4.2. The intercept, α , represents the expected probability of death in control plots at the average inter-tussock gap size (12 cm), β_1 is the effect of OTC, β_2 is the effect of average inter-tussock gap size, β_3 is the interactive effect of OTC and inter-tussock gap size and ε_{plot_k} is the residual error at the plot.

I used Bayesian inference and hence needed to specify prior distributions for all model parameters. In both growth rate and mortality models standard deviation parameters (i.e. $\sigma_{spp.}^{CTL}$, $\sigma_{spp.}^{OTC}$, σ_{plot} and σ_{ind}) were each estimated from weakly informative positive half Cauchy priors with scale parameters of 25. In both sets of models the intercept term α for inter-tussock seedling model and the mean hyper-parameter $\mu_{spp.}^{CTL}$ in the multispecies models were estimated from Cauchy priors with a scale parameter of 25. By contrast, β_1 , β_2 and β_3 for inter-tussock seedlings and the hyper parameter for the mean OTC effect $\mu_{spp.}^{OTC}$ were each estimated from Cauchy priors with a scale parameter of 10. I used Cauchy priors in order to prevent over-inflated estimates of variances due to the small number of plots and species (Gelman 2006).

In each model, OTC treatment, OTC_k , was a binary (0 = Control, 1 = OTC) plot level covariate. By contrast, inter-tussock gap size, Gap_i , was a continuous covariate at the individual seedling level. I estimated inter-tussock gap size by calculating the average distance to nearest tussock, across all censuses, for each inter-tussock seedling. Mean inter-tussock gap size ranged from 2.5 cm² to 26 cm² in both control and OTC plots. In order to compare the magnitude of effects between OTC treatment and inter-tussock gap size I log-transformed the distance data and then centered it on zero and divided by

two standard deviations (Gelman and Hill 2007). The advantage of centering and standardizing is that it allows for easier interpretation, with intercepts interpreted as average responses and slope terms as partial dependencies conditional on other continuous variables at their mean. Furthermore, standardizing by two standard deviations allows the magnitude of effects to be directly compared between binary and continuous covariates (Gelman and Hill 2007).

Seedling Survey

Observations were of seedling counts for each 1 m² plot i . I modeled these counts, $Count_i$, as random realizations from a Poisson distribution centred on λ_i , the fitted seedling count for each plot.

$$Count_i \sim \text{Poisson}(\lambda_i) \quad (3.5)$$

I modeled λ_i separately for *Grevillea australis* and *Asterolasia trymalioides* because the latter contained no measurements of adult density. The two models are structurally similar and only differ in that parameter β_5 is not included for *Asterolasia*. Below I outline the full model structure used to estimate λ_i .

I modeled λ_i using a log-link as a function in the following model:

$$\log(\lambda_i) = \gamma_{j[i]} + \delta_{k[i]} \quad (3.6)$$

where, $\gamma_{j[i]}$ and $\delta_{k[i]}$ represent the average seedling count for each site j and transect k within which plot i is located, respectively.

The average seedling count for each site, γ_j , was modeled using a varying intercept linear model:

$$\begin{aligned}\gamma_j &= \alpha_j + \beta_1 \times Alt_j + \beta_2 \times Wet_j + \beta_3 \times (1 - Burnt_j) \\ &\quad + \beta_4 \times (TD_j \times Burnt_j) \\ \alpha_j &\sim Normal(\mu_{site}, \sigma_{site})\end{aligned}\tag{3.7}$$

where, the intercept, α_j , varies by site and represents the average seedling count per plot at each site, assuming all other parameters are at their mean. I estimated α_j from a normal distribution centred on μ_{site} , the average seedling count per 1 m² plot for the average site. The parameters β_1 and β_2 are the effects of altitude and wetness, respectively, while β_3 is the effect of being an unburned site and β_4 is the effect of fire severity in burned sites.

The average transect seedling count, δ_k , was modeled as follows:

$$\begin{aligned}\delta_k &= \beta_5 \times ADen_k + \varepsilon_{tran_k} \\ \varepsilon_{tran_k} &\sim Normal(0, \sigma_{tran})\end{aligned}\tag{3.8}$$

where β_5 is the effect of mature *Grevillea* counts and ε_{tran_k} is the random error associated with transect k . Parameter β_5 was not included when modeling *Asterolasia* seedling counts because of a lack of mature individual counts. For this species $\delta_k = \varepsilon_{tran_k}$.

In order to validate growth rate findings in the OTC experiment I assessed how an elevation range of 200 m in elevation (equivalent to a temperature change of 1.5°C; Brown and Millner 1989) influenced *Grevillea* and *Asterolasia* seedlings heights in areas burned by the 2003 fires. I also assessed whether TWI and fire severity influenced these heights. Here, my observations were of maximum seedling heights for both species when at least one individual was present in a plot. I used maximum heights because these were likely to represent individuals that established immediately

post-fire, and would have had 9 years of post-fire growth. I modeled these heights, $maxht_i$, as a random realization from a log-normal distribution, a common distribution used for data, such as height, that are bounded between zero and infinity and tend to be positively skewed (Gelman and Hill 2007):

$$maxht_i \sim \text{log-normal}(\widehat{maxht}_i, \sigma_{obs}), \quad (3.9)$$

where, $\widehat{maxht}_i$ is the model fitted maximum height for each individual i and σ_{obs} is the standard deviation of the observation error. I modeled $\widehat{maxht}_i$ separately for *Grevillea* and *Asterolasia* using a varying intercept linear model:

$$\begin{aligned} \widehat{maxht}_i &= \alpha_j + \beta_1 \times Alt_j + \beta_2 \times TWI_j + \beta_3 \times TD_j, \\ \alpha_j &\sim \text{Normal}(\mu_{site}, \sigma_{site}) \end{aligned} \quad (3.10)$$

where, the intercept, α_j , varies by site and represents the average maximum seedling height of each site, assuming all other parameters are at their mean. I estimated α_j from a normal distribution centred on μ_{site} , the average maximum height for the average site. The parameters β_1 and β_2 are the effects of altitude and topographic wetness, respectively and β_3 is the effect of fire severity.

Here, I estimated each coefficient parameter in all seedling survey models (β_1 to β_6) using a vague normal prior distribution with a mean of 0 and a standard deviation of 100. All standard deviation parameters (σ_{obs} , σ_{site} , σ_{tran} and σ_{plot}) in each model were estimated from vague uniform distribution priors between 0 and 100.

In all models, $Burnt_j$ is a binary (0 = unburned, 1 = burned) site level covariate, which only affects seedling counts at unburned sites. By contrast, twig diameter (TD_j), a proxy for fire severity, was a continuous site level covariate that only affected seedling counts and maximum heights at burned sites. Altitude, TWI and mature *Grevillea* count ($ADen_k$) were also continuous covariates that affected all sites in both count and maximum height models. Before including the continuous covariates into the model I

checked that all were normally distributed. With the exception of twig diameter, which was square root transformed in order to meet this assumption; all covariates were normally distributed. I also checked for collinearity among covariates; all correlations were $r < 16\%$. The data from each continuous covariate was then centered on zero and standardized by two standard deviations (Gelman and Hill 2007).



Chapter 4:

General Discussion

4.1 Overview

In this thesis I had two objectives: (1) to determine how climate, disturbance and plant-plant interactions influence *rates* of compositional change (see Chapter 2); and (2) to determine whether heathland is likely to expand in a warmer, potentially more flammable alpine environment (see Chapter 3). To achieve both objectives, I developed novel statistical models to estimate rates of change in both vegetation growth and cover. I parameterized these models with data derived from multiple warming experiments and validated their predictions against height data collected along elevation gradients and compositional data from long-term monitoring sites. These models greatly advance current statistical tools used to examine the impacts of climate change on vegetation dynamics for two reasons: (1) they explicitly quantify how climate and other covariates (e.g. biotic interactions and measures of disturbance) alter *rates* (and therefore trajectories) of change as opposed to traditional approaches which only estimate differences between treatments (e.g. repeated measures ANOVA); and (2) they can implicitly (i.e. via logit link function; see Chapter 2) or explicitly (i.e. via logistic growth equation; see chapter 3) account for asymptotic growth - a non-linear growth response observed in many plants, animals and populations (Paine et al. 2011). As such, these models are biologically more realistic and capable of making predictions of vegetation change under multiple scenarios of environmental change.

In addition to developing, using and validating models that estimate rates of vegetation growth and cover change, I also conducted an extensive field survey and established a new warming experiment to examine questions related to shrub seedling dynamics. Specifically, I addressed 6 questions: (1) how does fire, elevation, adult density and topographic wetness influence shrub seedling establishment? (2) How do warmer post-fire conditions influence rates of seedling growth and mortality? (3) Are experimental growth responses consistent with observed along elevation gradients? (4) How does proximity to *Poa hiemata* (the dominant grassland species) influences shrub seedling growth and mortality rates? And (5) are *Poa* effects altered by warmer conditions? I then synthesized this information and determined whether global warming is likely to strengthen an existing feedback loop between shrubs and fire.

Below I summarize the major findings from the field and experimental work undertaken in this thesis. I then discuss the significance of these findings, their implications for on-going management of the Australian alpine vegetation and the potential directions for future research.

4.2 Summary of major findings

In **Chapter 2** I demonstrated the utility of modeling the interactive effects of experimental warming, disturbance and life form interactions on rates of cover change in alpine shrubs, graminoids and forbs. I found that the effects of experimental warming (and associated drying) on rates of life form cover change were contingent upon both the amount of bare ground (a measure of disturbance) and the cover of competing neighbouring life forms. Specifically, experimental warming altered rates of life form cover change in both burned and unburned heathland by reducing or mitigating the negative effects of neighbouring life forms and the positive effects of bare ground. Model simulations suggest that warming and drying in unburned heathland will decrease graminoid cover and increase forb and shrub abundance. By contrast, in burned vegetation, warming and drying is expected to slow post-fire regeneration for both graminoids and forbs, but increase it for shrubs.

In **Chapter 3** I examined how seedling dynamics of four dominant alpine shrubs would be affected by warmer, potentially more flammable alpine conditions. I found that fire increased shrub seedling establishment by more than 20-fold, and that this effect was exacerbated by the severity of fire and the number of adults at the site. I also found that experimental warming of 1.2°C had the capacity to double shrub seedling growth rates and increase survival in post-fire conditions. Warming also had the capacity to change the effect of tussock grass on shrub seedling survival from positive to negative. However, this effect was highly uncertain and likely to be of diminishing importance in areas with high levels of bare ground (e.g. following fire). As such, a likely consequence of global warming is that shrub cover will increase via enhanced seedling growth and survival thereby increasing landscape flammability. More frequent fires will create additional opportunities for shrub seedling establishment both within

existing heathland boundaries and within non-shrubby communities such as grasslands. In effect, warming is likely to strengthen an existing feedback loop that not only has the potential to cause rapid changes in the composition and structure of vegetation, but also have serious social, biodiversity and carbon sequestration consequences.

4.3 Management implications

4.3.1 Minimise disturbance

In Australian alpine landscapes shrub recruitment primarily occurs in bare ground (Williams and Ashton 1987b, 1988). Therefore, in order to minimise climate-induced increases in shrub cover, and as a consequence, increase landscape flammability in Australian alpine ecosystems, it is imperative that land managers invest in mechanisms that minimise the creation of bare ground. Landscape-scale fire is likely to be impractical to control in alpine environments, and methods currently employed or proposed to manage fire regimes (e.g. prescribed burning and livestock grazing) are themselves likely to create bare ground. Instead, effort should be focused at reducing disturbance from recreational use (e.g. walking and bicycle tracks) and grazing by deer, horses or domestic livestock. Minimising disturbance is also likely to be effective at reducing the spread and establishment of exotic plant species from nearby resorts, and residential and agricultural properties at lower elevations (McDougall et al. 2005).

4.3.2 Monitoring

Continued monitoring in experimental and non-experimental plots and sites is critical for parameterizing and validating predictive models of vegetation change (e.g. see Chapter 2). Monitoring programs that regularly sample vegetation and span decades also provide a rare opportunity to incorporate annual climatic fluctuations (e.g. annual precipitation) as predictor variables that will also improve model accuracy. To date, few such datasets exist, with most models incorporating climatic covariates relying on space-climate relationships (see Chapter 1). I recommend that monitoring programs particularly focus on changes in shrub and grass cover, because these life forms have

been documented worldwide to be highly responsive to climate change in alpine and arctic ecosystems (Myers-Smith et al. 2011).

4.4 Future research directions

1. It is commonly documented that species respond to climatic warming idiosyncratically (Dormann and Woodin 2002). I recommend that future research focus on elucidating the processes behind this variation. One possible avenue of research could involve determining whether species with fast growth rates are less responsive to warming than slow growing species. In Chapter 3 there is some evidence of this. *Asterolasia trymalioides* was the only shrub species not to benefit under experimental warming. However, this species exhibited the fastest growth rate (Appendix 3.1). In fact, *Asterolasia*'s unwarmed growth rate was equivalent to that observed in *Grevillea* and *Prostanthera* seedlings growing in warmed conditions. This indicates that *Asterolasia* is potentially already growing close to its maximum growth rate, and will be relatively insensitive to future warming.
2. Higher temperatures have been shown to increase the survival and growth of alpine shrub seedlings (Chapter 3). However, it is unknown whether warmer conditions will also alter the time required to reach reproductive maturity. One hypothesis is that because climatic warming allows individuals to reach larger sizes faster, they are likely to reach reproductive maturity sooner (i.e. based on the theory that reproductive output is related to plant size; Samson and Werk 1986). If this is the case then warming is likely to increase species resilience to short fire intervals and thus, potentially further exacerbate the shrub-fire feedback identified in Chapter 3. Because of this I recommend that seedling-warming experiments in combination with gradient studies be conducted to examine this particular hypothesis.
3. Future research should also focus on exploring other potential factors that may exacerbate or diminish the shrub-fire feedback loop identified in Chapter 3. For

example Post et al. (2008) provided experimental evidence suggesting that herbivory can mitigate climate-induced increases in shrub biomass. While Chapin et al. (2005) suggested that increases in shrub cover may reduce landscape albedo, which may further exacerbate shrub growth and expansion. There are also a number of other factors that warrant further research including the impacts of: decreased snow cover, heat stress, changes in the frequency of droughts and changes in nutrients.

4. Meta analyses of vegetation responses to climate change have predominately focused on reporting standardized effect sizes of experimental treatments (e.g. Ainsworth and Long 2005, Elmendorf et al. 2012a). While this information provides biome level information on the directions of vegetation responses to experimental treatments it does not provide information on how such treatments explicitly influence rates of change. As a consequence, the findings of these meta analyses are difficult to incorporate into models capable of predicting vegetation changes through time. As there are few studies that explicitly report treatment effects on rates (see Chapter 1) I recommend that experimental networks such as the International Tundra Experiment (ITEX; Henry and Molau 1997) and the Free-Air Carbon dioxide Enrichment experiment (Ainsworth and Long 2005) utilise their global datasets to model treatment effects on rates of vegetation growth and cover changes. Such analysis will reveal inter-continental similarities and differences but also provide the capacity for predicting biome level shifts in vegetation under multiple future climatic conditions.
5. Finally research effort should focus on making the models reported in this thesis spatially explicit. Extending this work to produce spatially explicit models can provide scientists, land managers and other stakeholders with the tools necessary to produce predictive maps of future vegetation change, which in turn can be used to determine areas most at risk or most susceptible to climate change. An example of such an application would be to predict which areas are

most susceptible to climate-induced shrub thickening or encroachment, for the purposes of fuel load management or biodiversity conservation.

4.5 Conclusion

In this thesis, I used data derived from multiple warming experiments and an extensive field survey to parameterize both conceptual and statistical models of vegetation change. I illustrate the benefit of modeling treatment effects on rates of vegetation growth and cover changes. I also highlight how climatic impacts on vegetation can be contingent on biotic interactions or plant responses to disturbances. Applying similar empirical approaches and models developed in this thesis to different plant communities, regions and biomes will test their robustness. Furthermore, the information obtained from these studies are likely to provide new insights into how climate change influences trajectories of vegetation change, which can then be used to improve our predictive and management capabilities.

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Appendices

Appendix 1.1 – Literature review table

Summary of experimental papers used in the Chapter 1 literature review.

Reference	Treatment	Yrs	Ecosystem	Disturb	Biotic	Seed	Rates
(Tercero-Bucardo et al. 2007)	Multiple	2	Forest	Yes	Yes	Yes	No
(Munier et al. 2010)	Multiple	5	Subalpine	Yes	Yes	Yes	No
(Bret-Harte et al. 2004)	Fertil/removal	2	Tundra	Yes	Yes	No	No
(Peñuelas et al. 2004)	Warm/water	2	Shrubland	Yes	Yes	No	No
(Post and Pedersen 2008)	Warm/herb	5	Tundra	Yes	Yes	No	No
(Kardol et al. 2010)	Multiple	5	Old-field	Yes	No	Yes	No
(Wan et al. 2005)	Warm/disturb	4	Grassland	Yes	No	No	No
(Peñuelas et al. 2007)	Warm/water	7	Shrubland	Yes	No	No	No
(Grime et al. 2008)	Warm/water	13	Grassland	Yes	No	No	No
(Jarrad et al. 2009)	Warm/disturb	3	Tundra	Yes	No	No	No
(Prieto et al. 2009b)	Warm/water	7	Shrubland	Yes	No	No	No
(Wahren et al. 2013)	Warm	9	Tundra	Yes	No	No	No
(Moser et al. 2011)	Multiple	15	Grassland	No	Yes	Yes	No
(Volder et al. 2012)	Warm/water	6	Savanna	No	Yes	Yes	No
(Klanderud 2005)	Warm/fertil	3	Tundra	No	Yes	No	No
(Klanderud and Totland 2005)	Warm/fertil	4	Tundra	No	Yes	No	No
(Wiedermann et al. 2007)	Warm/fertil	8	Boreal mire	No	Yes	No	No
(Price and Waser 2000)	Warm	4	Subalpine	No	No	Yes	No
(Lloret et al. 2004)	Warm/water	4	Shrubland	No	No	Yes	No
(Danby and Hik 2007)	Warm	3	Subalpine	No	No	Yes	No
(Erschbamer 2007)	Warm	7	Foreland	No	No	Yes	No
(Hovenden et al. 2008)	Warm/CO ₂	3	Grassland	No	No	Yes	No
(Classen et al. 2010)	Multiple	4	Old-field	No	No	Yes	No
(De Frenne et al. 2011)	Warm	2	Forest	No	No	Yes	No
(Piper et al. 2013)	Warm/water	2	Subalpine	No	No	Yes	No
(Rustad et al. 2001)	Warm	2-9	Multiple	No	No	No	No
(Shaver et al. 2001)	Fertil	15	Tundra	No	No	No	No
(Dormann and Woodin 2002)	Multiple	< 5	Tundra	No	No	No	No
(Kudo and Suzuki 2003)	Warm	5	Tundra	No	No	No	No
(Saavedra et al. 2003)	Warm	5	Subalpine	No	No	No	No
(Van Wijk et al. 2004)	Multiple	> 3	Tundra	No	No	No	No
(Weltzin et al. 2003)	Warm/water	5	Peatland	No	No	No	No
(Llorens 2004)	Warm/water	3	Shrubland	No	No	No	No
(Mack et al. 2004)	Fertil	20	Tundra	No	No	No	No
(Dukes et al. 2005)	Multiple	5	Grassland	No	No	No	No
(Hollister et al. 2005a)	Warm	5-7	Tundra	No	No	No	No

(Hollister et al. 2005b)	Warm	5-7	Tundra	No	No	No	No
(Jónsdóttir et al. 2005)	Warm	3-5	Tundra	No	No	No	No
(Takahashi 2005)	Warm	2	Tundra	No	No	No	No
(Wahren et al. 2005)	Warm/snow	8	Tundra	No	No	No	No
(Walker et al. 2006)	Warm	3-6	Tundra	No	No	No	No
(Biasi et al. 2008)	Warm	2	Tundra	No	No	No	No
(Klanderud 2008)	Warm/fertil	4	Tundra	No	No	No	No
(Gedan and Bertness 2009)	Warming	3	Salt marsh	No	No	No	No
(Jägerbrand et al. 2009)	Warm/fertil	5	Tundra	No	No	No	No
(Wipf et al. 2009)	Snow	2	Tundra	No	No	No	No
(Hudson and Henry 2010)	Warm	15	Tundra	No	No	No	No
(Dawes et al. 2011)	Warm/CO ₂	3-9	Tundra	No	No	No	No
(Elmendorf et al. 2012a)	Warm	20	Tundra	No	No	No	No
(Wu et al. 2011)	Warm/water	1-11	Multiple	No	No	No	No
(Barbeta et al. 2013)	Warm	13	Forest	No	No	No	No
(Campioli et al. 2013)	Warming	7	Tundra	No	No	No	No
(Newingham et al. 2013)	CO ₂	10	Desert	No	No	No	No
(Sistla et al. 2013)	Warm	20	Tundra	No	No	No	No

Appendix 2.1 – Table of logit transformed covariate means and standard deviations

Covariate	Logit mean (SD)
Shrub	-3.1 (1.3)
Graminoids	1.3 (1.1)
Forbs	-0.1 (0.7)
Bare ground	-3.6 (1.2)

Appendix 2.2 – JAGS code for modeling rates of life form cover change

The following is example code used to model rates of Graminoid cover change. This model has a varying intercept for site, which allows sites to have different rates of change. Once posterior distributions have been estimated for all life forms, parameter posterior distributions can then be combined from all models to make predictions under under different scenarios (not shown). For computational efficiency this is best done outside of JAGS.

Note: This model is structurally the same for other life forms with the exception that neighboring life form covariates will differ depending on the life form being modeled.

```

model {

  for (i in 1:n.plots) { # For each plot

    # Initialising first census cover + observation error
    cover[i, 1] ~ dbin(p[i, 1], 100)
    logit(p[i, 1]) <- Cover.hat[i, 1] # logit link
    Cover.hat[i, 1] ~ dnorm(0, 0.0001)

    # Estimating residual plot level error

    plot.err[i] ~ dnorm(0, sd.plot^-2)

    # Estimating subsequent census covers
    for (t in 2:n.census) { # For each census onwards

      # random realization from binomial distribution
      cover[i, t] ~ dbin(p[i, t], 100)
      logit(p[i, t]) <- Cover.hat[i, t] #logit link
      Cover.hat[i, t] <- r[i, t] + Cover.hat[i,t-1] # eqn. 2

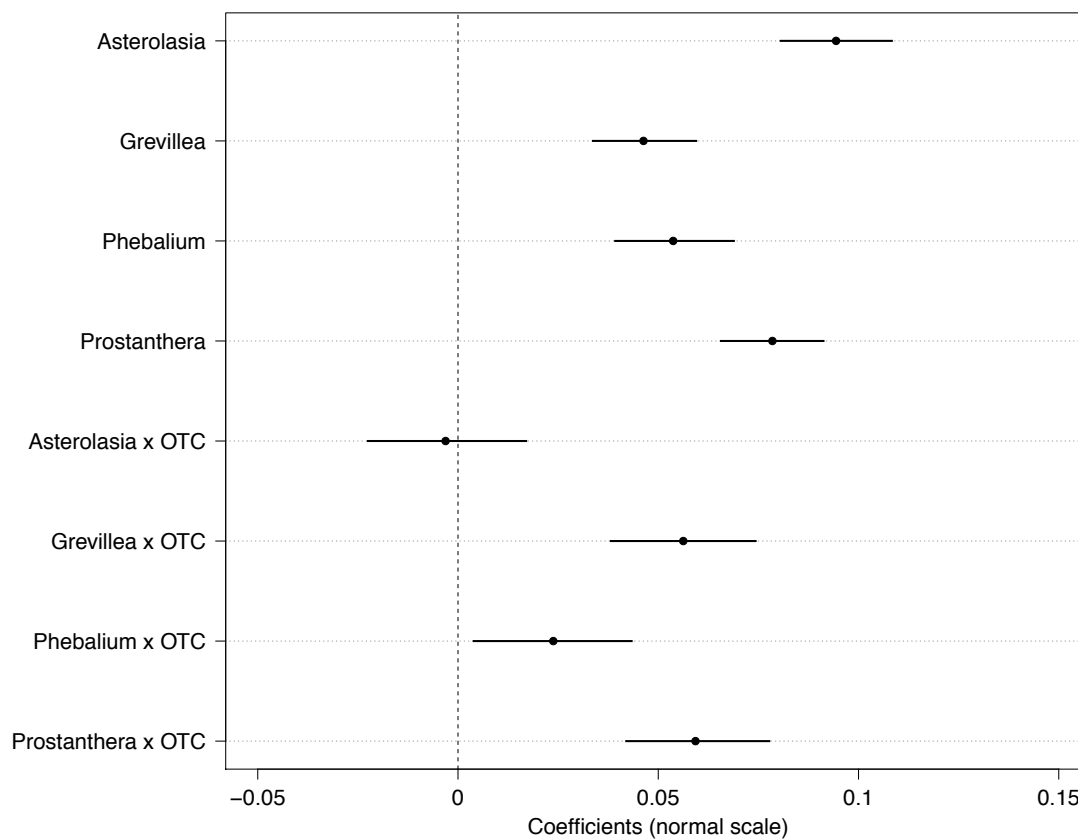
      r[i,t] <-
        alpha.site[site[i]] + # Varying intercept
        b.OTC * OTC[i] + # Effect of OTC
        b.Shrub * Shrub[i, t-1] + # Effect of shrub abundance @ t-1
        b.Forb * Forb[i, t-1] + # Effect of forb abundance @ t-1
        b.BG * BG[i, t-1] + # Effect of BG abundance @ t-1
        b.OTC_Shrub * (Shrub[i, t-1] * OTC[i]) + # OTC x Shrub
        b.OTC_Forb * (Forb[i, t-1] * OTC[i]) + # OTC x Forb
        b.OTC_BG * (Bareground[i, t-1] * OTC[i]) + # OTC x BG
        plot.err[i] # Residual plot level variation
      }
    }

  for (j in 1:n.site) { # For each site
    # Estimating site mean rates
    alpha.site[j] ~ dnorm(GM, sd.site^-2) #GM = average site rate
  }

  # Priors
  # Cauchy priors for coefficients & random effects
  GM ~ dt(0, .0016, 1)
  b.OTC ~ dt(0, .01, 1)
  b.BG ~ dt(0, .01, 1)
  b.Shrub ~ dt(0, .01, 1)
  b.Forb ~ dt(0, .01, 1)
  b.OTC_Shrub ~ dt(0, .01, 1)
  b.OTC_Forb ~ dt(0, .01, 1)
  b.OTC_BG ~ dt(0, .01, 1)
  sd.plot ~ dt(0, .0016, 1)T(0,) # Stdev of plot residual variation
  sd.site ~ dt(0, .0016, 1)T(0,) # Stdev of site residual variation
}

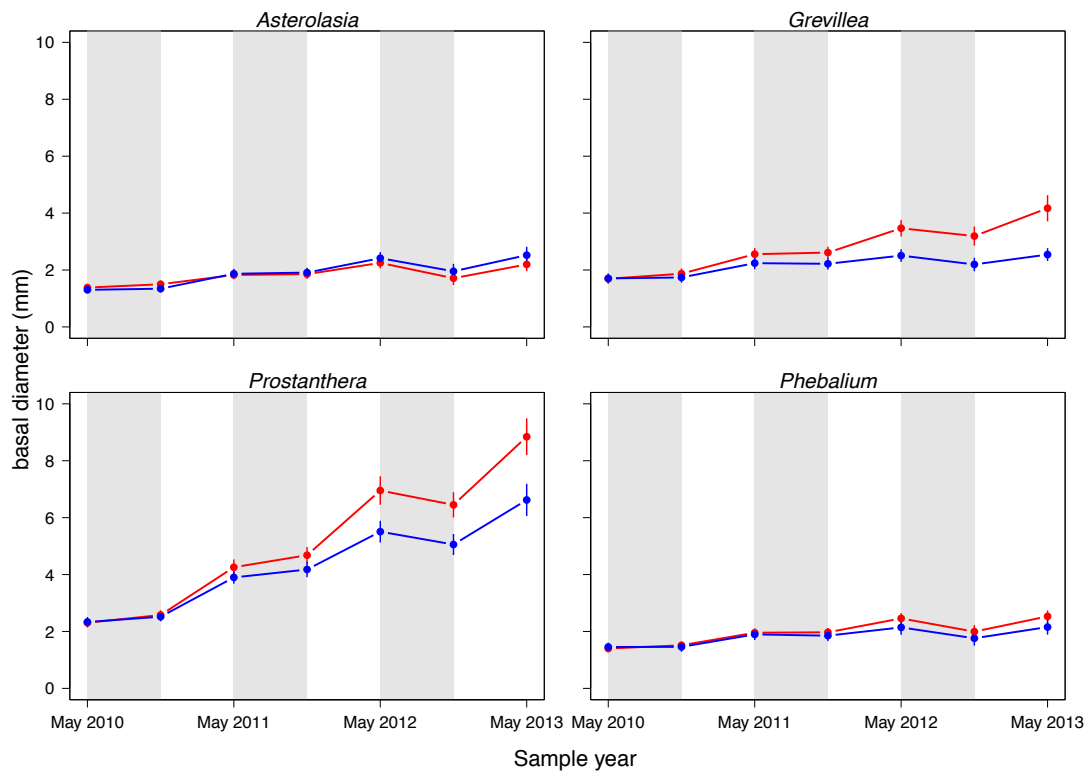
```

Appendix 3.1 – Coefficient plot of multi-species growth rate model.



Coefficient plot of multi-species growth rate model. Parameters: *Asterolasia*, *Grevillea*, *Prostanthera* and *Phebalium* represent growth rates for species in control plots. Genus name x OTC represents the OTC effect for associated species. This is an additive model. To determine the growth rate in OTCs add the two associated coefficients together (e.g. *Asterolasia* + *Asterolasia* x OTC = *Asterolasia* growth rate in OTC conditions).

Appendix 3.2 – Observed basal growth with experimental warming



Observed mean ($\pm$ 95% confidence intervals) basal diameters of seedlings from four dominant alpine shrubs during the 1064-day experiment. Shaded areas are the winter snow periods when warming treatment was not applied to plots. Red lines: warmed (OTC) conditions; blue lines: current (control) conditions.

Appendix 3.3 – JAGS code for multispecies seedling growth rate model

```
model {
  for (i in 1:n.Ind){ # For each individual
    for (t in 1:n.Year){ # For each year

      Height[i,t] ~ dnorm(Height.Hat[i,t], sd.Obs^-2) # including residual variation

      # Logistic growth rate model
      Height.Hat[i, t] <- Hmax[Species[i]] /
        (1 + (Hmax[Species[i]]/Init.Size[Ind[i]] - 1) * exp(-R[i] * (Days[t]/100)))
    }

    # Daily Growth Rate for each individual
    R[i] <-
      a.SPP_CTL[Species[i]] + # Intercept (CTL mean species growth rate)
      b.SPP_OTC[Species[i]] * OTC[Plot[i]] + # Effect of OTC
      ranef.ind[Ind[i]] + # Individual random effect
      ranef.plot[Plot[i]] # Plot random effect

    ranef.ind[i] ~ dnorm(0, sd.Ind^-2) # Estimating individual random effect
  }

  for (j in 1:n.Species) { # For each species

    # Estimating mean CTL growth rate for each species
    a.SPP_CTL[j] ~ dnorm(mu.SPP_CTL, sd.SPP_CTL^-2)

    # Estimating OTC effect for each species
    b.SPP_OTC[j] ~ dnorm(mu.SPP_OTC, sd.SPP_OTC^-2)
  }

  for (k in 1:n.Plots) { # For each plot
    ranef.plot[k] ~ dnorm(0, sd.Plot^-2) # Estimating random effect for plot
  }

  # Priors
  mu.SPP_CTL ~ dt(0, .0016, 1) # Mean CTL growth rate (across species)
  mu.SPP_OTC ~ dt(0, .01, 1) # Mean effect of OTC (across species)
  sd.SPP_CTL ~ dt(0, .0016, 1)T(0,) # CTL species variation
  sd.SPP_OTC ~ dt(0, .0016, 1)T(0,) # OTC species variation
  sd.Plot ~ dt(0, .0016, 1)T(0,) # Plot variation
  sd.Ind ~ dt(0, .0016, 1)T(0,) # Individual variation
  sd.Obs ~ dt(0, .0016, 1)T(0,) # Residual variation
}
```

Appendix 3.4 – JAGS code for modeling *Grevillea* seedling growth rates incorporating *Poa* effect

```
model {
  for (i in 1:n.Ind){ # For each individual
    for (t in 1:n.Year){ # For each year
      Height[i,t] ~ dnorm(Height.Hat[i,t], sd.Obs^-2) # including residual variation

      # Logistic growth rate model
      Height.Hat[i, t] <- Hmax /
        (1 + (Hmax/Init.Size[Ind[i]] - 1) * exp(-R[i] * (Days[t]/100)))
    }
    # Daily growth rate for each individual
    R[i] <-
      CTL + # Intercept (CTL mean growth rate)
      b.OTC * OTC[Plot[i]] + # Effect of OTC
      b.GapSize * GapSize[i] + # CTL gap size effect
      b.GapSize_OTC * GapSize[i] * OTC[Plot[i]] + # OTC gap size effect
      ranef.ind[Ind[i]] + # Individual random effect
      ranef.plot[Plot[i]] # Plot random effect

    ranef.ind[i] ~ dnorm(0, sd.Ind^-2) # Estimating individual random effect
  }

  for (k in 1:n.Plots) { # For each plot

    ranef.plot[k] ~ dnorm(0, sd.Plot^-2) # Estimating plot random effect
  }

  # Priors
  CTL ~ dt(0, .0016, 1) # Intercept (CTL mean growth rate)
  b.OTC ~ dt(0, .01, 1) # Effect of OTC
  b.GapSize ~ dt(0, .01, 1) # CTL gap size effect
  b.GapSize_OTC ~ dt(0, .01, 1) # OTC gap size effect
  sd.Plot ~ dt(0, 0.0016, 1)T(0, ) # Plot variation
  sd.Ind ~ dt(0, 0.0016, 1)T(0, ) # Individual variation
  sd.Obs ~ dt(0, 0.0016, 1)T(0, ) # Residual variation
}
```

Appendix 3.5 – JAGS code for multispecies seedling mortality model

```
model {
  for (i in 1:n.Ind) { # For each individual
    DIED[i] ~ dbern(p[i]) # Probability of death

    # Estimating probability of death
    cloglog(p[i]) <-
      a.SPP_CTL[Species[i]] + # Intercept (CTL mean probability of death)
      b.SPP_OTC[Species[i]] * OTC[Plot[i]] + # Effect of OTC for each species
      ranef.plot[Plot[i]] # Plot random effect
  }

  for (j in 1:n.Species) { # For each species
    # Estimating mean CTL mortality for each species
    a.SPP_CTL[j] ~ dnorm(mu.SPP_CTL, sd.SPP_CTL^-2)

    # Estimating OTC effect for each species
    b.SPP_OTC[j] ~ dnorm(mu.SPP_OTC, sd.SPP_OTC^-2)
  }

  for (k in 1:n.Plots) { # For each plot
    ranef.plot[k] ~ dnorm(0, sd.Plot^-2) # Estimating plot random effect
  }

  # Priors
  mu.SPP_CTL ~ dt(0, .0016, 1) # CTL mean probability of death (across species)
  mu.SPP_OTC ~ dt(0, .01, 1) # Mean effect of OTC (across species)
  sd.Plot ~ dt(0, .0016, 1)T(0, ) # Plot variation
  sd.SPP_CTL ~ dt(0, 0.0016, 1)T(0, ) # CTL species variation
  sd.SPP_OTC ~ dt(0, 0.0016, 1)T(0, ) # OTC Species variation
}
```


Appendix 3.6 – JAGS code for modeling *Grevillea* seedling mortality incorporating *Poa* effect

```
model {
  for (i in 1:n.Ind) { # For each individual
    DIED[i] ~ dbern(p[i]) # Probability of death

    # Estimating probability of death
    cloglog(p[i]) <-
      CTL + # Intercept (probability of death in CTLs)
      b.OTC * OTC[Plot[i]] + # OTC effect
      b.GapSize * GapSize[i] + # CTL gap size effect
      b.PoaDist_OTC * PoaDist[i] * OTC[Plot[i]] + # OTC gap size effect
      ranef.plot[Plot[i]] # Plot random effect
  }
  for (k in 1:n.Plots) { # For each plot
    ranef.plot[k] ~ dnorm(0, sd.Plot^-2) # Estimating plot random effect
  }

  # Priors
  CTL ~ dt(0, .0016, 1) # Intercept (CTL probability of death)
  b.OTC ~ dt(0, .01, 1) # OTC effect
  b.GapSize ~ dt(0, .01, 1) # CTL gap size effect
  b.GapSize_OTC ~ dt(0, .01, 1) # OTC gap size effect
  sd.Plot ~ dt(0, .0016, 1)T(0, ) # Plot variation
}
```

Appendix 3.7 – JAGS code for modeling *Grevillea* seedling density

```
model {  
  for (i in 1:n.plots) { # For each plot  
    SdlDensity[i] ~ dpois(lambda[i])  
    # Estimating seedling density  
    log(lambda[i]) <-  
      alpha.Site[Site[i]] +  
      b.Tran[Site[i], Tran[i]]  
  }  
  for (j in 1:n.sites) { # For each site  
    # Site level effects  
    alpha.Site[j] <- mu.site[j] + # Site intercept  
      (b.Alt * Alt[j]) + # Altitude effect  
      (b.Unburned * (1 - Burned[j])) + # Unburned effect  
      (b.Sev * (Sev[j] * Burned[j])) + # Severity effect (burned sites only)  
      (b.TWI * TWI[j]) # TWI effect  
    mu.site[j] ~ dnorm(GM.site, sd.site^-2) # Estimating intercepts for each site  
    for (k in 1:n.trans) { # For each transect  
      b.Tran[j,k] <- (b.AdultDen * AdultDen[j,k]) + # Effect of adult density  
      Tran.err[j,k] # Transect random effect  
      Tran.err[j,k] ~ dnorm(0, sd.tran^-2) # Estimating transect random effect  
    }  
  }  
  # Priors  
  GM.site ~ dnorm(0, 0.0001) # Mean density across sites  
  b.Unburned ~ dnorm(0, 0.0001) # Unburned effect  
  b.Alt ~ dnorm(0, 0.0001) # Altitude effect  
  b.Sev ~ dnorm(0, 0.0001) # Severity effect  
  b.TWI ~ dnorm(0, 0.0001) # TWI effect  
  b.AdultDen ~ dnorm(0, 0.0001) # Adult density effect  
  sd.site ~ dunif(0, 100) # Site variation  
  sd.tran ~ dunif(0, 100) # Transect variation  
}
```

Appendix 3.8 – JAGS code for modeling maximum *Grevillea* seedling heights across environmental gradients

```
model {  
  
  for (i in 1:n.obs) { # For each observation  
    SdlHeight[i] ~ dlnorm(mu.ht[i], sd.obs^-2) # Incorporating residual error  
    # Estimating mean seedling height  
    mu.ht[i] <-  
      mu.site[Site[i]] + # Site intercept  
      b.Alt * Alt[Site[i]] + # Altitude effect  
      b.Sev * Sev[Site[i]] + # Severity effect  
      b.TWI * TWI[Site[i]] # TWI effect  
  }  
  
  for (j in 1:n.sites) { # For each site  
    mu.site[j] ~ dnorm(GM.site, sd.site^-2) # Estimating mean density for each site  
  }  
  
  # Priors  
  GM.site ~ dnorm(0, 0.0001) # Mean height across sites  
  b.Alt ~ dnorm(0, 0.0001) # Effect of altitude  
  b.Sev ~ dnorm(0, 0.0001) # Effect of severity  
  b.TWI ~ dnorm(0, 0.0001) # Effect of TWI  
  sd.site ~ dunif(0, 100) # Site variation  
  sd.obs ~ dunif(0, 100) # Residual variation  
}
```




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Post-fire regeneration in alpine heathland: Does fire severity matter?

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Abstract Fire severity is thought to be an important determinant of landscape patterns of post-fire regeneration, yet there have been few studies of the effects of variation in fire severity at landscape scales on floristic diversity and composition, and none within alpine vegetation. Understanding how fire severity affects alpine vegetation is important because fire is relatively infrequent in alpine environments. Globally, alpine ecosystems are at risk from climate change, which, in addition to warming, is likely to increase the severity and frequency of fire in south-eastern Australia. Here we examine the effects of variation in fire severity on plant diversity and vegetation composition, 5 years after the widespread fires of 2003. We used floristic data from two wide-spread vegetation types on the Bogong High Plains: open heathland and closed heathland. Three alternative models were tested relating variation in plant community attributes (e.g. diversity, ground cover of dominant species, amount of bare ground) to variation in fire severity. The models were (i) 'linear', attributes vary linearly with fire severity; (ii) 'intermediate disturbance', attributes are highest at intermediate fire severity and lowest at both low- and high-severity; and (iii) 'null', attributes are unaffected by fire severity. In both heathlands, there were few differences in floristic diversity, cover of dominant species and community composition, across the strong fire severity gradient. The null model was most supported in the vast majority of cases, with only limited support for either the linear and intermediate disturbance models. Our data indicate that in both heathlands, vegetation attributes in burnt vegetation were converging towards that of the unburnt state. We conclude that fire severity had little impact on post-fire regeneration, and that both closed and open alpine heathlands are resilient to variation in fire severity during landscape scale fires.

Key words: competing model, disturbance, fire management, intensity, intermediate disturbance hypothesis, resilience, shrub.

INTRODUCTION

Fire influences the distribution, composition and structure of vegetation at global, regional and local scales (Bond *et al.* 2005) and therefore is integral to conservation management (Bradstock *et al.* 2002; Andersen *et al.* 2003; Bond & Archibald 2003). The spatial and temporal extent of fire is a function of fire regime (frequency, intensity, season, type), the variation in which can affect ecosystem state, ecological processes, landscape heterogeneity and biodiversity (Bradstock *et al.* 2002). The effects of fire-line intensity (the rate of energy release per metre of fire front) on ecosystems are difficult to investigate because quantifying intensity is rarely practicable. Fire severity is often used as a surrogate for fire intensity as it is more

readily quantifiable and directly assesses the effects of fire on ecosystem attributes (Keeley 2009). Patterns of fire severity may vary considerably during individual fires, including large severe fires, even under extreme fire weather conditions (Knox and Clarke 2012). Some points in the landscape burn severely, others only slightly or not at all (Turner *et al.* 1999; Schoenagel *et al.* 2008; Williams & Bradstock 2008).

The effects of variation in fire intensity or severity on ecosystems is the subject of considerable public and scientific debate. Some have argued that in temperate forests and shrublands large, severe fires are an unnatural expression of the historical fire regime, and are ecologically destructive (e.g. Adams & Attiwill 2011; Minnich 2001). According to this view, such fires are ecologically damaging because of the resultant homogenization of landscapes, loss of fine-grained patchiness, the death of many individuals of both plants and animals and the destruction of refugia.

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Conversely, others have shown that high severity fires in forests have few long-lasting effects on the vegetation (e.g. Keeley *et al.* 2008; Knox and Clarke 2012). These concerns regarding the role of large, potentially severe fires are emerging as major issues influencing the management of fire on public land in Australia, including National Parks, with calls for more prescribed burning to mitigate fire size and severity in the effort of maintaining biodiversity (e.g. Adams & Attwill 2011).

While large, severe fires undoubtedly threaten life and property, they are not necessarily threats to biodiversity (Williams & Bradstock 2008). Indeed, in many temperate regions of the world, occasional high severity fires are increasingly seen as integral to the historical fire regime (Bradstock 2008; Schoennagel *et al.* 2008; Veblen *et al.* 2008). Ecological processes such as mortality (Keeley 2006; Ryan & Williams 2011), recruitment (Hodgkinson 1991; Moreno & Oechel 1991; Turner *et al.* 1999; Myers & Harms 2011), ecosystem productivity (Hodgkinson 1991; Turner *et al.* 2003) and the maintenance of alternative stable states (Odion *et al.* 2010) have all been shown to vary with fire severity. Fire severity may also affect competitive interactions among plants in the post-fire environment (Ducey *et al.* 1996), which may affect succession (Moreno & Oechel 1991; Turner *et al.* 1999, 2003) and diversity (Schoennagel *et al.* 2008). Variation in severity may thus provide a fundamental template for the maintenance of ecological processes that underpin biodiversity.

Here we examine how variation in fire severity affects structure, composition and diversity of alpine heathlands. Australian alpine landscapes are ideal ecosystems to test the above contrasting hypotheses concerning fire regimes and biodiversity because they are subject to recurrent albeit infrequent fire; and typically burn only under severe fire weather and widespread drought (Williams *et al.* 2006b, 2008). Fires arrive via the forested slopes and foothills and the alpine vegetation burns with varying severity (Williams *et al.* 2006b, 2008). The vegetation is also diverse, consisting of a mixture of plant communities and life-forms, and is relatively slow-growing. Moreover, fires in south-eastern Australia are projected to become more intense as a consequence of climate change because the number of days with severe fire weather is likely to increase (Cary *et al.* 2012). Given that alpine ecosystems globally are threatened by climate change (IPCC 2007; Engler *et al.* 2011), understanding how these systems respond to changes in fire regime will be critical in devising strategies that conserve global biodiversity.

We examine how the structure and composition of alpine heathland varies as a function of fire severity 5 years after landscape scale fires burnt more than 1 million hectares across south-eastern Australia in

2003. We focus on heathlands because they occupy about 60% of Australian alpine landscapes (Williams *et al.* 2006a) and shrubby vegetation is common in most alpine and high latitude areas of the world (Sturm *et al.* 2001). As fire is relatively infrequent in alpine areas (Körner 2003) and post-fire regeneration may be constrained by low temperatures, the effects of fire on alpine vegetation may be long-lasting, particularly if severity is high (Kirkpatrick *et al.* 2010). Alternatively, as shown for a range of lowland shrubby vegetation types (Keeley *et al.* 2008; Keeley 2009), the effects of fire on alpine heathlands may be short-lived and independent of fire severity.

In this post-fire study we examined whether (i) there was a difference in community composition and structure between heathlands burnt in 2003 and those that were unburnt in 2003, and (ii) whether composition and structure of burnt heathland varied with fire severity. We assessed how variation in fire severity at the landscape scale affected six vegetation attributes in open heathland and closed heathland: species density and diversity, shrub cover, cover of the dominant snow grasses (*Poa* spp.), cover of bare ground and species composition. All are important measures of landscape state in relation to disturbance in Australian alpine vegetation (Wahren *et al.* 1994; Williams *et al.* 2006a). For the second question, we proposed three alternative models relating variation in cover and diversity to variation in fire severity: (i) 'linear', where attributes vary linearly (either positively or negatively) with fire severity; (ii) 'intermediate disturbance' (following Huston 1979), where responses to variation in severity are non-linear, and are highest at intermediate levels of fire severity and lowest at both low- and high-severity; and (iii) 'null', where there is no detectable effect of fire severity on the measured attributes.

METHODS

Study area

Our study was conducted across the Bogong High Plains in the Alpine National Park (37°S, 147°E), about 250 km north-east of Melbourne, Australia. Altitude ranged from 1600 to 1894 m a.s.l. Mean annual precipitation is 1228 mm. Winter snow cover lasts from June to September with low average annual temperatures (mean minimum = 2.5°C; mean maximum = 9.3°C) and frequent frost (Australian Bureau of Meteorology, unpubl. data, 2011). Soils are organic loams, and the vegetation is a mosaic of Eucalypt-woodland and treeless vegetation, with the latter ranging from closed and open heathlands, herbfields, tussock grasslands and wetlands. We studied closed heathland and open heathland, which together occupy about half the study area. Closed heathland occurs on steeper slopes; shrub cover is 70–100%, and grass and herb cover is generally <10%. The dominant shrub species range from 1–2 m tall and include *Bossiaea foliosa* (Fabaceae),

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Orites lancifolia (Proteaceae), *Phebalium squamulosum* (Rutaceae) and *Prostanthera cuneata* (Lamiaceae). Open heathlands occur on gentle slopes, shrub cover is 20–50%, and 0.2–0.5 m tall. The dominant shrub is *Grevillea australis* (Proteaceae), with the inter-shrub spaces dominated by snow grasses (*Poa* spp.) and herbs (Williams *et al.* 2006a).

Fires in Australia's south-eastern highlands in 2003 coincided with Australia's longest drought since 1900. Approximately 50% (400 000 ha) of the Alpine National Park was burnt, including about 10 000 ha of alpine treeless vegetation. Occurrence and severity varied substantially, with the scale of burning-induced patchiness ranging from square metres to square kilometres. Approximately 87% of closed heathland, 59% of open heathland and 13% of grassland vegetation was burnt (Williams *et al.* 2006b).

Study design

Immediately after the 2003 fires, we surveyed the patterns of burning (occurrence and severity where burnt) in four common vegetation types: grassland, snow patch herbfields, open heathland and closed heathland (Williams *et al.* 2006b). We established 419 randomly located survey points over an area of about 100 km². Latitude and longitude (± 10 m), whether the point was burnt or unburnt by the 2003 fires, slope, aspect, altitude and vegetation type were recorded. Fire severity in heathlands was based on minimum twig diameter, a proxy measure of fire severity (Whight & Bradstock 1999). Twig diameter was recorded between 1 and 10 months post fire, from 10 replicate samples of the two dominant shrub species, if present: *Grevillea australis* in open heathland, and *Orites lancifolia* in closed heathland. Twig diameters ranged from about 1–21 mm, with smaller diameters assumed to have experienced lower intensity of fire. This encompassed the full range of fire severity, from unburnt and lightly scorched shrubs, with only the tips of the outer branches burnt, to severely burnt shrubs where the majority of even large branches were consumed. Some sample sites, including those unburnt in 2003, are likely to have been burnt in 1939. However, the fire history of the sites prior to 2003 is unknown, and henceforth 'unburnt' will refer simply to sites that were not burnt in the 2003 fires.

All heathland points surveyed in 2003 were relocated in 2007/08 and a subset selected for the floristic survey, according to the following criteria: sites had to (i) be greater than 0.25 ha in area, so that the site could be sampled adequately by a 50 m transect (see below); (ii) be at least 50 m from wetlands, to minimize the chance of wetland species affecting the species composition of the heathlands, and (iii) have a measure of minimum twig diameter from the dominant shrubs (not all heathland sites surveyed for fire occurrence immediately after the 2003 fires had concomitant measures of twig diameter; Williams *et al.* 2006b). This yielded 150 sites that encapsulated the full range of fire severity, including unburnt vegetation, in both heathlands. From these we chose 40 sites at random from each community, of which 30 were burnt and 10 were unburnt. Half the sites were in the northern part of the Bogong High Plains, which had been ungrazed by cattle since their removal in 1991; the other half of the sites were

in the southern part of the Bogong High Plains, which were grazed by cattle at the time of the 2003 fires, and had been for over 150 years prior to that. Grazing ceased on the Bogong High Plains immediately after the 2003 fires, and has not recommenced. Grazing by domestic stock has long been a contentious issue in the ecology and management of Australia's alpine environments (Williams *et al.* 2006a) and this aspect of the design allowed us to test explicitly whether the effects of fire severity depended on grazing history. Average minimum twig diameter across burnt sites ranged from 4 to 21 mm in closed heathland, and from 2 to 13 mm in open heathland. The floristic composition at each sample site was determined using a single 50 m transect, along which five 6 m² quadrats were placed at 10 m intervals. Within each quadrat, the cover of all vascular plant species, total shrub cover and bare ground were estimated using the Braun-Blanquet cover abundance scale (Braun-Blanquet 1965). Difficult taxa, such as *Poa*, were identified to genus level, with the dominant grass in open and closed heathlands often being *Poa hiemata* and *Poa hothemensis*, respectively.

Data analysis

For all analyses, the transect was the experimental unit, with minimum twig diameter treated as a continuous variable. Braun-Blanquet cover data were converted to mid-point percent values. Average cover of each taxon at each site (transect) was then calculated from the five quadrats. Because minimum twig diameters are not directly comparable between open and closed heathlands (due to differences in stem architecture), diameters were standardized as a proportion of the maximum twig diameter found in each community. Sites in unburnt heathland were given a standard unburnt minimum twig diameter of 0.5 mm, allowing variation in the dependent variables to be presented as a function of twig diameter on the same scale for each community.

Data were analysed in two stages. First, to determine the difference between burnt and unburnt heathland, we compared the mean value of each variable between unburnt and burnt sites (pooling fire severity measures), using 95% confidence intervals. If the 95% confidence intervals of the unburnt samples did not overlap with the intervals for the burnt samples, we inferred a significant difference for that attribute (Cumming & Finch 2005). Second, to assess how fire severity affected response variables, we modelled the relationship between standardized minimum twig diameter and the mean site attribute in burnt heathland. Unburnt values were excluded from this second set of analyses because we were explicitly interested in discriminating between the three models only for burnt heathland. Including the unburnt data would also result in the independent variable being non-continuous between minimum and maximum values. We used general linear models with the 'glm' function from the statistical software package R (R Development Core Team 2011). To model cover, which is bound within the unit interval, data were logit transformed. We assumed normal error distributions for the density and diversity data. Though technically both of these community measures are bound at zero, neither approached this limit. For the null models, we fitted only an intercept term, that is,

without a parameter that accounted for a relationship with standardized minimum twig diameter. For the 'linear' models, we fitted both an intercept term and a slope term describing the relationship with standardized minimum twig diameter. For the 'intermediate disturbance' models, we fitted second order polynomial terms, which included a parameter for standardized minimum twig diameter and an additional parameter for its square. This was used because it can reflect the theoretical shape of the intermediate disturbance hypothesis. To display the uncertainty of model fits, we used an approximate Bayesian approach to construct credible intervals. We simulated posterior densities, based on parameter point estimates and standard errors returned by the 'glm' function, using the 'sim' function of the R package 'arm' (Gelman & Hill 2007). From these simulated densities, we used the inner 95% quantiles as approximate credible intervals. To compare alternative models and their corresponding hypotheses, we used an information theoretic approach based on Akaike's Information Criteria (AIC). Models having AIC values within 1–2 of the minimum were considered to have equal support; values within 4–7 of the minimum had considerably less support than the minimal model (Burnham & Anderson 2002). Where linear and intermediate disturbance models received support, the fitted models were used to calculate predicted values of the response variables as a function of standardized twig diameter.

To assess floristic compositional changes in relation to fire severity and grazing history, we used non-metric multidimensional scaling (NMDS) with the Bray–Curtis dissimilarity index based on both the presence/absence of species as well as their cover data for each transect. The contribution of environmental variables (fire severity, grazing history, altitude, slope) to the ordination pattern was assessed using the ADONIS function of the 'vegan' package (Oksanen *et al.* 2012). ADONIS is an alternative, more flexible permutation procedure to ANOSIM (e.g. Clarke 1993) that partitions the sums-of-squares of the Bray–Curtis dissimilarity matrix (Anderson 2001; Oksanen 2011).

RESULTS

Five years after fire, there was substantial regeneration in both closed and open heathlands. Total vegetation cover was generally >80%, with prolific growth and flowering of snow grasses, and substantial regeneration

of shrubs. In closed heathland, 75 species were recorded. Species density ranged from 3–24 per 6 m² quadrat, and 11–33 per 50 m transect. In open heathland, there were 78 species and species density ranged from 7–26 per quadrat and 18–36 per transect. There were some differences in the response variables between burnt and unburnt heathland, but the differences were generally slight to modest and not consistent for most variables (Table 1). Mean species density per transect was similar in burnt and unburnt vegetation in both closed heathland and open heathland. Shannon diversity was higher in burnt closed heathland compared with unburnt closed heathland, whereas in open heathland it was identical in both burnt and unburnt vegetation. Shrub cover was substantially lower in burnt compared with unburnt closed heathland, whereas the difference was more muted in open heathland. The cover of snow grass (*Poa* spp.) was substantially higher in burnt compared with unburnt closed heathland, but in open heathland, *Poa* cover was similar in burnt and unburnt samples. In both communities, the amount of bare ground in unburnt samples was substantially lower than that in burnt areas.

Species density, Shannon diversity and *Poa* cover were equally supported by all models (null, linear and intermediate disturbance) in both closed and open heathlands (Figs 1 and 2 respectively). In all cases the explained deviance was low (<13%). For shrub cover in closed heathland, the intermediate disturbance model had the most support (Δ AIC = 6; 22% of the deviance explained; Fig 1). The peak average shrub cover (about 30%) occurred for a standardized twig value of 0.585; this was about 11% greater than the expected shrub cover at the lowest twig diameters, and 13% greater than shrub cover at the highest twig diameters. In open heath, the effect of fire severity on open heath shrub cover was equally supported by all models (Fig. 2). For bare ground, the linear and intermediate disturbance models had equal support relative to the null model in open heathland (Δ AIC = 8 and 4, respectively; <30% of the deviance explained; Fig. 2). In this case, the linear model (model with greatest support) estimated average bare ground cover was 30% greater at high twig diameters than at low twig diameters. For bare ground in closed heathland, the

Table 1. Mean ($\pm$ 95% CI) vegetation attributes responses to burning in closed and open heathlands, 5 years post fire

Attribute (mean $\pm$ 95% CI)	Closed heath (burnt)	Closed heath (unburnt)	Open heath (burnt)	Open heath (unburnt)
Species density	22.1 $\pm$ 2.2	19.1 $\pm$ 2.9	26.9 $\pm$ 2.0	29.6 $\pm$ 2.5
Shannon diversity	2.1 $\pm$ 0.2	1.5 $\pm$ 0.2	1.8 $\pm$ 0.2	1.8 $\pm$ 0.2
Shrub cover, %	25.3 $\pm$ 2.7	81.5 $\pm$ 3.1	8.8 $\pm$ 1.2	14.2 $\pm$ 3.7
<i>Poa</i> cover, %	14.2 $\pm$ 2.4	1.7 $\pm$ 1.0	32.2 $\pm$ 6.3	33.2 $\pm$ 4.3
Bare ground, %	16.2 $\pm$ 1.6	2.0 $\pm$ 0.4	22.6 $\pm$ 2.1	2.0 $\pm$ 0.4

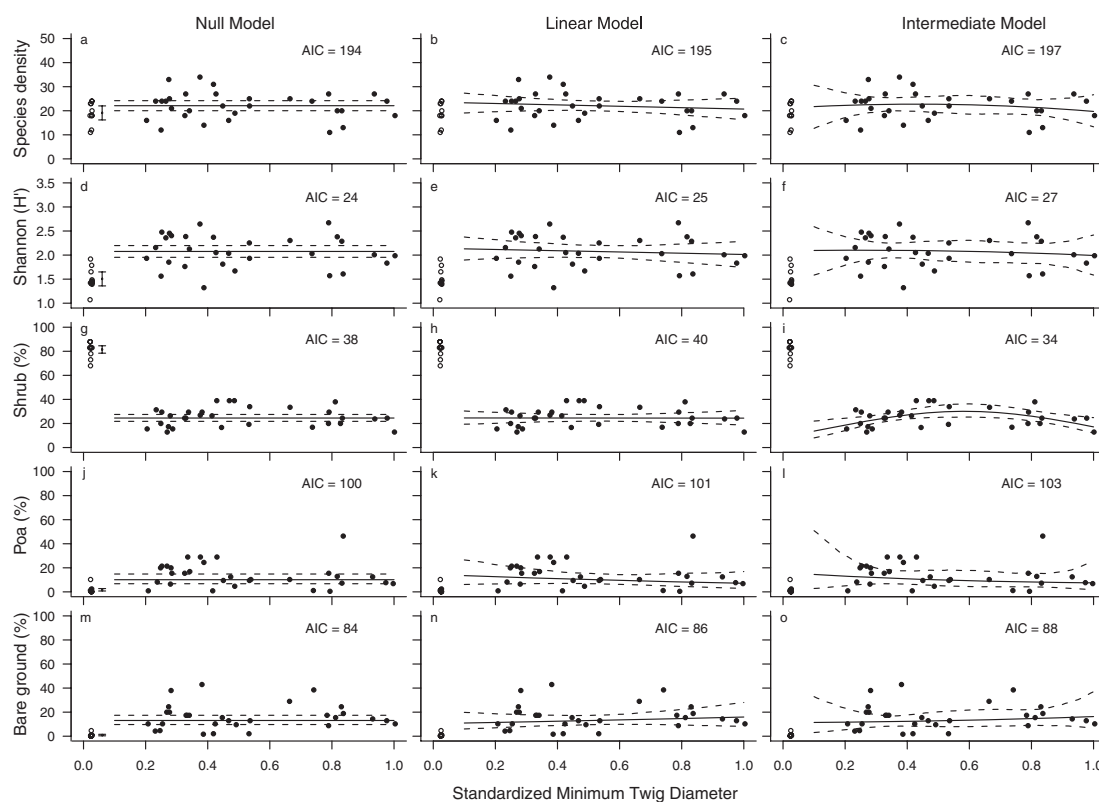


Fig. 1. Three competing models of fire severity effects on species density (a–c), Shannon diversity (d–f), and the cover of shrubs (g–i), *Poa* (j–l) and bare ground (m–o) in closed heathland. Left panels are null models (no severity effect); centre panels are linear models (positive or negative effects); right panels are intermediate disturbance models (greatest effects occurs at intermediate severity). Open circles on left side of figures signify unburnt sites, filled circles are burnt sites. Error bar in null model panels = mean from unburnt sites ($\pm 95\%$ CI). Model fit is based on burnt sites and is illustrated by a solid line, dashed lines are 95% credible intervals. AIC values are shown. AIC, Akaike's Information Criteria.

null model had the most support. Grazing history had no significant effect on diversity and life-form cover, and there were no significant severity $\times$ grazing interactions.

Ordination based on cover data found no significant differences between burnt and unburnt heathland and no significant correlation with fire severity (closed heathland: three-dimensional stress = 0.16, $R^2 = 0.05$, $P = 0.99$; open heathland: two-dimensional stress = 0.15, $R^2 = 0.07$, $P = 0.99$; Fig. 3) or any of other environmental variables (grazing history, altitude, slope, aspect or any interaction; $P = 0.99$, $R^2 < 0.09$, for all variables and interactions). Ordinations based on presence/absence data gave very similar results.

DISCUSSION

We proposed and tested three competing models for the impact of fire severity on post-fire regeneration in

alpine heathlands, finding strong support for the null model. Five years after landscape-scale fire, there were few differences in plant diversity and floristic composition across a strong fire severity gradient. Of the six measures of vegetation state assessed, the null model was most supported for all but two: shrub cover in closed heathland and bare ground in open heathland. In each case the model explained less than 30% of the deviance. Furthermore, ordination showed no difference between burnt and unburnt vegetation, nor was there a significant effect of fire severity on species composition in either burnt heathland community. Thus, 5 years post fire, the floristic composition of both alpine heathlands had converged towards that of the unburnt state. In Australian alpine and subalpine vegetation, most species re-establish within one or two years after fire (Wahren *et al.* 2001; Walsh & McDougall 2004), suggesting that these heathlands, like many temperate sclerophyllous shrubby vegetation types, follow the 'initial floristic composition' model of Egler

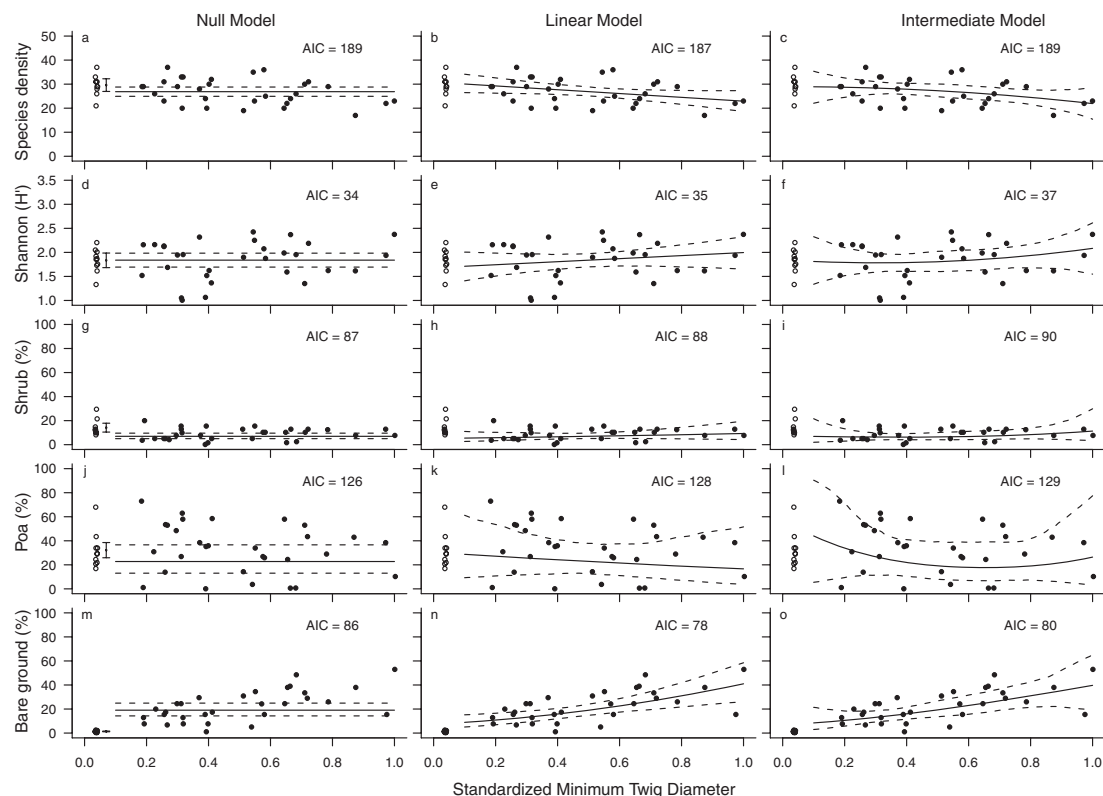


Fig. 2. Three competing models of fire severity effects on species density (a–c), Shannon diversity (d–f), and the cover of shrubs (g–i), *Poa* (j–l) and bare ground (m–o) in open heathland. Left panels are null models (no severity effect); centre panels are linear models (positive or negative severity effects); right panels are intermediate disturbance models (greatest effects occur at intermediate severity). Open circles on left side of figures signify unburnt sites, filled circles are burnt sites. Error bar in null model panels = mean from unburnt sites ($\pm 95\%$ CI). Model fit is based on burnt sites and is illustrated by a solid line, dashed lines are 95% credible intervals. AIC, Akaike's Information Criteria.

(1954) or the 'auto-succession' model of Keeley *et al.* (2005), whereby species diversity and composition is established rapidly post fire.

Post-fire regeneration in shrubby vegetation, whether vegetative or via seedlings, may be influenced by fire severity (Moreno & Oechel 1991; Bond & Midgley 2001; Myers & Harms 2011) which, in turn, could lead to different post-fire composition and diversity. However, we found no evidence that variation in fire severity affected community diversity and composition 5 years after fire. The muted effect of fire severity on compositional measures, and relatively rapid return to a pre-fire state, has also been documented in lowland shrubby vegetation types. Morrison (2002) found that fire intensity explained only 10% of the floristic variation in lowland Australian heath. Similarly, Knox and Clarke (2012) showed no effect of fire severity on fire-cued species in a temperate forest, and Knox and Clarke (2011) showed little long-term

effect of fire severity on woody plant resprouting ability. In Californian chaparral fire severity has been shown to have little long-lasting effects on vegetative regeneration (Keeley *et al.* 2005, 2008). This independence of post-fire regeneration patterns and fire severity appears to be very common in temperate heathlands. However, fire severity may interact strongly with other factors, such as productivity, rainfall and soil moisture to determine post-fire patterns of plant diversity (Safford & Harrison 2004; Pausas *et al.* 2008; Myers & Harms 2011).

The muted effect of fire severity on diversity and composition in alpine heathlands is likely due to the strong resprouting or seeding capacity of the Australian heathland floras in general (Williams *et al.* 2006a; Enright *et al.* 2012), and the long evolutionary history of recurrent fire in temperate shrublands worldwide (Keeley *et al.* 2011). Australian alpine heathlands are dominated by genera that are common in lowland

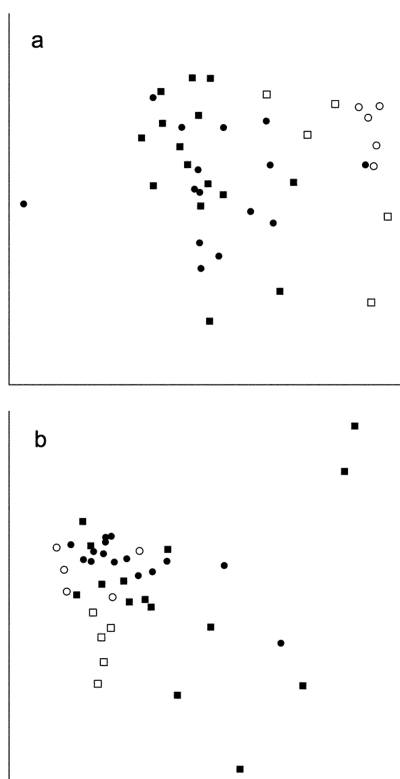


Fig. 3. Non-metric multidimensional scaling (NMDS) of floristic samples, showing. (a) closed heathland (showing the first two axis from three-dimensional solutions – minimum stress 0.16); (b) open heathland (two-dimensional, minimum stress 0.15). Configurations were based on relative species abundance. Burnt/grazed = black circle; burnt/ungrazed = black square; unburnt/grazed = open circle; unburnt/ungrazed = open square.

heathlands that have evolved in conjunction with recurrent fire over millions of years, with variation in fire intensity (and by implication, severity) being an integral part of fire regimes in Australian heathlands (Keith *et al.* 2002). Fires, of course, may result in substantial amounts of bare ground and although levels of bare ground are naturally low (1–2%) in long-unburnt alpine vegetation, the vast majority of the Australian alpine vascular flora is capable of recolonizing bare ground gaps that result from frequent small-scale disturbances associated with frost heave and insect attack (Williams *et al.* 2006a). Moreover, Australian alpine shrubs require bare ground for successful seedling recruitment. Thus, the patterns of regeneration in response to infrequent, large-scale and potentially severe fire rely upon the same traits of the Australian alpine flora that has allowed it to persist in the face of recurrent, frequent small-scale disturbances.

Climate change has already affected mountain ecosystems worldwide (e.g. Sturm *et al.* 2001; Chapin *et al.* 2005), while both severity and frequency of fire have been predicted to increase in many temperate ecosystems of the world (Flannigan *et al.* 2009), including Australian heathlands (Enright *et al.* 2012). Our data suggest that Australian alpine heathlands, even though they may be extensively burnt during occasional large fires, are resilient to variation in severity. Therefore, individual high severity fires, a feature of the current and future fire regimes of south-eastern Australia, are unlikely to result in the local extinction of alpine heathland species or communities (Williams *et al.* 2008). However, Australian heathlands more generally are known to be sensitive to variation in fire return-interval (Enright *et al.* 2012) and an increase in the frequency of fire may threaten alpine heathlands. Given that dominant obligate-seeding shrubs of the Australian alps take at least 5 years to flower and produce seed (C.-H. Wahren, unpubl. data, 2012), then detrimental intervals between fires are likely to be of the order of 10 years or less.

Our results have important implications for the conservation management of alpine ecosystems, under both current and future climate. Fire in some alpine environments may have long-lasting effects on some vegetation types, such as coniferous heaths in Tasmania (Kirkpatrick *et al.* 2010), and hygrophilous shrubs that occur in *Sphagnum* wetlands (McDougall 2007). However, our data show clearly that a single fire, albeit large and severe, did not reduce diversity or substantially change the composition of two of the most common alpine vegetation types in Australia – closed heathlands and open heathlands. Together these vegetation types account for over 60% of the alpine landscape. Recurrent, infrequent and large fires that result in parts of the alpine landscape being burnt severely are a part of the historical fire regime of the Australian Alps (Williams *et al.* 2006a, 2008). Propagation of these fires across the landscape is highly dependent on these two vegetation types (Williams *et al.* 2006b) but as our data show there are few long-lasting effects on diversity and composition in these heathlands when burnt, even if burnt severely.

Our data indicate there is no conservation imperative to limit fire severity in alpine landscapes through active fuel management in alpine vegetation (e.g. by prescribed burning or livestock grazing) based on the hypothesis that large, severe fire is unnatural and has deleterious impacts on biodiversity in southern Australia (e.g. Adams & Attiwill 2011). Although diversity and composition of the two-heathland communities were largely unaffected by fire severity, vegetation structure was. Bare ground was substantially higher in burnt vegetation than in unburnt, in both open and closed heathlands. Shrub cover was substantially lower in burnt closed heath than unburnt closed heath. At

least a decade post fire is likely to be required before the cover of dominant shrubs and the amount of bare ground return to pre-fire levels. Dense, mature shrub cover is required as habitat for a number of specialist alpine faunal species (Sanecki *et al.* 2006), and elevated levels of bare ground (>5%) increase the risk of soil loss in Australian alpine vegetation (Williams *et al.* 2006a, 2008). Thus, minimizing further disturbance to alpine heathlands that are regenerating post fire should be a fundamental management objective.

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Experimental warming and long-term vegetation dynamics in an alpine heathland

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Abstract. High mountain ecosystems are vulnerable to the effects of climate warming and Australia's alpine vegetation has been identified as particularly vulnerable. Between 2004 and 2010, we monitored vegetation changes in a warming experiment within alpine open grassy-heathland on the Bogong High Plains, Victoria, Australia. The study was part of the International Tundra Experiment (ITEX Network) and used open-topped chambers (OTC) to raise ambient growing-season temperatures by ~1°C at two sites. We assessed the effects of experimental warming on vegetation composition, diversity and cover using ordination, linear models and hierarchical partitioning. Results were compared with vegetation changes at four long-term (non-ITEX) monitoring sites in similar vegetation sampled from 1979 to 2010. The warming experiment coincided with the driest 13-year period (1996–2009) since the late 1880s. At the ITEX sites, between 2004 and 2010, graminoid cover decreased by 25%, whereas forb and shrub cover increased by 9% and 20%, respectively. Mean canopy height increased from 7 cm to 10 cm and diversity increased as a result of changes in relative abundance, rather than an influx of new species. These vegetation changes were similar to those at the four non-ITEX sites for the same period and well within the range of changes observed over the 31-year sampling period. Changes at the non-ITEX sites were correlated with a decrease in annual precipitation, increase in mean minimum temperatures during spring and increase in mean maximum temperature during autumn. Vegetation changes induced by the warming experiment were small rather than transformational and broadly similar to changes at the long-term monitoring sites. This suggests that Australian alpine vegetation has a degree of resilience to climate change in the short to medium term (20–30 years). In the long term (>30 years), drought may be as important a determinant of environmental change in alpine vegetation as rising temperatures. Long-term vegetation and climate data are invaluable in interpreting results from short-term (≤10 years) experiments.

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Introduction

Numerous experimental and observational studies have highlighted changes in vegetation communities in response to recent climate change (Root *et al.* 2003; Elmendorf *et al.* 2012a). Some of the largest and most well documented changes are in tundra vegetation, particularly in the Arctic, where biomass has increased, plant diversity has decreased and shrubs have expanded (Welker *et al.* 1997; Arft *et al.* 1999; Wahren *et al.* 2005; Tape *et al.* 2006; Hudson and Henry 2009). These findings were first noted in manipulative experiments, such as the International Tundra Experiment (ITEX Network), which use open-topped chambers (OTC) to passively warm ambient temperatures (Arft *et al.* 1999; Hollister *et al.* 2005a). Similar changes have also been observed in control plots (Wahren *et al.* 2005; Hudson and Henry 2009; Hill and Henry 2011). These

studies have documented changes in vegetation composition and structure, plant size and increases in leaf size, altered leaf chemistry (Hudson *et al.* 2011), and a tendency towards sexual reproduction. Such changes may ultimately increase plant cover and evolutionary rates (Klady *et al.* 2011). Similar responses are expected in other systems, particularly alpine and subalpine environments. In Europe, ecological models have indicated that over the next few decades, changes in precipitation and temperature will reduce the area suitable for alpine species by half (Engler *et al.* 2011). As in high-latitude tundra environments, results from experimental warming have suggested that alpine plants will increase in biomass and leaf size (Walker *et al.* 1995; Suzuki and Kudo 2000), and show changes in nitrogen content of leaves (Suzuki and Kudo 2000) and phenology (Hoffmann *et al.* 2010; Aldridge *et al.* 2011).

Such changes are likely to be due to a combination of direct and indirect environmental factors (Cleland *et al.* 2006). An increase in temperature and decrease in snow cover may directly influence phenology by lengthening the growing season and allowing some species to become larger (Thórhallsdóttir 1998; Studer *et al.* 2005). Indirect effects include increased rates of soil mineralisation, which can promote vegetative growth by the release of nitrogen and phosphorus (Chapin *et al.* 1995); a decrease in snow cover that leads to more frequent and severe frosts and greater plant mortality in spring (Inouye 2008); and changes in herbivore populations where these are affected by climate (Johnson *et al.* 2010; Li *et al.* 2011). Alternatively, and in contrast to lowland ecosystems, the effects of climate change on alpine plants may be reduced by local topography (Johnson *et al.* 2011; Scherrer and Körner 2011). For example, changes in elevation and aspect over only a few metres may be sufficient to provide climatically protected habitat (Scherrer and Körner 2011).

Because species typically respond individually to warming experiments (Hoffmann *et al.* 2010; Sherry *et al.* 2011), climate change is expected to alter community composition and diversity. In predicting such responses, short-term (≤ 10 years) studies at fine scales ($\leq$ several hectares) ideally need to be combined with data based on long-term experiments or monitoring that span several decades and covers larger areas (several square kilometres; Chapin *et al.* 1995; Price and Waser 1998; Arft Walker *et al.* 1999; Luo *et al.* 2010). Results from short-term warming studies in tundra suggest a decrease in diversity, particularly as a result of a decrease in cover of mosses and lichens (Walker *et al.* 2006), whereas long-term studies have not necessarily shown such changes in diversity (Hudson and Henry 2009). Some data series from the Arctic are beginning to span more than two decades (Hill and Henry 2011), but model simulations suggest still longer studies may be required (Epstein *et al.* 2004).

In Australia, treeless alpine and subalpine landscapes occupy only 0.15% of the continent, mostly in national parks (Williams *et al.* 2006a) and, as alpine environments elsewhere in the world, they are likely to be vulnerable to the effects of climate change (Hughes 2003). Much of the research in Australian alpine ecosystems has involved long-term monitoring (Williams *et al.* 2006a), and studies that have revealed successional changes and the effects of livestock grazing and fire (Costin 1954; Carr and Turner 1959b; Wimbush and Costin 1979c; Wahren *et al.* 1994; Kirkpatrick *et al.* 2010; Camac *et al.* 2012). Since 2003, the likely effects of climate change on alpine heathland have been studied

using open-topped chambers (Jarrad *et al.* 2008), with initial results showing significant phenological and compensatory responses (Hoffmann *et al.* 2010). Here, we report on changes in vegetation composition, cover and diversity from this experiment, and interpret results in the light of changes in similar vegetation monitored since 1979. We address the following four questions: (1) In Australian alpine heathlands, how does warming affect species composition, structure, diversity and cover? (2) To what extent are changes in experimentally warmed plots within the range of variability shown by longer-term monitoring studies? (3) Which environmental variables have influenced vegetation changes? (4) To what extent are vegetation changes in Australian alpine heathland consistent with changes in other alpine and tundra environments?

Materials and methods

Study sites

In 2003, we established two sites in unburnt open-heathland at ~1750 m asl on the Bogong High Plains, Victoria, Australia (Table 1, Fig. S1, available as Supplementary material on the journal's website). Treeline is at ~1800 m and the open-heathlands just below treeline are floristically similar to those above the treeline. Henceforth, we use the term 'alpine' open-heathlands, after McDougall and Walsh (2007). Open-heathland occupies ~25% of the area of treeless vegetation of the Bogong High Plains (McDougall 1982). In contrast to most tundra and alpine vegetation elsewhere, all shrubs in the Australian Alps are evergreen. The experimental design is described in detail in Jarrad *et al.* (2008) and Hoffmann *et al.* (2010); vegetation descriptions are given in McDougall and Walsh (2007) and Costin *et al.* (2000). At each of the two sites, we set up 26 1-m² plots: 13 controls plots and 13 plots passively warmed using OTC, following protocols of the International Tundra Experiment (Molau and Molgaard 1996). The OTC were placed over plots during the snow-free period, October to June, warming ambient temperatures by ~1.0°C (Jarrad *et al.* 2008). In addition to the two ITEX sites, we used four nearby open-heathland sites (hereafter, non-ITEX sites), initially established as part of a wider monitoring program that uses sets of permanent transects at a range of locations and plant communities across the Bogong High Plains. The aim of these monitoring sites has been to assess landscape state and the effects of domestic cattle grazing (Table 1). Cattle grazed the Bogong High Plains during the summer months from the 1850s to 2003 (Carr and Turner

Table 1. Site information for the two ITEX and four non-ITEX sites
Where sampling intervals are indicated, the sampling was annual. OTC, open-topped chambers

Site	Code	Year est.	UTM (zone 55H, WGS84)	Area (ha)	No. of replicates	OTC	No. of points (cm between points)	Sampling frequency, 1979–2010
ITEX 1	1	2003	0524305, 5915582	0.72	26	13	2600 (10)	2004, 2006, 2008, 2010
ITEX 2	2	2003	0523935, 5916094	0.54	26	13	2600 (10)	2004, 2006, 2008, 2010
Cope Creek	c	1979	0525073, 5914618	1.00	12	0	600 (20)	1979–1984, 1988–1995, 1997–2010
Cope Hut	h	1979	0525676, 5915238	1.00	12	0	600 (20)	1979–1985, 1988–1995, 1997–2010
PV-N	N	1991	0525937, 5915903	0.75	10	0	500 (20)	1992–1995, 1998, 2004–2010
PV-O	O	1945	0525786, 5915905	0.10	44	0	1110 (50)	1979, 1982, 1989, 1994, 1999, 2003, 2009

1959a; Wahren *et al.* 1994), but grazing ceased in 2003 and licenses were withdrawn in 2005 from the current Alpine National Park (Williams *et al.* 2006b).

Vegetation was sampled by point quadrats (Kent 2012). At the two ITEX sites, we used a 1-m² point-frame with a grid of 100 points, 10 cm apart (Molau and Molgaard 1996). At each point, we recorded top, intermediate and bottom species, canopy height, and condition of ground surface (bare soil, attached live or dead vegetation, and loose litter; for more information see Molau and Molgaard 1996). The four non-ITEX sites were sampled along fixed transects using a 4-mm diameter steel pin and, depending on site, inserted vertically at 20- or 50-cm intervals (Table 1). All species touching the pin were recorded, along with state of the ground surface. Unlike at the ITEX sites, canopy height was not recorded (Wahren *et al.* 1994).

Climate data

At the ITEX sites, microclimate data were recorded within plots using eight data loggers per site (4 controls, 4 OTC; data are summarised in Fig. S2, available as Supplementary material on the journal's website). A 15-channel weather station established at one of the ITEX sites recorded hourly ambient temperature, relative humidity, wind speed, photosynthetically active radiation, precipitation and soil-surface temperatures. Because some sensors malfunctioned, there were gaps in the microclimate data, especially in the spring 2008–09 data and weather-station data 2007–09. In analysing the ITEX-only data, we supplemented missing data with precipitation and ambient-temperature data from a nearby Bureau of Meteorology station (Falls Creek, Hoffmann *et al.* 2010). In analysing the non-ITEX and combined datasets, we used modelled temperature data based on historical gridded datasets available from the Bureau of Meteorology and optimised for individual locations (Jeffrey *et al.* 2001). From these and the microclimate data, we derived 42 climate variables, which we reduced to a final set of 11 after screening correlation matrices to assess multicollinearity, removing incomplete data and limiting climate variables to the snow-free growing period (September to May).

Data analyses

We tested for changes in vegetation composition, diversity and cover over time at the ITEX and non-ITEX sites, as well as the direct effects of experimental warming at the ITEX sites. We used multivariate approaches, with vector fitting, to test for community-level changes in vegetation composition. We assessed the association between univariate vegetation measures of change and environmental variables by using linear modelling and hierarchical partitioning.

Given that methods and sampling intensity differed between the ITEX and non-ITEX sites (Table 1), we first compared the two datasets using species accumulation curves (SAC, Ugland *et al.* 2003; Colwell *et al.* 2004). Results based on random resampling showed that the SAC were similar across the two datasets, asymptotic, and that 15 replicates captured 85% of the species pool (Fig. S3, available as Supplementary material on the journal's website). The rate of species turnover among samples was 0.02 and similarity 0.8 (methods below), suggesting that sampling intensity was adequate to reveal within- and between-

site variation in floristics, and that analyses using the two datasets were unbiased.

Vegetation composition was analysed by non-metric multidimensional scaling (NMDS), using the Bray–Curtis dissimilarity index (ter Braak 1995; Legendre and Legendre 1998). The stress functions for the two-dimensional solutions were 0.07 and 0.15, based on the ITEX-only and combined datasets, respectively, indicating that the rank order of dissimilarities was well represented by distances in the ordinations (Legendre and Legendre 1998). Using Site as a nested factor, we assessed groups (time, warming and their interaction) by a permutation procedure to partition sums-of-squares of the Bray–Curtis dissimilarity matrix (permanova, Anderson 2001; Oksanen *et al.* 2011). Hence, the permanova model was based on 2 sites $\times$ 26 plots $\times$ 4 sampling times (total degrees of freedom = 207). We selected environmental variables based on whether they maximised the correlation between the two matrices (Clarke and Ainsworth 1993; Oksanen *et al.* 2011). The correlation between matrices was then assessed using a Mantel test (Legendre and Legendre 1998). Because frost heave can create bare ground (Williams 1990b; Williams and Costin 1994), we treated bare ground as a causal variable, although it might also reflect climate change (stressful conditions decreasing plant cover).

Univariate response variables comprised cover of select species and growth forms (shrubs, graminoids, forbs), canopy height of growth forms and species diversity. We used linear models to assess the effects of explanatory variables for the ITEX data (warming, W ; time, T ; and their interaction, $W:T$) and the non-ITEX data (time only). Broadly following the recommendations of Gelman and Hill (2007) and Zuur *et al.* (2009), we began with a simple model (for the ITEX data: Response $\sim W + T + W:T + \text{error}$). We then assessed the random component of the model (normality, homogeneity of variances, independence) by examining raw and standardised residuals. This guided our decisions about whether or not to include one or more variance covariates to deal with heterogeneity, impose a temporal or spatial auto-correlation structure on residuals, allow coefficients to vary by group(s) (i.e. random effects), or use a combination of these. At each step of this procedure, we based model selection on the Akaike information criterion (AIC). For the fixed component of the model (i.e. the experimental treatments), we started with a saturated model (i.e. all terms and interactions). We then dropped the interaction term and compared the saturated and reduced model by using the log-likelihood ratio test (Zuur *et al.* 2009). This procedure was repeated until the model failed to improve. In no instance was transformation of the data necessary. Final models were one of the following forms: linear (LM), linear mixed (LMM, also called multilevel or hierarchical models, e.g. Gelman and Hill 2007), additive (AM) or additive mixed (AMM, Bates and DebRoy 2004; Wood 2006; Pinheiro and Bates 2009). Final models by functional type are given in Analytical methods (available as Supplementary material on the journal's website) where we also provide two worked examples.

Given the importance of diversity (Benayas *et al.* 2009; Isbell *et al.* 2011) and its projected decrease in tundra and alpine environments due to climate change (Walker *et al.* 2006), we used three measures of diversity: species richness, Shannon

entropy and the Gini–Simpson index. Prior to interpretation, we converted these indices to common units of *effective number of species* (MacArthur 1965; Hill 1973), as recommended by all participants of a recent Ecology forum (Ellison 2010) on diversity partitioning. Species richness needs no conversion, whereas Shannon entropy H (calculated using natural logarithms) is converted by taking the exponential, $\exp(H)$, and the Gini–Simpson index G is converted using the formula $1/(1-G)$. Unlike the unconverted Gini–Simpson and Shannon indices, these measures are linear with respect to addition of equally common species (Jost *et al.* 2010), and because they all have the same units, they can be directly compared with each other (Jost 2006, 2007). Such direct comparison is not possible using indices such as Shannon entropy. These effective numbers of species can all be written as

$${}^qD = \left(\sum_{i=1}^s p_i^q \right)^{1/(1-q)} \quad (\text{Jost 2007}),$$

where qD = effective number of species of order q , p = proportion of Species i , and s = number of species. 0D is species richness, 1D is the exponential of Shannon entropy, and 2D is the inverse Simpson concentration, the converted Gini–Simpson index. As increasing q places greater emphasis on common species, we used $q = 0, 1, 2$ to explore how rare and abundant species differ in response to treatment and time. Gamma diversity is the product of α and β diversity for all q (i.e. ${}^qD_\gamma = {}^qD_\alpha \times {}^qD_\beta$) and, unlike additively defined β diversity, this β diversity is independent of α and measures pure differentiation. Beta diversity can thus be normalised to produce Jaccard similarity indices and their abundance-based generalisations (S), measured by

$${}^qS = (1/{}^qD_\beta - 1/n)/(1 - 1/n) \quad (\text{eqn 20 in Jost 2007})$$

and the generalisation of Harrison's rate of species turnover (T) between groups,

$${}^qT = ({}^qD_\beta - 1)/(n - 1) \quad (\text{eqn 25 in Jost 2007}),$$

where n = number of samples. These complementary measures range from zero to one, where zero indicates no similarity or turnover and one indicates the reverse. We partitioned diversity based on samples (plots), such that α diversity was diversity within samples, β diversity the change in diversity between samples and gamma diversity the total diversity among samples.

The influence of environmental variables on the cover of growth forms was assessed using hierarchical partitioning (Chevan and Sutherland 1991; Mac Nally 2002). Our primary aim was to identify important variables rather than to develop a single 'best' linear model that may have excluded influential factors (Mac Nally 2002), and to guard against the potential problem of multicollinearity, which is more likely when using multiple explanatory variables or factors (Quinn and Keough 2002).

We used the *R* software (R Development Core Team 2011) and the following *R* packages: *vegan* (Oksanen *et al.* 2011) for all ordinations, identifying environmental variables that maximised correlations between distance matrices, fitting correlation vectors, assessing *a priori* groups, and contrasting distance

matrices; *ggplot2* (Wickham 2009) for all graphics; *nlme* (Pinheiro *et al.* 2011) for linear and linear mixed effects models; *mgcv* (Wood 2011) for additive and additive mixed effects models; and *hier.part* (Walsh and Mac Nally 2008) for hierarchical partitioning.

Results

Trends in climate, 1979–2010

Over the 31-year sampling period, there was a clear decrease in annual precipitation ($F_{1,29} = 5.05$, $P = 0.032$, $R^2 = 0.12$) and a clear increase in mean spring temperature ($F_{1,29} = 6.63$, $P = 0.015$, $R^2 = 0.16$; Fig. 1). This period spanned several El Niños and years when the Indian Ocean Dipole (IOD) was positive (Meyers *et al.* 2007; Wang and Hendon 2007). El Niño is generally associated with above-average temperatures during spring and summer months, the growing period in the Australian Alps, whereas a positive IOD is linked to below-average precipitation, especially from winter to early spring (Meyers *et al.* 2007; Murphy and Timbal 2008). Periods of negative or neutral IOD and La Niña usually produce the

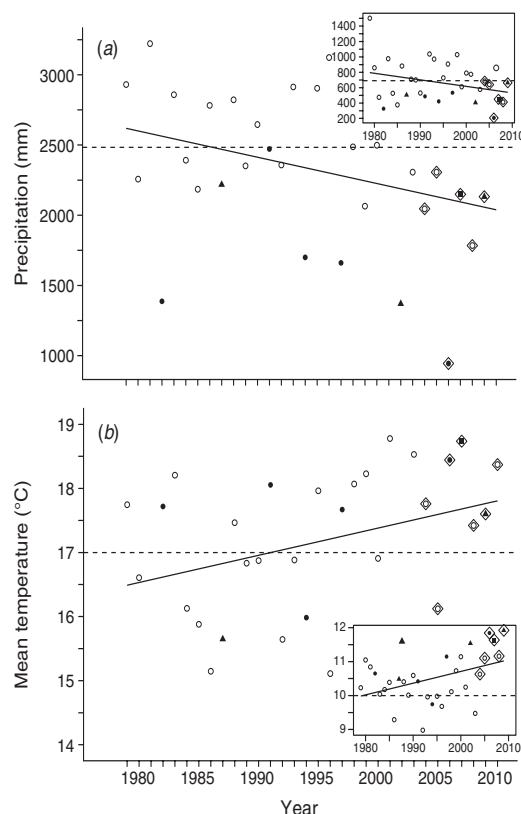


Fig. 1. Precipitation and ambient temperatures during the growing season at sampling sites during 1979–2010. (a) Annual and mean spring (inset) precipitation; (b) mean summer and spring (inset) temperatures. Symbols identify years as follows: non-El Niño and neutral or negative Indian Ocean Dipole (IOD) mode (white circle), El Niño (black triangle), positive IOD (black square), El Niño and positive IOD (black circle), and years of the ITEX experiment (white diamond). Linear model is shown by solid line, and the mean for reference period 1961–1990 is shown by dashed line.

opposite conditions. El Niño years have occurred at least 12 times during 1940–2010, six times after 1978 (Fig. 1). From 1979 to 2010, the strongest effects of El Niño and positive IOD were in 1982–1983 and 2002–2003, when there were severe droughts across south-eastern Australia. Since the late-1800s, when reliable instrumental climate data first became available, the years 1996–2009 were the driest on record in south-eastern Australia (Ummenhofer *et al.* 2009; CSIRO 2010). Using 1961–1990 as reference period (Solomon *et al.* 2007) when the mean annual precipitation was 2484 mm in the region of the study sites, precipitation was 151 mm (6%) lower in 1979–2010 and 425 mm (17%) lower in 2004–2010. The lowest annual precipitation was 944 mm in 2006, more than 60% lower than reference levels (Fig. 1a). The severity of the drought that affected south-eastern Australia after 2002–2003 is corroborated by the Palmer drought-severity index (PDSI, Dai *et al.* 2004; Ummenhofer *et al.* 2009). This index incorporates cumulative anomalies in local precipitation and moisture at the soil surface and has shown good correlation with soil moisture for the top 1 m of soil (Dai *et al.* 2004; Dai 2011, and references therein). For south-eastern Australia, PDSI declined from zero in 1995 to about –4 in 2001, the lowest level since reliable instrumental climate data have been available (Ummenhofer *et al.* 2009). Prior to 2001, the lowest PDSI occurred at the beginning of the 20th century, during one of the most severe droughts in south-eastern Australia, when PDSI reached about –1.5. By comparison, the PDSI in the drought of 1982–1983 was approximately –0.5 and returned to zero by 1985.

Mean spring temperatures in 1979–2010 and 2004–2010 were 0.4°C and 1.1°C higher, respectively, than during the reference period (10.1°C). Spring minima were 0.3°C and 0.6°C higher in 1979–2010 and 2004–2010, respectively, than the mean reference temperature of 4.6°C, whereas mean summer temperatures were 0.4°C and 0.7°C higher than the mean reference temperature of 16.9°C (Fig. 1b).

Experimental warming and vegetation change at the ITEX sites, 2004–2010

Both time ($F_{1,204}=33.96$, $P < 0.001$, $R^2=0.14$) and warming ($F_{1,204}=4.81$, $P < 0.001$, $R^2<0.10$) had significant effects on species composition and abundance, but there was no detectable interaction. Although the species composition of controls and OTC diverged with time, changes were broadly similar (Fig. 2, Table 2). Four environmental variables maximised the correlation between the species and environmental distance matrices (Fig. 2; Mantel test: $r = 0.60$, $P < 0.001$): mean spring maximum temperature ($r_{\text{cor}}=0.74$, $P < 0.001$), autumn precipitation ($r_{\text{cor}}=0.62$, $P=0.002$), minimum autumn temperature ($r_{\text{cor}}=0.54$, $P=0.007$), and to a lesser degree, bare ground ($r_{\text{cor}}=0.46$, $P=0.021$; Fig. 2, Table 2).

Cover of the main growth forms changed significantly over the 7 years ($P < 0.001$, Table 2, Table S1, available as Supplementary material on the journal's website, which provides detailed species-level data). Graminoids decreased, mainly because of declines in cover of the dominant *Poa* spp., whereas forbs and shrubs increased. Shrub cover increased at a greater rate in OTC than controls ($P < 0.001$) because of the expansion of established individuals of two common shrubs: *Asterolasia trymalioides*

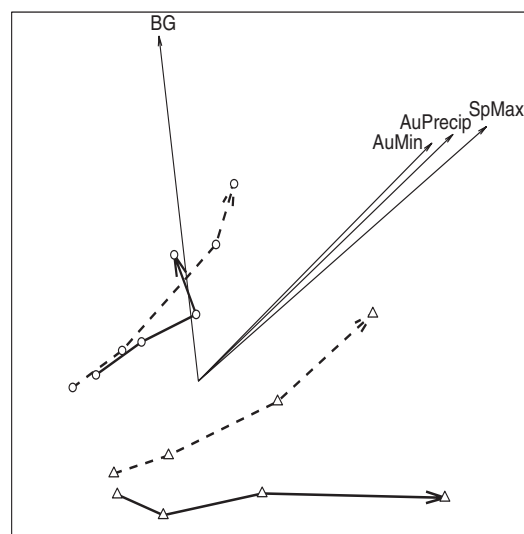


Fig. 2. Non-metric multidimensional scaling ordination of samples from ITEX Sites 1 (circle) and 2 (triangle), and vectors of environmental variables (fine arrows) that maximised the correlation between sample and environmental matrices. Length of arrows is proportional to the correlation between variables and ordination of sites. Arrows linking symbols indicate direction of time (2004–2010) for controls (solid line) and open-topped chambers (dashed line). BG, bare ground; AuMin, mean autumn minimum temperatures; AuPrecip, autumn precipitation; and SpMax, mean spring maximum temperatures.

(Rutaceae) and *Grevillea australis* (Proteaceae). Seedling recruitment was negligible (data not presented).

Changes in cover of forb species were idiosyncratic. *Leptorhynchus squamatus* (Asteraceae) remained unchanged, whereas the exotic *Acetosella vulgaris* (Polygonaceae) increased only in OTC (from <0.5% to 4%). *Microseris lanceolata* (Asteraceae) increased only in controls (from 0 to 1%) and *Scleranthus biflorus* (Caryophyllaceae) decreased in both treatments (from 3 to 1%; Table 2, also Table S1). Among the more common graminoids, the grass *Rytidosperma nudiflorum* and the sedge *Carex breviculmis* increased in cover, *Carex* more rapidly in OTC ($P < 0.001$; Table 2).

Environmental variables that influenced the cover of growth forms depended on the warming treatment. Hierarchical partitioning showed that all variables had a significant independent effect on the cover of graminoids within OTC and controls, whereas for shrubs and forbs, at least four environmental variables had significant independent effects on changes in cover (Fig. 3). The explanatory power of significant variables was mostly 10–20% and, except for the influence of bare ground on shrub cover, no variable dominated. The only variables with significant independent contributions across all growth forms were (1) mean minimum soil-surface temperatures during summer, which ranged from –6 to +16°C and –2 to +17°C in controls and OTC respectively, (2) mean ambient summer temperatures, which ranged from 0 to +25°C in both treatments, and (3) mean cover of bare ground. Of these three, only mean minimum surface temperature was significant for controls and OTC. Maximum soil-surface temperature in summer was significant for graminoids and shrubs in controls,

Table 2. Means $\pm$ 95% confidence intervals for cover, diversity and canopy height in control plots (CTL) and open-topped chambers (OTC) in 2004 and 2010 and the results from final models assessing effects of warming (W), time (T) and their interaction ($W:T$)

Model type (M) is indicated by symbols, as follows: §, linear; †, mixed; *, additive mixed. In additive mixed models, a significant interaction indicated that the shape of smoothers differed among warming treatments. Cover values for growth forms and species were based on percentage overlapping cover. Diversity was based on effective number of species, qD , where $q = [0.2]$. α , α diversity; β , β diversity. Thus α^1D is α diversity expressed as effective number of species of order 1. F, forbs; G, graminoids; n.s., non-significant ($P \geq 0.05$)

Parameter	Means $\pm$ 95% confidence intervals				M	M and results		
	2004		2010			Source of variation		
	CTL	OTC	CTL	OTC		<i>T</i>	<i>W</i>	<i>W</i> : <i>T</i>
Plant cover (%)								
Graminoids	88 $\pm$ 3.4	87 $\pm$ 2.8	64 $\pm$ 9.3	66 $\pm$ 7.1	†	<0.001	n.s.	n.s.
Forbs	42 $\pm$ 4.4	36 $\pm$ 5.7	60 $\pm$ 5.4	57 $\pm$ 3.9	§	<0.001	0.006	n.s.
Shrubs	5 $\pm$ 1.4	6 $\pm$ 1.9	11 $\pm$ 4.5	17 $\pm$ 5.0	†	<0.001	0.006	<0.001
Five most common species in 2004								
<i>Poa hiemata</i> (G)	85 $\pm$ 4.0	84 $\pm$ 3.1	56 $\pm$ 10.0	60 $\pm$ 7.8	†	<0.001	n.s.	<0.001
<i>Celmisia pugioniformis</i> (F)	21 $\pm$ 4.1	18 $\pm$ 3.7	30 $\pm$ 5.2	27 $\pm$ 4.8	†	<0.001	n.s.	<0.001
<i>Leptorhynchos squamatus</i> (F)	12 $\pm$ 4.8	9 $\pm$ 4.2	14 $\pm$ 4.8	9 $\pm$ 4.5	†	n.s.	n.s.	n.s.
<i>Carex breviculmis</i> (G)	5 $\pm$ 1.2	5 $\pm$ 1.1	6 $\pm$ 1.5	8 $\pm$ 2.2	†	n.s.	n.s.	<0.001
<i>Rytidosperma nudiflorum</i> (G)	4 $\pm$ 1.4	5 $\pm$ 1.2	6 $\pm$ 1.7	7 $\pm$ 2.5	†	n.s.	n.s.	n.s.
Ground cover (%)								
Bare soil	4 $\pm$ 1.0	4 $\pm$ 0.9	3 $\pm$ 1.8	4 $\pm$ 2.2	†	n.s.	n.s.	n.s.
Litter	14 $\pm$ 5.3	14 $\pm$ 4.3	17 $\pm$ 3.6	17 $\pm$ 3.5	†	n.s.	n.s.	n.s.
Diversity								
Richness (0D)	32 $\pm$ 1.8	36 $\pm$ 2.9	38 $\pm$ 2.2	33 $\pm$ 1.7	§	<0.001	0.006	n.s.
$\alpha(^1D)$	5 $\pm$ 0.2	5 $\pm$ 0.2	8 $\pm$ 0.3	8 $\pm$ 0.2	§	<0.001	n.s.	n.s.
$\alpha(^2D)$	3 $\pm$ 0.1	3 $\pm$ 0.1	5 $\pm$ 0.2	5 $\pm$ 0.2	§	<0.001	n.s.	n.s.
$\beta(^1D)$	1.2 $\pm$ 0.02	1.2 $\pm$ 0.02	1.4 $\pm$ 0.03	1.4 $\pm$ 0.03	§	n.s.	n.s.	n.s.
$\beta(^2D)$	1.1 $\pm$ 0.02	1.0 $\pm$ 0.02	1.2 $\pm$ 0.04	1.2 $\pm$ 0.02	§	n.s.	n.s.	n.s.
Canopy height (cm)								
Overall	7 $\pm$ 0.4	6 $\pm$ 0.4	7 $\pm$ 1.2	10 $\pm$ 2.0	*	<0.001	<0.001	<0.001
Graminoids	7 $\pm$ 0.4	6 $\pm$ 0.4	7 $\pm$ 0.5	10 $\pm$ 1.2	*	<0.001	0.001	<0.001
Forbs	6 $\pm$ 0.5	6 $\pm$ 0.6	8 $\pm$ 0.6	10 $\pm$ 1.0	*	<0.001	<0.001	<0.001
Shrubs	4 $\pm$ 1.1	4 $\pm$ 1.2	11 $\pm$ 3.0	16 $\pm$ 4.2	§	<0.001	0.001	0.001

where temperatures ranged from +1 to +69°C; it was also significant for graminoids and forbs in OTC, where temperatures ranged from +1 to +73°C.

Species diversity increased significantly over time, but there was no detectable effect of warming. Effective number of species ($^1D_\alpha$) was 60% higher in 2010 than in 2004 (Table 2). The difference in diversity between $^0D_\alpha$ (species richness) and $^2D_\alpha$ (greater emphasis on common species) remained similar over time and showed that the vegetation was dominated by five or six species (Table 2). The rate of species turnover among samples remained low (<0.01), but similarity among samples decreased over the sampling period and by the same amounts when pooled across the warming treatment, from 0.80 in 2004 to 0.69 in 2010. Over the same period, β diversity ($^1D_\beta$, the change in diversity among samples) increased from 1.2 to 1.4, suggesting that changes were in relative species abundance, rather than in composition.

Mean canopy height increased in the OTC from 6 cm in 2004 to 10 cm in 2010, but was unchanged in controls ($T: W, P < 0.001$; Table 2). Partitioning canopy height by growth form showed that in controls forbs increased in height – particularly the more common daisies, such as *Celmisia pugioniformis* (Asteraceae) and *Leptorhynchos* – as did the shrubs *Grevillea* and *Asterolasia*. The height of graminoids remained unchanged (Table 2, Fig. 4).

Trends in height varied by growth form. Graminoids and forbs had asymptotic growth curves that differed only in the first 2 years; graminoids showed little initial increase in height, resulting in a logistic curve, whereas forbs showed a rapid and early increase in height without an initial lag, resulting in a linear increase between 2004 and 2008, and no change to 2010. The shrub growth curve was linear throughout (Fig. 4). Environmental variables that most affected canopy height were similar to those influencing cover (data not shown). The independent contribution of mean minimum soil-surface temperature during summer ($\approx 20\%$) was significant across treatments and growth forms; mean minimum and maximum spring temperatures had similar explanatory power.

Vegetation change 1979–2010

Vegetation composition at the ITEX and non-ITEX sites changed significantly over the 31-year period (permanova: $F_{1,1180} = 155.7$, $P < 0.001$, $R^2 = 0.2$), particularly after 1999 (Fig. 5). This change was associated mainly with five environmental variables (Mantel test: $r = 0.27$, $P < 0.001$): decreases in bare ground ($P < 0.001$, $R^2 = 0.30$) and annual precipitation ($P < 0.001$, $R^2 = 0.30$); increases in mean minimum temperatures in spring ($P < 0.001$, $R^2 = 0.29$) and mean maximum temperatures in autumn

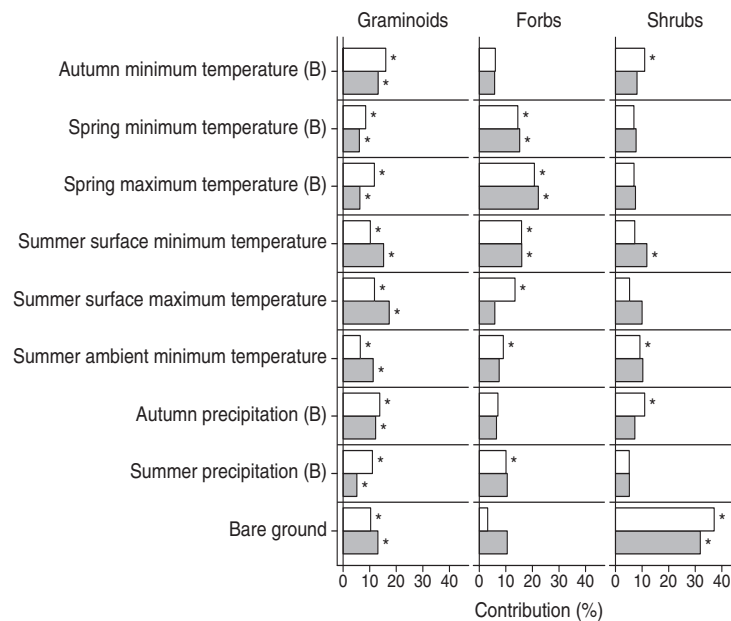


Fig. 3. Contribution (%) of environmental variables to the cover of the main growth forms for the warmed (white) and control (grey) plots of the ITEX sites. Analysis was based on hierarchical partitioning. Asterisks indicate significance ($P < 0.05$). B, data from Bureau of Meteorology.

($P = 0.011$, $R^2 = 0.10$). Bare ground decreased over time, and the rate of decline differed among sites (Fig. 6). Pooling across sites showed that between 1979 and 2005, bare ground decreased from a mean of 20 to 2.5%, then rose to 12% by 2010 (Fig. 7). The variation in composition at the non-ITEX sites between 1979 and 2010 was greater than the variation in composition within and between ITEX sites and treatments between 2004 and 2010 (Figs 5, 6).

Cover of the main growth forms at the ITEX and non-ITEX sites, although differing among sites, showed similar trends between 2004 and 2010: graminoids decreased, while forbs and shrubs increased (Fig. 6; species-level data are given in Table S2, available as Supplementary material on the journal's website). Compared with the full 31-year period, however, the changes between 2004 and 2010 were unusual, particularly those of graminoids and shrubs (Fig. 7). From 1979 to 2005, graminoid cover fluctuated between 80 and 90%, then declined sharply to 65% by 2010 (AMM: $P < 0.001$, $R^2 = 0.90$) because of declines in cover of the dominant *Poa* spp. In comparison, forb cover followed a sinusoidal response curve (AMM: $P < 0.001$, $R^2 = 0.70$), with minima of 40% in about 1985 and 2003, and maxima of 60–65% in 1995 and 2010. Most of this trend was due to variation in the cover of *Asperula gunnii* (Rubiaceae) and *Craspedia* spp. (Asteraceae; Fig. 7). *Celmisia* showed an exponential increase (AM: $P < 0.001$, $R^2 = 0.15$), from 5% in 1979 to about 28% by 2010, while *Leptorhynchos* decreased from 30% in 1979 to about 15% in 2010. Several minor forbs (<10% cover), such as *Ranunculus victoriensis*, *Brachyscome* spp. and *Erigeron bellidioides*, all fluctuated among years. The trend in shrub cover was weakest (AMM: $P = 0.04$, $R^2 = 0.11$), showing a gradual increase from 10% in 1979 to about 12% in 2005, followed by a more rapid rise to 17% by 2010 (Fig. 7). As at

the ITEX sites 2004–2010, changes in shrub cover were mainly due to increases in *Grevillea* and *Asterolasia*.

Hierarchical partitioning showed that variation in graminoid cover was largely explained by bare ground (60%) and annual precipitation (20%). In contrast, forb cover was associated with the independent effects of mean maximum autumn temperatures (30%), annual precipitation (22%) and mean maximum summer temperature (21%; Fig. S4, available as Supplementary material on the journal's website). Annual precipitation was non-significant for shrub cover, where significant variables were mean maximum summer temperature (34%), bare ground (22%) and mean maximum spring temperature (19%).

Species richness (0D) varied annually, largely because of the fluctuation in cover of minor forbs (<5% cover), and increased by 26% between 1979 ($^0D = 26$) and 2010 ($^0D = 32$). There was little change in measures of evenness (1D and 2D) and the rate of species turnover among samples was low (<0.05) throughout the monitoring period. Similar to the ITEX sites, non-ITEX sites were dominated by five or six species and changes in diversity were due mainly to fluctuations in species relative abundance, rather than appearance or disappearance of individual species.

Discussion

We first discuss results of the short-term warming experiment and then link these to observed changes at the long-term monitoring sites. This places the ITEX results within a broader context of longer-term rising temperatures and decreasing precipitation in south-eastern Australia since 1979 – our warming experiment occurred during the driest period on record (Hennessy *et al.* 2003; Timbal 2009; CSIRO 2010). We highlight the fact that species and growth forms have responded individually to warming,

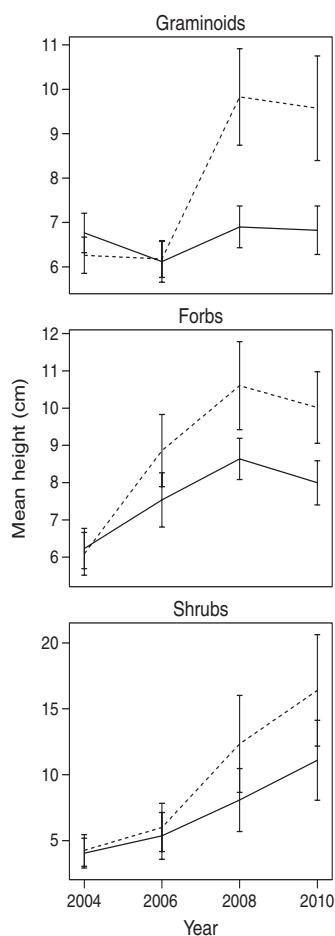


Fig. 4. Mean canopy height ($\pm 95\%$ normal confidence limits) by growth form in controls (solid line) and open-topped chambers (dashed line). Note that the height scale varies by growth form.

that long-term decline in precipitation is an important component of climate change in alpine environments, and that vegetation changes will depend on complex interactions among climate, disturbance regimes and species life history.

Effects of experimental warming on vegetation change, 2004–2010

Experimental warming clearly led to an increase in canopy height of all growth forms, an increase in shrub cover (but not in graminoids or forbs) and a small decrease in species richness. An increase in shrub cover has been a common response in many other studies assessing the effects of experimental warming in alpine and arctic landscapes (Harte and Shaw 1995; Dormann and Woodin 2002; Kudo and Suzuki 2003; Perfors *et al.* 2003; Jónsdóttir *et al.* 2005; Walker *et al.* 2006; Post *et al.* 2009; Elmendorf *et al.* 2012a, 2012b; but see Price and Waser 2000; Hollister *et al.* 2005b; Hollister and Flaherty 2010). Although our study certainly supports this finding, in the longer term, the woody–herbaceous balance in these heathlands will also depend on the interaction between disturbance regime, the effects of drought on bare ground and the dominant grasses

(*Poa* spp.), and the life-history characteristics of the dominant shrubs (Williams *et al.* 2006a).

Periods of reduced seasonal precipitation can lead to soil moisture in the top 30 cm falling below permanent wilting point (Griffin and Hoffmann 2011). As a consequence, *Poa* spp. may die, with a concomitant increase in bare ground where grass litter is disturbed. Such bare ground can persist for several decades (Costin Wimbush *et al.* 1959; Wimbush and Costin 1979a, 1979b, 1979c). In these heathlands, this process affects what happens to shrub cover. In our study, the main shrubs to respond to experimental warming were two common open-heathland species, *Grevillea* and *Asterolasia*. Unlike the majority of vascular plants in the Australian Alps, these species only regenerate from seed and their seedlings require patches of bare soil to establish (Williams 1992; Williams and Ashton 1988). Hence, if south-eastern Australia continues to become warmer and drier, with more bare ground, then an increase in shrub cover is highly likely. Such changes can alter the energy balance of the lower atmosphere (Sturm *et al.* 2001; Chapin *et al.* 2005), which may in turn lengthen the growing season, reduce the amplitude of diurnal temperatures at the soil surface, increase evapotranspiration and lower soil moisture. Similar to what appears to be happening in the Arctic and other tundra systems (Sturm *et al.* 2005; Tape *et al.* 2006; Myers-Smith *et al.* 2011; Elmendorf *et al.* 2012b), a positive feedback loop may result and lead to further expansion of shrubs at the expense of graminoids and forbs.

Consistent with several studies in arctic and alpine landscapes (Hobbie and Chapin 1998; Price and Waser 2000; Jónsdóttir *et al.* 2005; Jägerbrand *et al.* 2009; Rinnan *et al.* 2009; Hollister and Flaherty 2010), we found no detectable effect of experimental warming on the cover of graminoids. Some studies, however, have shown declines in graminoid abundance as a consequence of experimental warming. For example, Klein *et al.* (2007) in grassland and heathland on the Tibetan Plateau, Post and Pedersen (2008) in heathlands in Greenland, and Hudson and Henry (2009) in the high Arctic. Such results, and those from other studies based on meta-analysis (Walker *et al.* 2006; Elmendorf *et al.* 2012a), suggest that the effects of warming on graminoid cover depend on region and moisture regime. Experiments using warming and nutrient additions have generally resulted in a significant increase in the abundance of graminoids, although responses have varied with species and plant community (Klanderud 2008; Jägerbrand *et al.* 2009).

Although graminoids appeared unaffected by experimental warming, they decreased in cover in OTC and control plots, a trend associated most strongly with higher ambient and soil-surface temperatures, drought and higher amounts of bare ground. During the growing season, larger patches of bare ground ($>0.02 \text{ m}^2$) are subject to severe frost heave and high temperatures ($+80^\circ\text{C}$, Williams 1990a), to which graminoid seedlings are vulnerable. As mentioned above, such sites tend to be colonised by shrubs, whereas graminoids will mainly colonise areas with litter, small bare patches ($<0.02 \text{ m}^2$) or the edges of larger patches where the microclimate is less extreme (Williams 1990a, 1992). Hence, the microclimate of bare patches tends to influence what species will colonise a patch, rather than the cover of surrounding vegetation (Williams 1992).

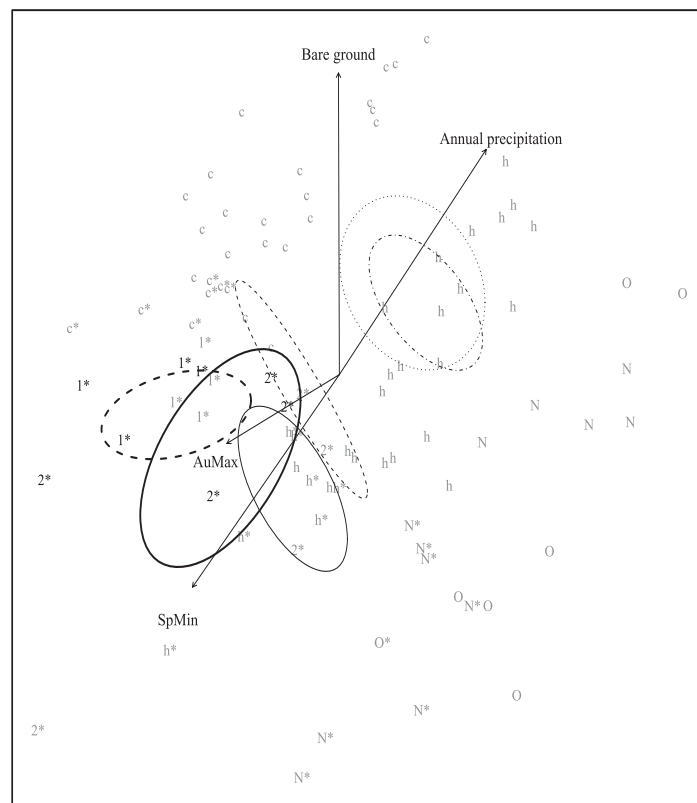


Fig. 5. Non-metric multidimensional scaling ordination of samples from the two ITEX sites (2004–2010) and four non-ITEX sites (1979–2010), with vectors of environmental variables (arrows) that maximised the correlation between the sample and environmental matrices. Length of arrows is proportional to the correlation between variables and the ordination of samples. Controls are represented by grey symbols, and open-topped chambers by bold symbols. Circles represent 95% confidence ellipses by sampling period and treatment: 1979–1989 (dotted line), 1990–1999 (dotted-dashed line), 2000–2003 (dashed line), 2004–2010 non-ITEX (solid line), 2004–2010 ITEX control plots (bold solid line) and 2004–2010 ITEX warmed plots (bold dashed line). Asterisks indicate post-2003 samples. AuMax, mean maximum temperatures in autumn; SpMin, mean minimum temperatures in spring; 1 and 2, ITEX Sites 1 and 2; c, Cope Creek; h, Cope Hut; N, PV-N; and O, PV-O.

We found no effect of warming on overall forb cover, as has been demonstrated in other warming studies (Price and Waser 2000; Jónsdóttir *et al.* 2005; Wahren *et al.* 2005; Walker *et al.* 2006; Klanderud 2008; Hudson and Henry 2009; but see Chapin *et al.* 1995; Harte and Shaw 1995; Hollister *et al.* 2005b). Species-level responses were idiosyncratic, a finding noted in several experiments involving warming (de Valpine and Harte 2001; Hollister *et al.* 2005a; Klein *et al.* 2007), nutrient addition (Jonasson 1992) and where these treatments have been used in combination (Dormann and Woodin 2002; Klanderud 2008; Jägerbrand *et al.* 2009).

The increase in canopy height in warmed plots concurred with theory (Bliss 1956; Wielgolaski 1966) and empirical findings (Stow *et al.* 2004; Tape *et al.* 2006). Although most species and growth forms were stimulated by experimental warming, species composition of the canopy and understorey remained similar throughout the experiment. These results differed from those of warming studies where expansion of shrubs has led to structural changes that have altered canopy composition from one of bryophytes and lichens to one dominated by woody species (Kudo and Suzuki 2003; Hollister *et al.* 2005b).

Warming resulted in complex changes to species diversity. Species richness (${}^0D_{\alpha}$) decreased in OTC, but there was no detectable effect on measures of evenness (1D and 2D); overall, α diversity (pooling treatment) increased. We conclude that in these alpine heathlands, the effects of experimental warming on plant diversity have been minor. This contrasts with ITEX studies in the northern hemisphere, where a pronounced decrease in diversity, especially in richness and evenness, has been a common effect of experimental warming, particularly when combined with nutrient addition (Chapin *et al.* 1995; Press *et al.* 1998; Shaver and Jonasson 1999; Klanderud and Totland 2005; Walker *et al.* 2006; but see Jónsdóttir *et al.* 2005; Hudson and Henry 2010; Elmendorf *et al.* 2012b). In the Arctic, changes in diversity have mainly been due to declines in the abundance of bryophytes and lichens (cf. Klein *et al.* 2004), functional groups that may have little effect on ecosystem function (Chapin *et al.* 2000; Thuiller 2007) and are minor components of Australia's alpine and sub-alpine flora. Further, no simple relationship appears to exist between any single measure of diversity and ecosystem function (Chapin *et al.* 2000), which means that to assess the effects of experimental warming on ecosystem function requires a combination of

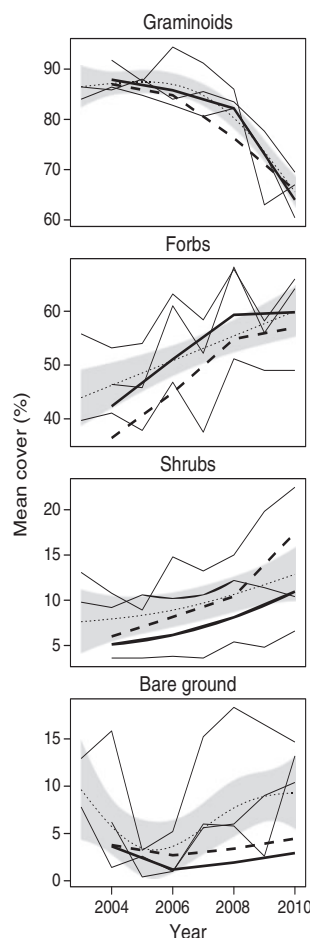


Fig. 6. Mean cover (%) of main growth forms and bare ground at the two ITEX sites and three non-ITEX sites, including additive model smoothers (dotted line) of overall cover change $\pm 95\%$ point-wise confidence bands. Controls are represented by solid lines, with the three non-ITEX sites indicated by finer lines; ITEX controls (solid line); OTC (dashed line). Cover scale varies by variable.

measures, including species evenness, composition and individual species traits (Chapin *et al.* 2000; Hooper *et al.* 2005; Klanderud and Totland 2005; Klein *et al.* 2007).

Vegetation change, 1979–2010 at ITEX and non-ITEX sites

Vegetation composition and cover of the main growth forms changed significantly at the non-ITEX sites over the 31 years, a period that included two significant droughts (1982–1983 and 1996–2009). The main changes were an increase in shrub cover, individualistic responses in the abundance of some forbs, and a sharp decline in graminoid cover over the period 2005–2010. Thus, vegetation changes at the non-ITEX and ITEX sites were broadly similar (e.g. Figs 5, 6). Most notably, trends at the ITEX sites between 2004 and 2010 were well within the range measured at the non-ITEX sites between 1979 and 2010.

Shrub cover increased at ITEX and non-ITEX sites, and the long-term data suggested a greater rate of increase after about 2003. This change in rate was likely caused by the cumulative

effects of long-term warming since 1979 and the cessation of cattle grazing in 2003. The main shrubs to increase in cover (*Grevillea* and *Asterolasia*) are palatable to cattle (van Rees 1982; van Rees and Hutson 1983) and *Asterolasia* has shown increases in cover following cessation of grazing at other sites (Wahren *et al.* 1994).

Trends in forb cover were similar at ITEX and non-ITEX sites, and both datasets showed idiosyncratic changes in cover of forbs. The long-term data revealed close links to seasonal climatic variation. For example, decreases in cover of several forbs with low cover (<10%), including *Erigeron*, *Craspedia* and *Ranunculus*, coincided with periods of well below-average seasonal precipitation, particularly in 1982, 1997 and 2006. Such individualistic responses to climatic extremes have been reported in other alpine ecosystems (de Valpine and Harte 2001) and several studies across the Australian Alps (Wimbush and Costin 1979c; Leigh *et al.* 1987; Paton 1988; Williams 1990b). These climatic fluctuations, with a duration of mostly 1–2 years, had no detectable effect on the cover of the two common forbs, *Celmisia* and *Leptorhynchus*, the former increasing and the latter decreasing in cover over the 31 years. Although the short-term ITEX data failed to predict the decrease in *Leptorhynchus* cover, such a response was expected with the expansion of the more robust *Celmisia* (Wahren *et al.* 1994). The long-term data also showed a clearer association between the trend in cover of two forbs (*Celmisia* and *Craspedia*) and both an increase in temperature and removal of grazing. These forbs are highly palatable to cattle (van Rees 1982), a relationship that was clearest in *Craspedia* spp. whose cover increased sharply after grazing ceased in 2003 (Fig. 7). Although patterns were less clear for *Celmisia* cover, its greater rate of increase after about 2000 may have been a response to reduced competition from *Poa* spp. and release from grazing in 2003.

The 25% drop in graminoid cover (mainly *Poa* spp.) between 2005 and 2010 was the largest reduction in *Poa* cover over the 31-year period. This decline was associated most with a decrease in annual precipitation and increase in bare ground, a relationship that was stronger in the non-ITEX than the ITEX data (Figs 2, 3; Fig. S4, available as Supplementary material on the journal's website). Ambient spring and summer temperatures during 2005–2010 were approximately 1°C higher and annual precipitation 60% lower than during the 1961–1990 reference period. Although drought is known to affect *Poa* (e.g. the 1967–1968 drought in the Kosciuszko National Park, Wimbush and Costin 1979c), its cover did not decline following the 1982–1983 drought – a result supported by the findings of Leigh *et al.* (1987) – or with the onset of the drought that began in 1996. This suggests that the decrease in *Poa* cover between 2005 and 2010 may have been due to the cumulative effects of drought and that five consecutive years of water deficit (e.g. PDSI < −0.5) could be necessary for *Poa* cover to decline significantly. Local mortality in *Poa* was linked to repeated periods of low soil moisture in 2007 (Griffin and Hoffmann 2011) and severe frost in 1982–1983 (Williams 1990b).

Vertebrate grazing may also affect the cover of graminoids in tundra environments. For example, Post and Pedersen (2008) and Klein *et al.* (2007, 2008) found that excluding ungulate grazers led to a decrease in graminoids. Although cessation of cattle grazing coincided with declining graminoid cover on the Bogong

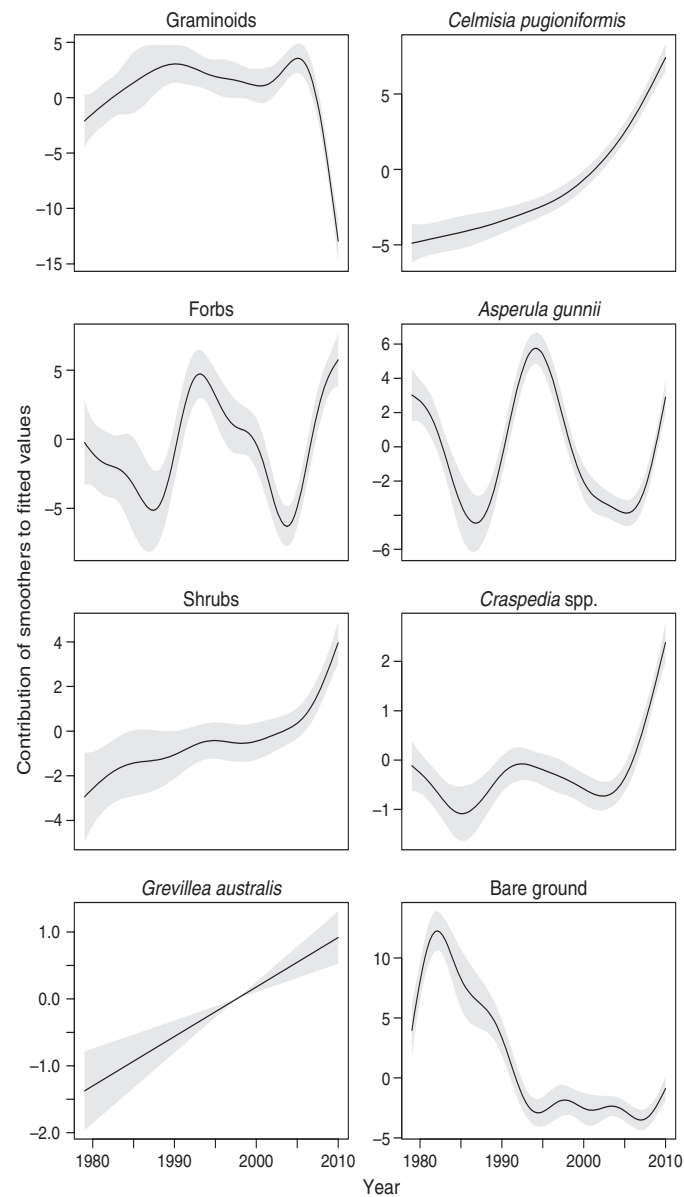


Fig. 7. Estimated smoothing curves $\pm 95\%$ point-wise confidence bands for optimal additive mixed models of the main growth forms, three common forbs (*Celmisia pugioniformis*, *Aperula gunnii* and *Craspedia* spp.), a common shrub (*Grevillea australis*) and bare ground. Data are based on cover values from control plots of the two ITEX sites (2004–2010) and four non-ITEX sites (1979–2010).

High Plains, we suggest that this trend was, as argued above, due to long-term decrease in precipitation. This conclusion is further supported by previous studies, which have shown that when cattle are excluded from these landscapes, the cover of *Poa* increases or remains unchanged, whereas the amount of bare ground decreases (Carr and Turner 1959b; Wimbush and Costin 1979a, 1979b, 1979c; Wahren *et al.* 1994). Hence, in line with expectations, the decline in cover of *Poa* between 2005 and 2010 was associated with a clear increase in cover of bare ground.

Changes in plant diversity were minor – a small increase in species richness and no change in measures of evenness – and similar to that recorded at the ITEX sites. These results suggest that in these heathlands, the long-term effects of warming on diversity may be similar to those predicted for the Arctic – an initial decline as local species disappear, followed by a gradual increase with the immigration of new species (Yurtsev 1997; Hollister *et al.* 2005b). At the non-ITEX sites, the species that appeared were almost all forbs, locally common and able to regenerate vegetatively, changes that were likely due to a

combination of individualistic responses to short-term climatic extremes and long-term warming.

Synthesis and conclusions

Results from the warming experiment and long-term monitoring sites suggested that vegetation changes in open-heathlands over the past 31 years have been small rather than transformative. Shrub cover increased, graminoid cover declined most likely because of drought, trends in forb cover varied with species, and changes in vascular plant diversity were minor. These broad responses were similar to what has been documented for other alpine and arctic systems as a consequence of rising temperatures (e.g. Elmendorf *et al.* 2012a). We also stress that in alpine vegetation, long-term vegetation change is likely to depend on drought as much as on rising temperatures.

Our results also suggested an inherent inertia or resilience (*sensu* Allen *et al.* 2011; the amount disturbance or disruption a system can recover from without transforming to another system) to climatic changes that had occurred up until 2010. In these alpine heathlands, such resilience has two components: first, individualistic responses within growth forms (e.g. forbs); and second, compensatory responses between growth forms (shrub–grass; forb–grass) to interactions between disturbance and climate change. The extent of warming over the past 31 years ($\approx 1^\circ\text{C}$) has been about the same as projected for next 20–50 years (Hughes 2003) and similar to that induced in the 7-year warming experiment. Nevertheless, recent vegetation changes, such as the rapid decline in *Poa*, sharp increase in variance of graminoid cover and increase in the amount of bare ground since 2005, all suggest that these heathlands may be altering in ways more fundamental and long-lasting than previously predicted (Wahren *et al.* 1994; Williams and Wahren 2005). Alternatively, if *Poa* spp. regenerate over the coming years, recent trends may provide an insight into the sort of community changes that can be expected with continued climate change.

Much will depend on the degree and rate of future climatic changes, the amount of bare ground resulting from such changes, and what species colonise bare ground. Further increase in the amount of bare ground and decrease in cover of *Poa* favour continued expansion of shrubs, a process contingent on the shrub species present. If the current dominant shrubs in these heathlands remain *Grevillea* and *Asterolasia*, then open-heathland is likely to continue expanding. If instead, taller, longer-lived, re-sprouting shrubs, such as *Prostanthera cuneata* and *Orites lancifolia*, colonise, then closed-heathland may develop, resulting in the broader landscape becoming substantially shrubbier, as has been occurring in parts of the Arctic (Tape *et al.* 2006; Myers-Smith *et al.* 2011). Alternatively, the forecast reduction in winter snow-pack in the Australian Alps (Hennessy *et al.* 2003) may favour forbs, because in this landscape most forbs able to colonise bare ground are hemicryptophytes and therefore less prone to frost damage than are shrubs, particularly early in the growing season (Williams 1990b; Körner 1999).

In assessing ecosystem state and predicting likely effects of a warming climate on alpine and tundra landscapes, our results have demonstrated the merit of hierarchical partitioning to evaluate the influence of multiple, potentially correlated,

environmental factors. The results also showed the value of an index such as PDSI and the importance of including, where possible, the interacting influences of short-term (1–2 years) seasonal climatic extremes and longer-term (decadal) fluctuations or trends in climate. For example, compositional changes at the ITEX sites were correlated, albeit weakly, with increasing autumn precipitation, a relationship that, in the longer term, was replaced by a strong correlation with decreasing annual precipitation (Figs 2, 5). Given the species-specific responses to such short- and long-term influences, our results clearly support the conclusions of several other studies (de Valpine and Harte 2001; Dormann and Woodin 2002; Hollister *et al.* 2005a; Klanderud 2008) – when assessing the effects of climate change on tundra vegetation, broad growth forms need to be used with caution. They can, nevertheless, be valuable where dominant species strongly influence community structure, composition or ecosystem processes, such as *Poa* in these heathlands.

Results also showed the benefit – in our case, the necessity – of interpreting trends from short-term field experiments (≤ 10 years) in the context of long-term changes. The long-term climate data revealed how unusual the climate had been during our warming experiment, leading to drying effects clearly captured by the PDSI. The long-term vegetation data was essential to reveal the unusual responses of *Poa* spp. and other species. Although the warming experiment linked vegetation changes to warming, we endorse Luo *et al.* (2010) in arguing for long-term, broad-scale, global-change studies of sufficient duration to include a wide range of climate variability that leads to novel or ‘surprising’ responses, especially to those likely to have significant effects on ecosystems. Hence, in any attempts to manage Australia’s rare and restricted alpine ecosystems in the face of climate change, continued monitoring of established sites is crucial.

Supplementary material

Supplementary information provides four figures and two worked examples that explain how the linear models were developed. The four figures show (1) site locations, (2) plot temperatures at ITEX sites (2004–2010), (3) species accumulation covers, and (4) results from hierarchical partitioning that indicate the influence of environmental variables on cover of growth forms based on ITEX and non-ITEX data.

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FIRE REGIMES AND BIODIVERSITY IN VICTORIA'S ALPINE ECOSYSTEMS

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Landscape-scale fires occur in Australian alpine ecosystems once or twice per century, primarily when ignition, regional drought and severe fire weather coincide. When alpine vegetation does burn, there is considerable variation in landscape flammability and fire severity. Regeneration following extensive fires of 2003 and 2006-07 across the Bogong High Plains is occurring in all plant communities (heathlands, grasslands, herbfields and wetlands). In heathland and grassland, vegetation composition has converged towards the long-unburnt state (> 50 years) eight years post fire. There was little effect of variation in fire severity on patterns of regeneration in heathland. In burnt wetlands, *Sphagnum cristatum* and other dominant species are regenerating; the cover of obligate seeding ericaceous shrubs two years post-fire was positively related to the cover of *Sphagnum*. The endangered mammal *Burramys parvus* is also capable of persisting in the alpine landscape after individual large, landscape fires. We conclude that there is no scientific evidence that these fires necessarily had 'disastrous' biodiversity consequences. After extensive landscape fires, the primary management objective should be to allow burnt alpine ecosystems to regenerate with minimal subsequent disturbance. Monitoring ecological change in the coming century will be essential for effective management of both fire and biodiversity in alpine ecosystems in Victoria and elsewhere in Australia.

Key words: alpine vegetation, grassland, heathland, fire severity, species diversity, conservation.

AUSTRALIAN alpine ecosystems are subject to recurrent fire. Alpine vegetation (hereafter we include the treeless vegetation above treeline, and floristically similar treeless vegetation at or below treeline in the high subalpine zone, in our definition of 'alpine'; Williams et al. 2006a) typically burns at landscape scales once or twice per century, under circumstances when ignition and severe fire weather coincide with widespread regional drought. Under these conditions, fire spreads to the treeless, alpine and subalpine vegetation via the foothill and montane forests and subalpine woodlands (Williams et al. 2008). Such fires occurred in the alpine regions of Victoria and New South Wales in 2003 and 2006-07. The 2003 fires burnt over 1 million hectares, the vast majority being forests and woodlands. About 10,000 ha of treeless, alpine vegetation was burnt, including about half of the Bogong High Plains (Williams et al. 2006b). The fires of 2003 and 2006-07 in north-eastern Victoria were the largest since 1939, when

much of the Victorian Alps burnt (Carr and Turner 1959). There have been other substantial fires in Victoria's treeless sub-alpine vegetation since 1939, such as on Wellington and Holmes Plains in 1998 (Wahren et al. 2001), and on Mt Buffalo, parts of which were burnt in 1972, 1984, 2003 and 2006-07 (Coates and Walsh 2010).

Much of the alpine and treeless subalpine vegetation burnt by the large fires of 1998, 2003 and 2006-07 occurred in national parks within the Victorian Alps. Well-informed fire management within national parks is essential to achieve nature conservation goals, but is controversial, with competing views concerning the ecology and management of large fires in south-eastern Australia. One view (e.g. House of Representatives 2003; Adams and Attiwill 2011) is that (a) fires such as those that occurred in 2003 were unnatural, and are (b) the resulted of inadequate fuel management in the surrounding forests, and are (c) a major threat to biodiversity and other natural

values within national parks, because of their size and intensity. On the other hand, there is evidence that large, intense fires are a natural part of the historical fire regimes of the temperate landscapes of south-eastern Australia, and the associated biota are resilient to individual large, intense fires (Bradstock 2008). According to this view, large individual fires, because they are a part of the historical fire regime, may not necessarily threaten conservation values in these landscapes. Evidence from the alpine and high subalpine ecosystems of SE Australia suggests that large fires, such as the 2003 fires, are part of the historical alpine fire regime (Williams et al. 2006b; 2008). Furthermore, regeneration following such fires, across a broad suite of taxonomic groups, can be both rapid and substantial (Wahren et al. 2001; Walsh and McDougall 2005; Williams et al. 2008; Camac et al. 2012).

Driscoll et al. (2010) highlighted key questions in relation to fire regimes (*sensu* Gill 1975) and their management for biodiversity conservation. They stressed the importance of natural experiments (e.g. studying major fires), studying species-level responses to variation in fundamental fire regime components (e.g. time since fire, intervals between fires, fire intensity) and the value of long-term monitoring. Victoria's alpine areas thus present a valuable opportunity to further this understanding, because (a) variation in occurrence and severity of fire across a diverse array of plant communities provides a robust natural experiment, (b) knowledge about species-responses to time since fire and fire severity is increasing and (c) the alpine vegetation of Victoria has been monitored systematically since the 1980s.

In this paper we explore the effects of recent, extensive fires on the major treeless plant communities (grasslands, heathlands and wetlands) from the alpine zone and high subalpine zone in the Victorian Alps. We draw on long-term monitoring data to make inferences about the effects of large fires on variation over time in key ecological attributes such as vegetation cover, species diversity and populations of species. We also present data on the ecological effects of variation in fire severity (a proxy for fire intensity; Keeley 2009). We also present data on post-fire recovery of an endangered small mammal, the alpine endemic Mountain Pygmy-possum (*Burramys parvus*).

DATA SOURCES, SELECTION AND ANALYSES

Victoria's alpine and treeless subalpine vegetation is a mosaic of shrub- and grass/herb-dominated communities. The major structural formations are closed- and open heathlands, herbfields, tussock grasslands and wetlands. We present data from monitoring sites in closed heathland, open heathland, grassland and wetlands, which collectively account for >95% of the treeless vegetation in alpine and high subalpine landscapes. Detailed community descriptions are found in Williams et al. (2006b). We use data from long-term, permanent monitoring sites established over the past 25 years across the Victorian alpine region (Papst et al. 1999). 'Burnt' monitoring sites were established within 2-4 weeks at sites affected by the fires of 1998, 2003 and/or 2006-07. Some 'unburnt' sites were established at the time of these extensive fires; others were established in the 1970s, 1980s and 1990s, as part of a wider as part of a wider program of long-term ecological monitoring. We present vegetation data from the 2003 and 2007 fires on the Bogong High Plains and the 2007 fires on Bennison-Moroka-Snowy Range. Sites were monitored at ca. 1-5 year intervals. For the purposes of this paper 'unburnt' refers to sites that were not burnt by any of these fires, and which have been unburnt since at least 1939. The data on *Burramys parvus* come from population monitoring sites across the Bogong High Plains-Mt Hotham region (Heinze 2010) established in the 1990s. Logistical constraints precluded assessment of all sites in all years. Nevertheless, our data are from a representative subset of monitoring sites from which we can derive robust measures of pre-fire state for a range of taxa, and change in state in those variables from immediately after the fire until 8 years post-fire.

Plant community data from heathlands and grasslands were collected from 11 monitoring sites, based on point quadrats along multiple (usually 10) 10m-long transects per site. Attributes collected include cover of vascular plant species, species diversity and composition, and the amount of bare ground (Wahren et al. 1994; 2001). Following the 2003 fires on the Bogong High Plains, fire severity in open and closed heathland was determined using 'minimum twig diameter', a proxy measure for fire severity (Williams et al. 2006b). In 2008, cover of vascular plant species, species diversity (measured as both richness and evenness; Jost et al. 2010) and

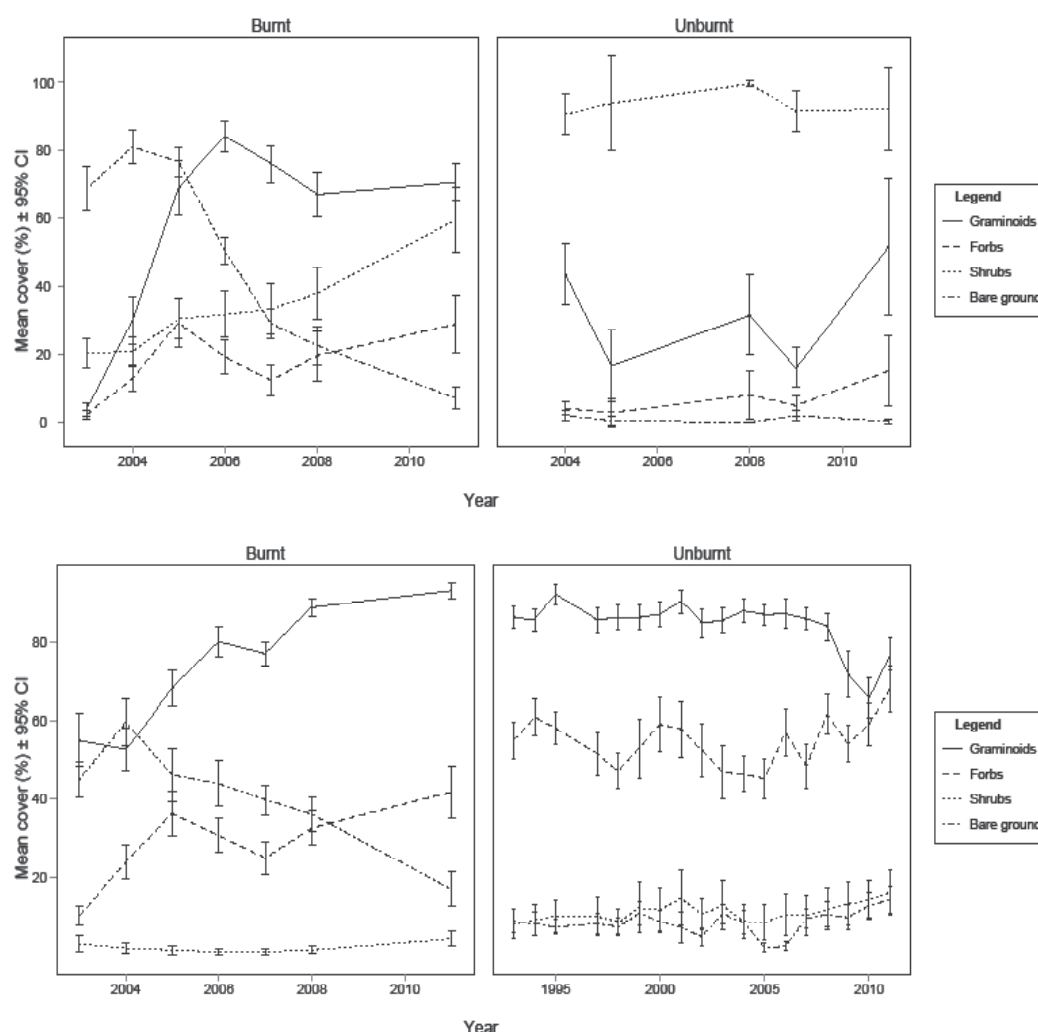


Fig. 1. Change in cover of major variables (graminoids, shrub, forbs, bare ground; mean + 95% CIs) in heathland (a, b) and grassland (c, d) on the Bogong High Plains following the 2003 fires. Data are for burnt (a, c) and unburnt (b, d) sample sites. Cover data collected from point quadrats along permanent transects according to methods in Warren et al. (1994; 2001).

species composition were assessed using five 6 m² plots along a 50 m transect at each of 40 sites (10 unburnt, 30 burnt to varying severity) per community; cover was estimated using standard Braun Blanquet methods (Camac et al. 2012). Data on wetlands were collected from 17 sites, based on contiguous 0.25m² quadrats along permanent 30m transects in each wetland. Primary attributes were the cover of dominant taxa: *Sphagnum cristatum*, ericaceous and myrtaceous shrubs, forbs and graminoids (Shannon 2012). Data on *Burramys* were based on 'capture-mark-recapture' protocols detailed in Heinze (2010). These techniques detect changes in populations over time, and determine survival, mortality and the structure of local populations, for males and females.

Statistical analyses were based on 95% confidence intervals, where the transect or trapping grid was the experimental unit. Where 95% confidence intervals of sample means did not overlap we inferred a significant difference (Cumming and Finch 2005).

RESULTS

Post-fire regeneration in heathland and grassland

The cover of the dominant life forms (shrubs, graminoids and forbs) and the amount of bare ground in heathland and grassland following the 2003 fires

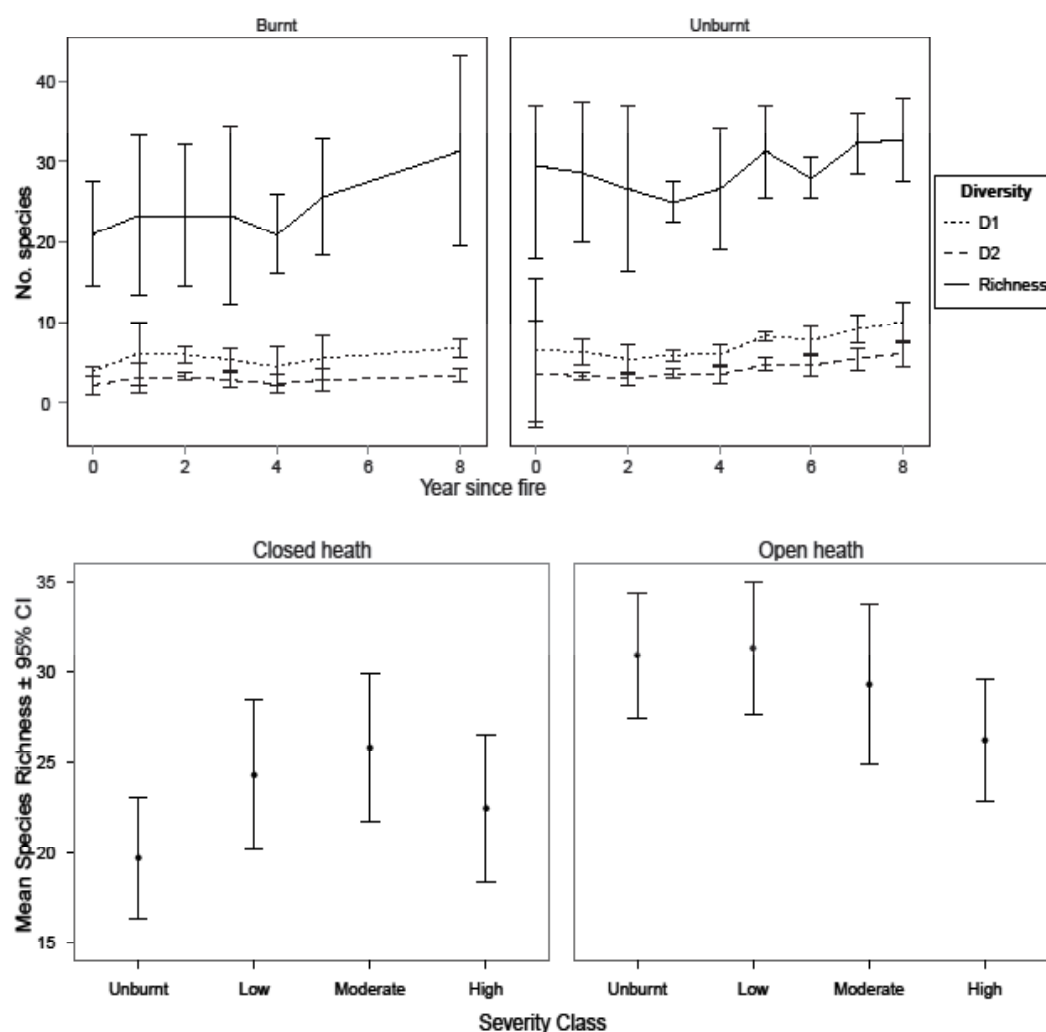


Fig. 2. Plant species diversity (mean + 95% CIs) as a function of time since the 2003 fires in grassland (a,b) and as a function of fire severity in heathland (c, closed heathland; d, open heathland) five years after the 2003 fires. Diversity measures in (a,b) are plant species richness ('Richness') and two measures of evenness (D1, D2; see Jost et al. 2010) per 10m transect. Data from Bogong High Plains. (Note that x-axis of both (a) and (b) represents time since the 2003 fires). In Fig 2c,d fire severity classes (unburnt, low severity, moderate severity and high severity) were measured in permanent reference sites in 2003-04 (Williams et al. 2006a) and diversity (plant species richness per 50 m transect) was recorded in December 2007 - January 2008 (Fig. 2c, d redrawn from data in Camac et al. 2012).

on the Bogong High are shown in Fig. 1. In heathland, regeneration commenced within days of burning. The cover of graminoids (mainly snowgrass, *Poa* spp) and forbs increased relative to that of the unburnt sites, especially in the initial 2-3 years post-fire. By 2011, shrub cover was about 60% of its pre-fire level of ca. 85-95%. Despite fire causing substantial increases in the amount of bare ground (from <5% to >80%), bare ground was about 10% by 2011 (Figs 1a,b).

In grassland (Fig. 2 c,d), post-fire regeneration was rapid for the snow grasses and forbs; the cover of snowgrass had returned to pre-fire levels of cover

(ca. 90%) within 5 years. On unburnt sites, the cover of snowgrass declined between 2005 and 2011, as a consequence of drought – the driest period on record in south-eastern Australia (CSIRO, 2010; Timbal, 2009; Ummenhofer, 2009). Bare ground was initially 40-60% in the first two years post fire on burnt sites, declining to ca. 20% in 2011. On unburnt sites, the cover of bare ground was ca. 5-10% over most of the monitoring period, increasing to 15% post-2005, as a consequence of the drought-induced decline in the cover of snowgrass. Although there were some significant differences between burnt and unburnt

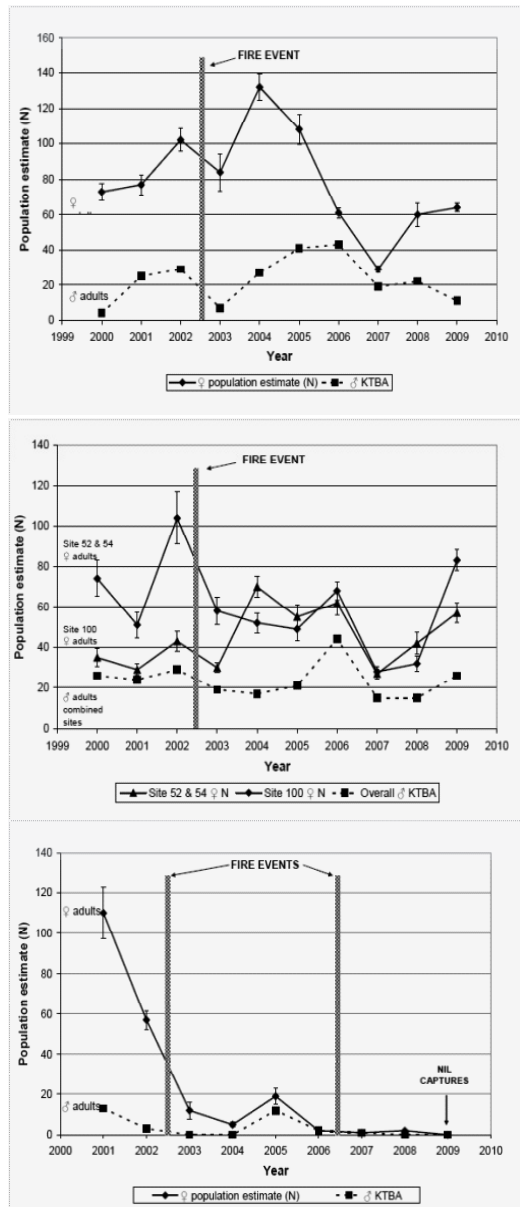


Fig. 3. Trends in the numbers of *Burramys parvus* males and females at three sites in Victoria, 1999/2000-2009. Adult female population (solid line) and 'known to be alive' male population. (a) Mt Loch; (b) Mt Higginbotham East and West (c) Mt McKay. (Source: Heinze 2010).

vegetation in the cover of some life forms in some years, after eight years the cover of shrubs, grasses and forbs in burnt grassland was similar to that of unburnt grassland. Bare ground, however, was significantly higher at burnt sites than unburnt sites, 8 years post-fire.

Plant diversity in burnt grasslands (both richness and evenness) was not significantly different from

that in unburnt grasslands over the monitoring period. Average total species richness per transect in burnt grassland two months post-fire was ca. 20, increasing to ca. 30 in 2010, compared with ca. 30 in unburnt grassland over the same period (Fig 2 a,b). There was no effect of variation in fire severity on plant diversity in heathlands on the Bogong High Plains (Fig. 2 c,d). Ordination of the sites over time also demonstrated convergence in floristic composition of burnt grassland and heathland towards the respective unburnt state within 3-5 years (Camac et al. 2012).

Post-fire regeneration in wetlands

The average cover of the major wetland species in 2006 (pooling sites) prior to the fires of 2006-07, and in 2007 and 2009 is given in Table 1. Sites are divided into 'bog' sites, where the pre-fire cover of the dominant mound-building moss, *Sphagnum cristatum*, is relatively high (>60%) and 'wet heathland' sites, where the pre-fire cover of *S. cristatum* is relatively low (<25%) but other typical wetland species, especially myrtaceous shrubs, are common. Both vegetation types are underlain by peat soils. Several post-fire responses are apparent. First, *Sphagnum* can regenerate post-fire; *Sphagnum* had reached ca. 80% and 70% of its pre-fire cover in bogs and wet heaths respectively. Second, the cover of the dominant graminoids, *Empodisma minus* and *Carex* spp., may increase in the short-term, post-fire. Third, the major ericaceous shrubs, *Richea continentis* and *Epacris* spp. and the major myrtaceous shrub *Baeckea gunniana*, were also regenerating. Importantly, regeneration of the ericaceous shrubs, which are obligate seeders, was substantially higher in the bogs, where the cover of *Sphagnum* is higher, than in the wet heaths. The cover of ericaceous shrubs pre-fire was similar in both bog and wet heath sites (ca. 33%) but was ca. 25% in the bogs in 2009, compared with ca. 7% in the wet heaths.

Post-fire trends in *Burramys parvus* populations

Burramys persisted in areas that were burnt in the 2003 fires at both Mt Loch and Mt Higginbotham, despite substantial population fluctuations (Fig. 3a,b). The situation was similar at other long-term monitoring sites such as Timms Lookout. However, the situation at Mt McKay was different (Fig. 3c). Following the 2003 fires, there was limited recovery

Table 1. Mean ($\pm$ SD) cover values of six dominant and/or common taxa in the subalpine wetlands of the Bennison-Moroka-Snowy Range region of Victoria. The wetlands were burnt in January 2007. Data were collected in April 2006; April 2007 (3 months post-fire) and April 2009. (Source: Shannon 2012).

Species	Bog			Wet heath		
	2006	2007	2009	2006	2007	2009
<i>Sphagnum cristatum</i>	62.8 ($\pm$ 9.0)	42.1 ($\pm$ 6.6)	51.4 ($\pm$ 5.7)	23.3 ($\pm$ 5.0)	7.9 ($\pm$ 3.0)	15.5 ($\pm$ 4.1)
<i>Empodisma minus</i>	17.3 ($\pm$ 7.1)	6.3 ($\pm$ 2.3)	22.9 ($\pm$ 8.7)	12.4 ($\pm$ 5.1)	0.8 ($\pm$ 0.2)	9.2 ($\pm$ 2.8)
<i>Carex gaudichaudiana</i>	0.8 ($\pm$ 0.1)	1.4 ($\pm$ 0.3)	2.7 ($\pm$ 0.3)	2.9 ($\pm$ 1.9)	3.8 ($\pm$ 1.7)	7.2 ($\pm$ 3.4)
<i>Baeckea gunniana</i>	9.6 ($\pm$ 2.8)	2.9 ($\pm$ 1.8)	5.4 ($\pm$ 1.7)	12.3 ($\pm$ 2.0)	1.5 ($\pm$ 0.3)	5.9 ($\pm$ 1.7)
<i>Epacris</i> spp.	18.0 ($\pm$ 3.0)	8.0 ($\pm$ 3.9)	15.7 ($\pm$ 6.2)	12.8 ($\pm$ 2.4)	1.1 ($\pm$ 0.4)	4.4 ($\pm$ 0.8)
<i>Richea continentis</i>	15.4 ($\pm$ 8.5)	5.9 ($\pm$ 4.2)	8.6 ($\pm$ 5.2)	20.9 ($\pm$ 9.7)	2.1 ($\pm$ 1.6)	2.9 ($\pm$ 1.9)

of the numbers of both males and females. The rate of recovery at Mt McKay was slower than at other sites such as Mt Loch and Mt Higginbotham, because the habitat at the McKay site is poorer than that at the other sites (closed heath with no nearby boulderfields; Heinze 2010). At Mt McKay the population was further affected by fires in 2007, which burnt heathland habitat that was also burnt in 2003. No animals were recorded at the McKay site in 2008 and 2009.

DISCUSSION

Vegetation

Alpine vegetation in Victoria has a strong capacity to regenerate after fire, including high severity fire. Our data show that there is clear evidence of convergence in floristic composition, diversity and some measures of ecosystem structure towards the long unburnt state (i.e. unburnt for > 50 years) within 5-10 years. This is especially apparent in the grasslands and heathlands, but may also occur in wetlands, especially where pre-fire cover of *Sphagnum* is high (>50%). This rapid recovery of diversity and composition occurs because most species of the alpine vascular flora can resprout from subterranean organs such as rhizomes, rootstocks and tubers, with many species also able to regenerate by seed (Williams et al. 2006a). Regeneration of the dominant life forms in heathland appears to be largely unaffected by variation in fire severity (Camac et al. 2012). Although diversity and composition show convergence to the unburnt state in 5-8 years in grasslands and heathlands, bare ground and shrub cover are likely to take more than a decade to return to unburnt/pre-fire levels. Importantly, we found no

evidence that any species failed to regenerate after fire. Our data are consistent with other studies of post-fire regeneration of alpine heathland and grassland on mainland Australia (Wahren et al. 2001; Walsh and McDougall 2005; Williams et al. 2008).

The data from wetlands indicate clearly the capacity of *Sphagnum cristatum* and other dominant species to regenerate post-fire, despite some wetlands having been moderately-severely burnt and that *Sphagnum* is relatively slow growing (Shannon 2012). Whether post-fire regeneration in *Sphagnum* is from shoots that have survived at or near the surface of the peat column, or from deeper-seated shoots, is unclear. However, *Sphagnum* spp in the UK can regenerate from decaying material 30 cm below the surface of the peat (Clymo and Duckert 1986). *Sphagnum* is an important mound-building species in Australian alpine wetlands (Williams et al. 2006a; Shannon 2012) and other species of *Sphagnum* are well-known as mound-builders in the northern hemisphere (Clymo and Hayward 1982). Our data also highlight the importance of *Sphagnum* as an ecological engineer (sensu Jones et al. 1994) in Australian alpine environments – the cover of obligate seeding ericaceous shrubs two years post-fire was significantly higher in bogs, with a relatively high cover of *Sphagnum*, than in wet heaths with relatively low *Sphagnum* cover.

Burramys parvus

Burramys parvus is a small, rare mammal that only occurs in restricted habitat in the Australian Alps (Mansergh and Broom 1994). On this basis, it may be expected to be highly vulnerable across its range to large severe fires. However, monitoring of *Burramys* populations before and after the 2003 and

2006 bushfires on the Bogong High Plains has shown that populations can persist in the landscape despite widespread fire. This is potentially because its core habitat (boulder fields) offers refuge from fire, and a major food source over summer, the Bogong Moth (*Agrotis infusa*), is migratory, aestivates among rocks in large numbers over summer, and is thus essentially independent of fire in the alpine zone. Moreover, because the fires on the Bogong High Plains in 2003 and 2006 were patchy (Williams et al. 2006b) unburnt patches of heathland could also have served as refugia. Nevertheless, numbers plummeted at Mt McKay after both the 2003 fires and 2006 fires extensively burnt habitat, such that no *Burramys* were trapped in 2009. The habitat at Mt McKay was heathland as opposed to boulderfields, hence it is not surprising that the loss of this vegetation cover coincided with a dramatic decline in *Burramys* numbers at this site. The *Burramys* population at Mt McKay may now be functionally extinct. Thus, although *Burramys* can persist post fire, it is at risk from subsequent disturbances (e.g. two fires < 5 years apart in closed heathlands). It is also at risk, post-fire, from predation by foxes, and drought (Green and Sanecki 2006).

Management implications

The primary management implication of our findings is that the alpine and high subalpine treeless vegetation of Victoria is resilient to the effects of occasional, large scale fires. This is clearly the case with respect to plant species composition and diversity in grasslands and heathlands, which together account for about 90% of the area of treeless vegetation. Importantly, our data also show that species that may be hypothesised to be vulnerable to large, severe fires – slow-growing plants such as *Sphagnum cristatum*, and rare and endangered mammals, such as *Burramys parvus* – can persist in the landscape following such fires. Although large fires undoubtedly have widespread and immediate effects on alpine landscapes, and may result in dramatic reductions in vegetation cover and faunal population numbers, we found no evidence, across a range of taxa, that the large, severe fires we studied were of themselves ‘ecologically disastrous’. Indeed, other ecological evidence suggests that this is the case for the fire regimes and associated biota of the widespread forests in the lowlands of south-eastern Australia in general (Bradstock 2008).

One major management concern in burnt grasslands and heathlands is the level of bare ground, which remained well above unburnt/pre-fire levels even 8 years post-fire. Minimising the amount of bare ground in alpine ecosystems is a primary objective for soil, water and nature conservation (Williams et al. 2006a). Thus, alpine vegetation that has been burnt needs to be protected from other, subsequent disturbances (prescribed fire, trampling, grazing by domestic livestock and feral animals; weed invasion) while it is regenerating, so that the rate of development of native vegetation cover over bare ground is maximised. Effective control of predators and exotic plants in the post-fire environment is very important. Although exhibiting broad resilience to large fires, *Burramys* is vulnerable to predation by foxes in the post-fire environment (Green and Sanecki 2006).

Management of fire regimes in alpine ecosystems also depends on effective long-term monitoring. We are able to make inferences about the nature and ecological effects of the recent large fires because of the array of monitoring sites first established in the 1940s. While grassland, heathland and even wetlands appear resilient to the effects of one-off large fires, and that regeneration in heathlands is independent of fire severity, we know little about ecosystem resilience in relation to intervals between fires. Parts of the Mt Buffalo Plateau (e.g. Five Acre Plain) have been burnt four times in the past four decades. Evidence from such sites indicates that short intervals between fires (<20 years) are likely to have detrimental effects on a range of species and ecosystem functions in alpine ecosystems (Coates and Walsh 2010). Monitoring of areas burnt in 2003 and 2006-07 that may be burnt again in the next 5-20 years will therefore provide important information on the responses of alpine ecosystems to variation in the intervals between fires, which will complement our developing understanding of how alpine ecosystems are affected by variation in fire intensity/severity.

Change in the biota in of the Australian Alps will be influenced by many factors, such as warming climate, changing fire regimes (Williams et al. 2009), a greater abundance of alien species (McDougall et al. 2005) and increasing human pressure. Burgman et al. (2007) have termed these interacting forces ‘threat syndromes’. It is these that are likely to emerge as the main threats to biodiversity and the capacity of protected areas to conserve biodiversity. Because such threats interact at different spatial and

temporal scales, it is essential to monitor changes in ecosystems, to determine whether such threats are emerging, how the biota is responding to them, and what level of change is acceptable (Bond and Archibald 2003). The alpine ecosystems of Victoria have a long-history of ecological monitoring. These monitoring sites and methods can be adapted readily to meet the emerging needs of understanding and managing fire regimes in Australia's alpine ecosystems in the coming century.

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Phenological changes in six Australian subalpine plants in response to experimental warming and year-to-year variation

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Summary

1. The likely phenological responses of plants to climate warming can be measured through experimental manipulation of field sites, but results are rarely validated against year-to-year changes in climate. Here, we describe the response of 1–5 years of experimental warming on phenology (budding, flowering and seed maturation) of six common subalpine plant species in the Australian Alps using the International Tundra Experiment (ITEX) protocol.

2. Phenological changes in some species (particularly the forb *Craspedia jamesii*) were detected in experimental plots within a year of warming, whereas changes in most other species (the forb *Erigeron bellidioides*, the shrub *Asterolasia trymalioides* and the graminoids *Carex breviculmis* and *Poa hiemata*) did not develop until after 2–4 years; thus, there appears to be a cumulative effect of warming for some species across multiple years.

3. There was evidence of changes in the length of the period between flowering and seed maturity in one species (*P. hiemata*) that led to a similar timing of seed maturation, suggesting compensation.

4. Year-to-year variation in phenology was greater than variation between warmed and control plots and could be related to differences in thawing degree days (particularly, for *E. bellidioides*) due to earlier timing of budding and other events under warmer conditions. However, in *Carex breviculmis*, there was no association between phenology and temperature changes across years.

5. These findings indicate that, although phenological changes occurred earlier in response to warming in all six species, some species showed buffered rather than immediate responses.

6. **Synthesis.** Warming in ITEX open-top chambers in the Australian Alps produced earlier budding, flowering and seed set in several alpine species. Species also altered the timing of these events, particularly budding, in response to year-to-year temperature variation. Some species responded immediately, whereas in others the cumulative effects of warming across several years were required before a response was detected.

Key-words: flowering, ITEX, phenology, subalpine plants, temperature variation

Introduction

Phenological changes have now been widely linked to recent global warming in a range of plants and animals (Parmesan & Yohe 2003; Menzel *et al.* 2006; Miller-Rushing & Primack 2008). Key phenological shifts detected in plants include earlier

budding, flowering time and seed maturation under warmer and drier conditions (Root *et al.* 2003; Menzel *et al.* 2006). These shifts in phenology can influence the fitness of plants directly or indirectly through interactions with other organisms. Plant reproduction may be vulnerable to the effects of warming (Hedhly, Hormaza & Herrero 2009). Plants that develop early might suffer a decrease in seed set and offspring survival because conditions for seed development and/or seedling growth are suboptimal (Harrington, Woiwod & Sparks 1999; Wagner & Simons 2009). Early budding and flowering

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may also lead to altered seed set because of changes in levels of damage from insect herbivores and activity of pollinators (Both *et al.* 2009).

Nevertheless, plants may compensate for climate-induced changes in individual phenological events. Earlier budding or flowering may lead to earlier seed set or be compensated for by later development and maturation of seed, so that the timing of seed production and release is unaltered (Post *et al.* 2008). Apart from these plastic responses, there is also the possibility that evolution will change individual phenological events. For instance in *Brassica rapa*, flowering time has shifted in response to drier conditions during development (Franks & Weis 2008). To predict the long-term impact of phenological changes on plant fitness, the effects of compensation and evolution need to be considered and assessed (Post *et al.* 2008).

The effects of global warming on phenology might be particularly evident in alpine and arctic plants where temperature variation can have a large impact on phenological events (Parmesan & Yohe 2003; Root *et al.* 2003). Potential changes in these environments have been investigated as part of the International Tundra Experiment (ITEX) (Henry & Molau 1997), which involves passive warming in open-top chambers (OTCs) that cover plots of c. 1–2 m². In general, plants in warmed plots show earlier budding and flowering (Arft *et al.* 1999), although species also differ in their responses and may even show later flowering (Hollister, Webber & Bay 2005). There is variation in the speed at which plants shift phenology after experimental warming is started. Some perennial species shift rapidly, whereas in others it appears that cumulative effects of warming are required across multiple growth years (Arft *et al.* 1999). This suggests that plastic changes in phenology are complex.

Much of the research on ITEX sites has so far focused on testing for general effects of warming on phenology and species composition, but there is also a growing opportunity to link variation detected in experimental plots to year-to-year changes seen in control plots across monitoring periods. For instance, changes in the composition of vegetation in warmed plots involving an increase in woody vegetation match the increase in this type of vegetation seen in control plots as conditions in the arctic have warmed (Wahren, Walker & Bret-Harte 2005). Year-to-year variation can also be used to assess the importance of factors that are not manipulated in ITEX plots, such as changes in seasonal rainfall patterns and snow melt known to influence phenological events in alpine and sub-alpine plants (Walker, Ingersoll & Webber 1995; Wagner & Reichegger 1997).

Here, we use replicated ITEX plots and year-to-year variation in temperature conditions to investigate phenological changes in six diverse plant species from a subalpine area close to the tree line in south-eastern Australia. Conditions in this region have become warmer with a rise of c. 0.2 °C per decade since the 1970s (Hennessy *et al.* 2003). There has also been a decrease in rainfall (<http://www.bom.gov.au>), snow depth and snow cover (Osbourne, Davis & Green 1998; Hennessy *et al.* 2003; Nicholls 2005). Herbarium records suggest potential changes in flowering time in some species from this region (Gallagher, Hughes & Leishman 2009). In an earlier study on

these ITEX experiments based on data from 3 years (Jarrad *et al.* 2008), there was suggestive evidence that warming resulted in earlier occurrence of key phenological events in some species.

We consider the following questions. Is there evidence for divergence in phenology in six common subalpine species after 5 years of experimental manipulation? Is there evidence of compensation across phenological events? How do the detected effects of ITEX manipulations compare with year-to-year variation in phenology in control sites? To what extent can this variation be predicted by models based on degree-day (DD) accumulation? Do species that show the most rapid responses to warming also track year-to-year variation more closely? We also discuss the implications of these results on the selection of species used to monitor the effects of global warming near the tree line.

Materials and methods

PLOTS

The OTCs used in ITEX experiments are inexpensive and robust and provide protection from wind, but they are only suitable for warming a small area of 1–2 m in diameter. Establishment of the OTCs is described in Jarrad *et al.* (2008) and only a brief overview is provided here. The OTCs (1.7 m in diameter; 110 cm at the top, 168 cm at the base) were set up at c. 1750 m a.s.l. in November 2003 on the Bogong High Plains, Victoria, Australia, according to the ITEX protocol (Molau & Molgaard 1996). The OTCs were placed over the plots throughout the snow-free period, from snow melt, when 50% of the ground was free of snow (October or November), until 50% of the snow cover returned (June).

This study focuses on results from the two unburnt sites located 0.5 km apart described in Jarrad *et al.* (2008). There were 13 OTCs and 13 controls (CTL) at each of these sites. The sites had a similar subalpine open heathland community – community 26 in McDougall (1982). The tussock grass *Poa hiemata* and forb *Celmisia pugioniformis* predominated in this community at both sites, but there were also various other grasses, daisies, rushes, sedges, forbs and shrubs. Air temperature was recorded at 5 cm above the surface with Onset Hobo data loggers in eight plots (four OTC; four CTL) per site. The OTCs warmed the air by 0.9 °C during the day and 1.0 °C at night based on 2004/2006 data. The OTCs also warmed soil by 1.2–1.4 °C at the surface and 0.9–1.0 °C at 5 cm depth (Jarrad *et al.* 2008).

We focused on six common subalpine species for monitoring that included the main families and growth forms consisting of grasses (Poaceae), sedges (Cyperaceae), shrubs (Rutaceae) and forbs (Asteraceae, Ranunculaceae). We measured the phenology of plants in the central 1-m² region of the plots following the ITEX protocol. The species occur in the alpine and high subalpine zones. Plant communities in these zones on the Bogong High Plains are the same floristically and not geographically separated, being part of the same dissected plateau. *Celmisia pugioniformis*, which occurred in all plots, was not included because it does not flower every year and there were insufficient data points to test for patterns. Plots were visited every 2–4 days during the snow-free period from November 2003 to March 2008. The dates of first flower bud, opening of flower and seed maturation as defined by Jarrad *et al.* (2008) were recorded when the first plant exhibited the trait for each plot following the ITEX protocol (<http://www.geog.ubc.ca/itex/>). These pheno-phase dates were expressed in

days since 1 June to be more consistent with northern-hemisphere studies.

ANALYSIS

ITEX comparison

To test if phenology has shifted as a consequence of experimental warming, repeated-measures ANOVAs are often carried out on ITEX phenology data from the same plots across years. However, if this analysis is applied to our data from the first and last years, many plots are excluded, because often the same plots did not flower in both of these years. This results in few degrees of freedom for the error term and low power for detecting warming effects.

To overcome this problem, we considered two approaches. First, we used ANOVAs to analyse the effect of treatment on phenological traits for each sampling year (i.e. data were not combined across years). Site was also included in the ANOVA but not presented because the focus of this study is on treatment effects and because site differences were mostly not significant. When presenting the data graphically, site effects were removed by adding or removing the signed difference between site means and the overall mean to individual data points. We analysed traits separately and expected some species–trait–year combinations to differ between treatments by chance, and warming effects are therefore interpreted cautiously except where significance was maintained following Bonferroni correction of probabilities for the number of comparisons per species. For some of the species–trait–year combinations (budding in *Erigeron bellidioides* 2006/2007, 2007/2008 and in *Ranunculus victoriensis* 2004/2005; flowering in *Craspedia jamesii* 2005/2006, *E. bellidioides* 2007/2008, *R. victoriensis* 2006/2007, *Carex breviculmis* 2003/2004; seed maturation in *Carex breviculmis* 2003/2004), data were not normally distributed by Kolmogorov–Smirnov tests or graphically via probability plots (Quinn & Keough 2002), so non-parametric Mann–Whitney *U*-tests were used instead. All statistical tests were run with SPSS for Windows (SPSS, Chicago, IL, USA) or SYSTAT 12 (Crane, Bangalore, India).

Second, we combined adjacent early years (to represent the early period) and adjacent late years (to represent the late period) to increase the number of plots with data suitable for a repeated-measures ANOVA. To be included in the analysis, plots had to exhibit the trait in at least one of the years in each of the periods. When combining data from the adjacent early growth years (2003/2004 and 2004/2005, except for *R. victoriensis* where 2004/2005 and 2005/2006 data were combined because only a few plants flowered in 2003/2004), we initially corrected for differences between the overall mean value for adjacent years. For instance, if flowering time in *P. hiemata* had a mean of 220 days in 2003/2004 across all plots that flowered and a mean of 230 days in 2004/2005, we added 5 days to all plot values where flowering occurred in 2003/2004 and took away 5 days from all plot values where flowering occurred in 2004/2005. We combined data from the later growing seasons (2006/2007 and 2007/2008) in the same way. ANOVAs were then run with treatment as a fixed factor and period (early or late) as a random factor. There were insufficient data points for budding and seed maturation in the shrub *Asterolasia trymaloides* for these analyses. Site was also included as a factor in the ANOVA but site (and interaction terms involving site) was only significant for *P. hiemata*, and these analyses are not presented. Data for the repeated-measures ANOVAs were normally distributed based on Kolmogorov–Smirnov tests and also using probability plots, and variances were similar between treatments based on Levene tests.

Fruit development period

Plants might alter seed maturation time to compensate for warming effects on flowering time, to ensure that they produce seed at a similar period within the growing season. To test this, we computed the time of seed maturation minus the time of flowering in each plot where both seed maturation and flowering time were available for a particular plot in a given year. This measure (referred to as the fruit development period) might reflect the ability of plants to compensate for differences in flowering time by changing the rate at which fruit matures. Two-way ANOVAs were used to test for treatment and site effects on fruit developmental period for each species–year combination. We also ran repeated-measures ANOVAs (corrected for site as described above) with year and treatment as factors to test for changes in fruit development period over time using the 2003/2004 and the 2007/2008 data. However, for two species (*R. victoriensis* and *Carex breviculmis*), there were insufficient early data in a single year and we therefore combined plots that flowered in either the 2003/2004 or 2004/2005 periods after adjusting for year effects as described before. These data were all normally distributed by Kolmogorov–Smirnov tests and graphical assessments.

Year-to-year variation

To test if year-to-year variation in temperature affected phenological traits (budding, flowering, seed maturation) in the different species, a thawing DD model was used. Development of a species towards a phenological event was assumed to depend on air temperature (a threshold of 0 °C was adopted to represent thawing – although higher values did not improve prediction) and degrees accumulated across days. Temperature data were obtained from the air conditions recorded at the sites 5 cm above the ground inside and outside OTCs. However, there were occasional gaps in the data set where temperatures were not recorded because of malfunctioning sensors. In this case, we substituted data from a local weather station (Falls Creek, 36.86°S, 147.28°E) (<http://www.bom.gov.au>); air temperatures at plots within the growing season were predicted through linear regression from records collected at the weather station ($R^2 > 0.95$).

We initially computed the mean time of an event for each species and trait (averaged across all plots). We then computed the cumulative DD for this mean separately for each combination between plot, site, year and treatment. The cumulative DD was obtained by adding up the number of degrees in a day where the maximum temperature exceeded zero, this was then accumulated across days. DDs for flowering time were computed based on the combined DDs to budding and between budding and flowering, whereas DDs for seed maturation time also encompassed the flowering to seed maturation period. If phenological events depend on temperature, we predicted that there would be a negative relationship between days to the phenological event and cumulative DD for each site–treatment–year combination; i.e. earlier occurrence of phenological event with increasing DD values. These relationships were tested through linear regression analyses of cumulative DDs onto days to the phenological event. We also included time of snow melt in these regression analyses as a separate variable, but found that inclusion of this variable did not improve the fit because this factor is already contributing to the cumulative DD values. We also included treatment (OTC vs. control) in the analyses, but this factor did not significantly influence the regression slope ($P > 0.05$) in any instance, again probably because the OTC difference was already accounted for in the DD values.

COMBINING PROBABILITIES AND EFFECT SIZES

To examine the consistency of trends across the different species, we followed the Z method as outlined in Whitlock (2005) to combine probabilities from comparisons across individual seasons or single species, initially treating the probabilities as one-tailed but then testing the combined value as a two-tailed test. We also computed effect size by year following the approach of Gurevitch & Hedges (2001). This allowed us to directly compare the effects detected to those from other similar studies.

Results

PHENOLOGY ACROSS YEARS

Changes in phenology across the 5 years measured are presented Figs 1–3 along with *P*-values for ANOVAS testing if there were shifts in phenology between warmed control plots each year. These results indicate that, in some species, a number of years were required for the warming treatment effect to be expressed (to produce significant differences between the OTCs and control plots), whereas warming effects were expressed more quickly in other species. The results also indicate that year-to-year variation in phenology was generally larger than the treatment effects.

For the shrub *A. trymalioides*, flowering time differed significantly (even after Bonferroni correction) between treatments in 2006/2007 and 2007/2008 when the shrub flowered earlier in the OTCs by c. 10 days (Fig. 2). In the repeated-measures ANOVA testing for a shift in phenology between the early and late monitoring period, there was a significant effect of treatment and a Treatment $\times$ Year interaction (Table 1), indicating that treatment differences have developed since 2003/2004.

For the forb *Craspedia jamesii*, buds, flowers and seeds emerged on average 2–10 days earlier in the OTCs, and the effects of treatments on each of the traits was significant in at least 1 year (Figs 1–3). In the repeated-measures ANOVAS, the

effects of treatments on each of the traits was significant and there were no interactions (Table 1), suggesting no difference in response between early and late years. The forb *E. bellidioides* showed consistently earlier flowering and seed maturation in the OTCs after 2003/2004, and the effects of treatments on each of the traits was significant in 2007/2008 (even after Bonferroni correction) when plants in the OTCs flowered and set seed on average 7–8 days earlier than in the control plots. In the repeated-measures ANOVAS on flowering, both the main effect of treatment and Treatment $\times$ Year interaction were significant, whereas for budding only the Treatment $\times$ Year interaction was significant (Table 1). In contrast, in the forb *R. victoriensis*, the effect of treatments was only significant in 2007/2008 due to earlier flowering in the OTCs by an average of 3 days. Treatment effects were not detected in the repeated-measures ANOVAS for this species (Table 1).

In the sedge *Carex breviculmis*, budding and flowering occurred earlier in the OTCs in later years (2006/2007 and 2007/2008) by 5–10 days on average (Figs 1 and 2). Patterns for seed maturation were inconsistent, but maturation was significantly earlier by 7 days in the OTCs in the final phenological season (Fig. 3). In repeated-measures ANOVAS, there was a significant effect of treatment for budding and significant interactions for flowering and budding (Table 1). Budding and flowering in the grass *P. hiemata* occurred significantly earlier in the OTCs by on average 4–12 days in 2005/2006 to 2007/2008 (Figs 1 and 2). In the repeated-measures ANOVAS, treatment and Treatment $\times$ Year interactions were significant for flowering but not for budding and seed maturation (Table 1).

Comparing patterns across traits and species, events in 2007/2008 occurred on average earlier in the OTCs than in the controls for all 16 trait–species comparisons (with nine of these being significant and a combined probability of $P < 0.001$ based on the Z method; Whitlock 2005). Flowering, seed mat-

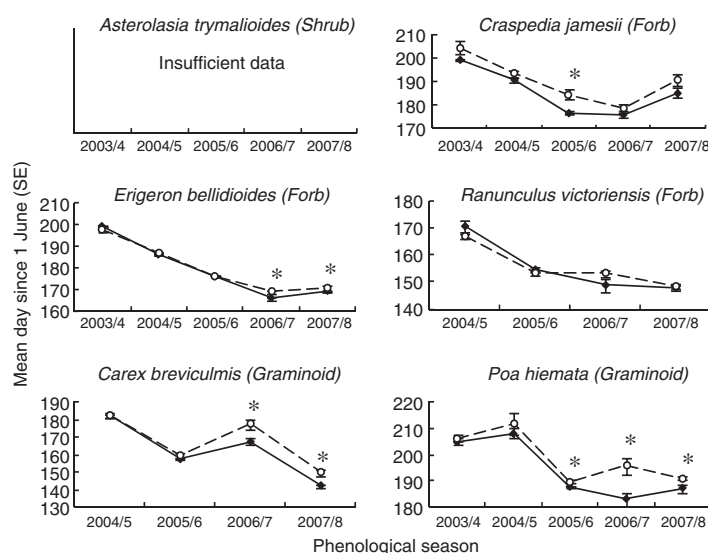


Fig. 1. Effects of warming in open-top chambers (OTCs = solid line with black square) relative to controls (CTL = dashed line with open circle) on days to first budding across 4–5 years where data were available. Asterisks indicate significance ($P < 0.05$) between treatments based on ANOVAS or Mann–Whitney *U*-tests. Data points are based on 11–26 replicate plots. Error bars represent ± 1 SE.

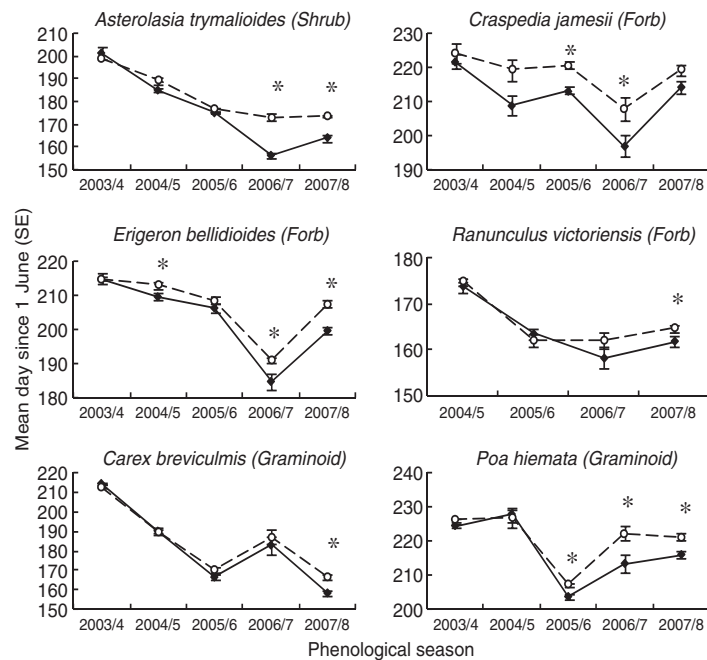


Fig. 2. Effects of warming in open-top chambers (OTCs = solid line with black square) relative to controls (CTL = dashed line with open circle) on days to first flowering time across 4–5 years where data were available. Asterisks indicate significance ($P < 0.05$) based on ANOVAs or Mann-Whitney U -tests. Data points are based on 10–26 replicate plots. Error bars represent ± 1 SE.

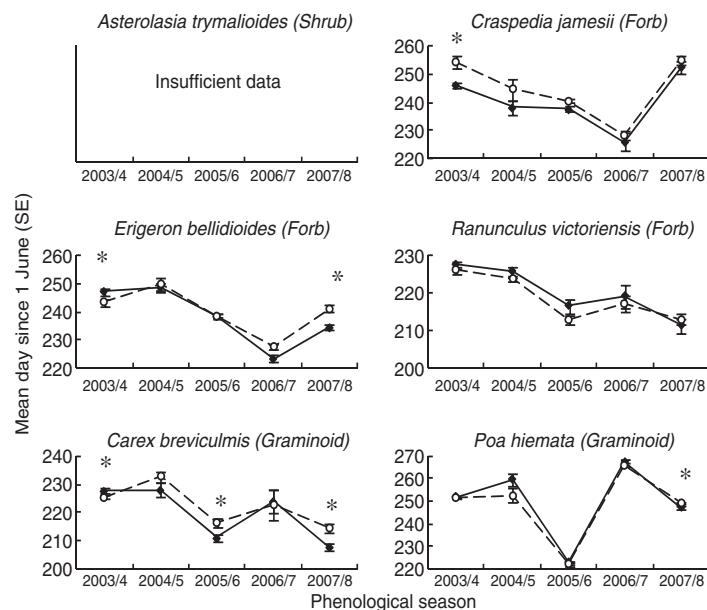


Fig. 3. Effects of warming in open-top chambers (OTCs = solid line with black square) relative to controls (CTL = dashed line with open circle) on days to first seed maturation time across 4–5 years where data were available. Asterisks indicate significance ($P < 0.05$) based on ANOVAs or Mann-Whitney U -tests. Data points are based on 5–26 replicate plots. Error bars represent ± 1 SE.

uration and budding all took place significantly earlier in the warmed plots ($P < 0.001$, except for budding where $P = 0.012$) when compared across all species. In contrast, in 2004/2005 only 9 of the 16 species–trait comparisons among treatments were on average earlier in the warmed plots (with only one significant in the expected direction, and a combined P -value > 0.05).

For the effect size analyses, results for days to flowering (Fig. 4) indicate that where differences emerge in later years (CIs of effect size do not cross 0), the effect size is $c. 1$ in

some species (e.g. *P. hiemata*) but greater in others (e.g. *A. trymalioides*). For budding and seed maturation, effect sizes were also $c. 1$ when differences among treatments were significant.

FRUIT DEVELOPMENT PERIOD

The period between the seed maturation and flowering phases was compared to test whether it had altered in the OTCs due to warming. Treatment differences were significant in several

Table 1. Results from repeated-measures ANOVA of phenological events in six subalpine species

Species	Trait	Mean squares				
		Treatment (d.f. = 1)	Between subjects error (d.f.)	Year (d.f. = 1)	Treatment × Year (d.f. = 1)	Within subjects error (d.f.)
<i>Asterolasia trymalioides</i> †	Flowering	666.8**	27.2 (29)	0.5	235.7**	11.7 (29)
<i>Craspedia jamesii</i>	Budding	330.4*	46.7 (19)	0.8	40.4	34.3 (19)
	Flowering	1780.0*	243.8 (23)	21.1	319.1	193.9 (23)
	Seed maturation	312.6*	68.7 (24)	27.8	107.6	31.9 (24)
<i>Erigeron bellidioides</i>	Budding	3.5	24.2 (36)	5.4	0.5	17.1 (36)
	Flowering	462.6**	25.6 (37)	3.7	102.3*	14.5 (37)
	Seed maturation	58.6	32.1 (38)	6.3	228.6*	28.1 (38)
<i>Ranunculus victoriensis</i> ‡	Budding	0.7	18.8 (31)	34.1	21.3	23.2 (31)
	Flowering	54.8	27.5 (44)	1.9	18.6	20.4 (44)
	Seed maturation	113.7	3557.4 (43)	47.4	52.8	3487.5 (43)
<i>Carex breviculmis</i>	Budding	257.9*	35.0 (23)	10.4	346.4**	19.1 (23)
	Flowering	227.5	69.0 (38)	3.0	240.2*	38.9 (38)
	Seed maturation	22.2	794.0 (31)	7.7	155.9	741.8 (31)
<i>Poa hiemata</i>	Budding	251.0	59.3 (18)	4.2	142.1	65.7 (18)
	Flowering	362.2**	24.0 (43)	13.3	238.3*	22.6 (43)
	Seed maturation	3.4	10.1 (38)	0.1	26.4	13.2 (38)

Comparisons were between the average of the first two (2003/2004 and 2004/2005) and the last two (2006/2007 and 2007/2008) growth years unless otherwise indicated. Days from 1 June until first appearance of phenological trait was used.

* $P < 0.05$, ** $P < 0.001$.

†Insufficient data collected on other traits

‡First 2 years based on 2004/2005 and 2005/2006 data

instances (Fig. 5). For *Craspedia jamesii*, the period between seed maturation and flowering was greater in the controls than in the OTCs in 2003/2004 but this switched in later seasons

(significantly so in 2005/2006), although treatment and interaction effects were not significant in the repeated-measures ANOVA (across 2003/2004 and 2007/2008) (Table 2). For

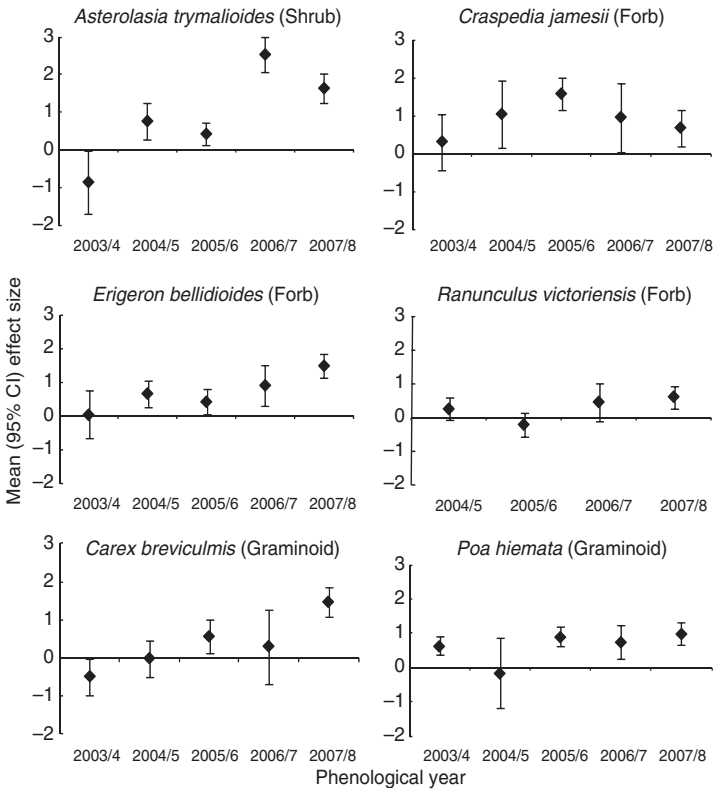


Fig. 4. Plots of effect sizes of warming effects for first flowering event across 4–5 years where data were available for the different species. Error bars represent 95% confidence intervals.

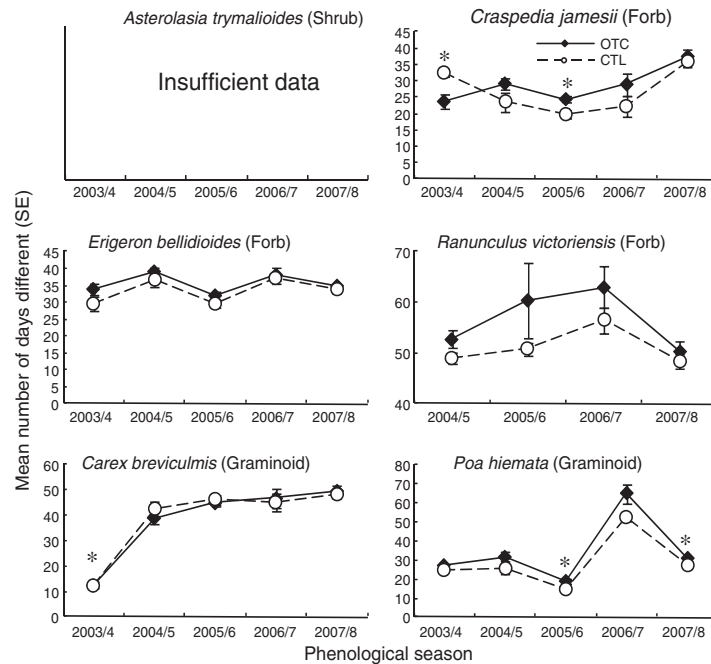


Fig. 5. Changes in fruit development period (defined as time of first seed maturation minus first flowering within a treatment) in open-top chambers (OTCs = solid line with black square) relative to controls (CTL = dashed line with open circle) across 4–5 years where data were available. Asterisks indicate significance ($P < 0.05$) between treatments based on ANOVAS. Data points are based on 14–52 replicate plots. Error bars represent ± 1 SE.

Table 2. Results from repeated-measures ANOVA of compensation of phenological events (first seed maturation minus first flowering time) in six subalpine species

Species	Mean squares				
	Treatment (d.f. = 1)	Between subjects error (d.f.)	Year (d.f. = 1)	Treatment $\times$ Year (d.f. = 1)	Within subjects error (d.f.)
<i>Craspedia jamesii</i>	101.2	47.0 (23)	13.3	30.6	61.0 (23)
<i>Erigeron bellidioides</i>	49.8	27.4 (37)	0.0	11.0	35.9 (37)
<i>Ranunculus victoriensis</i> †	604.5*	107.3 (43)	1.0	71.0	112.5 (43)
<i>Carex breviculmis</i> †	75.9	75.2 (34)	4.2	83.9	28.3 (34)
<i>Poa hiemata</i>	253.1**	16.3 (38)	1.9	72.3	21.1 (38)

Comparisons were between the average of the first two (2003/2004 and 2004/2005) and the last two (2006/2007 and 2007/2008) growth years unless otherwise indicated.

* $P < 0.05$, ** $P < 0.001$.

†First 2 years based on 2004/2005 and 2005/2006 data.

E. bellidioides and *Carex breviculmis*, differences between treatments were consistently small (Fig. 5) and not significant in the repeated-measures ANOVAS (Table 2), although in *Carex breviculmis* compensation increased across years in both OTCs and controls. Warming treatment effects were significant in the repeated-measures ANOVAS for *R. victoriensis* and particularly for *P. hiemata* (Table 2). In these two species, plants from OTCs had extended fruit maturation periods in all years (significant in two years for *P. hiemata*) indicative of compensation (Fig. 5).

YEAR-TO-YEAR VARIATION

Regression analyses were undertaken to test if year-to-year variation in phenology could be predicted by differences in

DDs. For the shrub *A. trymalioides*, these analyses indicated that budding and flowering were significantly earlier in years with higher cumulative DDs, and patterns were consistent for the OTCs and controls (Fig. 6). No pattern was evident for seed maturation although only a few data points were available.

For the forbs *Craspedia jamesii*, *R. victoriensis* and *E. bellidioides*, there were negative relationships between phenology and DDs for most traits (Fig. 6). R^2 values were particularly high for *E. bellidioides*. For the graminoid *Carex breviculmis*, changes in phenology were not associated with year-to-year variation in DDs (Fig. 6). However, for the graminoid *P. hiemata*, phenology and DD were negatively associated and the regression coefficient for budding was significant.

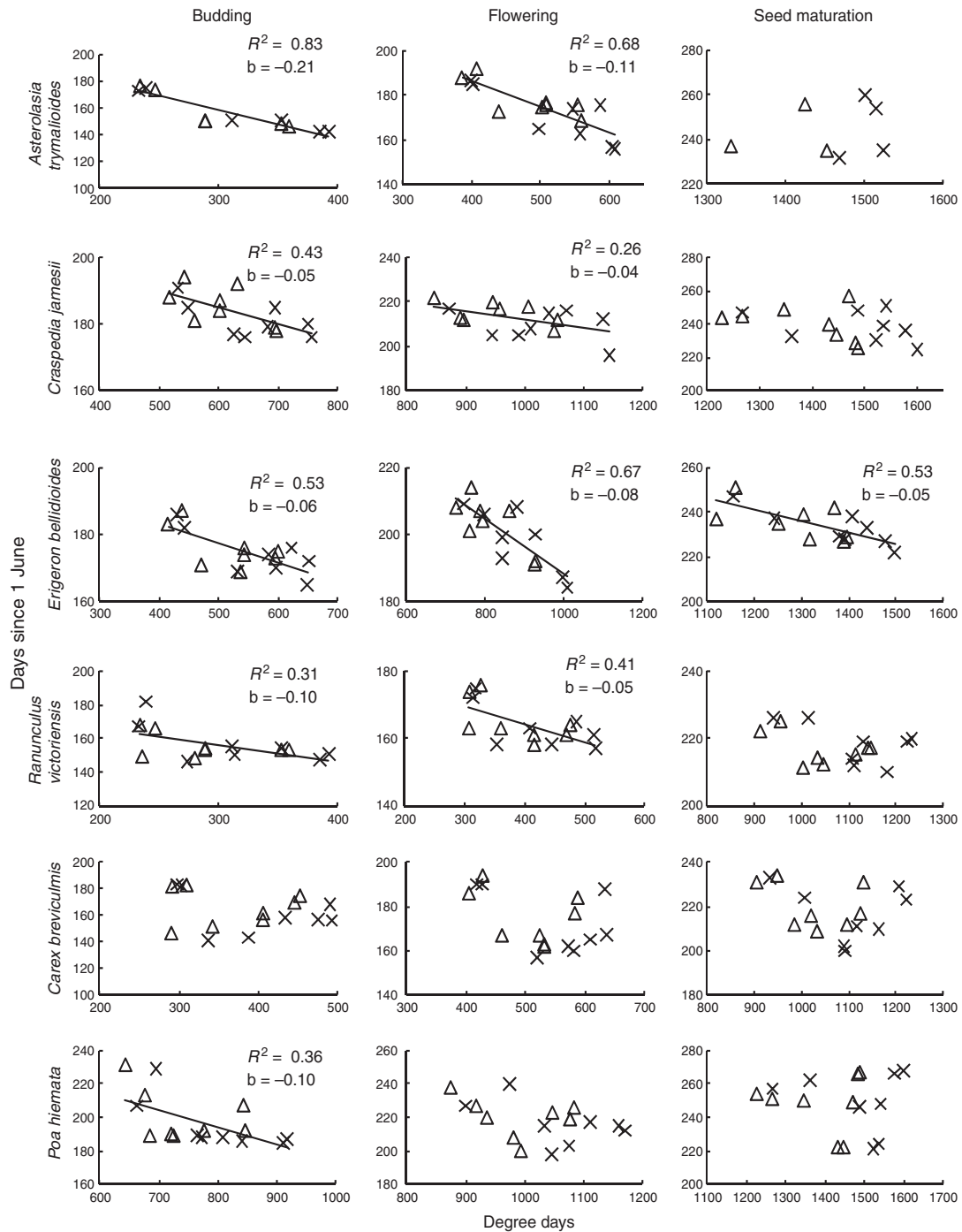


Fig. 6. Association between cumulative degree days since snowmelt and phenological events in the subalpine species. Open triangles indicate OTCs, crosses indicate control plots. For the linear regressions that were significant ($P < 0.05$) the slope and R^2 are provided.

Overall across the species, timing of budding was negatively associated with DDs across years and treatments in five of six species (all five relationships significant, with a combined prob-

ability based on the Z method < 0.001). When OTC and control treatments were considered separately, there was a negative relationship in 10 of the 12 comparisons. For flowering

time, associations were negative rather than positive for the same number of comparisons as for budding (5 of 6 combined, or 10 of 12 with treatments separated), and the combined *P*-value across species was < 0.001 . For seed maturation, the relationship between timing and DDs was negative in five of six comparisons (9 of 12 if treatments are considered separately), but the combined *P*-value across species was not significant (> 0.05).

Discussion

The results complement the early findings on these ITEX plots that suggested phenological responses to warming among Australian subalpine species (Jarrad *et al.* 2008). However, the use of additional monitoring years has produced much more consistent effects across species compared with idiosyncratic changes noted in the earlier work. Effect sizes are similar in magnitude to those observed for phenological events in other ITEX experiments (e.g. Arft *et al.* 1999). Moreover, temperature effects were evident from year-to-year variation in phenology being linked to thawing DD predictions.

Species tested differ markedly in the speed at which they have responded. The delayed response of many species is consistent with observations from other ITEX sites (Arft *et al.* 1999; Molau 2001; Hollister, Webber & Bay 2005). Responses in reproductive traits in some species may take several years to emerge, presumably because the formation of flower buds occurs one to several seasons prior to flowering (Billings 1974). In our study, one of the later species to flower (*Craspedia jamezii*) was the fastest to respond, whereas one of the earlier-flowering species (*R. victoriensis*) did not respond until the end of the monitoring period. Another member of the *Ranunculus* genus exhibits little response to warming in ITEX chambers over 3 years at an alpine site in Norway (Totland & Alatalo 2002). Perhaps early flowering species respond less rapidly to warming because development starts while plants are still covered with snow. Early flowering species might be more vulnerable to climate change if an inflexible flowering time in response to temperature entails fitness costs, such as through a mistiming of flowering and the availability of pollinators (Kameyama & Kudo 2009).

The present findings indicate that subalpine plants from the Australian Alps respond to shifts in temperature. One other detailed study on this flora suggested that temperature might not be important; Venn & Morgan (2007) found that in three species from the Bogong High Plains (*Celmisia pugioniformis*, *Luzula acutifolia*, *Poa fawcettiae*), flowering time and seed maturation were independent of the time snow melted and might instead be driven by photoperiod rather than temperature. However, Gallagher, Hughes & Leishman (2009), using herbarium records, noted long-term changes in flowering time associated with temperature shifts over the last 50 years in several alpine species. This is consistent with our year-to-year records, which indicate that the phenology of most species from this region is likely to be altered by changes in thermal conditions. Large-scale surveys from other regions have also shown that average temperatures within a year prior to flower-

ing influence flowering time of a range of plants (e.g. Menzel *et al.* 2006; Miller-Rushing & Primack 2008).

Although budding and flowering time were influenced by temperature, we also found that the period between flowering time and seed maturation could be extended when flowering was early, particularly in one grass (*P. hiemata*). Due to changes in the fruit development period, there were only minor differences in the timing of seed maturation in this species between the OTC and control plots in 2007/2008, compared with much larger differences in flowering and budding time. Our data on fruit development are consistent with the results of Post *et al.* (2008) who found that the alpine chickweed *Cerastium alpinum* could compensate at later stages of development for an effect of experimental warming on emergence, although these authors also found no evidence of such changes in two other species. *Poa hiemata* is a dominant species in the alpine and subalpine community, and this species may be able to respond to warmer climatic conditions through delaying fruit maturation. In previous work involving transplants of *P. hiemata* across an environmental gradient, this species showed substantial adaptive capacity both through plastic changes and genetic variation (Byars, Papst & Hoffmann 2007). It remains to be seen if an extended fruit maturation period in the OTCs increases the fitness of *P. hiemata*.

The changes we observed in the OTCs were smaller than phenological changes occurring from year to year, which were also related to temperature. We found that the timing of budding in particular was linked to cumulative DDs. This approach provides an opportunity to test the importance of the immediate within-season effects of post-thawing temperature on plant development. If sufficiently long time series were available on across-season variation, it might even be possible to test if there is an influence of temperature (and rainfall) in past growth seasons on phenology, as suggested by the delayed phenological responses of several plants in our current ITEX experiments.

Based on herbarium records, Gallagher, Hughes & Leishman (2009) suggested that flowering time in the alpine groundsel, *Senecio pectinatus* var. *major*, may be an indicator of climate change in the Australian Alps. Our results indicate that some species respond rapidly to experimental warming, others respond more slowly requiring cumulative effects across multiple years, while there are also sharp differences in responses to year-to-year variation in thermal conditions. Given these diverse patterns, what makes a good indicator species? An ideal species is likely to be one that responds to the cumulative effects of warming over time, is fairly common (unlike *S. pectinatus* var. *major*), flowers consistently and does not alter its flowering time dramatically in response to year-to-year variation. Such a species might then show a gradual shift in phenology but a reduced immediate response to thermal conditions within the season where flowering is being measured. Its phenology is more likely to reflect the cumulative effects of several years. In terms of the species considered here, we suspect that two good candidates are flowering time in *P. hiemata* and flowering time as well as budding in *Carex breviculmis*. Flowering time in *E. bellidioides* and *A. trymalioides* might also be suitable

because of the large effect sizes we detected for these species in later years, although phenology in both species did respond to year-to-year variation in temperature. *Craspedia jamesii* probably responds too quickly and might even be in the process of acclimating to warming given the apparent reduction in effect size in later years (Fig. 4). A related species (*Craspedia lamicola*) shows a high level of plasticity in its morphological growth form when transplanted across altitudinal gradients (Byars & Hoffmann 2009).

We have so far only considered the effects of temperature on phenological changes, whereas the timing of plant development may also depend on changes in water availability, fire and perhaps CO₂ (e.g. Franks & Weis 2008; Hovenden *et al.* 2008). A reduction in wind exposure might influence phenology in OTCs, although only the central area of the OTCs was monitored in the current experiments. Predictions about phenological changes in alpine and subalpine environments will ultimately require an understanding of how changes in temperature, rainfall and CO₂ interact to influence plant development. This will require more complicated models that include variables other than DDs. Ideally, these models will also include predictions about fitness effects, so that the ecological consequences of changes in phenology in perennial plants can be considered. Changes in phenological traits might influence the amount and dispersal of seed in plants due to altered interactions with pollinators and seed dispersers (Kudo & Hirao 2006; Kameyama & Kudo 2009). Finally, although we have considered the timing of first budding, flowering and seed maturation as in other ITEX experiments, it is not clear whether these traits accurately reflect the distribution of phenological events across a season. The estimation of first flowering time will also depend on the size of the flowering plant population (Miller-Rushing, Inouye & Primack 2008). In our plots, where the number of plants of different species in the ITEX chambers was similar from year to year, there was nevertheless variation in the number of plants that flowered.

To conclude, we have found that experimental warming using the ITEX protocol has led to phenological changes in plants in the Australian Alps, particularly in flowering time. Effect sizes were similar to those observed in other ITEX sites in the Northern Hemisphere. Species differ in whether they express these changes soon after warming started or after a number of years, and species also differ in their ability to compensate for shifts in flowering time by the time seed has matured. Most species respond to year-to-year variation in thermal conditions at the budding stage but this source of variation is less apparent at the time of seed maturation. Phenological responses of Australian subalpine plants may therefore involve immediate responses to temperature conditions within a growth season as well as cumulative effects across years.

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6 Alpine ecosystems

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SUMMARY

Australian alpine ecosystems are of great national significance for nature conservation and catchment protection for high-quality water. Ecological research has been undertaken in the alpine and high subalpine ecosystems of New South Wales, the Australian Capital Territory, Victoria and Tasmania for many decades, with many monitoring sites and plots in all major plant communities. Some plots from this monitoring network date from the 1940s. This network of monitoring plots has helped ecologists and managers quantify basic ecological patterns, processes and trends. In addition, this long-term ecological research has been important for the development of conservation management strategies, including the establishment of national parks, the protection of rare species such as the Mountain Pygmy Possum (*Burramys parvus*) and limiting damage to catchments from land-use practices that disturb the fragile alpine environment. Long-term monitoring and experiments have shown that ungulates (hard-hooved animals), both domestic and feral, have no place in Australian alpine ecosystems and should be removed. Livestock grazing in alpine ecosystems has no environmental benefits; it does not mitigate the extent or severity of fire in alpine ecosystems. Occasional large fires such as those of

2003 and 2006–07 are not necessarily a catastrophic threat to alpine biodiversity; the available evidence from long-term monitoring indicates that alpine ecosystems on mainland Australia are resilient to such fires in the long term. Experimental investigations of the potential impacts of climate change over an 8 year period in open grassy heathlands indicate relatively minor effects on plant diversity and species composition and a variable capacity of the flora to adapt genetically to warming. This indicates a degree of resilience to a 1–2°C increase in mean annual temperature over the coming decade. The most serious threat to the natural values of Australian alpine ecosystems is the expanding range and numbers of exotic plants and animals. Without such an extensive network of long-term monitoring plots in Australia's alpine ecosystems, assessing the effects of land use on soils and vegetation, interpreting the patterns of ecological change following major fires, anticipating potential ecological response to climate change and identifying and managing the invasion of exotic species would not have been possible. Such important findings demonstrate the need for long-term monitoring to be continued, adapted, and in some cases expanded, so that the numerous threats to alpine ecosystems in the 21st century can be detected and mitigated.

Box 6.1: Key discoveries

Several major discoveries in alpine ecosystems could not have been made without long-term ecological research. These include:

- Long-term vegetation change is a feature of alpine ecosystems, and documenting this has been a feature of research in the Australian Alps. Changes in the balance between shrubs, grasses and forbs can be substantial, and depend on interactions between disturbance and species life history.
- The conservation management of the Mountain Pygmy Possum is a success story for long-term ecological research and landscape management, but is also a cautionary tale.
- Ungulates (hard-hooved animals) such as cattle, sheep, horses, deer and pigs have no place in Australian alpine ecosystems.
- Alpine vegetation of mainland Australia has a strong capacity to regenerate after large fires such as those of 2003. Grazing by domestic livestock does not reduce the incidence or severity of fire in Australian alpine ecosystems.
- Alpine grasslands and open heathlands may be resilient to warming of 1–2°C over the coming decade.
- Exotic, invasive plants and animals pose a clear and present major threat to alpine ecosystems.
- Assessing the potential effects of climate change on alpine ecosystems, and interpreting the patterns of ecological change following landscape-scale fires such as those of 2003, would not have been possible without long-term monitoring plots.

INTRODUCTION

Alpine landscapes occur at altitudes above 1600–1900 m on mainland Australia and 1000 m in Tasmania; they occupy 270 000 ha or ~0.04% of the Australian continent (Kirkpatrick 1997; Williams *et al.* 2006a; McDougall and Walsh 2007). Despite this relatively low altitude and very small area, Australia's alpine landscapes are of national and international significance, because of their tectonic, geomorphic, biotic and cultural values (Good 1989; Kirkpatrick

1994). The headwaters of some of Australia's major temperate river systems arise in the Australian Alps and the alpine and surrounding subalpine ecosystems have high soil, water and nature conservation value (Worboys and Good 2011). Globally, high mountain environments are vulnerable to the effects of climate warming. Australian alpine ecosystems have been identified as particularly vulnerable because the alpine altitudinal zone is comparatively narrow, affording limited potential for the migration of alpine biota (Brereton *et al.* 1995; Hughes 2003; Laurance *et al.* 2011). Understanding how global change may affect Australia's alpine ecosystems has important implications for the conservation management of the world's high altitude ecosystems.

The Australian Alps are of great scientific significance (Good 1989) (Box 6.1). Detailed studies of environmental change in the Australian Alps commenced in the early 1940s and, at present, there are numerous long-term monitoring sites in New South Wales, Victoria and Tasmania. More than 100 plots have been established to examine landscape responses to livestock grazing, landscape rehabilitation, fire and, more recently, invasive, exotic species and climate change (Box 6.2).

The current, designated primary land use in alpine ecosystems is nature conservation and this use is compatible with the provision of high-quality water to the Murray–Darling Basin – Australia's food bowl. The majority of Australia's alpine ecosystems are in protected areas such as the Kosciuszko National Park in New South Wales, the Alpine National Park in Victoria, Namadgi National Park in the Australian Capital Territory and numerous reserves in Tasmania, such as the Cradle Mountain National Park. Recreational uses of the alpine landscape, such as skiing, bushwalking and other outdoor adventure activities, have increased in the latter decades of the 20th century. In the coming century, it is likely that the ecosystem services provided by the alpine ecosystems will be increasingly valued.

Free-range livestock grazing over summer was a widespread land use in the 19th and 20th centuries and has historical and cultural significance (Good 1992). The stock were primarily cattle and sheep, but horse numbers were also high at the beginning of the 20th century. Concern over the effects of grazing on

land condition in the Australian Alps arose as early as the 1890s, with observations by Richard Helms and JH Maiden of the damaging effects of livestock grazing and deliberate burning (Hancock 1972; Good 1992). Byles (1932) further noted the damaging effects of such grazing and burning on the vegetation and soils of the Snowy Mountains region. Detailed scientific studies to investigate these concerns commenced immediately after the Second World War (Good 1992). The establishment and maintenance of long-term monitoring sites to assess the effects of disturbance by grazing on alpine ecosystems was an important development in Australian ecological science.

This chapter discusses how long-term monitoring plots have influenced our understanding of environmental change, both natural and human-induced. We start with a description of alpine ecosystems, their distribution, the primary drivers that shape their dynamics and the threats to them. We then present the finding from four core case studies that have used long-term monitoring and research: long-term vegetation dynamics; the biology of the Mountain Pygmy Possum; post-fire regeneration; and climate change impacts. We conclude with a consideration of how the long-term studies have influenced our understanding of the ecology of Australian alpine ecosystems, the applications of ecological understanding in land man-

agement, future challenges and threats, and policy considerations.

We focus on alpine ecosystems in Victoria, and the Bogong High Plains and Mount Hotham regions in particular. We do not describe the detail of the plots and findings from all monitoring sites elsewhere in the Australian Alps, such as New South Wales and Tasmania. However, the findings from the Victorian research described in this chapter illustrate general principles that are applicable elsewhere.

A DEFINITION OF AUSTRALIAN ALPINE ECOSYSTEMS

The term 'alpine' generally refers to the treeless vegetation above the climatic limit of tree growth (Fig. 6.1A) (Costin *et al.* 2000). On mainland Australia, the treeline occurs at ~1700–1900 m above sea level, and at ~1000 m in Tasmania. However, trees and treeless vegetation may occur in mosaic near the upper treeline (e.g. Fig. 6.1B). Moreover, the treeline may be inverted in valleys, below the climatic treeline, because of the accumulation of cold air in landscape depressions during the growing season (Williams 1987). This prevents trees on the slopes from establishing in the valley bottoms (Williams *et al.* 2006a). Thus, there may be extensive areas of treeless vegetation near or below the climatic treeline. Wimbush and Costin (1979b) and Costin *et al.* (2000) describe such treeless vegetation below the treeline as 'subalpine'. However, in such situations, the treeless plant communities of this high subalpine zone may be floristically and structurally similar to those above the treeline. On this basis, the treeless plant communities below treeline have also been described as 'alpine' (e.g. McDougall 1982; Walsh *et al.* 1984; Kirkpatrick 1989) and in this chapter we follow this latter convention for such treeless communities.

The distribution of Australian alpine ecosystems

Australian alpine ecosystems occur exclusively in the high mountain areas of south-eastern Australia and are contained within the single Interim Biogeographic Region 'Australian Alps' (AUA; Table 6.1). They also occur within a single Agro-climatic zone (B1, *sensu* Hutchinson *et al.* 2005; Fig. 6.2; Table 6.2). Vegetation

Box 6.2: Links between TERN and the core studies in alpine ecosystems

In 2012, each of the core study datasets featured in this chapter became part of the Long Term Ecological Research Network (LTERN) within the Terrestrial Ecosystem Research Network (TERN). However, one core alpine study, the International Tundra Experiment, which was established in 2003–04, is linked to the International Long Term Ecological Research network (ILTER, www.ilternet.edu), which was founded in 1993 (see Box 1.4, p. 15). The International Tundra Experiment is a major climate change experiment on alpine ecosystems, taking place on the Bogong High Plains in Victoria.



Figure 6.1: The alpine environment of the Bogong High Plains: (A) treeless vegetation above the treeline in summer; (B) the high subalpine environment in winter, with treeless vegetation in mosaic with stands of snow gum (*Eucalyptus pauciflora*) (photos by Colin Totterdell).

units within the National Vegetation Information System (NVIS) (Department of the Environment and Water Resources 2007) germane to alpine ecosystems are heathlands (MVG18), tussock grasslands (MVG19) and other grasslands, herblands, sedgeland and rushlands (MVG 21; Table 6.1).

The most extensive areas of alpine vegetation are found in the Snowy Mountains in New South Wales, the Brindabella Ranges on the border of the Australian Capital Territory and NSW, the Bogong High Plains and nearby peaks in Victoria, and the Central Plateau and south-west regions of Tasmania (Kirkpatrick 1989, 1997; Williams and Costin 1994; Crowden 1999; Costin *et al.* 2000; Williams *et al.* 2006a).

Australian alpine ecosystems encompass several plant communities, soil types, habitats and species. McDougall and Walsh (2007) identified 56 plant communities on the mainland, while up to 74 have been described for Tasmania (Kirkpatrick 1997). There are 10 major structural formations in the mainland Alps and the Tasmanian Alps (Kirkpatrick and Bridle 1999; Williams *et al.* 2006a; McDougall and Walsh 2007). These are coniferous heath, heathlands, alpine sedge-land, tall alpine herbfield, short alpine herbfield, grassland, bog and fen, and the specialised alpine formations feldmark and bolster heath. These structural types occur in a mosaic with each other, and with woodlands in the high subalpine zone. The major

Table 6.1: Classification and relative coverage of Australian alpine ecosystems

Classification	Relative coverage
Terrestrial Ecoregions of Australia (Department of Sustainability, Environment, Water, Population and Communities 2012b)	Montane grasslands and shrublands http://www.environment.gov.au/parks/nrs/science/pubs/ecoregions.pdf
Interim Biogeographic Regionalisation for Australia, version 7.0 (Department of Sustainability, Environment, Water, Population and Communities 2012a)	Australian Alps (AUA)
National Vegetation Inventory System (NVIS) (Department of the Environment and Water Resources 2007)	Heathlands (MVG 18); Tussock grasslands (MVG 19); Other grasslands, herblands, sedgeland and rushlands (MVG 21)
Natural Resource Management regions	ACT (Australian Capital Territory); Murrumbidgee (New South Wales); Southern Rivers (New South Wales); East Gippsland (Victoria); North-east (Victoria)

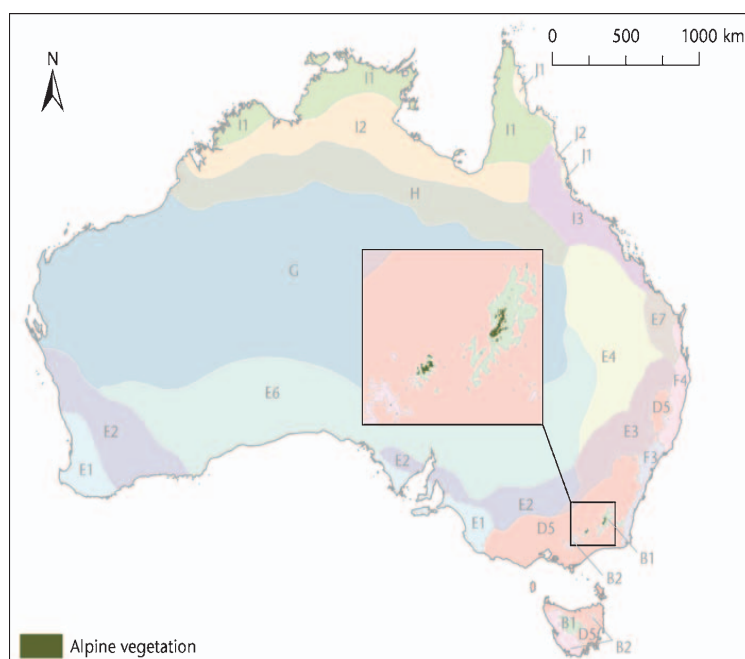


Figure 6.2: The extent of Australian alpine ecosystems relative to agro-climatic zones developed by (Hutchinson *et al.* 2005). See Table 6.2 for more information on the agro-climatic zones.

vegetation types of the Bogong High Plains were mapped at a scale of 1:15 000 in the early 1980s (McDougall 1982). The maps and associated data provided a sound basis for ongoing monitoring. Detailed accounts of the floristics, structural formations and the factors controlling their distribution are found in Williams and Ashton (1987a), Kirkpatrick and Bridle

Table 6.2: The single agro-climatic class (after Hutchinson *et al.* 2005) that coincides with all of Australia's alpine ecosystems, their approximate locations and common land uses

See Fig. 6.2 for a spatial representation of the agro-climatic zones. See Chapter 3 for a definition of the agro-climatic zones.

Code	Agro-climate	Location and land use
B1	Very cold winters with summers too short for crop growth	Alpine areas of NSW, ACT, Victoria and Tasmania. Water harvesting, hydroelectricity, tourism and nature conservation

(1999), Costin *et al.* (2000) and Williams *et al.* (2006a). On the Bogong High Plains, closed heathland predominates on the relatively steep, rocky, sheltered slopes, where alpine humus soils are shallow (<0.3 m deep). The shrubs are 1–2 m tall, with a canopy cover of >70%. In open heathland, shrubs and snow grasses are co-dominant and occur where the alpine humus soils are deeper than in closed-heath. Grassland occupies level ground on slopes and hollows, which may be subject to severe winds and frost, and where the alpine humus soils are deepest (generally up to 1 m). Short herbfields ('snow-patch vegetation') occur on steep, leeward, south-facing slopes where snow persists well into the spring or summer. Wetland complexes of heathlands, bogs and fens occupy valley bottoms, drainage lines and some stream banks, which are waterlogged for at least 1 month per year.

A fundamental feature of many Australian alpine ecosystems is the well-developed mantle of soil. The most widespread soil type, occurring on most geological substrata on well-drained terrain, is alpine humus soil. This is a friable, organic loam up to 1 m deep



Figure 6.3: Invertebrates of alpine ecosystems: (A) Chloropidae fly and moth on flowering head of *Brachyscome decipiens*. (B) thousands of Bogong Moths in a rock crevice (photo A by Michael Nash, B by Ian Mansergh).

(Costin 1954; Gibbons and Rowan 1993; Kirkpatrick and Bridle 1999). Peats, consisting almost entirely of organic matter, occur in waterlogged areas. All alpine soils in Australia are relatively low in clay, high in organic matter, highly acidic (pH 4–5; except on small areas of limestone), nutrient-poor and highly erodible.

The abundance and activity of the alpine fauna is regulated by the seasons (Green and Osborne 1994; Mansergh and Broome 1994; Mansergh *et al.* 2004; Williams *et al.* 2006a). Animals must cope with large seasonal variations in temperature and food supply, and deep winter snow. The fauna consists of seasonal immigrants, lower altitude species and alpine specialists. Highly mobile species (birds, bats and some insects) migrate to lower altitudes (Green and Osborne 1994). Less mobile species seek winter shelter either underground (reptiles) or beneath the snow (some mammals). Some species hibernate (e.g. the Mountain Pygmy Possum). Species diversity in the alpine zone is generally low compared with montane forested environments, and there are relatively few native terrestrial mammal species. Large vertebrate herbivores, such as macropods, generally avoid alpine areas of mainland Australia (Williams and Costin 1994), but occur in Tasmanian alpine vegetation (Bridle and Kirkpatrick 2001). The biota and ecosystems of the Australian Alps have not evolved in conjunction with grazing pressure from large vertebrate herbivores, especially ungulates (hard-hooved animals) such as

sheep, cattle, horses, pigs and deer (Costin 1954). The cool, moist environments of the Alps support reptiles and amphibians that have highly restricted geographical ranges (Clemann and Howard 2011), and several species are endemic. Invertebrates (Box 6.3; Fig. 6.3) constitute the majority of the alpine fauna and appear to be distinctive. However, there has been little detailed research on the taxonomy (Box 6.3) and ecology of the alpine invertebrate fauna, and the impact of different environmental factors on invertebrate diversity is currently unclear (Nash *et al.* 2013).

Conservation status

Most of Australia's alpine ecosystems are within the National Reserve System (NRS). The Mount Buffalo National Park is one of the oldest in Australia, with the first land set aside in 1898. Kosciuszko National Park in New South Wales and the Alpine National Park in Victoria are both large parks (690 000 ha and 650 000 ha, respectively). Thus, by definition, the primary land use for these ecosystems is nature conservation (Good 1992; Worboys and Good 2011). Because of the critical contribution that the Australian Alps make to the water resources of south-eastern Australia, protection of catchments has long been a primary land use objective, and one that is complementary with nature conservation (Costin 1954; Costin *et al.* 2000; Worboys and Good 2011). Monitoring of attributes describing soil, water and nature conservation values has been integral to the development of

Box 6.3: Alpine invertebrates

Australia's invertebrate alpine fauna is distinct from other global alpine systems, with Orthoptera (grasshoppers, crickets and katydids) and Hymenoptera (wasps, bees and ants) dominant in Australian mountains (Green and Osborne 1994). Other high-elevation arthropod orders found in the Australian alps that occur worldwide include: Plecoptera (stoneflies); Coleoptera (beetles); Lepidoptera (butterflies and moths; Fig. 6.3A); Diptera (flies); and Collembola (springtails) (Somme 1989).

Invertebrates are vital for facilitating the movement of energy and genes (both for fauna and floral systems) between and within alpine ecosystems. The best example of energy flow is the annual migration of Bogong Moth (*Agrotis infusa*, Fig. 6.3B) from the flood plains of central NSW to the mainland Alps, where the adults congregate and aestivate in huge numbers in rock crevices. They accumulate fat over winter and provide a major food for a variety of animals, including the Mountain Pygmy Possum.

Invertebrates can regulate structure, diversity and function of plant communities. Examples include pollination and the predation of seed (Pickering 2009) and damage to snowgrass tussocks (*Poa* spp.) by Swift and Case Moths. This natural disturbance allows the establishment of other species and life-forms within open heathland and grasslands (Chadwick 1966).

Diversity in Victorian alpine and subalpine grasslands (>1200 m above sea level) is often high and may be extremely localised in comparison to low elevation grasslands (<500 m asl). On the Bogong High Plains, species richness did not decline with increased elevation (Nash *et al.* 2013), which contrasts with findings from overseas studies (e.g. Wimbush and Costin 1979c; Wimbush and Forrester 1988; Lessard *et al.* 2011). For example, 18 species of Carabidae have been identified so far from the Victorian alps, where four species had been reported from the Victorian alpine or subalpine areas previously (Moore 1987) and nine species from above the treeline in Kosciusko National Park (Green 2002). In comparison, low-elevation grassland sites in western Victoria exhibit lower Carabidae diversity; seven species from one study (Nash *et al.* 2008) and 15 from another (Yen *et al.* 1994). Similarly, four species of alpine wolf spiders (Lycosidae) have recently been identified from the Bogong High Plains, including two new species, bringing the total number of known Australian alpine Lycosidae to six. Three species had been reported from four locations in Kosciusko National Park (Green 1988, 2002).

However, the diversity of ants (Formicidae), an important ecological engineer, does appear to decline with increasing elevation. On the Bogong High Plains, four species have been recorded (Nash *et al.* 2013). Studies from low-elevation studies show much higher diversity: 38 species from 20 vineyards (Chong *et al.* 2011) and 19 species from 29 western Victorian lowland grassland locations (Yen *et al.* 1994).

Stoneflies are an important faunal group. They are key indicators of water quality, with a high divergence of species within the key genera investigated. Three new alpine species within the genus *Riekoperla* have been identified examining larvae using molecular taxonomic techniques (Mynott *et al.* 2011). Furthermore, similar phylogeographic patterns from high altitude areas of the Australian Alps and the Strzelecki ranges have been observed between genetically distinct populations of stoneflies and mayflies (Mynott *et al.* 2011). One of the few invertebrate species listed on the EPBC Act is the endangered stonefly *Thaumatoperla alpina*, which may be locally abundant, but has a restricted distribution.

The few previous invertebrate studies carried out in other Australian subalpine areas (e.g. Green 2002) are clearly insufficient for a detailed understanding of local species diversity or function. Limited results point to a unique and largely undescribed invertebrate fauna in Australian alpine ecosystems, with some interesting patterns of diversity and distribution that may differ between taxonomic groups. A formal inventory of arthropods is long overdue for this region and should cover a wide variety of sites in order to maximise the chance of detecting patchily distributed rare species. The ability to apply established genetic techniques rapidly to abundant groups will illuminate underlying phylogeographic patterns and any barriers to gene flow that are vital for evolutionary processes. Knowledge of such processes will be vital to underpin conservation management in the face of climate change.

this scientific understanding of the ecology and management of alpine ecosystems (Good 1989).

The Australian Alps National Parks and Reserves were listed in November 2008 as a National Heritage Place (i.e. in the National Heritage List) under subsection 324C(3) of the Commonwealth *Environmental Protection and Biodiversity Conservation (EPBC) Act* (1999). Numerous plant communities and species in alpine ecosystems have been listed under both Australian Government and state government legislation. Fauna listed under the *Victorian Flora and Fauna Guarantee Act (1988)* (the Act) include Mountain Pygmy Possum; Alpine Egernia Skink (*Egernia*

guthega); Alpine Water Skink (*Eulamprus kosciuskoi*; listed as *Sphenomorphus kosciuskoi*); Alpine Tree Frog (*Litoria verreauxii alpina*); Alpine Stonefly (*Thaumatoperla alpina*). Plant species listed under the Act include Mountain Daisy (*Brachyscome* sp. 3; listed as *Brachyscome tenuiscapa*); Silky Snow-daisy (*Celmisia sericophylla*); Bogong Eyebright (*Euphrasia eichleri*); Cushion Rush (*Juncus antarcticus*); Bogong Apple-moss (*Bartramia subsymmetrica*; listed as *Bartramia bogongia*). Plant communities listed under the Act include the alpine bog community; the alpine snow-patch community; *Caltha introloba* herbland community; and fen (bog pool) community. Further details

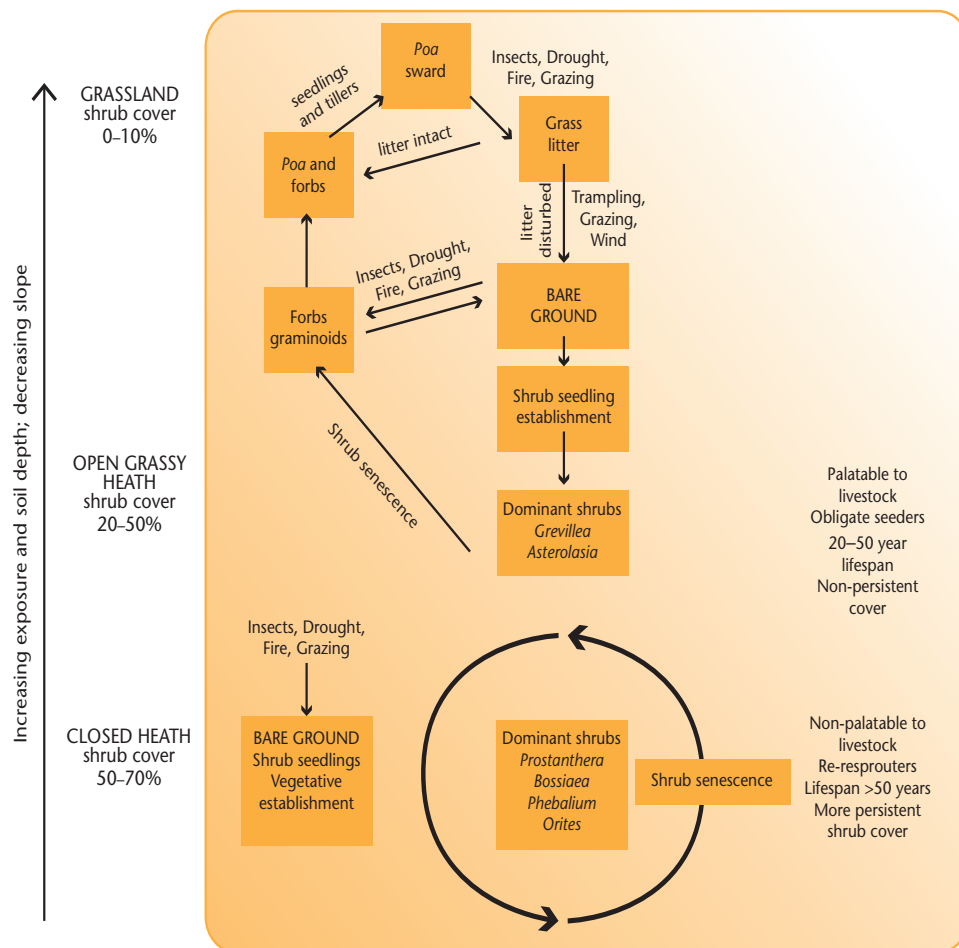


Figure 6.4: Conceptual diagram of dynamics of the grasslands and heathlands on the Bogong High Plains. These plant communities occupy >90% of the area of the Bogong High Plains, and their distribution is determined by gradients of exposure and mineral soil depth and rockiness. Snow-patch herbfields occur on steep slopes where snow persists well into the spring or even summer. Wetlands and fens occur where water accumulates and organic, peat soils form.

are available at http://www.dse.vic.gov.au/—data/assets/pdf_file/0014/103136/20101021_FFG_threatened_list_Oct_10.pdf and http://www.environment.gov.au/cgi-bin/sprat/public/publicspecies.pl?taxon_id=25289.

ECOSYSTEM DRIVERS AND THREATS IN ALPINE ECOSYSTEMS

Natural driving processes

Like all high altitude and high latitude ecosystems, alpine ecosystems are temperature limited. Frosts are frequent (>100 per year) and nocturnal temperatures near the ground on clear nights in autumn may be -20°C (Williams 1987; Williams *et al.* 2006a). Annual precipitation in alpine areas on the Australian mainland ranges from 1000 mm to ~ 2500 mm, much of which falls as persistent snow during winter. The distribution of the major plant communities is controlled by soil type, depth and fertility, moisture, geomorphology, topography, waterlogging, exposure to wind and frost, the persistence of snow and disturbance (Williams *et al.* 2006a).

Disturbance (*sensu* White and Pickett 1985) is a fundamental driver of the dynamics of Australian alpine vegetation and occurs at different scales and frequencies (Williams 1990). The alpine landscape is subject to recurrent, natural disturbances as a result of frost heave, soil movement on steep slopes, water

flow, seasonal drought, wind, fire and herbivory. Despite this recurrent disturbance, which is generally small-scale ($\sim 0.01\text{--}1\text{ m}^2$), most alpine plant communities usually produce a more or less complete cover of vegetation. Bare ground occurs in all plant communities, but its abundance is generally low (<5%). Soil can be moved by water, frost and wind following removal of vegetation. At the micro-scale, bare ground is integral to the regeneration cycles of obligate seeding shrubs such as *Grevillea australis* (Fig. 6.5; Williams and Ashton 1987b, 1988). However, at meso- and macro-scales, maintenance of natural, high levels of vegetation cover (as close to 100% as possible) is critical for catchment condition and water quality (Costin 1957; Costin *et al.* 2000).

The alpine landscape is also subject to periodic larger scale disturbances, in particular fire and long-term drought. Both have major effects on ecosystem dynamics. Recurrent drought is a feature of the climate of south-eastern Australia. Since the late-1800s, when reliable instrumental climate data were first collected, major multi-year droughts have occurred in 1895–1903, 1936–46 and 1996–2009, with occasional additional drought years in the alps (e.g. 1967–68, 1982–83). The years 1996–2009 constitute the driest period on record in south-eastern Australia (Ummenhofer *et al.* 2009; CSIRO 2010). During the drought of 1967–68, there was substantial mortality of the dominant snow-grasses in the Kosciuszko region of New South Wales. However, the death of the dominant snowgrass (*Poa*



Figure 6.5: *Grevillea*–*Poa* open heathland (foreground) on the Bogong High Plains. Open heathlands such as this occupy $\sim 25\%$ of the treeless vegetation of the Bogong High Plains (photo by James Camac).



Figure 6.6: Dead snowgrass, *Poa* spp., beneath Snowgum woodland (*Eucalyptus pauciflora*) on the Bogong High Plains following the drought of 2003–2006 (photo by Pip Griffin).

spp.) was associated with mass recruitment of other sub-dominant herbs such as *Craspedia* (Wimbush and Costin 1979c). During the recent, extended drought that commenced in the alpine area in 2003, very low levels of soil moisture have caused high mortality of the dominant alpine grasses (Griffin and Hoffmann 2012). The timing of long rain-free periods was more important than their duration in the Victorian Alps (Griffin and Hoffmann 2012), and these and/or cumulative rainfall deficits provide potential predictive frameworks for the effects of altered precipitation under projected climate change scenarios (warming and drying) for south-eastern Australia. Importantly, despite mortality of snowgrass, dead litter can remain fixed to the soil (Figs 6.4 and 6.6), thus offering the soil surface protection from wind, frost and rain (Wimbush and Costin 1979c; Scherrer and Pickering 2005).

Fire is another natural agent of disturbance in Australian alpine ecosystems (Kirkpatrick and Dickinson 1984; Wahren *et al.* 2001b; Williams *et al.* 2006a, b, 2008). Multiple lines of evidence indicate a fire frequency of about twice per century for both Snowgum woodland and treeless alpine communities, and that occasional extensive fires (e.g. 1939 and 2003) are a natural component of the alpine fire regimes (Leigh *et al.* 1987; Wimbush and Forrester 1988; Banks 1989; Williams *et al.* 2008).

Aborigines burnt parts of the high country in summer (Flood 1980), but the frequency or extent of such fires is not known. It is unlikely that Aboriginal people used broadcast fire ('fire stick-farming') in the alpine zone, if for no other reason than the major food species so typical of lower altitudes (e.g. kangaroos and wallabies) did not occur there (Williams *et al.* 2006a). Anthropological evidence (Mooney 2004; Zylstra 2006) supports this view. Graziers also deliberately burnt alpine vegetation to improve the quality and quantity of the fodder (Costin 1954; Leigh *et al.* 1987; Williams *et al.* 2008).

Alpine ecosystems were extensively burnt by the fires of January 1939, January 2003 and December 2006 – January 2007, in both New South Wales and Victoria (Fig. 6.7). In 2003, ~50% (6000 ha) of the Bogong High Plains burnt; heathland was clearly more flammable than grassland and herbfield. In the 2003 fires, ~87% of closed heathland was burnt,



Figure 6.7: Fire in New Species Gully, Bogong High Plains, January 2003 (photo by Henrik Wahren).

compared with ~60% of open heathland and 15% of grassland; snow-patch herbfields were mostly unburnt (Williams *et al.* 2006b). The alpine landscape exhibits a mosaic of fire frequencies – some patches may be burnt twice per century, whereas others remain unburnt for centuries (Williams *et al.* 2008).

Alpine vegetation is capable of vigorous regeneration after fire; where mass flowering is common in the grasses, shrub recruitment is stimulated and with most species re-establishing within weeks of fire, and being well established within 2 years (Wahren *et al.* 2001b; Walsh and McDougall 2004). However, bare soil is likely to take at least a decade to return to low, pre-fire levels. There is also variation in fire severity during large fires (Williams *et al.* 2006b; Camac *et al.* 2012). The dominant alpine heathlands on the Bogong High Plains appear to be resilient to variation in fire severity (Camac *et al.* 2012).

THREATENING PROCESSES

Land clearing for agriculture is not a threatening process in Australian alpine and subalpine landscapes. This is because of the harsh climate, which makes the land unsuitable for clearing, cropping and improved pastures, and because the land has remained principally in public ownership. Judging from aerial photos from the 1940s, there was some clearing of Snowgum woodlands in high subalpine regions of the Kosciuszko National Park (Keith McDougall *pers. comm.*). There has also been locally intensive clearing of vegetation and soils in the past 70 years for hydroelectric project

and alpine resort development. Invasion by weeds and feral animals, soil disturbance accompanying development for tourism are current threats, and climate change will increase pressure on the natural alpine environment in the coming century.

Livestock grazing and degradation and loss of habitat by feral horses are both listed as a 'potentially threatening process' under the Victorian *Flora and Fauna Guarantee Act 1988* (http://www.dse.vic.gov.au/-/data/assets/pdf_file/0016/103138/Updated-FFG-processes-list-February-2012.pdf).

Australian alpine ecosystems evolved in the absence of grazing pressure from large hooved vertebrate herbivores and these ecosystems are not pre-adapted to livestock grazing (Costin 1954). It is not surprising, then, that a century or more of free-range livestock grazing has had a substantial impact on Australian alpine ecosystems. Damage to vegetation and soils from grazing and associated prescribed burning was first observed in the late 19th century (as noted previously; Hancock 1972). By the 1930s and 1940s, there was considerable concern over the impact of livestock on soils and vegetation. At the highest elevations (above 1800 m), damage to vegetation and soils from grazing and associated burning off was substantial (Costin 1954; Australian Academy of Science 1957). Grazing ceased on the highest peaks of the Kosciuszko area in 1944 and in the entire Kosciuszko National Park by the late 1960s (McDougall *et al.* 2013). In the mid-1940s, burning off on the Bogong High Plains was banned, and the number of stock and the duration of

the grazing season were regulated (Wahren *et al.* 1994). Grazing ceased in the Victorian Alpine National Park in 2005. Grazing also changed historical fire regimes; deliberate burning by graziers resulted in an increase in the frequency and likely extent of fires (Costin 1954; Leigh *et al.* 1987; Banks 1989; Zylstra 2011).

The impacts of livestock grazing on Australian alpine ecosystems have been extensively studied and documented. They include selectivity of both species and plant communities, trampling, deposition of dung and urine, and the spread of weeds. Cattle prefer to graze in plant communities such as herbfields, grasslands and open heathlands (Fig. 6.8A) (van Rees and Hutson 1983); they tend to avoid dense, closed heathlands. The common snowgrasses (*Poa* spp.), major tall herbs such as *Celmisia* spp. and *Craspedia* spp. and some shrubs (*Grevillea australis* and *Asterolasia trymalioides*) are major dietary components (van Rees and Holmes 1986). Although not a preferred grazing community, wetlands have been used by domestic stock both for drinking water and grazing of palatable species, especially sedges; wetlands have been also deliberately burnt by graziers (Costin 1954). As a consequence of grazing, vegetation cover is reduced, species composition may change and bare ground increases, leading to enhanced soil loss and declines in catchment condition (Costin 1954; Australian Academy of Science 1957; Costin *et al.* 1960; Wahren *et al.* 1994; Williams *et al.* 2006a; McDougall *et al.* 2013). It is popularly hypothesised that grazing mitigates fire risk – or, as the popular slogan would

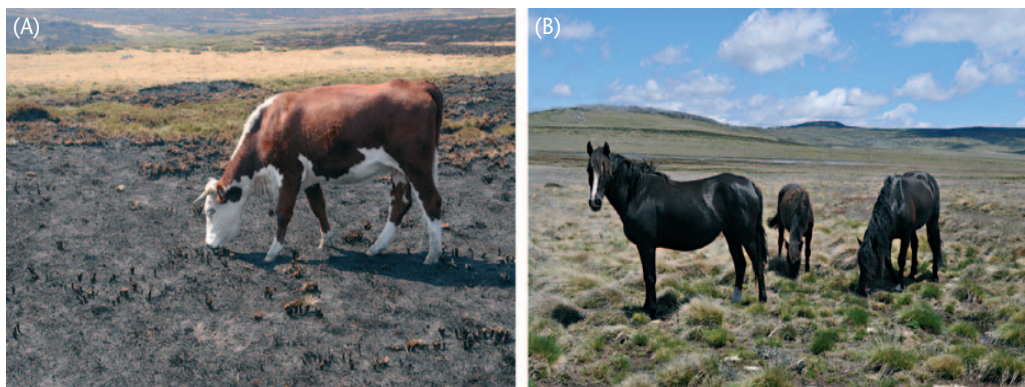


Figure 6.8: (A) Cow grazing on grassland burnt by the 2003 fires, Mount Cope region, Bogong High Plains; (B) feral horses in Pretty Valley, 2010 (photo A by Henrik Wahren, B by James Camac).

have it, 'alpine grazing reduces blazing' (House of Representatives Select Committee 2003). However, there is no scientific evidence that grazing by domestic livestock reduces fire occurrence or severity in Australian alpine ecosystems (Williams *et al.* 2006b, 2008). Moreover, the combination of livestock grazing and fire, deliberate or otherwise, has long been known to threaten the conservation of soils and biota in Australian alpine ecosystems (Costin 1954).

The second half of the 20th century saw the expansion of land uses, in addition to grazing, many of which have brought potential threats to alpine ecosystems. The development of hydroelectricity in the 1950s and 1960s in the New South Wales and Victorian Alps led to alteration of drainage patterns, removal of soil for dam and road constructions, and the use of exotic plant species to stabilise exposed soil. Ski resort development accelerated in the 1970s and has continued apace. This has led to substantial soil and vegetation disturbance accompanying the erection of buildings and ski lifts and the development of ski slopes. Exotic plant species also have increased in abundance. Although the current proportion of the alpine flora that is exotic is still relatively small, compared with the lowland flora, climate change, fire and more frequent disturbance associated with resort development is likely to increase the proportion and impact of exotic species in alpine ecosystems in the future (McDougall *et al.* 2005). Management and control of exotic species is likely to place substantial resource constraints on conservation management in alpine areas. Feral animals such as horses (Fig. 6.8B) (Nimmo and Miller 2007), pigs and deer (particularly Sambar Deer *Rusa unicolor*) are increasing in numbers and moving to higher altitudes. With declining snow cover, these exotic, invasive species pose present and accelerating threats to alpine ecosystems (Mansergh *et al.* 2004).

OVERVIEW OF CORE STUDIES SHOWCASED

There is a rich history of research in the Australian Alps. The ecology of alpine ecosystems has been examined over the past 140 years through monitoring, experiments and detailed observations – to better

understand soils, vegetation dynamics, land condition, fauna, disturbance regimes, the ecology and management of exotic species and the implications of climate change. The cool alpine climate results in slow growth and consequently slows rates of ecological change. Long-term monitoring of responses to various influences and interactions are therefore central to alpine research. Ecological disturbances, both natural and human-induced, have been a major focus of this long-term research. Disturbances of greatest concern to researchers and managers include the effects of fire and hooved animals on soils and vegetation, and the clearing of vegetation and soil for infrastructure developments.

The following four core studies have at their centre observations and principles gleaned from this critical long-term monitoring. Without the long-term perspective, key insights may have been overlooked. The four core studies investigate: long-term change in vegetation composition and structure; the ecology and management of the rare Mountain Pygmy Possum; post-fire regeneration of vegetation; and potential responses to climate change.

Long-term monitoring in Australian alpine ecosystems has been located at many hundreds of sites in NSW, the ACT, Victoria and Tasmania. The sites particular to the four core studies from the Victorian Alps featured in this chapter are mapped in Fig. 6.9; features are summarised in Table 6.3. Together, they illustrate how long-term ecological research has developed from its beginnings in the 1940s, and consider what climate change might bring in the future.

History of ecological monitoring in alpine ecosystems

Monitoring commenced in the 1940s in Victoria and the 1950s in NSW (Carr and Turner 1959a; Wimbush and Costin 1979a, b, c; Wahren *et al.* 1994). Plots were first established on the Bogong High Plains in 1944 and 1946 by Mrs Maisie Carr (nee Fawcett) and Prof John Turner from the University of Melbourne. These plots were representative of the major grassland and heathland communities, and included grazed and ungrazed plots.

With increased interest in the Alps (e.g. Johnson 1974), and public land-use questions in general,

throughout the 1960s and 1970s (Land Conservation Council of Victoria 1977), issues and hypotheses raised by these early studies formed the basis of additional studies. Comprehensive vegetation mapping commenced in the early 1980s (McDougall 1982), providing landscape context for monitoring and experimental studies. The Carr and Turner plots were supplemented with additional monitoring sites established in grassland at numerous locations in 1979–80.

Experimental investigations of ecological processes also commenced in the 1980s on the Bogong High Plains. These include shrub regeneration (Williams and Ashton 1987b) and the diet and behaviour of cattle (van Rees and Hutson 1983; van Rees and Holmes 1986). Over the ensuing decades, additional sites were established and at present there are more than 100 plots across the Victorian Alpine National Park, most of which are on the Bogong High Plains and adjoining peaks. These plots are located in all of the major alpine plant communities in Victoria: grassland, open- and closed heathland, wetlands, boulder-field heathland and snow-patch herbfields (Wahren *et al.* 1994, 2001a, c). Long-term vegetation change is discussed in Core Study 1.

There was a major discovery in the Australian Alps in 1966: a single, male Mountain Pygmy Possum hereafter *Burramys*). Previously known only from fossils, and thought to be extinct, the animal was found at the University Ski Club, near Mount Hotham. Other individuals and small populations of the species were subsequently found in the Kosciuszko area (NSW), and elsewhere in the Victorian Alps. *Burramys* is a small, rare mammal and the only Australian mammal restricted to the alpine and subalpine environment. It is listed as Endangered throughout its range (Mansergh and Broome 1994; Heinze *et al.* 2004; Heinze 2010). Considerable research has been devoted to understanding its ecology, genetics and management. Conservation management strategies for *Burramys*, informed by long-term monitoring, include: protection of critical habitat in ski resorts; recovery following the fires of 2003 and 2007; provision of innovative habitat and experimental reconnection of populations (Mansergh *et al.* 1989; Mansergh and Scotts 1989; Weeks *et al.* 2012). There are also major monitoring plots for other fauna in alpine

ecosystems, which have allowed assessment of faunal responses to variation in climate and disturbance (Green and Sanecki 2006). Monitoring of *Burramys* populations is discussed in Core Study 2.

In 1998, 2003 and 2006–7, there were major fires in the Australian Alps. Given the rarity of landscape-level fire in alpine ecosystems, both globally and nationally, these fires presented researchers and managers with a golden opportunity to examine the place of such fires in the general fire regime of the Australian Alps, and to measure post-fire recovery of both flora and fauna in long-term plots. Monitoring plots to examine post-fire regeneration were established following the 1998 fires on Wellington and Holmes Plains (Wahren *et al.* 2001b) and following the 2003 fires on the Bogong High Plains (Williams *et al.* 2006b; Camac *et al.* 2012). Data from these plots have been used to examine long-term vegetation dynamics, the recovery of vegetation following the cessation of grazing, patterns of burning in different plant communities, and post-fire regeneration in relation to fire severity. Post-fire vegetation monitoring is discussed in Core Study 3.

In 2003–04, a major climate change experiment – the Australian Tundra Experiment – commenced on the Bogong High Plains as part of the International Tundra Experiment (ITEX; Molau and Mølgaard 1996). A series of small ($\leq 2 \text{ m}^2$), open-topped, clear-perspex chambers (OTCs) was established around plant communities, to passively raise ambient temperatures by 1–2°C, compared with control, unwarmed plots. This experiment is designed to test the effects of experimental warming on: plant phenology and growth; plant and invertebrate species diversity and community composition; reproductive output and fitness; and soil nutrient dynamics (Jarrad *et al.* 2008, 2009; Hoffmann *et al.* 2010). Climate change and long-term monitoring is discussed in Core Study 4.

In association with the climate change experiment, complementary experiments were established to determine: the capacity of different plant species to adapt genetically to warming (Byars *et al.* 2007; Byars and Hoffmann 2009); patterns of gene flow in the landscape affecting adaptive capacity (Walsh *et al.* 1984; Byars *et al.* 2009); the evolutionary uniqueness of alpine vegetation (Griffin *et al.* 2011); and the effects of drought on alpine grasses (Griffin and Hoffmann 2012).

Table 6.3: Summary details of the four core studies of long-term research in Australian alpine ecosystems, featured in this chapter

Note that the post-fire vegetation plots (Core Study 3) are a subset of the long-term vegetation plots (Core study 1)

Plot network/ core study name	Major vegetation group	NRM	Data custodian	Data type (fauna/flora/ vegetation structure)	Spatial extent	No. of plots	Plot size (ha)	Start year	Current status	Temporal revisit
1. Victorian Alpine Network; Long-term vegetation plots	Heathlands (MVG 18) Tussock grasslands (MVG 19) Other grasslands, herblands, sedgeland and rushlands (MVG 21)	ACT (Australian Capital Territory); Murrumbidgee (New South Wales); Southern Rivers (New South Wales); East Gippsland (Victoria); North-east (Victoria)	Research Centre for Applied Alpine Ecology, La Trobe University (Papst, Wahren, Williams, Morgan)	Vegetation composition and structure	100 km ²	76	0.05–0.1	1946	active	2–10 years
2. Victorian Alpine Network; Burrumbys sites	Heathlands (MVG 18) Tussock grasslands (MVG 19) Other grasslands, herblands, sedgeland and rushlands (MVG 21)	ACT (Australian Capital Territory); Murrumbidgee (New South Wales); Southern Rivers (New South Wales); East Gippsland (Victoria); North-east (Victoria)	Dean Heinze and Ian Mansergh vertebrate ecologists.	Small Mammal population numbers; sex, age, weight	400 km ²	12	0.5	1982	active	1–5 years

Table 6.3: (Continued)

Plot network/ core study name	Major vegetation group	NRM	Data custodian	Data type (fauna/flora/ vegetation structure)	Spatial extent	No. of plots	Plot size (ha)	Start year	Current status	Temporal revisit
3. Victorian Alpine Network; post-fire vegetation plots	Heathlands (MVG 18) Tussock grasslands (MVG 19) Other grasslands, herblands, sedgeland and Rushlands (MVG 21)	ACT (Australian Capital Territory); Murrumbidgee (New South Wales); Southern Rivers (New South Wales); East Gippsland (Victoria); North-east (Victoria)	Research Centre for Applied Alpine Ecology, La Trobe University (Wahren, Papst, Williams)	Vegetation composition and structure	100 km ²	24	0.05–0.1	1998	active	2–10 years
4. Victorian Alpine Network; Australian Tundra Experiment and Phenology sites	Heathlands (MVG 18) Tussock grasslands (MVG 19) Other grasslands, herblands, sedgeland and rushlands (MVG 21)	ACT (Australian Capital Territory); Murrumbidgee (New South Wales); Southern Rivers (New South Wales); East Gippsland (Victoria); North-east (Victoria)	Genetics Dept, University of Melbourne; Research Centre for Applied Alpine Ecology, La Trobe University (Hoffmann, Wahren)	Microclimate; Vegetation composition, structure, growth, phenology; invertebrate assemblages	0.1 km ²	22	0.1–1	2003	active	1–2 years

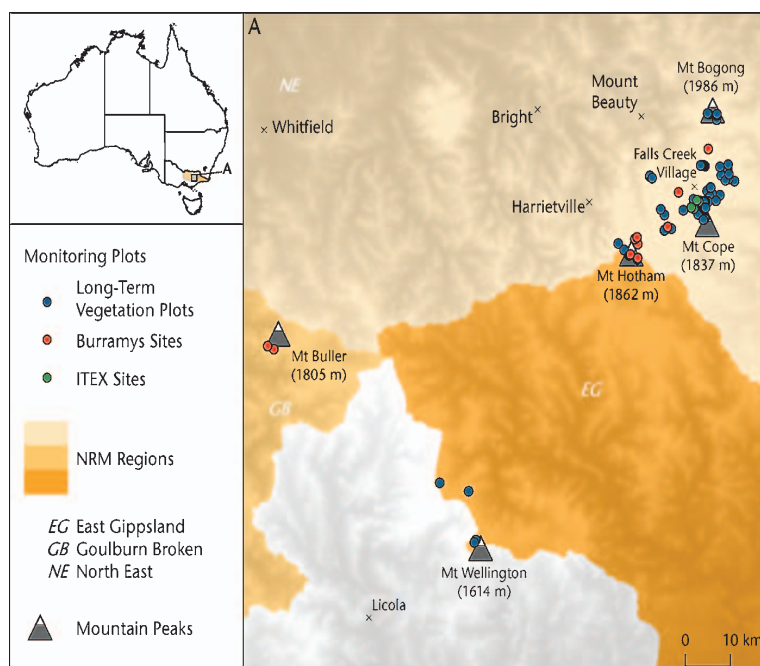


Figure 6.9: The location of the four core studies in alpine ecosystems. 1. Long-term vegetation monitoring plots, Bogong High Plains and elsewhere. 2. Mountain pygmy possum (*Burramys*) monitoring sites. 3. Post-fire monitoring plots (a subset of the long-term vegetation monitoring plots). 4. The climate change (Australian Tundra Experiment) sites.

The plots encompass different species and communities, and cover a wide geographic range, both in latitude and altitude (Fig. 6.9). We recognise that there are also numerous monitoring sites in alpine ecosystems in NSW (Good 1989, 1992; Scherrer and Pickering 2005) and Tasmania (Bridle and Kirkpatrick 2001). These are important monitoring sites, but a detailed discussion of them is beyond the scope of this chapter. However, some pertinent findings are presented in feature boxes.

TRENDS IN ENVIRONMENTAL CHANGE AND BIODIVERSITY IN ALPINE ECOSYSTEMS

In this section we discuss the design and observed trends of the four core studies. We highlight the dynamics of vegetation change, how knowledge of population dynamics and genetics have helped in the conservation of Mountain Pygmy Possum, the role of

fire in alpine ecosystems, how alpine ecosystems respond to landscape-scale fires and how climate change may affect alpine ecosystems.

Core Study 1. Long-term vegetation monitoring plots

The plots established on the Bogong High Plains in the 1940s by Carr and Turner are known as the 'Rocky Valley' and 'Pretty Valley' plots (Fig. 6.10A, B). They were established 'partly to determine the status of the communities and partly to investigate the effects of cattle grazing' (Carr and Turner 1959b). From the outset, the plots were designed for long-term ecological research and monitoring. There is one grazed and one ungrazed plot in each of the two vegetation communities (Fig 6.10B). The ungrazed plots are located inside fences that exclude stock (Carr and Turner 1959a, b; Wahren *et al.* 1994). Each plot is 0.05–0.1 ha in area, with each plot having 600–1000 point quadrats along fixed transects. From the point quadrats,



Figure 6.10: Long-term experimental plots on the Bogong High Plains. These plots were established by Mrs Maisie Carr and Prof John Turner in 1946–47. In each case, the fences exclude domestic stock. (A) Rocky Valley plots in 1954; (B) Pretty Valley plots in 1993. Ungrazed plot on left of photo; grazed plot on the right (photo A by Alec Costin, B by Henrik Wahren).

botanical composition and ground cover (cover of litter, bare ground and density of overhanging cover) are determined. Measurements were taken annually from 1945/6–1951, then once or twice per decade. The most recent sampling was in 2013. There were parallel developments in the Kosciuszko region of NSW. However, the first long-term monitoring plots in that region – several experimental grazing plots and numerous permanent transects – were not established until the late 1950s (Wimbush and Costin 1979a, b, c).

Carr and Turner (1959a, b) describe the plots and present data from 1947 to 1958. Wahren *et al.* (1994) describe the main changes at these plots from 1945–6 to 1994. At Pretty Valley, cattle grazing reduced the cover of several tall forbs (e.g. *Celmisia* and *Craspedia* spp.; Fig. 6.11) and short shrubs (e.g. *Asterolasia trymalioides*). On the ungrazed plot, these species increased in cover over time. Subsequent analyses of diet selection showed that all three species are highly palatable to cattle (van Rees and Holmes 1986). The amount of bare ground and loose litter was consistently and significantly greater over time on the grazed compared with the ungrazed plot (Fig. 6.12). The cover of the taller shrubs, such as *Phebalium squamulosum* and *Prostanthera cuneata* at Rocky Valley and *Grevillea australis* at Pretty Valley, all increased in both grazed and ungrazed treatments. This increase in the cover of the taller shrubs at both sites was primarily a consequence of shrub regeneration following the 1939 bushfires that burnt much of the Bogong High Plains.

The grassland monitoring plots established since 1979 are designed to investigate the state of the grassland across the Bogong High Plains and complement the Pretty Valley plots established in the 1940s. At present there are 17 such sites and include some sites burnt in 2003. Each site is sampled using 500 point quadrats along permanent transects distributed over an area of ~0.5 ha. From these point quadrats, vegetation composition, the amount of bare ground and the density/quality of cover is determined (Fig. 6.13). Complementary experimental work on the diet and behaviour of cattle (van Rees and Hutson 1983; van Rees and Holmes 1986), and vegetation dynamics (Williams and Ashton 1988) allowed strong inferences regarding grazing effects on alpine grasslands and heathlands to be made (Figs 6.11 and 6.12) (Wahren *et al.* 2013).

Importantly, the grazing treatment at the Pretty Valley and Rocky Valley sites is not replicated within communities – there is only one grazed and one ungrazed plot in each of the grassland and heathland sites. However, the variation in the cover of key species over time detected at the additional monitoring plots has allowed the patterns quantified over time at these plots to be interpreted at the landscape scale (Wahren *et al.* 1994).

Numerous additional vegetation monitoring plots have been established in other plant communities on the Bogong High Plains. These include 13 plots in wetlands and 35 in snow-patch vegetation. Additional plots are used to monitor weed invasions

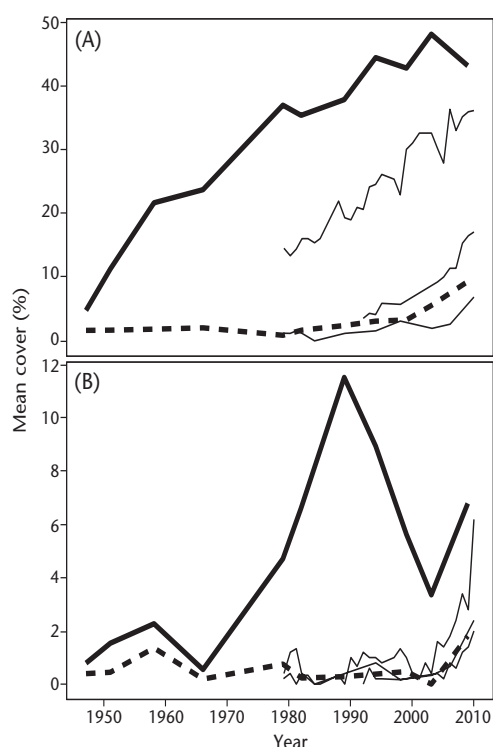


Figure 6.11: Change in percentage cover of (A) *Celmisia pugioniformis* and (B) *Craspedia* spp. from 1947 to 2010 at monitoring sites in alpine grassland on the Bogong High Plains, Victoria. The bold lines represent changes at the Pretty Valley plots established by Carr and Turner in 1946; ungrazed plot, solid line; grazed plot broken line. The fine solid lines (grey) represent changes in the same species at three additional grassland monitoring sites, with a similar sampling density to the Pretty Valley plots. Two of these were established in 1979 and one in 1992.

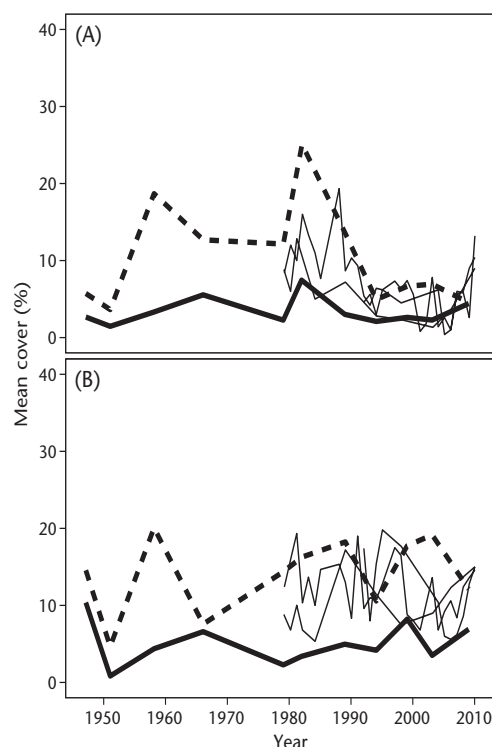


Figure 6.12: Change in percentage cover of (A) bare ground and (B) poor-quality ground cover (cover class 3 of (Wahren *et al.* 1994) from 1947–2010 at monitoring sites in alpine grassland on the Bogong High Plains, Victoria. The bold lines represent changes at the Pretty Valley plots established by Carr and Turner in 1946; ungrazed plot, solid line; grazed plot, broken line. The fine solid lines (grey) represent changes in the same species at three additional grassland monitoring sites, with a similar sampling density to the Pretty Valley plots. Two of these were established in 1979 and one in 1992.

along roadside corridors and the rare plants *Oreomyrrhis brevipes* and *Plantago glacialis*. There are also monitoring plots at other locations in the Victorian Alps, such as the Dargo High Plains (four plots), on Wellington and Holmes Plains (11 plots, established in 1991 and 1998; Wahren *et al.* 2001b; Williams *et al.* 2012) and in the Kosciuszko region of NSW (see Box 6.4).

Core Study 2. Monitoring populations of the Mountain Pygmy Possum (*Burramys*)

In the late 1970s, potential impacts of the expanding ski industry led to the first systematic survey of the Mountain Pygmy Possum (Fig. 6.14A) to quantify the

habitat requirements of the species (Gullan and Norris 1979). Within an original grid, a smaller configuration of replicated sample sites (0.2 ha site – 60 trap sites × 3 days) was developed and this methodology has been used consistently thereafter (Mansergh 1984). The monitoring program uses ‘capture–mark–recapture’ trapping protocols, along with the CAPTURE program to estimate population parameters (details in Mansergh 1984; Heinze 2010). Vegetation quadrats have been surveyed for all sites since 1990. Hair samples (for genetic analysis) have been routinely collected. Populations have been monitored regularly (annually to biennially) at most sites, and annually since the early 1980s at sites in the Mount

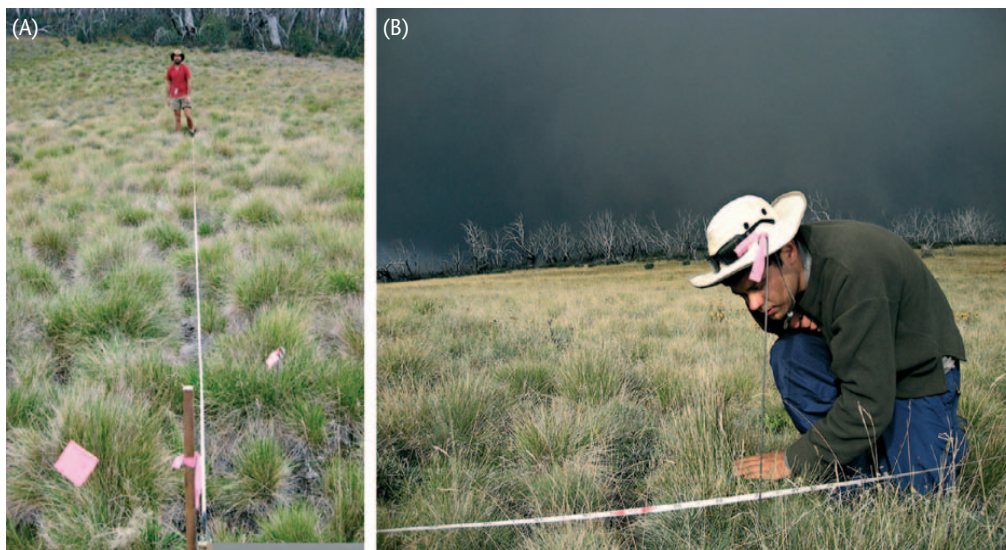


Figure 6.13: Example of a long-term, permanent transects in alpine grassland vegetation. Such transects are used to quantify vegetation composition and cover using point quadrats. (A) Grassland transect at Holmes Plain; (B) grassland transect on Bogong High Plains (photo A by James Camac, B by Sarah Bartlett).

Box 6.4: Alpine and subalpine range transects and photoquadrats at Kosciuszko, NSW

Long-term monitoring plots were established in the 1950s in the Kosciuszko region of NSW. Transects were monitored from 1957 to 1979; measurements were taken of species composition and ground cover conditions along permanent transects using point quadrats. Trends over this period were reported in Wimbush and Costin (1979b, c). Importantly, they were revaluated in the early 2000s (Scherrer and Pickering 2005). The transects were designed to examine effects of removal of grazing over decadal periods. As with the Bogong High Plains plots, the Kosciuszko plots were established explicitly to be long-term.

Experimental studies that complemented the monitoring studies were also established in the 1960s. Wimbush and Costin (1979a) report on a 14 year manipulative grazing experiment with various other experiments examining the factors affecting soil erosion undertaken in the 1950s and 1960s (Costin *et al.* 1960, 2000).

Monitoring on these plots showed that the main effect of grazing was to reduce the vegetation cover and biomass in general, particularly the cover of palatable forbs. In so doing, grazing prevented or slowed natural regeneration. This resulted in persistently higher levels of bare ground compared with ungrazed situations. Removal of grazing can reverse these trends (Wimbush and Costin 1979b, c)

Increases in shrub cover on subalpine range transects were generally proportional to the amount of bare ground initially exposed. These long-term studies also demonstrated substantial inter-annual fluctuations in the cover of major life forms due to climatic variability, especially drought (Wimbush and Costin 1979c). This was an early demonstration that drought was a fundamental factor in the dynamics of Australian alpine ecosystems.

Together, the monitoring and experiments demonstrated: the highly selective nature of grazing of domestic stock; the fundamental importance of maintaining high levels of vegetation cover for catchment protection purposes; and the threat that livestock grazing poses to nature, soil and water conservation purposes in alpine ecosystems. Critically, the trends detected over time at both monitoring and experimental sites at Kosciuszko were very similar to those detected using similar monitoring protocols in similar vegetation types on the Bogong High Plains.

Higginbotham–Mount Hotham region. Research began in NSW in 1981 (Caughley 1986) and led to the establishment of monitoring sites on the Main Range of Kosciuszko National Park, which have been observed annually since 1986 (Broome 2001). After the discovery of a third, genetically distinct population at Mount Buller in Victoria, monitoring began there in 1996 (Heinze and Williams 1998). The extensive alpine fires in 2003 and 2007 triggered a major effort to examine effects of this large-scale disturbance on all known populations several years post fire (Heinze 2010). There are now over 70 plots across alpine habitat in Victoria and additional plots in New South Wales.

The aims of the monitoring program are to: develop and implement a conservation management plan for the species; discover and secure populations outside ski resorts (e.g. on the Bogong High Plains); monitor population levels; provide evidence of sustainable land use within resorts; and to gauge the effects of extreme events such as floods (1988) and fires (2003 and 2006–2007) and provide control sites for innovative conservation management such as the genetic rescue of the Mount Buller population (see below; Mansergh *et al.* 1989; Weeks *et al.* 2012). New monitoring sites have emerged as new information has become available. For instance, air photo interpretation in the 1990s indicated potential suitable boulder-field habitat (Fig. 6.14b) for additional trapping. This approach led to the discovery of small, satellite colonies within the meta-population on the Bogong

High Plains (Ruined Castle, Basalt Hill, Pretty Valley West) and expansion of monitoring plots.

Monitoring has been successful in detecting changes in populations over time, and in determining survival, mortality, genetics and the structure of local populations. The total population nationally is ~2500 adults. Population genetics studies were initiated by Osborne *et al.* (2000) and a detailed analysis was undertaken by Mitrovski *et al.* (2007). These studies have shown that *Burramys* occurs in three genetically distinct populations (Mansergh and Scotts 1989; Osborne *et al.* 2000; Broome 2001; Mitrovski *et al.* 2007). Two are in Victoria, (Bogong High Plains region and Mount Buller) and one in New South Wales (Kosciuszko National Park). Some local populations can be as small as a few individuals while others may support hundreds of individuals. Populations fluctuate in size from year to year. Monitoring has also quantified the fundamental habitat and life history characteristic of the species. Males and females use separate habitats and typically occur in peri-glacial boulder fields and associated dense heathlands. This habitat is cool in summer and insulated in winter, and is also the critical habitat through which males move to and from female habitat during the breeding season. Critical foods include the Bogong Moth (*Agrotis infusa*; see Box 6.3) and fruit of the Mountain Plum Pine *Podocarpus lawrencei*. *Burramys parvus* is the only marsupial known to both store food and hibernate (Mansergh and Broome 1994).



Figure 6.14: (A) *Burramys parvus* the Mountain Pygmy Possum; (B) typical *Burramys* habitat, boulder-field heathland, Charlotte Pass, Kosciuszko National Park, NSW (photo A by Timothy Arch, B by Linda Broome).

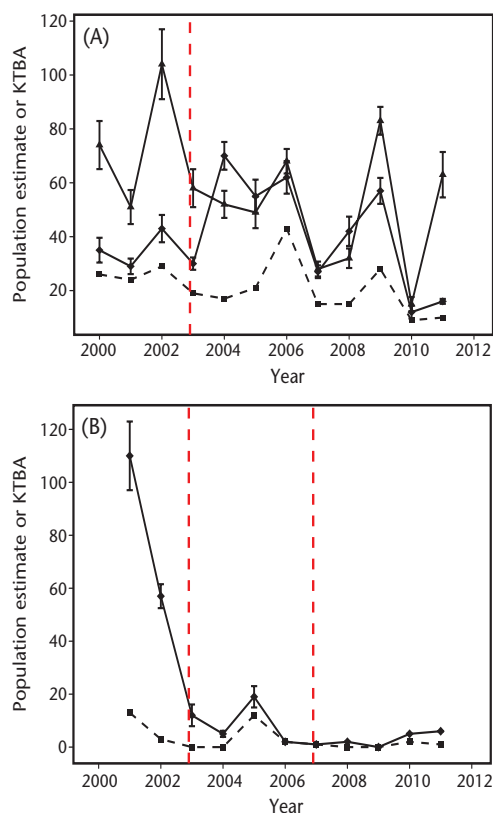


Figure 6.15: Trends in the numbers of *Burramys parvus* males and females at two monitoring sites in Victoria, 1999–2011: (A) Mount Higginbotham; (B) Mount McKay. Error bars represent 95% confidence intervals (KTBA: known to be alive). Vertical red dotted lines indicate fires in January 2003 at Mt Higginbotham, and in January 2003 and January 2007 at Mt McKay.

Burramys is a highly seasonal breeder (October–November), is polyoestrous and bears more young than available teats (four; supernumerary). After a short (14 day) gestation, young are weaned after 4–6 weeks in the natal nest. Sex ratios are at parity at birth but become skewed towards females in the breeding season because survival of males post-hibernation is reduced (Heinze *et al.* 2004). Hibernating over winter, adult females may live up to 12 years (it is the longest lived small terrestrial mammal known) and where resources are highly clumped, their social organisation has been described as female resource polygyny (Mitrovski *et al.* 2008). Adult females are polygamous and remain sedentary in habitat of high food

availability and protective resources (Mansergh and Scotts 1989). Males migrate annually into these areas, beneath boulder fields and dense heath, to mate and then vacate to peripheral areas of lesser food and shelter resources. Males may live for 5 years. At lower densities, this form of social organisation may weaken.

Monitoring both before and after the 2003 and 2006 bushfires on the Bogong High Plains has shown that populations of *Burramys* can persist in the landscape despite widespread fire (Williams *et al.* 2008, 2012; Heinze 2010), for example at Mount Higginbotham (Fig. 6.15A). This is potentially because the core habitat (boulder fields) offers refuge from fire, and a major food source over summer, the Bogong Moth, aestivates among rocks in large numbers over summer (Mansergh and Broome 1994). Although the *Podocarpus* overstorey may burn, the substratum and food sources provide buffering from fire in the alpine zone. Moreover, *Burramys* can use unburnt patches of heathland as temporary refugia and connectivity pathways for recolonisation (Williams *et al.* 2008). However, numbers plummeted at the Mount McKay site (Fig. 6.15b). The heathland at this site was burnt by both the 2003 and 2007 fires, and no *Burramys* were trapped in 2009 (Heinze 2010). A few individuals have been trapped since 2009, pointing to a partial population recovery and the reliance on dispersal and recolonisation with genetic input from other colonies. Recovery from fire can be complicated by predation pressure from Red Foxes and feral cats (e.g. at Blue Cow at Kosciuszko).

At Mount Buller, the population collapsed due to habitat destruction and fragmentation within the resort, resulting in a dramatic loss of genetic variation (Mitrovski *et al.* 2008) and imminent extinction of that genetically distinct population. In 2010 and 2011, translocation of males from Mount Higginbotham allowed wild cross breeding to restore genetic diversity to the Mount Buller population – an Australian first for this cost-effective methodology to make isolated populations more genetically resilient (Weeks *et al.* 2012).

Core Study 3. Post-fire monitoring plots

A subset of the long-term vegetation monitoring plots (described in Core Study 1 above) was established in the Victorian Alpine National Park following the fires of 1998 on Holmes and Wellington Plains, and the

2003 fires on the Bogong High Plains. Some plots were pre-existing and others were established within weeks of the fires in both grassland and heathland, and include some in unburnt vegetation. The aim of the monitoring program at these sites was to document: (1) the rate of regeneration of vegetation cover; (2) the modes of regeneration of the major species (e.g. whether vegetative or by seed or both); and (3) post-fire patterns of vegetation composition and diversity. The protocols were similar to those used for the long-term vegetation monitoring sites on the Bogong High Plains. There are multiple sites, all geo-located, with replicate permanent transects within sites. Point quadrats are used to determine vegetation composition and structure. The post-fire monitoring sites on the Bogong High Plains were established in 2003 in both burnt and unburnt heathland and grassland, with three replicates in each (C-H Wahren *pers. comm.*). In addition to these sites, 400 sample points were established on the Bogong High Plains immediately after the 2003 fires, in grassland, closed heathland (Fig. 6.16), open heathland and snow-patch herbfield. The patterns of burning (burnt/unburnt) and severity of burning within heathland were determined from these geo-located sample points (Williams *et al.* 2006b). In 2008, a subset of 80 sample points (40 in open heathland; 40 in closed heathland) were also revisited and 50 m transects established to examine the effect of variation in fire severity on heathland regeneration 5 years post-fire (Camac *et al.* 2012).

Both the dedicated post-fire monitoring plots described here, and the longer term vegetation monitoring plots described in Core Study 1, were integral to determining post-fire successional patterns and likely rates of recovery in alpine vegetation. Data from these plots have shown that alpine vegetation in Victoria has a strong capacity to regenerate after fire, including high-severity fire. There are some very strong pyrogenic responses, such as growth and flowering in the dominant snow grasses (*Poa* spp.; Wahren *et al.* 2001b). Our data show that there is clear evidence of convergence in floristic composition and diversity towards the long unburnt state (i.e. unburnt for >50 years) within 5–10 years. This is especially apparent in the grasslands and heathlands (e.g. Fig. 6.17). There is no evidence from any of these monitoring plots that



Figure 6.16: Measuring twig diameter (a proxy for fire severity) at closed heathland site burnt by the 2003 fires, Watchbed Creek, Bogong High Plains. March 2003 (photo by Henrik Wahren).

the large fires of 1998 and 2003 have had a detrimental effect on alpine plant diversity. Thus, the alpine grasslands and heathlands of the Victorian Alps have a degree of resilience to occasional large fires, which are a feature of the natural disturbance regime of the mainland Australian Alps (Williams *et al.* 2008, 2012; Camac *et al.* 2012). Nevertheless, despite rapid recovery of initial, pre-fire floristic condition, some variables have not returned to pre-fire levels, 8 years post-fire. For example, the amount of bare ground remains two to five times above the long-term average for long-unburnt, ungrazed grassland and heathland. In contrast to the grasslands and heathlands of the Bogong High Plains, some species and communities in the mainland Alps and the Tasmanian Alps are much less resilient to fire (Walsh and McDougall 2004; Kirkpatrick *et al.* 2010). Importantly, these flora share characteristics with threatened alpine fauna – that is, they are alpine specialists with disjunct habitats, which persist in patches scattered though the spatially predominant alpine heathland and grassland.

Core Study 4. Climate change experiment in open heathland/grassland, Bogong High Plains

High latitude and high altitude vegetation is threatened globally by climate change (Huber *et al.* 2005) and in the past 20 years numerous experiments have been set up that have manipulated temperature, soil

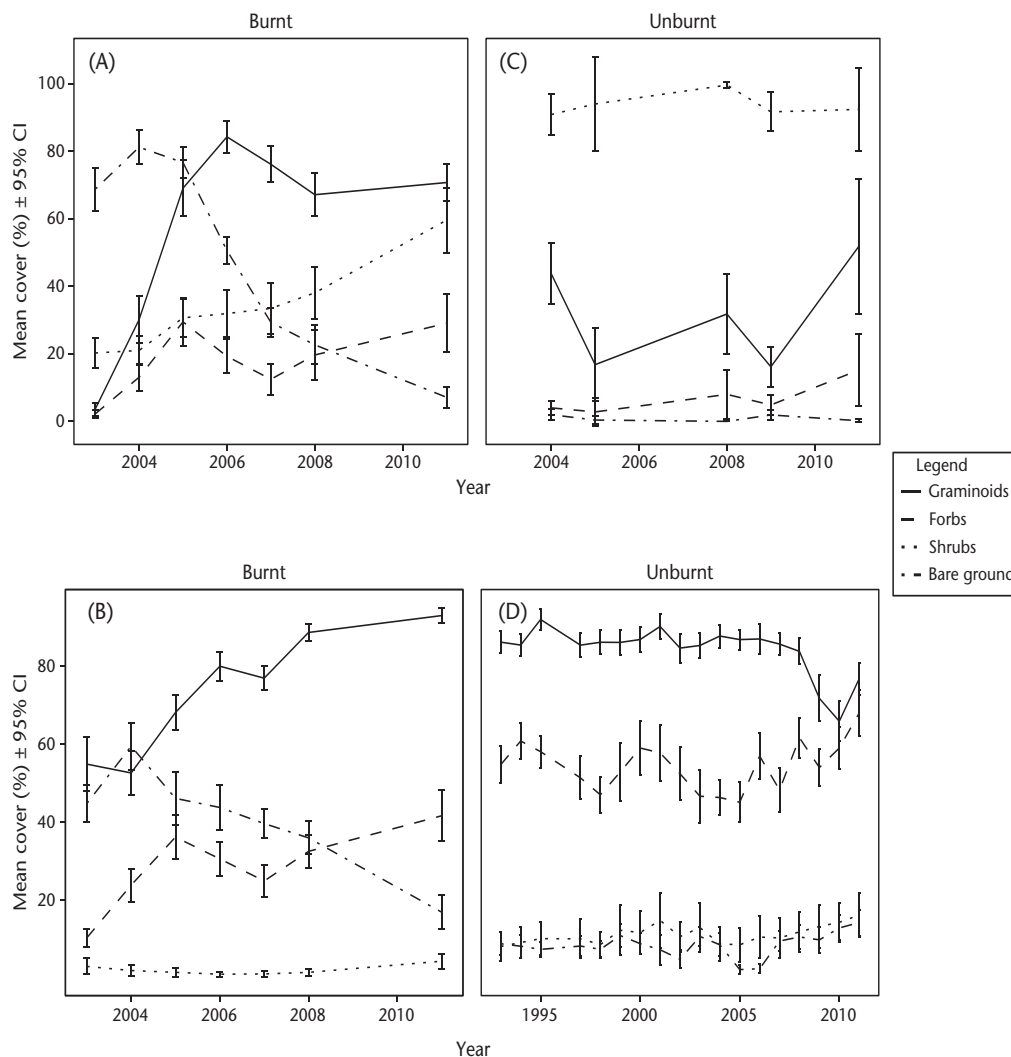


Figure 6.17: Change in cover of major variables (graminoids, shrub, forbs, bare ground; mean $\pm$ 95% CIs) in heathland (A, B) and grassland (C, D) on the Bogong High Plains following the 2003 fires. Data are for burnt (A, C) and unburnt (B, D) sample sites. (Source: Williams *et al.* 2012).

nutrients and snow. One of the larger international studies is the International Tundra Experiment (ITEX; Arft *et al.* 1999; Walker *et al.* 2006; Elmendorf *et al.* 2012). As part of this global experimental network, a warming experiment – the Australian Tundra Experiment – commenced on the Rocky Knobs region of the Bogong High Plains in 2003–4. The experimental design follows the protocols of the International Tundra Experiment (Molau and Mølgaard 1996; Jarrad *et al.* 2008; Hoffmann *et al.* 2010). Two sites (Fig. 6.18A) were established in open heathland, unburnt by the

2003 fires, at ~1750 m asl. At each site, 26 plots of 1 m² were established: 13 plots were passively warmed using perspex open-topped chambers (OTCs; Fig. 6.18B) and 13 were control plots. Two additional plots, each consisting of seven experimentally warmed and seven control plots were established ~1 km from the unburnt plots, in heathland sites burnt by the 2003 fires.

The OTCs are placed over the vegetation during the snow-free spring–autumn period, from October to June. The temperature of the plots is measured every hour. The chambers raise ambient air and

near-surface soil temperatures by $\sim 1.0\text{--}2.0^\circ\text{C}$ during the growing season compared with the controls (Jarrad *et al.* 2008). Measurements of plant phenology (Jarrad *et al.* 2008; Hoffmann *et al.* 2010) and growth are taken at weekly-monthly intervals; botanical composition (Wahren *et al.* 2013), invertebrate composition (Nash *et al.* 2013) and soil nutrient status are measured annually or biennially.

The experimental design thus allows the interactive effects of warming and fire to be studied. Critically, the vegetation changes detected on the long-term vegetation monitoring sites (described in Core Study 1 above) can be used to interpret the changes observed in the experimentally warmed plots. This is one of the few ITEX sites in the world that has this capacity. Moreover, a series of validation transects has been established at four other sites. These transects are ~ 1 km long, with an elevational gradient 200–300 m, which corresponds approximately to a 2°C difference in mean annual temperature.

Some effects of experimental warming are apparent from the first 8 years of the experiment. Warming induces earlier flowering (by 2–10 days) in numerous species across life forms (Jarrad *et al.* 2008) although this depends on the species being considered (Hoffmann *et al.* 2010), a finding also demonstrated in other ITEX studies (Sherry *et al.* 2011). Moreover, the effect size due to warming is less than the inter-annual variability over the same experimental period in the onset of flowering. There is also evidence in the

dominant snow grass, *Poa*, that the fruiting period becomes extended in warmed plots, thus compensating for any earlier flowering (Hoffmann *et al.* 2010). Significantly, plant diversity did not decline in the warmed plots, as has been reported in other ITEX studies (Walker *et al.* 2006). Furthermore, changes in the floristic composition of vegetation in OTCs between 2004 and 2010 was similar to that of the controls and well within the spatial and temporal range of floristic variation exhibited by the same broad vegetation type on the long-term vegetation monitoring plots (Wahren *et al.* 2013). The growth of shrub seedlings can be greatly enhanced by warming, but the effect is species-specific (Fig. 6.19).

Genetic factors were found to contribute to fitness differences between high- and low-elevation populations of the dominant snow grass, *Poa hiemata* (Byars *et al.* 2007). In contrast, for the widespread forb *Craspedia lamicola*, differences between populations were entirely accounted for by plastic changes (Byars and Hoffmann 2009). This suggests that *Poa* is more likely to evolve in response to changing climatic conditions than *Craspedia*. Evolutionary changes in the genus *Poa* may be assisted by hybridisation among species. A comparison of *Poa* species from different regions using next-generation DNA sequencing indicated that different species from the same regions were often more similar to each other genetically than the same species from different regions, pointing to extensive hybridisation (Griffin *et al.* 2011).

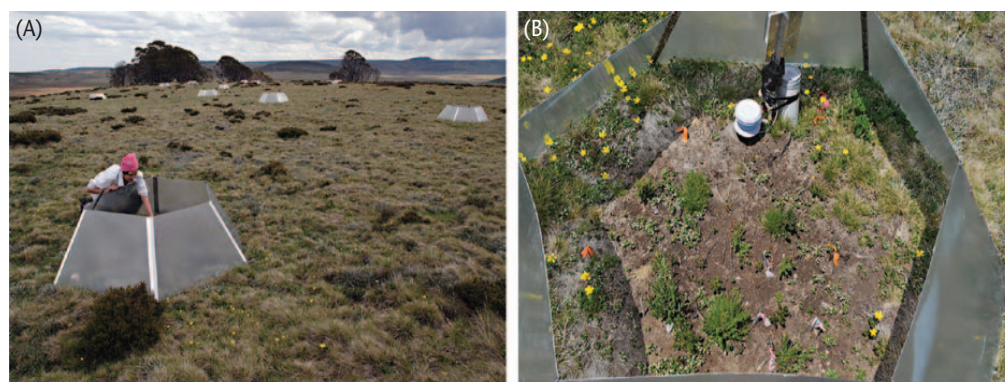


Figure 6.18: The Australian Tundra Experiment on Bogong High Plains: (A) one of four open-heathland sites, with multiple open-top chambers; (B) close-up of open-top chamber, showing transplanted shrub seedlings growing in burnt patches and Hobo data logger for measuring microclimate (photo A by Henrik Wahren, B by James Camac).

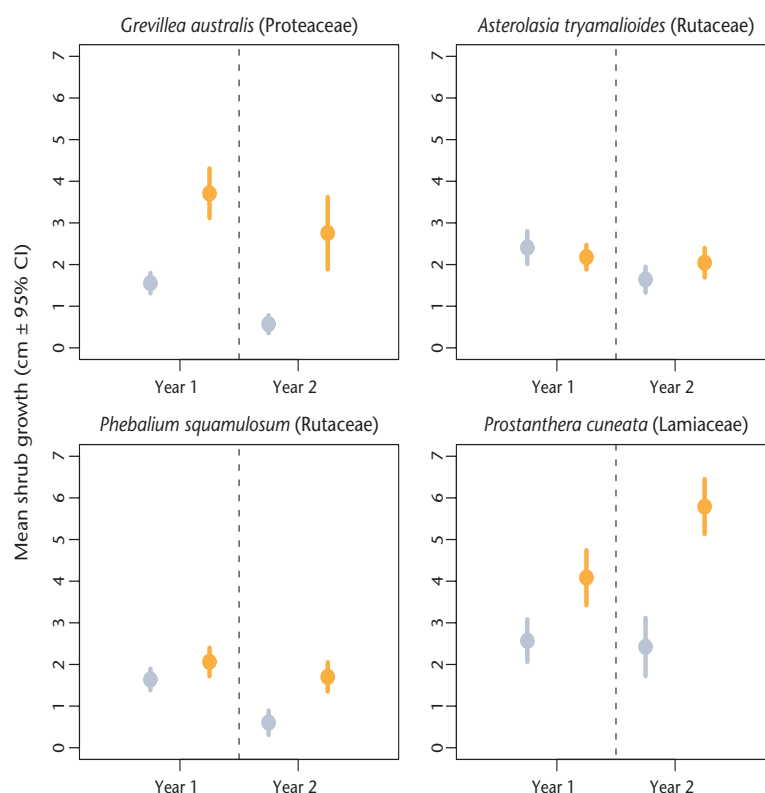


Figure 6.19: Mean height growth (95% CI) of seedlings of common open heathland shrub species (*Grevillea australis* and *Asterolasia tryamalioides*) and closed heathland species (*Phebalium squamulosum* and *Prostanthera cuneata*) in experimentally warmed plots (Red) and unwarmed (Blue) plots for seasons 2010/11 and 2011/12 (source: James Camac *pers. comm.*).

These findings – individualistic responses, compensation, no major decline in plant diversity and relatively small experimental effects compared with ambient variation – may indicate a degree of resilience in alpine grasslands and open heathlands to warming of 1–2°C over the coming decades. However, further monitoring of the plots at the experimental sites and the long-term vegetation sites discussed in Core Study 1 is critical to test this hypothesis.

In addition to the Australian Tundra Experiment plots, climate change impacts are being studied using a new set of 13 long-term monitoring sites established in November 2011. The sites range in elevation from 1400 m to 1880 m. These monitoring sites are designed to record changes in phenology and abundance of alpine plants along elevation gradients in the Bogong High Plains. At each site, a 30 m transect has been established and phenology (budding, flowering and

seed set) is recorded on three occasions during the growing season for a total of 18 species of monocots, forbs and shrubs; 12 of the species are common in the Victorian Alps and six of the species are uncommon. The relative abundance of the species at each site is also recorded. These data will be used to determine the impact of environmental variables (including temperature, rainfall and snow cover) on phenological events and to build models predicting changes in phenology with environmental conditions (cf. Hoffmann *et al.* 2010). The extent to which phenological responses influence resilience, and susceptibility to local extinction, will also be evaluated as data accumulate.

DISCUSSION

Below, we discuss how the major findings from the long-term monitoring and experiments have shaped our

ecological understanding of alpine ecosystems. We also outline the management implications and applications of these findings. We then highlight some current and emerging challenges and threats that may not be detectable with the current network of plots. We conclude with some policy and management considerations.

Long-term monitoring and the development of ecological understanding of alpine ecosystems

Five fundamental conclusions can be drawn about alpine ecosystem dynamics from the above core studies in long-term ecological change.

1. Documenting long-term vegetation change has been a feature of research in alpine ecosystems

Data from long-term monitoring sites in the Australian Alps represent some of the longest-running monitoring trials in Australia. Data from long-term plots have provided the context for interpreting the results of short-term ecological manipulative experiments examining regeneration ecology (Williams and Ashton 1987b, 1988); diet and behaviour of livestock (Wimbush and Costin 1979a; van Rees and Holmes 1986); restoration of habitat and genetic connectivity (Mansergh and Scotts 1989; Weeks *et al.* 2012) and climate change (Jarrod *et al.* 2008, 2009; Hoffmann *et al.* 2010), as well as natural experiments examining post-fire regeneration (Camac *et al.* 2012; Williams *et al.* 2012). Changes in the balance between shrubs, grasses and forbs can be substantial, and depend on interactions between disturbance and species life history (Williams 1990).

2. Grazing by domestic livestock can have substantial ecological effects on alpine ecosystems

Monitoring plots have been indispensable in the development of our understanding of the ecological impacts of past grazing and trampling by livestock on alpine ecosystems. Livestock grazing changes plant species composition because stock are highly selective in their grazing habits, as demonstrated by experiments (Wimbush and Costin 1979a; van Rees and Hutson 1983; van Rees and Holmes 1986). Grazing also increases the abundance of bare ground, which has implications for both ecosystem dynamics (shrubs, for example, require bare ground to establish:

Carr 1962; Williams and Ashton 1987b; Wahren *et al.* 1994) and catchment protection (a more or less full cover of vegetation over the soil is both the long-term norm and is required for effective catchment protection in alpine ecosystems (Costin 1954, 1957).

Monitoring in two states for over half a century has confirmed the propositions put forward over half a century ago by Costin (1954) and the Australian Academy of Science (1957) that livestock grazing is a threat to soil, water and nature conservation in Australian alpine ecosystems. No environmental benefits of grazing have been detected anywhere in the mainland Australian Alps during more than half a century of detailed, targeted monitoring. Importantly, long-term monitoring has shown that grazing effects can be reversed, and that land and water condition and conservation values can and do improve, albeit slowly, following the cessation of grazing (Australian Academy of Science 1957; Wimbush and Costin 1979b, c; Wahren *et al.* 1994; Scherrer and Pickering 2005). This, however, does not mean that grazing can safely be re-introduced periodically, because environmental conditions (e.g. climate and grazing pressure from introduced ungulates) are changing. The classical studies showing recovery were done at a time when the new threats of exotic species and climate change were small. Alpine ecosystems might not recover from future sustained grazing. Any re-introduction of livestock grazing would only further compound these threats to catchment condition and the internationally significant conservation values of Australian alpine ecosystems.

The findings and principles derived from long-term research into cattle and sheep in Australia's alpine ecosystems can be applied to these other ungulates (horses, deer and pigs). Indeed, incursions of feral horses and Sambar Deer to higher altitudes means that the alpine region has an ever increasing pressure from grazing and trampling. These species all present clear threats to Australian alpine ecosystems and should be removed.

3. The Mountain Pygmy Possum: successful use of ecological science for effective and innovative conservation management

Long-term research has been pivotal in understanding the ecology and management of this Endangered

mammal. The monitoring program has enabled accurate estimates of the population dynamics of the species. We now have a robust understanding of biology, genetics and ecology of the species (e.g. Caughley 1986; Mansergh and Scotts 1989; Mansergh and Broome 1994; Heinze *et al.* 2004; Mitrovski *et al.* 2007). The habitat, distribution, biology and ecology of this species are now among the best known of all Australian mammals. These data have provided a strong basis for conservation actions in the face of change, particularly from ski resort development. The management implications of the *Burramys* population and genetic data are discussed further below.

Successful interventions, such as the ‘tunnel of love’ (Fig 6.20) and translocation of animals, have been based on providing low intrusive, permanent solutions to assist *Burramys* to self-adapt. The translocation at Mount Buller may well have wider use for the species (and many others) in future. However, the history of *Burramys* also provides sobering lessons. Known, significant habitats were destroyed and fragmented during the course of the development of alpine resorts. The cautionary tale is clear – conservation as a legitimate land use relies on more than good science. Strong societal and regulatory values and, perhaps most importantly, the competent ‘goodwill’ of land management also must be nurtured. Many *Burramys* populations are in or adjacent to ski resorts and the indirect pressures remain real and elevated. For example, high predator densities and risk of mesopredator release if Red Foxes are controlled, but not cats, may lead to greater overall predator impact (e.g. particularly Mount Buller and Blue Cow). Although some populations have been brought back from the brink, the edge remains nearby. Sustaining the rare and endangered in the face of rapid and or persistent change requires constant vigilance.

4. Alpine vegetation of mainland Australia has a strong capacity to regenerate post-fire

The data from post-fire monitoring plots established in Victoria and New South Wales, in conjunction with data from longer term monitoring plots, clearly indicate a high degree of resilience of alpine vegetation of mainland Australia to major landscape fires such as those of 2003 (Williams *et al.* 2008, 2012; Camac *et al.*

2012). However, decades are needed between fires for vegetation to fully recover to the pre-fire state.

5. Responses to climate change have been demonstrated experimentally

Many responses to changes in climate in Australian alpine ecosystems are consistent with experimental observations at ITEX sites in the Northern Hemisphere. These include earlier flowering (Jarrad *et al.* 2008), a capacity to adapt genetically (Byars *et al.* 2007) as well as via plasticity (Byars and Hoffmann 2009). However, the experiments have also produced several surprising results, such as phenological compensation (Hoffmann *et al.* 2010) and potential resilience in the flora (Wahren *et al.* 2013). There is also the likely generation of evolutionary novelty through hybridisation (Griffin *et al.* 2011). Data from these experiments have contributed to global meta-analyses of warming effects (e.g. Walker *et al.* 2006). Importantly, the magnitude of the shorter term, decadal experimental effects could not have been interpreted without reference to the multi-decadal trends elucidated from the long-term monitoring plots (Wahren *et al.* 2013).

Applications of ecological understanding in land management

The fundamental ecological insights into long-term ecosystem dynamics and ecological processes that have been demonstrated from long-term ecological monitoring have direct and obvious applications in land management in the Australian Alps. This includes setting aside of alpine ecosystems within the National Reserve System, the gradual phasing out of grazing as a land use, the importance of species life history in designing conservation actions and the understanding of ecosystem resilience when considering management responses to fire and climate change. We discuss these themes below.

1. Rarity as a driver of conservation management

Alpine ecosystems are globally important and rare within Australia. The soil–vegetation–fauna assemblages occupy a small fraction of the land area, and by that measure alone are of considerable conservation significance. This has been recognised for many decades (Good 1989, 1992; Costin *et al.* 2000; Worboys

and Good 2011). The scientific understanding that has resulted from long-term ecological studies has guided the Australian Government and state governments in their conservation directions. A fundamental response has been to conserve alpine ecosystems within the National Reserve System (NRS) and currently the overwhelming majority of alpine and sub-alpine ecosystems are within the NRS. The Mount Buffalo National Park was one of Australia's earliest (first accessions in 1898). Since then, there have been large additions to the NRS – Kosciuszko National Park in NSW in 1967, Cradle Mountain National Park in Tasmania in 1971, Namadgi National Park in the ACT, 1984 and the Alpine National Park in Victoria in 1989. Long-term ecological monitoring has also underpinned the listing of rare species and communities under both Commonwealth and state law.

2. The sensitivity of alpine ecosystems to human-induced disturbance

Response to disturbance has been a consistent theme from six decades of studying the effects of livestock grazing. Long-term monitoring has revealed that Australia's alpine ecosystems are characterised by an almost complete cover of vegetation. There are very few exceptions to this (for example, feldmarks; Costin *et al.* 2000). Ergo, the key to managing alpine landscapes is to maintain and/or restore vegetation cover and minimise the amount of bare ground. The way to achieve this is to minimise anthropogenic disturbance. The natural disturbance regimes of alpine ecosystems of the mainland are well understood and need to be accommodated in long-term management (Costin 1954; Williams 1990; Williams *et al.* 2008). These findings underpin nature, water and soil conservation in the Alps and have done so for more than half a century (Australian Academy of Science 1957). Early findings from NSW and Victoria influenced decisions to restrict and/or remove grazing from high mountain catchments; ecologists and soil conservationists recognised the importance of maintaining vegetation cover for the purposes of catchment protection. As a consequence, livestock were removed from the Main Range at Kosciuszko in 1944 and from the whole Kosciuszko National Park in 1967. Similarly, in Victoria, stock were removed from Mount Buffalo

in 1952, from high peaks such as Mounts Bogong, Feathertop and Hotham in the 1960s, from the northern region of the Bogong High Plains in 1991 and from the whole of the Victorian Alpine National Park in 2005.

3. Species life history information and conservation management

As noted above, the seminal example of science-based conservation management in the Australian Alps is *Burramys*. Following its initial discovery, the potential impacts of the then expanding ski industry led to the first systematic survey of the species that was able to refine habitat characteristics (Gullan and Norris 1979). Resort development remained a constant driver of monitoring and research, which had a strong conservation imperative – avoidance of extinction. There was a clear impetus: to develop and implement a management plan; to discover and secure populations outside resorts (e.g. on the Bogong High Plains); to resolve issues of habitat fragmentation and destruction; to provide evidence of sustainable land use within resorts; and to gauge effects of extreme events (floods in 1988, and fires in 2003 and 2007). *Burramys* has been included in bioclimatic modelling for adaptation to climate change (e.g. Brereton *et al.* 1995).

In Victoria, the 'tunnel of love' (Fig. 6.20) was constructed in 1986 under the main road into and out of the Mount Hotham Ski Resort. This engineering



Figure 6.20: The 'tunnel of love' at Mount Hotham Ski Resort (photo by Ian Mansergh).

project successfully restored habitat and population connectivity within the resort on Mount Higginbotham that had been disrupted by habitat destruction and fragmentation (Mansergh and Scotts 1989). This form of ecological re-connectivity was adopted in NSW and later at Mount Buller.

The discovery of the third, genetically distinct population at Mount Buller in 1996 and subsequent monitoring (Heinze 2005) showed dramatic population decline and terminal genetic erosion and loss of diversity (Mitrovski *et al.* 2007). This led to a major innovative effort: the translocation of males from other, wild-breeding populations. This resulted in the ‘genetic rescue’ of the Mount Buller population in 2011–12 (Weeks *et al.* 2012). Annual reporting of the population status of *Burramys* is now a key performance indicator for reporting on both business and sustainability criteria of Alpine Resorts (e.g. Heinze 2005). These high-profile and successful conservation actions could not have been conceived or executed without detailed knowledge of the life history of *Burramys* that came from decades of monitoring population size and structure and genetic variation.

4. Ecosystem resilience and management for fire and climate change

An emerging issue, and one with profound importance for managing alpine ecosystems in the face of fire and climate change, is ecological resilience (*sensu* Holling 1973; Allen *et al.* 2011). Resilience is the amount of disturbance or disruption a system can recover from without transforming to another system. Multiple lines of evidence have been compiled from long-term monitoring studies in both NSW and Victoria that most alpine ecosystems are resilient to fire (Walsh and McDougall 2004; Williams *et al.* 2012). Alpine heathlands are resilient to variation in fire severity (Camac *et al.* 2012). Alpine snow-patch communities were virtually unburnt during the 2003 fires (Williams *et al.* 2006b). The management implication of these findings is clear and compelling: large fires are not of themselves an ‘ecological disaster’, as has been posited generally for southern Australia by Adams and Attiwill (2011). It follows that there is no ecological need to modify fire regime components,

whether by prescribed fire or livestock grazing, to ‘protect’ alpine ecosystems from ‘devastating large fires’. There are two fundamental reasons for this. First, grazing by domestic livestock does not mitigate fire extent or severity – ‘alpine grazing’ does NOT ‘reduce blazing’ (Williams *et al.* 2006b). Second, there is no need, on conservation grounds, to ‘reduce blazing’ (either the severity or occurrence). This is because the biota, including elements that may be thought of as vulnerable to any fire (*Sphagnum*; *Burramys*) can persist in the landscape following large, potentially severe fires (Williams *et al.* 2008, 2012). The effect of variation in inter-fire interval on conservation values is uncertain, but it is highly likely that intervening with prescribed burning for fuel reduction purposes in alpine ecosystems at 5–10 year intervals will have adverse biodiversity outcomes.

The climate change experiment on the Bogong High Plains is indicating potential resilience of alpine open heathland to warming, at least to a warming of 1–2°C over a decade. We could not have interpreted the results from the warming experiment on the Bogong High Plains over the 2003–2010 period without reference to trends documented over the 1979–2010 period on the long-term monitoring plots (Wahren *et al.* 2013). These findings mean that managers have the time and the opportunity to reflect and be confident in directing resources to known, current and pressing ecological management problems such as exotic/feral species (Mansergh and Doolan 2012).

5. Global scientific connections

Alpine ecosystems are globally significant and it is important to build and maintain international research links. Data from the Bogong High Plains have contributed to ITEX meta analyses (Walker *et al.* 2006; Elmendorf *et al.* 2012). The high peaks of the Main Range in the Kosciuszko and Bogong High Plains regions are part of the Global Observation Research Initiative in Alpine Environments (GLO-RIA) network (Fig. 6.21A; Box 6.5). Altitudinal transects in Kosciuszko National Park are part of the global monitoring system of the Mountain Invasion Research Network (MIREN; see Box 6.5; Fig. 6.21B), which aims to detect movements of both exotic and native species (Pauchard *et al.* 2009). It is imperative

Box 6.5: The Global Observation Research Initiative in Alpine Environments – GLORIA

Australian alpine and high mountain areas are considered to be highly vulnerable to climate change (Laurance *et al.* 2011). High altitude alpine vegetation may be replaced by species typical of lower altitudes as species respond to climatic changes, rising temperatures and longer growing seasons. Indeed, re-surveys of mountain summits from the European Alps, using data from as far back as 1835, have revealed upward shifts of alpine plants and an associated increase in species richness primarily related to recent (late 20th century) climate warming (Grabherr *et al.* 1994; Holzinger *et al.* 2008).

Empirical evidence of vegetation shifts in response to recent climate change is largely unavailable in Australia. Studies instead report the indirect links of climate change and climate variability with vegetation change, such as investigating the inter-annual variability of snow cover on vegetation patterns (e.g. Edmonds *et al.* 2006) and encroaching subalpine treelines into grassy plains (Wearne and Morgan 2001), and using space-for-time studies over altitudinal gradients to infer future vegetation change (Venn and Morgan 2005).

The Global Observation Research Initiative in Alpine Environments monitoring network (GLORIA; <http://www.gloria.ac.at>) was established to detect long-term alpine vegetation change, particularly changes in species richness with respect to local temperatures and altitude, on high mountain summits (Fig. 6.21A). Using a standard monitoring protocol (Pauli *et al.* 2004), five mountain summit survey sites were established in Kosciuszko National Park in 2004 and several in the Victorian Alpine National Park in 2006.

The Australian summits cover an altitudinal range of 301 m. At each site, the top section of each summit was divided into eight summit area sections, four covering the area down to 5 m below the summit (the 5 m isoline) for each of the four cardinal compass bearings and another four covering the four compass bearings down to the 10 m isoline.

At each of the four cardinal bearings at the 5 m isoline, a cluster of four 1 m² quadrats was established and species composition was recorded. The flora on 11 mountain summits has been monitored in Victoria since 2003 (Venn and Morgan 2005, 2009, 2010). This study asks: are changes in species richness with time related to altitude of the summit? Do different life-forms respond at different rates? Is there any evidence of migration of species from lower altitudes to summits?

The study is in its infancy, but has already shown that mean species richness has increased at the summit scale between 2004 and 2011 (Venn *et al.* 2012). At this scale, the rate of species richness increase was almost one new species per year. Shrub and graminoid species showed the largest increases. Future re-surveys of the summits will confirm whether these short-term variations in species richness, particularly increases in shrubs, are indeed signals of longer term trends and interactions with a changing climate. Long-term monitoring using the GLORIA protocol is timely and essential for detecting and predicting the responses of Australian alpine species to local climate change. A larger network of sites in Australia is advisable to detect changes in summit floras that are likely to be most vulnerable to rapid environmental change.

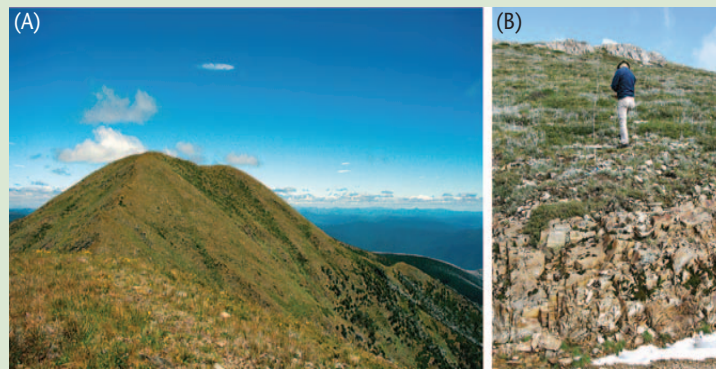


Figure 6.21: (A) Summit ridge of Mount Feathertop Alpine national Park, Victoria (1922 m), part of the GLORIA network of mountain observation sites; (B) a MIREN (Mountain Invasion Research Network) transect at Rawson's pass, Kosciuszko National park, NSW (photo A by John Morgan, B by Keith McDougall).

Box 6.6: Plant invasions in the Australian Alps

In the 20th century, the threat of plant invasion in Australian high mountain areas was regarded as low because of a climatic barrier (Costin 1954). Management therefore focused on the control of exotic species required under legislation, most of which were species of agricultural importance (e.g. *Rubus* spp.). Although Plans of Management provided legislative support for control of exotic species in natural vegetation, few species were deemed to warrant such attention (an exception being English Broom, *Cytisus scoparius*). In the past decade, there has been invasion by two *Hieracium* species (*H. aurantiacum* and *H. praealtum*). *H. aurantiacum* did not require major disturbance to establish in natural vegetation and was highly competitive when it did invade, making it a significant threat to biodiversity.

The scale of the threat was largely determined from assessments of threats in other mountain regions, which have proven to be accurate (McDougall *et al.* 2005). Costly eradication programs are underway but have been challenging partly because these species have established in rugged terrain. The choice of control measure had to be determined largely by trial and error (McDougall *et al.* 2011).

Populations of *H. aurantiacum* were sprayed with herbicide and marked to determine whether plants had been killed. It quickly became obvious that the species was spreading faster than it was being controlled. A more systematic eradication program involving search and control was then developed, together with the repeated monitoring of treated areas. With the need to monitor treated populations and survey a larger area each year, the cost of survey and monitoring is becoming prohibitive, and impossible without a large number of volunteers.

The importance of the eradication programs has been promoted in brochures and newspaper articles. This has aided public acceptance of the program's cost and minor disruptions to visitor movement because of quarantine closures. It has also led to the early detection of new infestations and increased the likelihood of eradication. Monitoring has led to a sudden increase in awareness of the threat of exotic species to natural mountain values and the realisation that mountains are not invulnerable to destructive invasion because of their colder climate.

The investment in control and eradication has increased dramatically over the past decade but new incursions continue to be detected. A recent incursive element, the Ox-eye daisy (*Leucanthemum vulgare*), has spread rapidly and will test the capacity of managers to deal with plant invasions in Australian mountains (Fig. 6.22).



Figure 6.22: Not snow, but the white flowers of the exotic, invasive plant *Leucanthemum vulgare* (Ox-eye Daisy) in Kellys Plain near Tantangara Dam, Kosciuszko National Park. Horses are believed to be the main dispersal vector for this species (photo by Keith McDougall).

to remain part of this global network of experiments, sites and scientists. What we detect in Australia, and how management agencies respond, is therefore internationally significant.

Current and future challenges and threats

Historically, the research and monitoring in Australian alpine ecosystems has focused on understanding

species and ecosystem dynamics in relation to disturbance. This includes natural disturbance regimes, for example, small-scale frequent disturbances such as insect attack (Williams 1990), large-scale infrequent disturbances such as drought (Griffin and Hoffmann 2012) and landscape-scale fire (Williams *et al.* 2006b, 2008; Camac *et al.* 2012; Williams *et al.* 2012), non-native disturbance regimes such as livestock grazing

and the combination of grazing and fire (Costin 1954; Australian Academy of Science 1957; Williams *et al.* 2006a).

Some future changes can be anticipated on the basis of current knowledge (e.g. expansion of woody vegetation; see below). Moreover, future scenarios of climate and land use will interact ('threat syndromes'; Burgman *et al.* 2007). How such interactions between various factors will affect alpine ecosystems is uncertain, but may lead to surprises and novel assemblages (Dunlop and Brown 2008). Moreover, how less-common, but high-conservation-value ecosystems, such as wetlands and snow-patch herbfields, will respond to changing climate is poorly understood. A key issue is the extent to which current understanding can anticipate such threats and whether current monitoring sites and protocols can detect the directions and rates of such change. Management may need to adopt new techniques (e.g. variations on translocation) for fragmented alpine populations. Climate change will also affect land use and the way society values key ecosystem services from landscapes (i.e. water production, quality and quantity, and bio-sequestration of carbon). We suggest that such adaptation options will further enhance support for conservation of the region.

Below we highlight some challenges to achieving effective conservation management of alpine ecosystems and how the long-term monitoring may need to be modified to detect emerging threats and provide a basis for decision making:

1. Warming and the expansion of woody species

The alpine treeline is increasing in elevation globally and there is some evidence that this is happening on the Bogong High Plains (Wearne and Morgan 2001). Shrubs are also expanding in arctic and alpine environments globally, as a consequence of warming (Wahren *et al.* 2005; Walker *et al.* 2006). Both phenomena are likely in alpine ecosystems across Australia. The current long-term monitoring plots in grassland are likely to be adequate for detecting change in shrub cover in this community. However, shrub expansion also will be likely within open-heathland and at the boundaries between grassland and heathland. Thus, additional plots have been

established in such sites to detect such changes in the cover of shrubs (JS Camac, unpublished data). Some changes to treeline and shrub cover on the Bogong High Plains and at Kosciuszko may be detectable from aerial photography (K McDougall, unpublished data). However, preliminary analyses suggest that separating the influence of climate change from that of land use change on the expansion of woody species may not be possible.

Shrub expansion due to climate change also may provide a positive feedback to fire regimes. More severe fire weather is projected for south-eastern Australia as a consequence of climate change (Clarke *et al.* 2013). Shrubs are also the most flammable fuels in the alpine environment (Williams *et al.* 2006b). Hence, a combination of expanding shrub cover and increasing severity of fire weather may increase the chance of fire in alpine vegetation. Occasional extensive fire is not of itself a threat to alpine biodiversity (Williams *et al.* 2008, 2012). However, the effects of increased fire frequency are unknown. Biodiversity patterns in relation to fire frequency in areas known to be burnt at relatively short intervals (e.g. Mount Buffalo National Park) need to be examined.

2. Climate change and nationally listed communities and species of high conservation significance

Most of the published long-term monitoring and experimental work on the Bogong High Plains has been undertaken in the grasslands and heathlands, which together constitute ~90% of the alpine landscape. Other plant communities such as wetlands/bogs and snow-patch herbfields occupy a relatively small proportion of the landscape, but have high conservation significance. Alpine bogs are listed under the Commonwealth EPBC Act and *Victorian Flora and Fauna Guarantee (FFG) Act*; alpine snow-patch vegetation is also listed under the FFG Act. Both communities are at risk from warming and drying associated with climate change (Venn and Morgan 2007; White 2009; Venn *et al.* 2011). In the past decade or so, these communities have received considerable attention from scientists, conservationists and national park managers, and now are included in scientific monitoring programs.

Wetlands occupy ~10% of the alpine landscape (McDougall 1982). Monitoring of wetlands on the Bogong High Plains initially concentrated on mapping wetland vegetation at a few sites and the patterns and processes in the pavement component of the wetland complex, which is listed separately under FFG Act (Wahren *et al.* 2001c; McDougall 2007). Shannon (2011) established numerous monitoring plots in a variety of wetlands on the Bogong High Plains, Snowy Range and several other locations. The current array of plots in wetlands is probably sufficient to document long-term ecological processes in Australian alpine ecosystems. However, this array does not sample the more remote areas of the Australian Alps (e.g. the Davies Plain and Cobberas in Victoria). Moreover, the existing plots may not be sufficient to monitor the impacts of current threats such as exotic plants and feral animals, and disturbance due to alpine resort and other tourist development. There has been preliminary modelling of potential effects of climate change on alpine wetlands, showing potential contraction as a consequence of warming and drying (White 2009).

Snow-patch vegetation occupies less than 1% of the alpine landscape (McDougall 1982). Field evidence at Kosciuszko suggests some potential effects of climate change on snow-patch herbfields (Venn *et al.* 2011). Almost all snow patches in Victoria are on the Bogong High Plains and nearby summits and ridges. The structure and composition of the vegetation at 37 of these sites have been monitored since 1996; the large (22 ha) snow-patch site on Mount Nelse has been monitored since 1982 (Wahren *et al.* 2001a, b, c; McDougall and Walsh 2007). Recent data from the Bogong High Plains indicates shrub invasion at sites below the treeline and consequent contraction of herbfields, and demonstrates the risks that exotic plants and feral animals pose to this community (C-H Wahren *pers. comm.*).

Several plant species are listed under the EPBC Act and/or FFG Act (e.g. Snow Daphne *Kellaria laxa*, Marsh Leek-orchid *Prasophyllum niphopedium*) and some others only occur in very restricted habitats (e.g. *Orreomyrrhis brevipes*, *Plantago glacialis* and *Abrotanella nubigena* on pavements in wetlands). These

species deserve careful monitoring because they are likely to respond to environmental changes more rapidly than communities. Most of these rare species are monitored occasionally by individual scientists but a formal monitoring program, coordinated and supported by the Australian Government and state conservation agencies, is required. A large proportion of the alpine herpetofauna (reptiles and amphibians) is listed as threatened under the Commonwealth EPBC Act or the Victorian FFG Act. Trends in populations of these species may also be indicative of changes in the habitat(s) they occupy. Victoria's Arthur Rylah Institute has an active program monitoring listed herpetofauna, which was expanded after the 2003 bushfires (Clemann and Howard 2011). Aquatic macroinvertebrates are important functional components of alpine streams and indicators of stream health (Mynott *et al.* 2011). Some local endemic species of stoneflies are listed under the FFG Act; because temperature is considered a determinant for distribution of population of these rare species, a rigorous monitoring program is essential.

Given the national conservation significance of wetlands, snow-patch vegetation and listed species, and the potential sensitivity of alpine ecosystems to climate change, then continued monitoring of these plant communities and species, using the existing arrays of plots, is essential. Additional sites may need to be established to monitor change in these communities and species. Additional techniques (e.g. for monitoring water tables and snow lie) will also be required. Mansergh and Doolan (2012) have recommended identification and monitoring of climatic refugia for alpine specialists and the assessment and protection of areas of ecological and genetic connectivity for these species. Where genetic evidence indicates inbreeding and/or loss of genetic resilience, gene transference by wild cross breeding (translocations) should be facilitated (e.g. see *Burramys*, Core Study 2).

3. The threat to Australian alpine ecosystems posed by invasive plants and animals

Plant invasions in the Australian Alps continue to be a risk (see Box 6.6). Climate change will further increase

Box 6.7: Assessment of impacts of feral horses in the Kosciuszko and Alpine National Parks

There are large numbers of feral horses in the alpine and high subalpine landscapes of south-eastern Australia. Australian ecosystems, and alpine ecosystems in particular, have not evolved in the presence of large grazing vertebrate herbivores such as horses. Thus, horses, like cattle and sheep, have major impacts on plant community structure and composition, wetland condition and streambank erosion. This has resulted in their listing as a 'Potentially Threatening Process' under the Victorian *Fauna and Flora Guarantee Act 1988*.

In Victoria, feral horse numbers have been estimated to be at least 8000 animals (Thiele and Prober 1999; Dawson and Miller 2008), most of which occur within the Cobberas-Tingaringy unit of the Alpine National Park. In 1999, a long-term experimental monitoring program was established to assess feral horse impacts at two sites in the Alpine National Park. The aims of the monitoring program were to determine the effects of exclusion from feral horses on floristic composition and structure of favoured grazing areas (grasslands) and on bank condition and disturbance of streams draining these areas (Thiele and Prober 1999; Prober and Thiele 2007).

Replicated exclusion trials were established at two sites: Cowombat Flat and Native Cat Flat. Both sites are naturally treeless damp grasslands. At each site, eight 10 m × 10 m plots were established in pair-wise fashion (four replicate pairs) either side of a small stream line. Plots were established adjacent to the streamline, but beyond the zone of direct riparian influence, and permanently marked using steel star posts. Plots in each pair were randomly assigned to one of two treatments: fenced to exclude horses but not other grazers (European Rabbits, wombats and macropods), and unfenced so that grazing by all animals was unrestricted. Fences were erected in the winter of 1999.

Detailed vegetation monitoring was undertaken in 1999, 2005 and 2012. All plant species present within each plot were recorded and their abundance estimated using 100 non-permanent points (5 mm diameter pin). Plot-scale (total species per plot) and point-scale richness (average number of species per point) for a range of species groups (total, native, exotic, herb, shrub, grass and sedge) were calculated. In addition to detailed floristic monitoring, several structural vegetation variables are estimated for each plot (average height of the groundlayer, tree seedling and shrub density and cover). Permanent photopoints were established at one corner of each plot.

Results to date show that exclusion from horse grazing has had striking visual effects on vegetation and streambanks at both sites (Prober and Thiele 2007; Wild and Poll 2012). There is evidence that vegetation change is occurring after 13 years of exclusion from horse grazing. The most significant effect of exclusion at both sites was an increase in the height of the vegetation, with a reduction in small-scale species richness also emerging. Increases in the coverage of the dominant grasses and sedges have been noted within exclusions, partially at the expense of low-growing perennial herbs. Decreases in stream depth and reductions in streambank slumping have also been recorded.

The floristic plots at both sites should be maintained. The effects of horses, and other feral animals such as deer, are poorly documented across the Australian Alps, so it is recommended that new monitoring points be established to identify the spatial and temporal effects of feral animals on high mountain ecosystems.

the risk of invasion of alpine vegetation by exotic plant species (McDougall *et al.* 2005), as may fire (e.g. the case of willows *Salix cinerea* invading alpine bogs following the 2003 fires; Pascoe 2007). The Mountain Invasion Research Network (MIREN) has established a series of geo-located floristic plots in Kosciuszko National Park (Seipel *et al.* 2012). These plots have

detected increases in the diversity of exotic plants over the past 5 years. Although this is perhaps partly attributable to drought at the time of the first measurement, 25 new exotic species were recorded at the second measurement. This suggests an alarming rate of invasion. The plots and observations made during the measurements also indicate that, in addition to

exotic species, at least three native species are using roads to increase their altitudinal range. Future movements of native plants may be just as perplexing an issue for land managers as movement of exotic plants.

Exotic herbivores are a clear threat to alpine ecosystems. Horses (Nimmo and Miller 2007) and Sambar Deer (IM Mansergh and C-H Wahren *pers. comm.*) appear to be expanding their range and abundance. Monitoring of the impacts of these species (Box 6.7) is in its infancy (Nimmo and Miller 2007). There are permanent horse exclosures in the Cobberas region of Victoria. Horse impacts on wetlands are being monitored in Kosciuszko National Park and the program is being extended to Victoria (G Robertson, NSW Office of Heritage and Environment *pers. comm.*). Available evidence suggests horses have a substantial impact on wetlands (Fig. 6.23A). Pigs can also have substantial impacts in alpine vegetation (Fig. 6.23B). Action on these species is needed particularly because, without intervention, both are likely to continue to expand their range.

Exotic invertebrates also pose a risk to alpine ecosystems. Exotic pollinators (e.g. Western Honey Bee *Apis mellifera*) have been recorded above 1500 m and this species has the potential to change gene flow patterns between isolated populations of the dominant flowering plants (MA Nash *pers. comm.*).

4. Ecological connectivity

Most alpine endemic species persist in isolated 'island' populations of varying size. Small populations with an impoverished genetic base have a heightened extinction risk through both adverse extreme events and an inability to adapt to gradual environmental changes such as changing climate. To minimise extinction risk, climatic refugia should be identified and natural connectivity between them maintained. Genetic markers also should be used to identify vulnerable populations as well as patterns of hybridisation. Human-assisted restoration of ecological connectivity and genetic interchange (as evidenced in *Burramys*; Weeks *et al.* 2012) may be required to boost genetic variation in isolated populations. In this context, the alpine region is a microcosm for many remnant populations across Australia and may act as a model for management. Ecological re-connectivity for fragmented populations is a major management imperative under climate change to which the *Burramys* work has contributed innovative empirical evidence supporting the efficacy of such approaches. A rigid policy of quarantining local genetic variation (particularly in threatened species) may have a perverse outcome (i.e. quicker extinction) whereas increasing genetic resilience may be a more prudent policy (Mansergh *et al.* 2004; Mansergh and Doolan 2012).

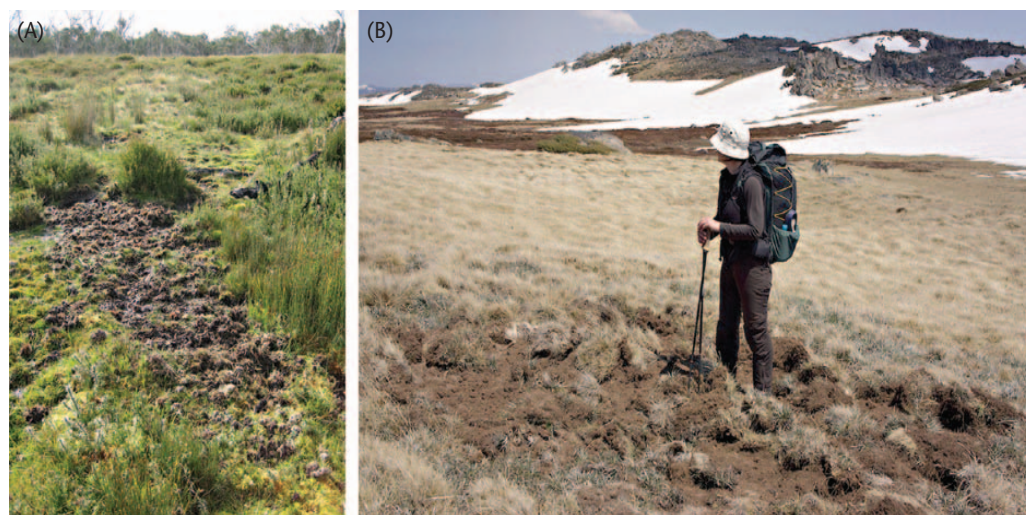


Figure 6.23: (A) Trampling damage by horses in a high subalpine wetland on Forlorn Hope Plain, in 2012; (B) pig damage at 2000m in alpine grassland at Kosciuszko (photo A by James Shannon, B by Henrik Wahren).

Policy considerations

Our data have relevance for contemporary and future land-use policies in alpine ecosystems. We highlight four below:

1. Invasive, exotic plant species are a clear and present threat that is under-recognised

There are considerable threats to conservation values and ecosystem resilience from weeds and feral animals. With respect to invasive plants, the current array of monitoring sites is probably not sufficient to detect establishment and growth of exotic species; early detection and eradication of founder populations is crucial. Many exotic, invasive plants in alpine ecosystems have originated from ski resorts (McDougall *et al.* 2005; McDougall and Walsh 2007). Crucial elements to effective control of such species are systematic detection and eradication programs, together with the repeated monitoring of treated areas and studies of dispersal and general ecology (Moore *et al.* 2011). After a brief establishment phase, many new introductions now have a sufficient foothold to spread rapidly, which reduces the chances of eradicating them. It is crucial that experience gained with treatment protocols is documented and analysed, so that managers may be better prepared for dealing with future invasions. Climate change and fire may exacerbate these threats.

2. Hard-hooved animals (ungulates) do not belong in Australian alpine ecosystems

Six decades of monitoring and experiments have shown the threats posed to Australian alpine ecosystems by livestock grazing. We infer that all ungulates (horses, Sambar Deer and pigs) will pose similar threats. On this basis, we contend that there is ample scientific justification for the removal of all ungulate grazers from the whole of the Australian Alps. There are several reasons for this. First, long-term monitoring has shown that nationally listed plant communities such as alpine wetlands are heavily impacted by sheep and cattle, and there is substantial evidence of trampling of these ecosystems by horses (e.g. wetlands; Shannon 2011). Second, some of the plants known to be highly palatable to sheep and cattle (e.g.

Craspedia; Fig. 6.24) have little genetic capacity to adapt to rising temperatures (Byars *et al.* 2007). On this basis, we infer that grazing by feral horses and deer is likely to elevate the risk that climate change poses to such plants.

There is no scientific basis for the use of domestic livestock to mitigate fire risk in the Australian Alps, nor is there any compelling reason to undertake further research on how livestock grazing may reduce fire risk. Alpine grazing has been shown to be an ineffective fire mitigation tool at landscape scales (Williams *et al.* 2006b). Grazing is highly likely to be ineffective in other high mountain ecosystems such as subalpine woodlands, because the tall, flammable but non-palatable alpine shrubs that dominated heathlands that burnt in 2003, also occur as major understorey components in subalpine woodlands. Importantly, no scientific evidence has been provided in any forum, including the 2009 Victorian Bushfire Royal Commission (Teague *et al.* 2010), to suggest that there is a conservation management problem related to inappropriate fire regimes in Australian alpine or subalpine ecosystems for which livestock grazing may provide a solution. Scarce scientific and management resources should be directed towards more pressing conservation management problems such as



Figure 6.24: *Craspedia* species (Alpine Billy Buttons). Alpine *Craspedia* species are highly palatable to domestic livestock, as shown by experimental grazing trials and long-term monitoring. Genetics studies have shown that *Craspedia lamicola* has a limited capacity to adapt genetically to climate change. These findings would not have been possible without long-term ecological research (photo by Henrik Wahren).

identifying climate refugia and the management of invasive, feral plants and animals.

3. Changes in society will affect land use and how alpine ecosystems are valued

Climate change and other global changes (e.g. increased urbanisation) are likely to lead to changes in land use in the Australian Alps. These changes will also cause society to re-evaluate ecosystem services from the landscape – for example, carbon sequestration and water production will have increasing economic value. Although our ecological knowledge of vegetation and disturbance is good, likely changes under rapidly shifting conditions need to be more accurately predicted. More understanding is required of soils, fungi and invertebrates, and the ecosystem services provided by the alpine landscape as an inter-related system. Land use in land adjoining Australia's alpine national parks is also changing. In addition to traditional agricultural and forestry uses, land is now being increasingly used for amenity, recreation and carbon sequestration. A decline in winter use of alpine resorts may also occur as a consequence of climate

change (Mansergh *et al.* 2004; Barr 2008). If the winter snow pack declines as a consequence of climate change, then tourism infrastructure (alpine resorts, etc.) will increasingly be used for summer recreation. These changes need to be better understood because they will influence the development of land-use and land-management policies in Australian alpine ecosystems in the coming decades.

Governments and their agencies can increase public awareness of the value of alpine ecosystems. In particular, there needs to be greater awareness of the threat that invasive plants pose, and of the need to prevent invasive plants establishing in the first place. The public also needs to be aware of the damage that horses, deer and pigs have wrought on alpine ecosystems, and the need for eradication programs.

There is an ongoing need to communicate the natural values of Australian alpine ecosystems to the people of Australia and how long-term ecological research has played an important role in managing these systems for catchment protection, nature and soil conservation and other land uses. The Alpine Ecology Course (Box 6.8; Fig. 6.25) has been instrumental in

Box 6.8: Training and education outcomes

The Alpine Ecology Course had humble beginnings in 1987 as a weekend gathering of conservationists, farmers and graziers interested in the Alps and how ecology could be applied to manage the land. Over the following years, it grew into a week-long training course for park rangers and resort workers in the Australian Alps, teachers and research students, land managers and others interested in conservation – indeed anyone who has a passion for the Alps. Since its inception almost 1000 people have attended.

The course is run on the Bogong High Plains by La Trobe University's Research Centre for Applied Alpine Ecology. It includes a 'crash course' in principles of the main disciplines of ecology – soils and geomorphology, vertebrate and invertebrate fauna, alpine vegetation and plant ecology – and how alpine ecosystems function. Long-term monitoring plots, including the ones established in the 1940s, are used to demonstrate ecological patterns and processes.

Field exercises are devised to tackle ecological and land-use problems; field data are collected, analysed and interpreted. Participants sample vegetation quadrats, search streams for macro-invertebrates and bogs for rare skinks, and explore rock scree and other ancient landscape features. The results of the exercises are presented in a course forum.

What has it achieved? Those who attend gain an understanding of the importance of the Alps and that ecology matters, they become familiar with techniques of field ecology, and they learn that science can be understood and easily applied to better manage the land.



Figure 6.25: Participants in the Alpine Ecology Course at the head of New Species Gully, Bogong High Plains, with geomorphologist Neville Rosengren. Communication of how ecological principles can be applied in land management will be critical in the coming decades (photo by Jack Reilly).

communicating the ecology of the Australian Alps, and the role of ecological science in land management, to a wide audience of people with an interest in the Alps.

4. Long-term ecological monitoring and research is an investment

Long-term monitoring has provided researchers and managers with extensive knowledge about the ecology of alpine ecosystems and has been important for the definition of standards of vegetation cover for nature conservation and catchment protection. Future management context (Boxes 6.9 and 6.10) is likely to

Box 6.9: Future, ongoing and emerging research and information needs

- Cost-effective ways of reducing or eliminating populations of invasive, exotic species, both plant and animal.
- Resilience of alpine ecosystems to changing climate and fire regimes.
- Capacity of alpine biota to adapt to climate change.
- The role of climate refugia.
- How best to apply various ecological indicators of ecosystem condition, derived from long-term research, in landscape management.

involve uncertainty, complex trade-offs and potentially reduced financial resources. Monitoring protocols that identify potential 'red flag' changes that are of concern to land managers are required. This is a global concern in environmental management. Thus, the long-term monitoring sites and protocols in the alpine region need to be regularly evaluated, and potentially re-configured, to detect environmental threats and challenges in the 21st century. Genetic tools will need to be brought more into the monitoring and management to avoid extinction of threatened species and to maintain landscape resilience; some cost-effective techniques for such monitoring have been developed (e.g. *Burramys*).

GENERAL CONCLUSIONS

The alpine region is a natural area of importance in its own right and for the water it supplies to the catchments, landscapes and people of temperate south-eastern Australia. It also holds an iconic place in the way the people of Australia view the Australian landscape. The legacy of well-documented sites and science from the 1940s onwards have allowed long-term environmental monitoring to reveal key impacts of human

Box 6.10: Key management recommendations

- Weeds and feral animals are the most pressing threats to Australian alpine ecosystems. While existing populations require control, early detection and eradication of founder populations is needed urgently. Appropriate monitoring and eradication protocols are needed.
- Hooved animals should be removed from all Australian alpine ecosystems.
- Maintain the existing network of long-term monitoring plots.
- Governments to support programs to monitor the state of rare species of plants and animals.
- Develop partnerships and protocols that allow ecological knowledge gained from long-term research to be evaluated and applied in land management.

management and response to natural phenomena. This evidence base has assisted society to make more prudent land-use decisions, such as removal of live-stock grazing and expanding the network of protected areas. The evidence base and supporting infrastructure will be vital to future management needs (see Box 6.10). Environmental conditions and human perceptions of value will undoubtedly change in the future, as climate changes, population increases and society's preferences for land use change. In the face of such complex scenarios of change, it is imperative that the natural heritage of the mountains is conserved. Long-term monitoring has been, is, and will continue to be, an essential part of protecting this precious part of Australia's natural estate.

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of the Australian High Country. Finally, this work was supported by the Australian Government's Terrestrial Ecosystem Research Network (www.tern.org.au).

RECOMMENDED READING

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2. Costin AB, Gray M, Totterdell CJ, Wimbush DJ (2000) 'Kosciuszko Alpine Flora'. 2nd edn. (CSIRO Publishing: Melbourne.)
3. Green K, Osborne W (1994) 'Wildlife of the Australian Snow-Country'. (Reed Press: Sydney.)
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5. Williams RJ, McDougall KL, Wahren C-H, Rosengren NJ, Papst WA (2006) Alpine landscapes. In 'Ecology: an Australian Perspective'. 2nd edn. (Eds PM Attiwill and BA Wilson.) pp. 557–572. (Oxford University Press: Oxford.)

RECOMMENDED WEB LINKS

1. The Australian Alpine Research Network, <http://www.taarn.org.au/>
2. Research Centre for Applied Alpine Ecology, <http://australianalpineecology.org/>
3. Australian Institute of Alpine Studies, <http://www.aias.org.au/>
4. Australian Alps National Parks, <http://www.australianalps.environment.gov.au/>
5. Threatened alpine species and communities, Australian Government and State Government listings, (a) Australian Government Species Profile and Threats Database; alpine species and alpine communities: (i) [http://www.environment.gov.au/cgi-bin/sprat/public/spratlookupspecies.pl?name=alpine&searchtype=Sciname](http://www.environment.gov.au/cgi-bin/sprat/public/spratlookupspecies.pl?name=alpine&searchtype=Sciname;); (ii) <http://www.environment.gov.au/cgi-bin/sprat/public/spratlookupcommunity.pl?name=alpine&searchtype=name> (b) Victorian Government Department of Sustainability and Environment *Flora and Fauna Guarantee Act 1988*, Threatened List, http://www.dse.vic.gov.au/—data/assets/pdf_file/0019/141580/201207-FFG-threatened-list.pdf

BIOS

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