Response of montane plant communities to wildfires in the South Island of Aotearoa New Zealand

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Abstract

Measuring and predicting the response of plant communities to ecological disturbances require characterising community dynamics over multiple timescales, both before and after disturbance events. With global climate change, fire regimes are expected to increase in some regions, including parts of New Zealand. These increases are predicted to be particularly impactful in ecosystems in regions with historically low fire frequencies, such as montane plant communities in New Zealand's South Island. Species functional traits or sets of traits such as those represented by growth form and biostatus, can influence the ecological effects of fire and are likely to influence rates of recovery of individual plants and plant communities after fire. Thus, flammability at the plant community level can be estimated using plant community composition, plant traits and experimental measurements of plant shoot flammability. In this thesis, I measured plant community structure and trait variation of plants within South Island montane plant communities that had been impacted by wildfires over a range of sites and timescales. This research showed that most plants in these communities can survive wildfires and that most aspects of plant community structure recover rapidly, in less than 15 months after fire. However, longer-term data from permanent monitoring plots showed that historical fires have a lasting signature on plant community composition. In addition, plants with different biostatus (native or exotic) and growth forms (forbs, graminoid, or woody) showed different responses to fire. These long- and short-term dynamics in plant community structure result in dynamics in estimated plant community flammability that primarily reflects changes in key plant traits and species' relative abundance. However, both experimentally measured shoot flammability and plant traits, including leaf nutrient concentrations, show phylogenetic patterns suggesting both ecological and evolutionary processes that drive plant flammability, and therefore influence community flammability. This study highlights the need for ongoing future trait-based fire ecology research in these montane plant communities because, although native plants were not disproportionately impacted by these instances of wildfires compared to exotics, long-term data show that repeated fires are likely to alter community structure over longer timescales.

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Attestation of Authorship

To the best of my knowledge and belief, this submission is my own work. It does not contain material previously published or written by another person, except where explicitly defined. Nor does it contain any material which has been submitted to a substantial extent for a degree or diploma award by a university.

Shanta Budha Magar

Co-Authored Works

Chapter 2 Shanta Budha-Magar, Nicola J. Day, Hannah L. Buckley, Timothy J. Curran Short-term recovery of plant community after wildfires in montane grasslands (Submitted to Fire Ecology)	Budha-Magar, S 80 % Day, N.J. 9 % Buckley, H.L. 9 % Curran, T.J. 2 %
Chapter 4 Shanta Budha-Magar, Nicola J. Day, Hannah L. Buckley, Olivia R. Burge, Sarah J. Richardson, Dylan W. Schwilk, Ruby R. Ross, Timothy J. Curran Leaf morphological and nutrient traits are associated with plant flammability in sub-alpine vegetation, New Zealand (Submitted to International Journal of Wildland Fire)	Budha-Magar, S 80 % Day, N.J. 4 % Buckley, H.L. 4 % Burge, O.R. 1 % Richardson S.J 1.5 % Schwilk, D.W. 2 % Ross, R.R 0.5 % Curran, T.J. 7 %

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Chapter 1 General introduction

1.1 Fire and climate change

Fire is an ecological disturbance that has shaped ecosystems and biodiversity through both ecological and evolutionary processes (Bowman et al., 2020; He et al., 2019; McLauchlan et al., 2020; Pausas & Ribeiro, 2017). Due to global climate change effects, such as changes in temperature, precipitation, and vapour pressure deficit, the Earth’s fire regimes are rapidly changing and there are now extremely large fires occurring on a regular basis in many parts of the world (Bowman et al., 2020; Duane et al., 2021; Grillakis et al., 2022). These wildfires are anticipated to increase further in wildfire size, frequency, and severity far beyond historical norms (Clarke et al., 2011; Duane et al., 2021; Jain et al., 2022; Wu et al., 2021). Through ecological and evolutionary drivers, these increases are highly likely to cause changes in plant communities globally (Gallagher et al., 2022; Nolan et al., 2022; Triepke et al., 2019).

1.2 Response of plant communities to fire

Over time, plant species adapt to ecological disturbance regimes through their recovery response (Le Breton et al., 2020). So, predicting community responses to various environmental factors related to disturbance must be conducted by accounting for plant species adaptations, or traits. Ecological research has increasingly focused on identifying how ecosystems respond to wildfire disturbances by measuring plant community structure (Abrahamson et al., 2021; Gallagher et al., 2022; Springer et al., 2022; Steel et al., 2021). Plant community structure refers to plant species composition, richness, relative abundances, trait composition and diversity. Dynamics in these community structure variables over time can provide simple summaries of ecosystem change (Abella et al., 2021; Avolio et al., 2019; Matthews et al., 2013). Fire can impact community by causing change in species composition species’ relative abundances, and decreases in species richness (Kimball et al., 2018; Nolan et al., 2021; Paudel et al., 2022). However, plant community will recover after fire whereby composition, relative abundances and richness may return to their pre-fire condition (Abella et al., 2021; Knox & Clarke, 2012). If plants in the community are resilient to fire, they will recover rapidly; however, if they are sensitive to fire and/ or source populations are altered, the compositional trajectory will not return to the prior state and species can be permanently lost or gained over time, thus forming a novel type of community (Abella et al., 2021; Lamothe et al., 2019).

Measuring pre- and post-fire community patterns at different time scales is vital for understanding these patterns in plant community dynamics and resilience (Abrahamson et al., 2021; Arnoldi et al., 2018; Bagchi et al., 2017; Bowd et al., 2021; Dickinson et al., 1992). In particular, the spatial and temporal scales of pre-fire (background) community dynamics can determine the detectability of changes induced by fire. Comparing pre- and post-fire dynamics for the same location or in similar environments will provide reliable conclusions on the response of a community to fire (Arnoldi et al., 2018; Steel et al., 2021). Such understandings are essential to inform biodiversity conservation and ecosystem management, particularly where fire regimes are shifting (Perry et al., 2014; Tolhurst, 2012). Repeated measurements of community structure before and after fire can be used to predict successional temporal changes of plant community in any ecosystem (Bowd et al., 2021; Springer et al., 2022).

Investigating changes in plant community dynamics in relation to biostatus (exotic or native) and growth forms can inform on how they will respond to fire, such as which groups of plants may prevail over time (Bowd et al., 2021; Lentile et al., 2007). This is because plant species from different biostatus and growth forms are affected differently by the fire (Biondini et al., 1989; Miller et al., 2020) and their recovery after fire varies (Rodhouse et al., 2020; Watson et al., 2021). Some growth forms can survive or recover from fire better than others. For instance, grass cover increased following fire in steppe community structure in a study in dry steppe of Kazakhstan (Freitag et al., 2021), which is a typical pattern of grassland and savannah ecosystems that have evolved under a regular fire regime showing that grasses are adapted to recover after fire (Bruckerhoff et al., 2020; Pausas & Paula, 2020; Simpson et al., 2022). Furthermore, slow growing plants and small forbs that are fire-tolerant can cause fires to be less intense and where communities are dominated by such species, they can recover rapidly (Ladwig et al., 2018). In contrast, fire intolerant plants that grow from large underground parts, they are more impacted by fire and communities dominated by such species can take time to recover to pre-fire condition (Cruz et al., 2003). Thus, post-fire temporal patterns in community structure are the consequence of differential survival of growth forms after fire (Zomer & Ramsay, 2021).

Biostatus has been a key ecological variable of interest in fire ecology research; invasive exotic species have previously been shown within floras to possess a suite of traits related to ‘weediness’, i.e., the rapid sequestration of resources after disturbance (Das et al., 2019; Molinari & D’Antonio, 2020). Exotic plant species can often recover following disturbance and can outcompete native perennials in post-fire environments (Balshor et al., 2017; Wainwright et al., 2012). For instance, a study in a sagebush steppe community in the USA found that exotic grasses increased in response to burn severity while native species did not show any trend, suggesting that exotic species can recover rapidly following fire in that system (Rodhouse et al., 2020). However, the response of exotic species to disturbance varies depending upon the structure of the native community and the local ecological conditions (D'Antonio et al., 2000; Gedalof et al., 2022; Prevéy et al., 2010). Thus, studies on fire that seek to understand responses of plants of different biostatus should consider the context of the invasion.

1.3 Plant traits and fire

Fire can affect ecosystems both positively and negatively. Some ecosystems demonstrate positive feedback where plants are adapted to rapidly recover and grow following fire (Vilà et al., 2001), e.g., savannahs and Mediterranean shrublands (Ratnam et al., 2011; Staver et al., 2011). Some ecosystems show negative feedback where fire temporarily reduces fuel loads and decreases the potential for repeated burning for a period of years to some decades, e.g., boreal forests and several temperate coniferous forests (Parks et al., 2015). Plants can impact fire behaviour via their traits (Prior et al., 2017). For example, grasses provide fine fuel, and this promotes fire spread in grasslands, while forbs with less fine fuels and higher moisture content can suppress fire (Simpson et al., 2022; Wragg et al., 2018). Some plants possess traits that make them either resistant or tolerant to fire, e.g., thick leaves with high moisture content or thin, dry leaves and low meristems that resprout rapidly after fire. Thus, different plants that are either more or less flammable can co-exist in fire-prone ecosystems (Bond & Scott, 2010).

Depending on their traits, when plants are perturbed, their recovery rate may vary (Cardoso et al., 2018; Clarke et al., 2013; Simpson et al., 2016; Simpson et al., 2022); this variation can be related to either morphological traits, fuel loads, moisture content of leaf and shoot tissues, plant architecture, and/ or leaf nutrient contents (Bowd et al., 2021; Krix et al., 2019; Landesmann et al., 2021). Plants having high specific leaf area, moisture content and low dead material retention decrease plant shoot flammability (Alam et al., 2020; Wyse et al., 2016). Thus, the prediction is that, if there are many plants with these traits in a community, it would burn less readily than community with different trait composition (Padullés Cubino et al., 2018). In contrast, community with many relatively more flammable plants burn readily, and may be more resilient to fire disturbance (Bond & Midgley, 1995; Schertzer & Staver, 2018).

Thus, the structure of the existing community in the landscape determines the size and severity of fires (Estes et al., 2017; Viedma et al., 2020). With increasing fire regimes, changing land-use types and biological invasions, montane environments, an ecosystem type with novel diversity, are becoming more susceptible to increasing fires (Le Breton et al., 2022; Nolan et al., 2022).

1.4 Fire and flammability in the indigenous grasslands and sub-alpine ecosystems of New Zealand's South Island

New Zealand has a unique range of vegetation and animal life, which developed as a consequence of both in situ evolution and long-distance dispersal events during the country's prolonged isolation for about 80 million years from the rest of world (Gibbs, 2006; Lee et al., 2001; McGlone et al., 2001; Müller-Doblies, 1995). It is estimated that before human settlement ~800 years ago, dense, evergreen forests covered around 90% of the country, except wetlands and grasslands above tree line and in low elevation areas that could not support forests (McGlone, 2001; Perry et al., 2014). However, with human settlement, extensive anthropogenic fires occurred, after which grasslands become more widespread in montane and lowland areas (McWethy et al., 2013; Perry et al., 2014). Thus, even though grasslands are widespread as a result of fires in New Zealand, these communities have evolved in environments with low fire frequency (McGlone, 2001; Perry et al., 2014). Tussock-dominated (represents both tall tussocks; dominated by *Chionochloa* spp. and short tussocks; dominated by *Poa* spp., and *Festuca* spp.) montane grasslands are now one of the most extensive vegetation types in New Zealand and, by definition, are dominated by graminoid species (Mark, 1969; Mark et al., 2010; O'Connor & Alison, 1963; Wardle 1991). These native grasslands are under risk from invasion by exotic trees, shrubs (Hua & Ohlemüller, 2018) and forbs (Day & Buckley, 2013; Mark et al., 2010), particularly as invasive forb species can easily establish in new environments with limited resources (Mark et al., 2010).

Numerous studies have been conducted on post-fire vegetation in tussock-dominated montane grasslands and sub-alpine areas before the 2000s (Allen & Partridge, 1988; Calder et al., 1992; Calder & Wardle, 1969; Cockayne, 1898; Cockayne & Calder, 1932; Gitay et al., 1992; Gitay & Wilson, 1995; Lee et al., 1993; Mark, 1994; Payton et al., 1986; Payton & Mark, 1979; Rogers & Leathwick, 1994; Yeates & Lee, 1997). Most of these studies were focussed on plant biomass and tiller regeneration of *Chionochloa* species after prescribed burning. Some were conducted in wildfire areas, but measurements were done many years after the fire. For example, at one site vegetation plots were set up 35 years after fire (Burge et al., 2020; Cockayne & Calder, 1932).

After 2000, a few studies have investigated plant species recovery and succession in post-fire in tussock-dominated grasslands (Glogoski, 2017; Payton & Pearce, 2009), sub-alpine areas (Arnst et al., 2020; Burge et al., 2020), peatlands (Johnson, 2001) and forest ecosystems (Christensen, 2022; Kitzberger et al., 2016; Richardson et al., 2018; Teixeira et al., 2020). Some studies have been conducted relating to fire and weather conditions (Pretorius et al., 2020; Simpson, et al., 2014), flammability and plant traits (Alam et al., 2020; Cui et al., 2020; Cui, Paterson, Wyse, et al., 2020; Mason et al., 2016; Pausas et al., 2012; Wyse et al., 2016). A few studies have investigated pattern of community flammability in tussock-dominated montane grassland (Padullés Cubino et al., 2018) and forest ecosystems (Lord et al., 2022).

In tussock-dominated montane grasslands, species such as *Chionochloa* spp. are believed to be fire-adapted species (Payton & Pearce, 2009; Perry et al., 2014). Payton and Pearce (2009) found that recovery of tall tussocks in post-fire was determined by pre-fire moisture conditions in two different seasons (spring and summer). Glogoski (2017), found that exotic grasses and herbaceous weeds recovered better than native vegetation in post-fire vegetation recovery. In peatlands, low-growing species (forbs and grasses) peaked in abundance 15-22 months post-fire but in successional recovery they declined and woody species became dominant (Johnson, 2001). In low-productivity sub-alpine ecosystems, plant community has been taking longer time to converge to pre-fire conditions (Arnst et al., 2020; Burge et al., 2020). In forest ecosystem, the recovery of woody species were slower than exotic grasses (Richardson et al., 2018). Most of the smaller trees and shrubs recovered by resprouting and these were related to species composition and abundance of the site that can result in similar responses in post-fire (Teixeira et al., 2020). The local weather and environmental conditions for instance an increase in hot, dry and windy foen and slope increased fire frequency and severity (Pretorius et al., 2020; Simpson, et al., 2014); these are further associated with availability of fuel and flammable plants that can increase burn. For example, associated plant traits such as retention of dead material, low moisture content and low specific leaf area accounted for the high flammability of invasive species (Wyse et al., 2016). Other studies (eg.

Alam et al., 2020; Cui et al., 2020; Mason et al., 2016) have shown that plant morphological and chemical traits play an important role in plant flammability. These species trait variation in community can influence flammability at community level. For example, Padullés Cubino et al. (2018) found that community flammability was declined in tussock-dominated montane grasslands due to increase in invasive forbs. However, there are no studies where pre- and post-fire data are used to assess temporal changes in community structure. Determining trajectories of post-fire community by comparing with pre-fire community structure are important to determine future community pathways. Testing the plant community pattern and comparison between pre- and post-fire community structures, in particular in natural fires are rare around the world (Bowd et al., 2021; Lipoma et al., 2016).

1.5 Thesis aims, and objectives

This thesis broadly aimed to evaluate plant community structure and plant traits that influence fire and are influenced by fire in montane environments in predicted fire-prone ecosystem. The specific objectives of this study were to:

1) quantify and understand short-term community dynamics after wildfires in tussock-dominated areas of montane grasslands at two sites in the South Island of New Zealand (Chapter 2);

2) test for community resilience by comparing pre- and post-fire plant community structure in tussock-dominated areas of montane grasslands at one site in the South Island of New Zealand (Chapter 3);

3) quantify change in community flammability over nine decades of post-fire vegetation change in multiple vegetation types in montane areas in the South Island of New Zealand (Chapter 4); and

4) understand relationships among flammability, leaf nutrients and morphological plant traits in montane areas of the South Island of New Zealand (Chapter 5).

Recently, large wildfires in New Zealand have affected several sites in tussock-dominated grasslands in the South Island montane environment (Fire and Emergency New Zealand, 2020, 2021). In the face of this increasing wildfire activity in Aotearoa New Zealand, using repeated measurement datasets of over two and half years after wildfire, Chapter two quantifies the short-term response of community structure to wildfire at two different locations.

Community structure was compared over time for areas with three different fire histories of which some were burnt twice, and some were burnt once. Patterns were compared for species of different biostatus (native and exotic species) and growth form (forbs, graminoids and woody).

Using a dataset that incorporated long-term pre-fire measurements with short-term post fire measurements, Chapter three tested for community resilience in tussock-dominated montane grassland after a recent wildfire. Pre- and post-fire community structures were compared, and patterns were assessed for species of different biostatus (native and exotics) and growth form (forbs, graminoids and woody). Field measurements of plants that survived the wildfire were used to assess patterns for species with different regeneration traits (clonality and meristem position).

Chapter four used experimental shoot burning to estimate community flammability for different plant community types measured over nine decades in one of the oldest permanent vegetation monitoring plots in the world. Phylogenetic patterns and relationships between morphological traits and plant flammability were assessed. Chapter five used the same plots, flammability measurements and plant morphology trait data to test the relationships among flammability, morphology and leaf nutrient contents.

Chapter 2 Short-term recovery of plant communities after wildfires in montane grasslands

2.1 Introduction

Disturbance regimes around the world, such as fire, are changing beyond historical norms due to climate change, with fire regimes shifting due to changes in ignition patterns, fuel continuity, drought and fire weather (Collins et al., 2022; Pausas & Keeley, 2021; Sage, 2020). Changes in fire regimes can impact plant community structure and recovery, sometimes causing widespread shifts or losses of dominant species (Baltzer et al., 2021; Nolan et al., 2021). Species common in the initial period after fire can give good indications of future community structure in forests (Day et al., 2017; Johnstone et al., 2020; Turner et al., 2016) and grasslands (Zomer & Ramsay, 2021). Repeated measurements of plant community in the initial stages after fire can therefore facilitate understanding of future vegetation dynamics by capturing immediate responses such as plant survivability, recovery, and changes in community structure, however, few studies have done this.

Plants can recover from fire by two responses: surviving to resprout or germinating from seed either from on-site seed banks or spores dispersed from unburnt areas (Bond et al., 2004; Bond & Midgley, 2003; Day et al., 2020; Nolan et al., 2021). At an individual level, plants need time to build up reserves for structures to regrow after fire (such as rhizomes, tillers) and/ or time to reach reproductive maturity. If fires become too frequent outside of historical norms and beyond ecological tolerances of the species, then this compromises the ability of plants to recover, i.e., ‘interval squeeze’ (Enright et al., 2015). This can cause dramatic changes in plant community structure and even declines in dominant species (Baltzer et al., 2021; Le Breton et al., 2022). For example, one study showed that excluding fires from cerrado savannah in Brazil led to increased woody species cover (Rodrigues & Fidelis, 2022). Moreover, community composition was different from areas that had burnt annually or biennially in the six years prior. Such impacts on community structure under different fire frequencies may be detectable for many decades and potentially through multiple fire cycles and may impact initial patterns of recovery in plant communities after fire.

Species with different growth forms and biostatus (i.e., exotic, or native origin) can differ in how they are impacted by fire and, therefore, their recovery (D’Antonio & Vitousek, 1992; Day et al., 2020). Growth forms with meristems close to the ground are probably less likely to be damaged by fire, particularly fast-moving surface fires, so they may survive and rapidly recover following fire. For instance, grasses and forbs have low meristems and they can rapidly recover post-fire from basal buds but slower-growing woody plants with higher meristems are more susceptible to mortality or at least take longer to recover (Bellingham & Sparrow, 2000; Kraaij et al., 2017; Pekin et al., 2012). While over decadal time periods grassy ecosystems can become dominated by woody species in the absence of fire (Mark & Dickinson, 2003), recovery of different growth forms may be observable in the first few months after fire. Exotic species, particularly those that become invasive, are often more tolerant to disturbances than native species in the same environments and are proficient at outcompeting natives for resources such as light, nutrients and water (Molinari & D'Antonio, 2020). In a grassland in California, USA, exotic graminoids survived fire better than surrounding native species because they had higher moisture content than natives; hence, they may outcompete native graminoids (Livingston & Varner, 2016). In New Zealand native grasslands, disturbance-tolerant exotic graminoids, such as *Agrostis capillaris* L., are often highly abundant after fire (Allen & Partridge, 1988; Calder et al., 1992). In this system, invasive exotic forbs had lower flammability than other species in this community (Padullés Cubino et al., 2018), suggesting they may be less impacted by fire and may be able to survive and outcompete native species. These studies suggest recovery of plants after fire may differ depending on a combination of both biostatus and growth form.

Fine-scale environmental conditions or microhabitats influence the ability of plants to survive and resprout or germinate from seed (Day et al., 2020; Day et al., 2022; Moore et al., 2019). Substrate availability may be particularly important. For instance, mosses have high water-holding capacity and may support survival of plants by reducing impacts of heat-damage of plant tissue by fire (Gavini et al., 2019; Michel et al., 2013). Alternatively, mosses may inhibit seed germination due to allelopathy and competition with vascular plants for space, moisture, and light (Jeschke & Kiehl, 2008; Michel et al., 2011). Interactions between micro-sites and post-fire plant community structure and dynamics are little understood.

In Aotearoa New Zealand, parts of the landscape currently covered by native-dominated grasslands are projected to experience the greatest increases in fire risk compared to other parts of the country (Melia et al., 2022; Pearce et al., 2011) and some of the largest fires in recent New Zealand history have occurred in montane grasslands. These montane grasslands in New Zealand became widespread only after the arrival of humans and increased fire activity ~800 years ago (McGlone, 2001; McWethy et al., 2010; Perry et al., 2014). Fires are thought to have been extremely rare prior to human arrival, so it is generally thought that native plants are not well adapted to recover from fire (Bond et al., 2004; Ogden et al., 1998; Perry et al., 2014). While species in grasslands and savannas in many regions globally have evolved in frequent fires and are adapted to fire, this may not to be the case in New Zealand grasslands (Bond & Keeley, 2005; MacDermott et al., 2017). However, we know that some native plants are capable of rapid recovery after fire. For example, snow tussocks (*Chionochloa* spp.) can survive fire by rapidly resprouting followed by flowering, but seeds produced after burns have lower viability rates than other grasses and unburnt snow tussocks (Mark, 1965, 1969). Several species of mountain daisies (*Celmisia* spp.) can also resprout (Allen & Partridge, 1988). A study using prescribed burns demonstrated that losses of snow tussock biomass was higher in summer burns than spring burns (Payton & Pearce, 2009), but recovery of the full plant community was not investigated. Several studies showing changes in plant community structure and long-term succession decades after fire (20 years or more) have been conducted in tussock grasslands, in New Zealand (Burge et al., 2020; Calder et al., 1992; Gitay et al., 1992), but immediate, short-term dynamics in montane grassland plant community has not been studied. These short-term dynamics likely affect the longer-term successional changes, and with increased fire frequency, they may become increasingly important.

Here, we aimed to quantify and understand short-term community dynamics after wildfires in tussock-dominated areas of montane grasslands at two sites in the South Island of Aotearoa New Zealand. We undertook repeated measures of post-fire vascular plant community to investigate short-term changes over 2-26 (Deep Stream) and 1-16 (Pukaki) months since fire. Deep Stream was an area where prescribed burns had been conducted in 2001, where some areas were burnt in spring, some in summer, and others left unburnt; the entire area reburnt in a wildfire November 2019. Pukaki had not burnt since before the 1970s (Molloy & Hodder, 1976) and burnt in a wildfire in August 2020. We asked: 1) how does post-fire community structure (composition and richness) change in the months immediately following wildfire?; 2) Do different fire histories lead to differences in plant recovery or community dynamics?; 3) Do species of different biostatus (native vs exotic) and growth forms recover at the same rate?; and 4) Does biostatus, substrate (moss), or meristem height influence the probability of individual plants recovering from seed? The significance of this study is improving our understanding of the response of plant communities to wildfires in montane grasslands, which will help community ecologists to better predict trajectories of post-fire composition changes and, thus, the public will be better informed about the effects of wildfires.

2.2 Methods

2.2.1 Study locations and field sampling

Two sampling sites were sampled in the recently burnt area in this study: a tall tussock dominated grassland site at Deep Stream (inland from Dunedin), on land owned and managed by the Dunedin City Council and both short and tall tussock grassland at Pukaki, a land close to the highway and owned by Department of conservation (Figure S2.1). The Deep Stream site, which is on gently sloping terraces (640–700 m a.s.l.) between Barbours and Clarkes Streams at the eastern end of the Lammerlaw Range, is typical of lower-altitude tall-tussock grasslands that are coming under increasing pressure for pastoral development. The Pukaki site, situated at the side of highway and close to farmland, represents highly disturbed mixed short and tall tussock grassland is progressively being retired from grazing and incorporated into conservation land.

Deep Stream

Deep Stream lies between 640 to 700 m a.s.l. in the Lammerlaw Range in Otago, New Zealand. The vegetation was dominated by the perennial narrow-leaved snow tussock (*Chionochloa rigida* (Raoul) Zotov, Poaceae) interspersed with native perennial forbs, such as *Aciphylla aurea* W.R.B.Oliv. (Apiaceae) and *Celmisia gracilenta* Hook.f. (Asteraceae), and exotic perennial forbs, such as *Pilosella officinarum* Vaill. (Asteraceae) and *Hypochaeris radicata* L. (Asteraceae; Figure S2.1, Appendix A). Small native woody shrubs are distributed throughout the tussock matrix. Mean annual precipitation and mean seasonal temperature amplitude (difference between summer and winter) were 667.67 ± 3.02 mm, and 10.67 ± 0.05 °C (Wratt et al., 2006). Mean summer temperature and mean winter temperature were 11.76 ± 0.05 °C and 2.54 ± 0.06 °C respectively. This area is managed by Dunedin City Council and was not grazed or burnt since at least the 1970s until prescribed burns occurred in 2001 (Payton & Pearce, 2009). Our experimental design at this site consists of replicated areas that burnt within 18 years of each other, and others that burnt in 2001 (Figure S2.1a, Appendix A). In 2001, Deep Stream was the site of prescribed burns (Payton & Pearce, 2009) and then the whole area burnt in a wildfire in spring of 2019 (November). There were nine, 1 ha (100 × 100 m) plots set up in 2001: three plots were unburnt in 2001 and burnt in November 2019 (hereafter unburnt 2001); three burnt in spring 2001 (2 October) and reburnt in November 2019 (hereafter spring burnt 2001); and three plots were burnt in 2001 (7 March) and reburnt in November 2019 (hereafter summer burnt). Payton and Pearce (2009) reported that the 2001 summer burn was hotter than the spring burn due to high biomass and low moisture content. The cause of the 2019 fire is still unknown but burnt ca. 5400 hectares, which is a large fire for this region (Fire and Emergency New Zealand, 2021).

We conducted vegetation surveys three times after the wildfire in November 2019: 2 months (January 2020), 13 (December 2020), and 26 (January 2022) months post-fire (Figure S2.2, Appendix A). We undertook vegetation surveys within 12, 20 × 20-m plots within the larger 1 ha plots. There were nine, 20 × 20-m plots that were subjectively chosen for an experimental burn to avoid slope effects and other environmental effects in 2001 (Payton & Pearce, 2009). These nine plots were groups of three adjacent plots with different burn treatments (unburnt, spring burnt, summer–autumn burnt) in each group. Three additional 20 × 20-m plots were set up in an area that did not burn in 2001 or in 2019 ~1 km from the burnt plots (hereafter unburnt). Within each 20 × 20-m plot, we randomly established three 1 × 1-m subplots, which comprised of four, 0.5 × 0.5-m quadrats with reference to pre-existing wooden or metal poles that were placed for sampling during experimental burning in 2000 and 2001 (Figure S2.1a, Appendix A). However, we did not get any community structure data from that study. In each quadrat, we recorded presence of live vascular species (plants with green leaves) at the three measurement times in the experimental burn plots (Figure S2.2 Figure S2.3, Appendix A). The vascular plant species were identified using flora books of New Zealand (Mark 2012; Wilson 1978; Champion et al. 2012). For those plants that could not be reliably identified to species, a sample was collected from nearby plot and were identified later. Nomenclature follows the Landcare Plant Names Database (https://www.nzflora.info). The voucher specimens were collected and deposited at AUT. Assuming less change due to slow growing nature of tussock grassland species which is previously described (Mark, 1969; Connor & Vucetich, 1964), the unburnt plots were only measured once at 2 months after fire. We also undertook destructive sampling of plant individuals in two, 2 × 2- m plots 2 months after fire in the burnt areas on each end of 10-m transect, but not in the vegetation survey plots, to assess whether plants were recovering from seed or had survived the fire. We excavated plants at nine locations in 18 plots aiming to collect data for five individuals of each species at each location. We also recorded the substrate of each plant was growing in, in terms of moss or not on moss. These transects were made close to, but outside, the permanently marked vegetation survey plots to ensure that excavated individuals did not affect community composition in future surveys. About 45% of the total species recorded in the surveyed plots were excavated in the plots at these transects.

Pukaki

Pukaki lies at 620 to 650 m a.s.l. in the Pukaki Scientific Reserve, Canterbury, New Zealand. This site is comprised of native shrubs such as *Corokia cotoneaster* (Argophyllaceae) and small invasive exotic conifer trees (*Pinus contorta*¸Pinaceae), with patches of narrow-leaved snow tussock-dominated grassland (Figure S2.1, Appendix A). The reserve is managed by the Department of Conservation and had not been burnt or grazed since the establishment of the reserve in 1996. Mean annual precipitation was 593.7 ± 2.58 mm and mean seasonal temperature amplitude was 13.84 ± 0.05 °C (Wratt et al., 2006). Mean summer temperature and mean winter temperature were 14.75 ± 0.02 °C and 2.81 ± 0.03 °C respectively. We established two plots for vegetation surveys in October 2020, one month after the wildfire in spring of 2020 (30 August 2020) (Figure S2.1b, Appendix A). The fire was an accident and burnt ca. 3000 hectares (Fire and Emergency New Zealand, 2020).

We conducted vegetation surveys three times after the wildfire in October 2019: one month (October 2020), four (January 2021) and 16 (January 2022) months after fire (Figure S2.2 & Figure S2.4, Appendix A). Two plots were randomly located in mixed short and tall tussock dominated grassland habitat that are similar to the Deep Stream site. Then, to capture highly spatially dispersed species data, we used a modified Whittaker's plot design where, within each 20 × 20-m plot, we established a 1 × 1-m subplot at each corner then divided this into four, 0.5 × 0.5-m quadrats (Figure S2.1b, Appendix A; Morrison et al. 1995). As at Deep Stream, we recorded vascular species' presence (with green leaves) within each 0.5 × 0.5-m quadrat, identified and deposited voucher specimens. We also undertook destructive sampling within two, 2 × 2-m plots on each end of a 10-m transect, but not in the vegetation survey plot 4 months after fire to assess whether individual plants were recovering from seed or had survived the fire, and the substrate they were in, using the same methods described for Deep Stream. These transects were established adjacent to, but outside, the permanently marked vegetation survey plots to ensure that the excavated individuals did not affect community composition in future surveys. About 31% of the total species recorded in the surveyed plots were excavated in the plots at these transects.

Fire severity

Field sampling was undertaken at both sites to compare three methods for assessing fire severity: minimum branch diameters of woody plants and percent covers of burnt and live vegetation and litter (Appendix B). The results were inconclusive and so these data are not presented in this chapter.

2.2.2 Data analyses

For each species at each site, we collated plant data to explore the post-fire plant community trait change: plant biostatus (native or exotic), growth forms (forb, graminoid, woody) and meristem height (high or low based on Raunkiær's life form (Raunkiaer, 1934; Raunkiaer, 1905; Table S2.1 & Table S2.2, Appendix A; Breitwieser et al., 2010; Manaaki; New Zealand Plant Conservation Network, 2022). Those plants having bud close to the soil surface or inside soil are low meristem and those plants having bud high up on the plant are meristem high. Sites were analysed separately due to different sampling designs and fire histories. Species present at each measurement time in each1ha, 20 × 20 m plot at each site was visualised by Venn diagram using 'ggVennDiagram' (Gao, 2022). All other analyses were conducted at the quadrat level in R v.4.2.1 (R Core Team, 2022) with 'tidyverse' (Wickham et al., 2019), 'ggreppel' (Slowikowski et al., 2021), 'gghighlight' (Yutani, 2022), and 'egg' (Auguie, 2019) for data visualization and others where specified.

Post-fire changes in plant community structure

Composition

To investigate short-term changes in post-fire composition over time, we used species' presence in each quadrat at each site at each time (species' presence matrix). We performed a principal coordinate analysis (PCoA) on the species' matrix using Jaccard dissimilarity in 'vegan' (Oksanen, 2021). We then calculated the weighted average scores for each species using function 'wascores' over PCoA and species presence absence data matrix. To assess changes in composition over time, we ran separate PERMANOVAs for each fire history (Deep Stream) or plot (Pukaki), specifying the species matrix as the response and months since fire as a categorical predictor, implemented using 'pairwise.adonis2' (Anderson, 2006; Oksanen et al., 2022). We then assessed changes in compositional variance (following Avolio et al., 2019). We measured the distance between centroids of each subplot at each time within each fire history (Deep Stream) or plot (Pukaki) using 'betadisper'. We then assessed significant changes in compositional variance using function ‘permutest’ in ‘vegan’. High values of compositional variance suggest there is a lot of variation in species composition in quadrats within fire history or plots (i.e., variation around the centroid), while low values suggest there is little variation.

Species richness

We calculated quadrat species richness by biostatus and growth form for each quadrat at each time. We used generalized linear mixed effect models assuming a Poisson error distribution (glmmTMB; Brooks et al., 2017). Since quadrats were joined to each other, to avoid spatial autocorrelation and subplots were not adjacent to each other, the random effect was subplot. Data were subsetted into species groups of interest and multiple models were run. At Deep Stream, to assess significant differences in richness over time within fire histories, we ran six models for biostatus (3 fire histories × 2 biostatus) and nine models for growth form (3 fire histories × 3 growth forms). We were also interested in if there were differences in richness among fire histories at each time, so we ran additional models with fire history as a predictor: six models for biostatus (3 measurement times × 2 biostatus) and nine models for growth form (3 measurement time × 3 growth forms). At Pukaki, to assess significant differences over time within plots, we ran four models for biostatus (2 plots × 2 biostatus) and six models for growth form (2 plots × 3 growth forms); we were not explicitly interested in differences between plots at this site. Significant differences were assessed using ‘emmeans’ (Lenth, 2022).

Probability of germination from seed or survival

To evaluate the probability of plants recovering from seed under different conditions, we used the destructive sampling data at Deep Stream (two months after fire) and Pukaki (four months after fire). Individual plants were assigned one if they were growing from seed (if seeding is coming from any seed and has remains of seed coat or decayed seed attached to) or zero if they had survived (i.e. plants that were found green and live growing from vegetative part but not sure either they were resprouters or not). We used generalised mixed effect model (glmmTMB) assuming a binomial error distribution to model the proportion of plants that were from seed out of the total number of plants excavated as a function of three predictor variables (run as 3 separate models at each site): biostatus, meristem height (high or low), or substrate (moss or not moss). At Deep Stream, the random effect was location at which plants were excavated. We did not use a random effect at Pukaki due to low sample size. These models tell us whether particular plant traits or substrate variables impacted how plants recovered.

2.3 Results

2.3.1 Post-fire community structure changes following wildfire in relation to fire history at Deep Stream

We observed a total of 42 vascular plant species in 36 m^2 at Deep Stream across three measurements 2-26 months post-fire (Table S2.1, Appendix A). Most species were native (n = 35) compared to exotic (n = 7). Most species that were present 2 months after fire were also present 13 and 26 months after fire (Figure 2.1). The number of species and species richness increased with time since fire across all fire history treatments (Figure 2.2).

Composition

The first two axes of the PCoA explained 46% of the total variation in plant species composition across time. On plots that had reburnt (spring burnt 2001 and summer burnt 2001), quadrats were different in composition compared to quadrats that burnt only in 2019 (unburnt 2001) which were close to the reburnt in the same habitat (Table 2.1 & Table 2.2; Figure 2.3). Over time (2, 13, and 26 months after fire), unburnt 2001 quadrats differed in how they changed in composition compared to the spring burnt 2001 and summer burnt 2001 quadrats (burnt in 2001 and 2019) (Table 2.1). Quadrats that did not burn in 2001 or 2019 (unburnt) had different composition from the quadrats that burnt either once or twice (Table 2.2; Figure S2.5, Appendix A). Post-fire change in composition and change in variance of the quadrats were large at two months after fire and low in later measurements (13-26 post-fire) (Table 2.1 & Table 2.2; Figure S2.6, Appendix A). Together, these results show that among fire histories, composition immediately after fire was more different and more variable than they were a longer time after fire (Figure 2.2). Change in richness was significantly higher in spring burnt 2001 than unburnt 2001 (Table 2.2; Figure 2.4).

Table 2.1. Post-fire change in the mean and variance of community composition in montane grasslands at Deep Stream, and Pukaki, New Zealand over time across 14 plots of fire history treatments and plots, respectively, across measurement times. Change in composition was measured as the mean pairwise Jaccard dissimilarity in species presence within 0.25-m^2 quadrats (*n* = number of quadrats compared). Comparisons were made among measurement times (months post-fire) for each fire history treatment; 12, 400-m^2 plots at Deep Stream and 2, 400-m^2 plots at Pukaki. Asterisks represent significant differences between measurement times, where *** = $P < 0.001$, ** = $P < 0.01$ and * = $P < 0.05$, based on permutational analysis of variance.

Site	**Fire history treatment / Plot**	**Months post-fire compared**	***n***	**Change in composition**	**Change in variance**
Deep Stream	Unburnt 2001	2-13	36	0.36 ± 0.17**	-0.05 ± 0.01*
	Unburnt 2001	13-26	36	0.33 ± 0.13**	-0.08 ± 0.02
	Unburnt 2001	2-26		0.57 ± 0.14**	-0.08±0.01*
	Spring burnt 2001	2-13	36	0.36 ± 0.11**	-0.02 ± 0.01
	Spring burnt 2001	13-26	36	0.28 ± 0.11**	-0.01 ± 0.02
	Spring burnt 2001	2-26		0.52 ± 0.11**	-0.03±0.01*
	Summer burnt 2001	2-13	36	0.37 ± 0.15**	-0.03 ± 0.02
	Summer burnt 2001	13-26	36	0.21 ± 0.12**	0 ± 0.02
	Summer burnt 2001	2-26		0.49 ± 0.14**	-0.03±0.03
Pukaki	Plot 1	1-4	16	0.74 ± 0.08***	0.1 ± 0.05*
		4-16	16	0.54 ± 0.17***	-0.05 ± 0.03*
		1-16	16	0.86 ± 0.06***	-0.05 ± 0.03
	Plot 2	1-4	16	0.71 ± 0.13***	0 ± 0.03
		4-16	16	0.54 ± 0.16***	-0.06 ± 0.04*
		1-16	16	0.85 ± 0.09***	-0.06 ± 0.04

Table 2.2. Differences in mean and variance in species composition among fire history treatments within each measurement time in montane grasslands at Deep Stream, New Zealand. Variation in composition was quantified using the pairwise Jaccard dissimilarity among 0.25-m^2 quadrats within fire history treatment 12, 400-m^2 plots (*n* = number of quadrats compared). Asterisks represent significant differences between fire histories at each measurement, where *** = *P* < 0.001, ** = *P* < 0.01 and * = *P* < 0.05, based on permutational analysis of variance and on generalised linear mixed effects modelling for species richness.

Fire history treatments compared	**Months post-fire**	***n***	**Composition change**	**Change in variance**	**Change in richness**
Unburnt 2001 and Spring burnt 2001	2	24	0.63 ± 0.12***	0.02 ± 0.09**	-1.61 ± 0.53
Unburnt 2001 and Summer burnt 2001	2	24	0.63 ± 0.11***	0.02 ± 0.08**	-1.14 ± 0.47
Spring burnt 2001 and Summer burnt 2001	2	24	0.51 ± 0.13	0 ± 0.08	0.47 ± 0.43
Unburnt 2001 and Spring burnt 2001	13	24	0.56 ± 0.12***	0.01 ± 0.1*	-1.83 ± 0.42*
Unburnt 2001 and Summer burnt 2001	13	24	0.57 ± 0.11***	0.02 ± 0.1*	-1.64 ± 0.43
Spring burnt 2001 and Summer burnt 2001	13	24	0.47 ± 0.12	0.01 ± 0.1	0.19 ± 0.48
Unburnt 2001 and Spring burnt 2001	26	24	0.53 ± 0.11***	0.01 ± 0.1*	-1.42 ± 0.45
Unburnt 2001 and Summer burnt 2001	26	24	0.54 ± 0.11***	0.01 ± 0.1*	-0.61 ± 0.48
Spring burnt 2001 and Summer burnt 2001	26	24	0.47 ± 0.1	0 ± 0.09	0.81 ± 0.52
Unburnt 2001 and Unburnt	2	24	0.72 ± 0.12***	-0.01 ± 0.1	-0.28 ± 0.53
Spring burnt 2001 and Unburnt	2	24	0.74 ± 0.1***	-0.02 ± 0.09**	1.33 ± 0.58
Summer burnt 2001 and 2019 and Unburnt	2	24	0.74 ± 0.11***	-0.03 ± 0.09**	0.86 ± 0.57

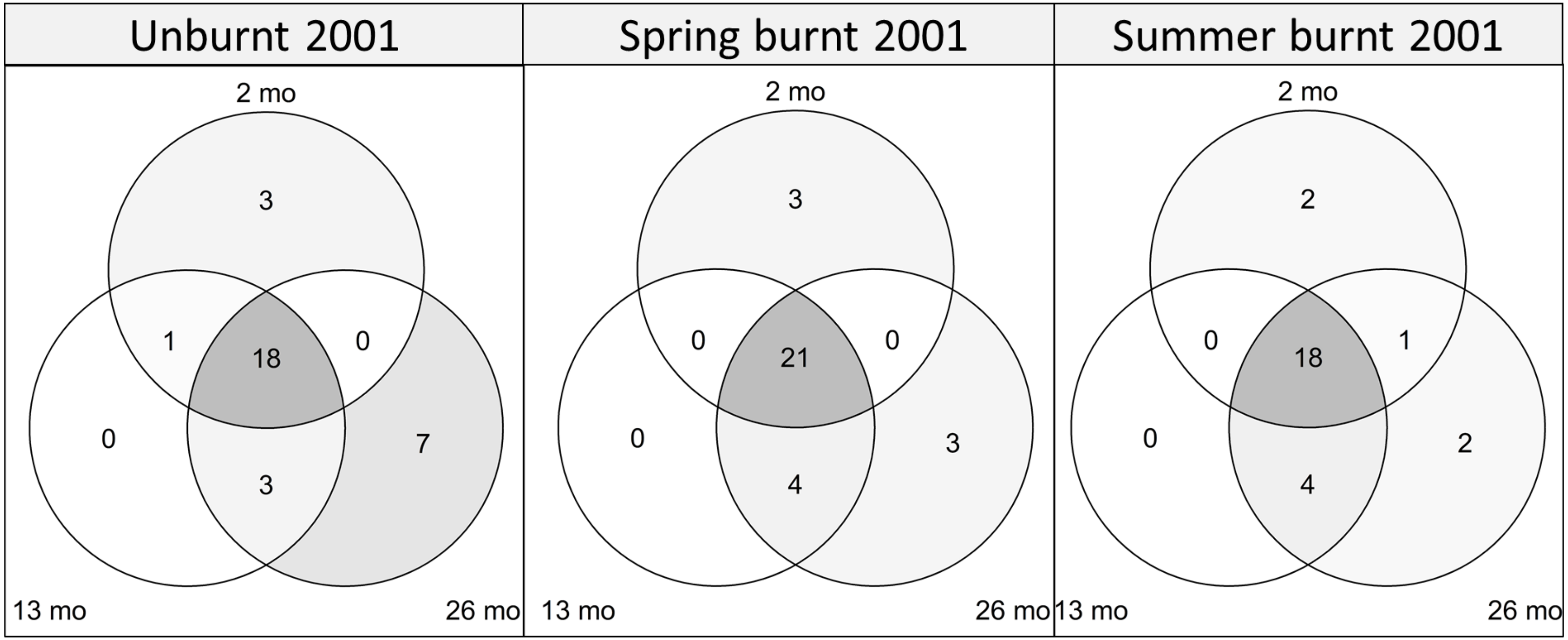

Figure 2.1. Venn diagrams of species recorded in 36, 0.25-m^2 quadrats in 9, 400-m^2 plots at 2, 13, and 26 months after the November 2019 wildfire (summer) across three fire history treatments in montane grasslands at Deep Stream, New Zealand.

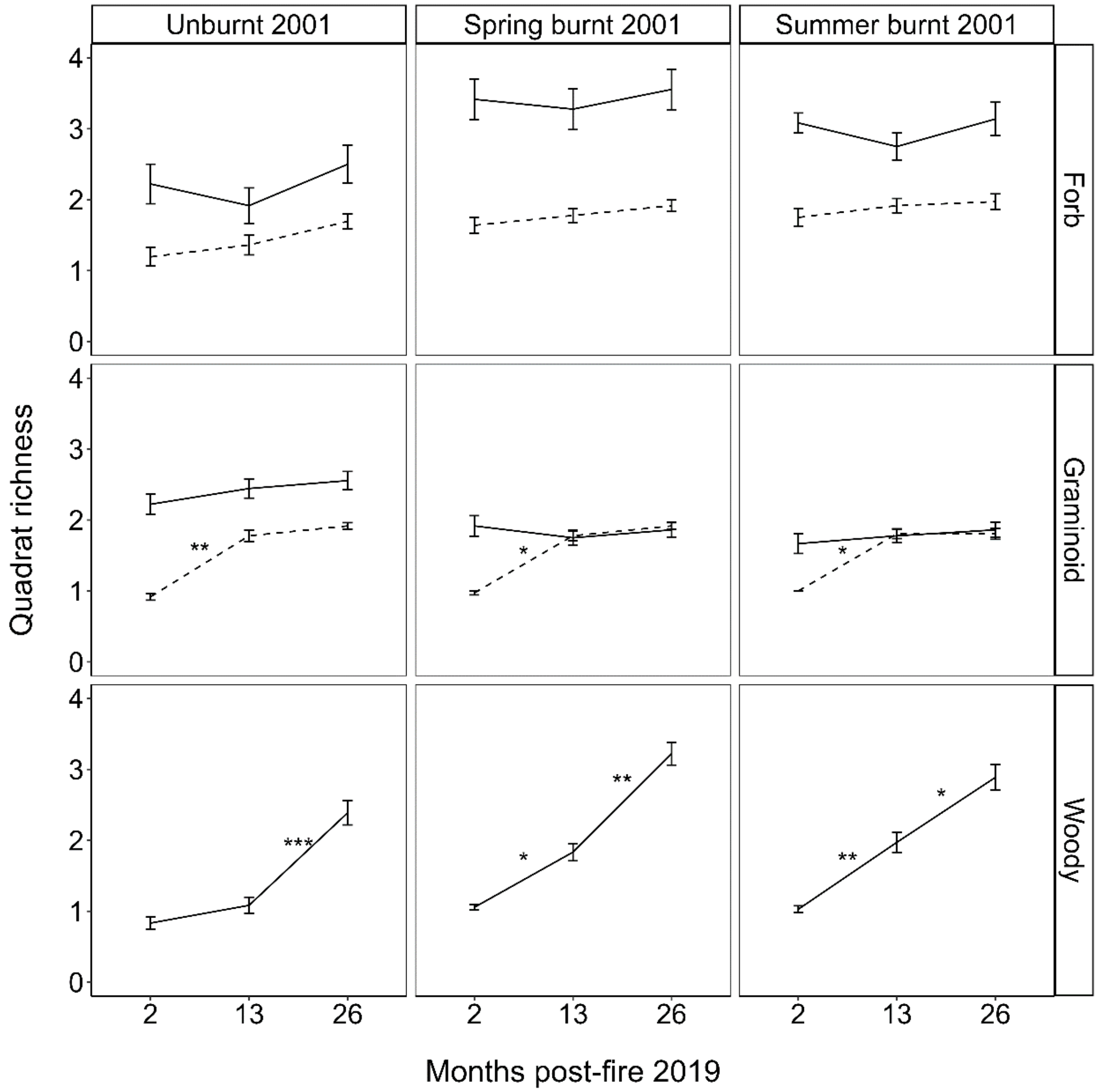

Figure 2.2. Post-fire quadrat vascular plant species richness (± standard error) of native (solid lines) and exotic (dashed lines) species of different growth forms over time on the plots that were burnt either once or twice in different seasons in montane grasslands at Deep Stream, New Zealand. A total of 12, 0.25-m^2 quadrats were measured in each 400-m^2 plot at each measurement. The *x*-axis represents the measurement time in months relative to November 2019 wildfire (spring). The panel rows show the results for growth forms and the columns show the results for plots from different fire history treatments. Asterisks represent significant differences in mean quadrat richness between the measurements, based on the generalised linear mixed effects models (* = $P < 0.05$, ** = $P < 0.01$) and *** = $P < 0.001$).

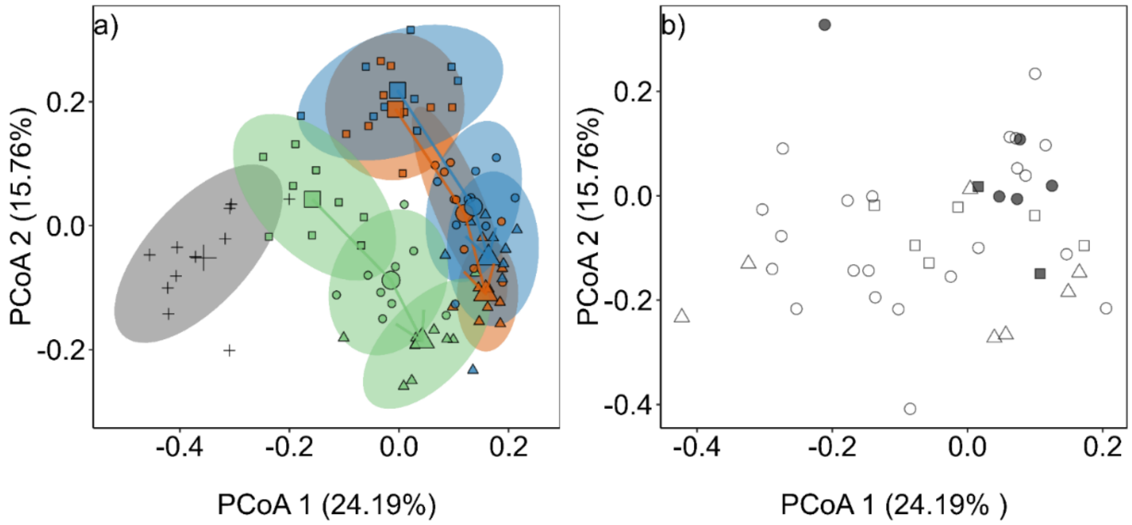

Figure 2.3. Principal coordinate analysis diagrams for Jaccard dissimilarity of plant species presence in 0.25-m^2 quadrats showing a) site scores and b) species scores in montane grasslands at Deep Stream, New Zealand. This study took place in a permanently marked study site where 9, 400-m^2 plots were subjected to experimental burning treatments in 2001 (3 unburnt, 3 burnt in spring, or 3 burnt in summer); subsequently, in November 2019 (summer), a wildfire occurred in the area, burning all experimental plots and 3 400-m^2 unburnt plots in an area that was not burnt. Large symbols represent the centroids of the fire history treatments (12, 0.25-m^2 quadrats in each fire history at each measurement time). Ellipses represent 95% confidence intervals for centroids. Lines represent the trajectories in composition between each measurement where the arrowhead is the most recent measurement. Ellipse and trajectory line colours represent fire history treatments: unburnt in 2001 and burnt in 2019 (green), spring burnt in 2001 and 2019 (blue), summer burnt in 2001 and 2019 (orange) and unburnt in 2001 and 2019 (grey crosses). Point shapes represent the number of months the measurement was taken after the November 2019 wildfire: 2 months (rectangle), 13 months (circle), and 26 months (triangle). Unburnt quadrats (cross) were measured 2 months post-fire. Species' scores represent exotic (filled) and native (hollow) species categorised as forbs (circle), graminoids (rectangle), and woody (triangle).

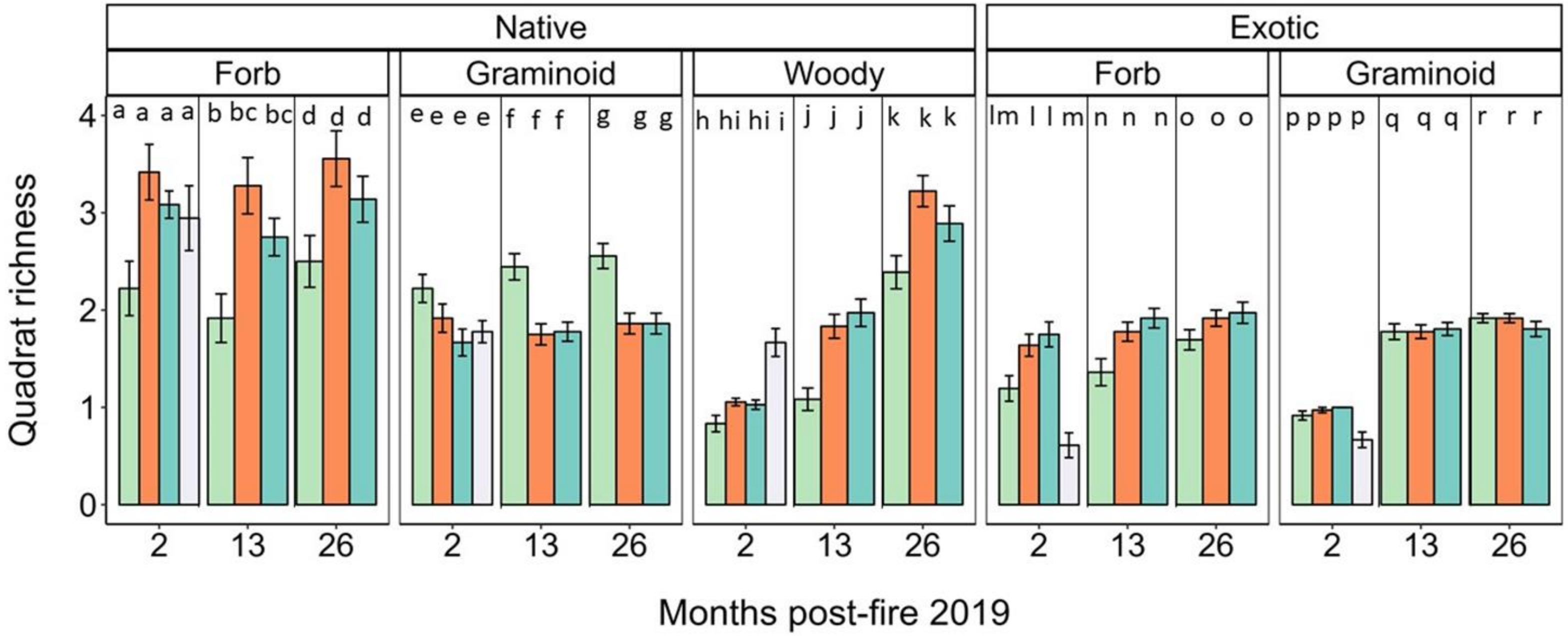

Figure 2.4. Post-fire quadrat vascular plant species richness (± standard error) of native and exotic species of different growth forms comparison in between fire history plots that were burnt either once or twice in different seasons at each measurement in montane grasslands at Deep Stream, New Zealand. Colour of bars represents the plots that had different fire history treatments of 2001 [bar: light green (unburnt 2001), orange (spring burnt 2001), blue (summer burnt 2001) and grey (unburnt)] in addition to 2019 wildfire at Deep Stream. A total of 12, 0.25-m^2 quadrats were measured in each 400-m^2 plot at each measurement. The *x*-axis represents the measurement time in months relative to November 2019 wildfire (spring). Quadrat richness was significantly different between unburnt 2001 and spring burnt in 2001 for native forbs and native woody ($P < 0.05$). In between unburnt 2001 and summer burnt 2001, native woody richness was significantly different at 13 months ($P < 0.05$) and between unburnt and unburnt 2001, native forbs were significantly different at two months ($P < 0.05$). Native woody species richness was significantly different in between unburnt, and spring and summer burnt 2001 at two months ($P < 0.01$). Significant differences between fire history were determined by generalised linear mixed effects models.

Recovery by biostatus and growth form

Changes in species richness by biostatus and growth form were similar among fire histories (Figure 2.2). Quadrat richness of exotic graminoids significantly increased 2-13 months after fire in all fire history treatments, but not 13-26 months after fire (Figure 2.2; Table S2.3, Appendix A). Quadrat richness of woody species, which were all native at this site, was the lowest 2 months post-fire and increased significantly over the time of the study; the exception to this was in the spring burn 2001 quadrats where only woody species richness increased 13-26 months after fire. Quadrat richness of forbs was high two months post-fire but did not change significantly both in natives and exotic species. Overall, these results show richness of both exotic graminoids, and native woody species increased 2-13 months after fire. Richness of woody natives continued to increase 13-26 months after fire but exotic graminoids did not. Richness of native forbs and native woody species was significantly higher on spring burnt 2001 and 2019 quadrats compared to unburnt 2001 quadrats 13 months post-fire (Figure 2.4). Richness of woody species was also significantly higher on summer burnt 2001 and 2019 quadrats than unburnt 2001 quadrats at the same measurement time. Richness of native woody was significantly higher in unburnt quadrats than the unburnt 2001 but burnt 2019 quadrats. Richness of exotic forbs were significantly lower in unburnt quadrats compared to spring and summer burnt 2001 and 2019 quadrats.

2.3.2 Probability of plants recovering from seed at Deep Stream

We destructively sampled 360 individual plants across 19 species (biostatus: 15 natives and 4 exotics; meristem height: 5 high and 14 low) (Table S2.1 &Table S2.4, Appendix A). A total of 58 plants were recovering from seed compared to 302 plants that survived the fire. All 19 species survived the fire, but of them, ten species were also recovering from seed. Among, the total species, *Pilosella officinarum* Vaill. and *Agrostis capillaris* L. were the dominant species that survived fire. *Agrostis capillaris* L. was also a dominant species recovering from seed. At 2 months after fire, the probability of recovering from seed was significantly higher in exotics and on non-moss substrate compared to natives and on moss (Table 2.3). In contrast, meristem height did not significantly impact the probability of plants recovering from seed.

Table 2.3. Generalised mixed effect modelling results for the probability of individual plants regenerating from seed in relation to three predictors: biostatus (native vs. exotics), substrate type (moss vs. not on moss), and meristem height (low vs. high meristem) in post-fire in montane grasslands at two months at Deep Stream, and four months at Pukaki, New Zealand (*n* = the number of individuals excavated). Significant predictors ($P < 0.001$) are shown in bold. The probability of regenerating from seed were all on not moss so model was not possible to run for substrate at Pukaki

Site and time	Model	Predictor	Coefficient	S.E.	*z* - value	*P* - value
Deep Stream (*n* = 360) at 2 months	Biostatus	**Exotic (vs. native)**	**-1.24**	**0.31**	**-4.03**	**0.00**
	Substrate	**Moss (vs. not on moss)**	**1.81**	**0.49**	**3.65**	**0.00**
	Meristem height	High (vs. low)	22	19826.43	0.001	0.999
Pukaki (*n* = 37) at 4 months	Biostatus	Exotic (vs. native)	0.92	0.92	0.99	0.31
	Substrate	Moss (vs. not on moss)	NA	NA	NA	NA
	Meristem height	High (vs. low)	23.12	60407.76	0	1

2.3.3 Post-fire community structure changes following wildfire at Pukaki

We observed a total of 48 vascular plant species at Pukaki across the three measurements 1-16 months post-fire (Figure S2.6; Table S2.3, Appendix A). Most species were native (*n* = 30) compared to exotic (*n* = 18). Similar to Deep Stream, most species that were present 1 month after fire were also present 4 and 16 months after fire (Figure 2.5). The number of species and species richness increased with time since fire in both plots (1-16 months) (Figure 2.6).

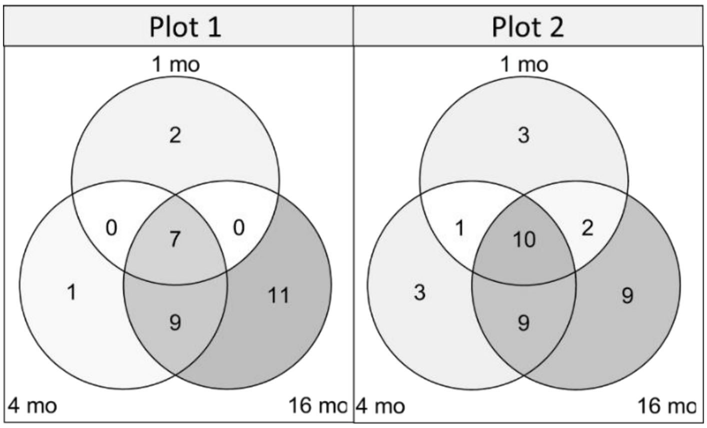

Figure 2.5. Venn diagrams of species recorded in 16, 0.25-m^2 quadrats in two 400-m^2 plots at each of three measurement times from one to 16 months after the August 2020 wildfire (spring) in montane grasslands at Pukaki, New Zealand

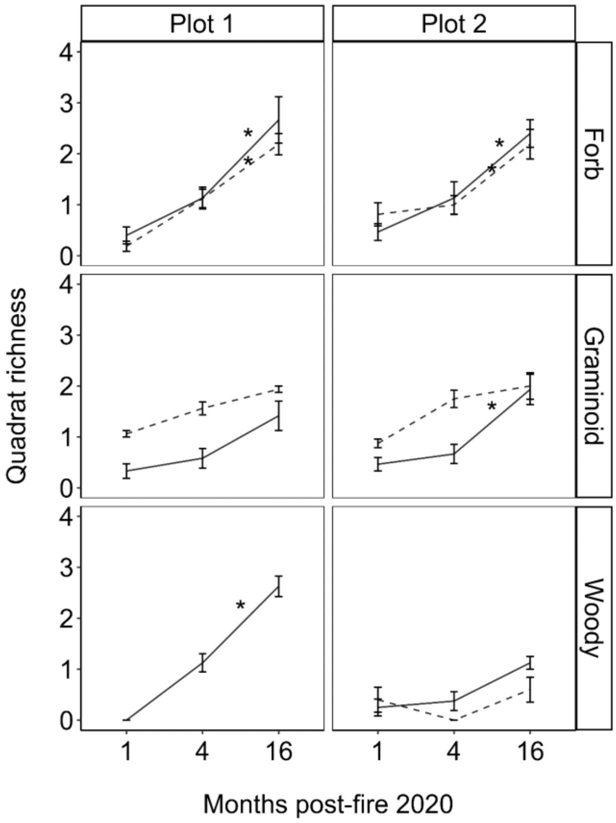

Figure 2.6. Post-fire quadrat richness (± standard error) of native (solid lines) and exotic (dashed lines) species different growth forms over time in montane grasslands in two 400-m^2 plots at Pukaki, New Zealand. The *x*-axis represents vegetation measurement time in months relative to the August 2020 wildfire (spring). Asterisks represent significant differences (*** = $P < 0.001$, ** = $P < 0.01$ and * = $P < 0.05$, based on the generalised linear mixed effects models) between measurements for all the growth forms on each plot

Composition

The two plots had similar composition 1 month after fire and became more similar over time. The first two axes of the PCoA explained 19.97% of the total variation in species composition (Figure 2.7; Figure S2.7, Appendix A). Post-fire changes in composition and change in compositional variance were higher 1-4 months post-fire compared to 4-16-months post-fire (Table 2.1; Figure 2.7; Figure S2.8, Appendix A). This shows that among plots, composition immediately after fire was more different and more variable than they were a longer time after fire (Figure 2.6).

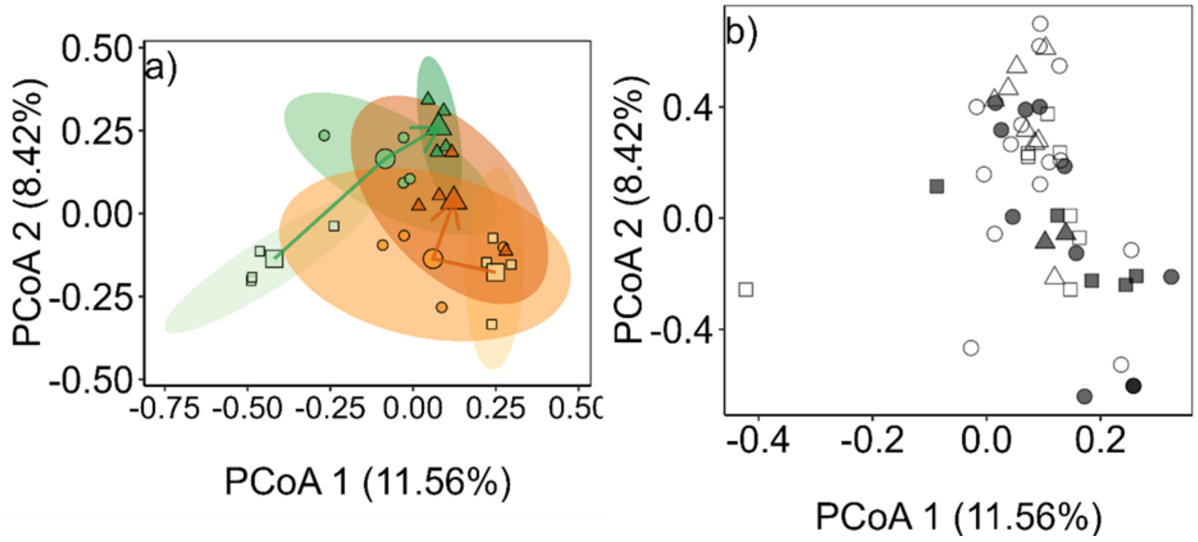

Figure 2.7. Principal coordinate analysis diagrams for Jaccard dissimilarity of plant species presence in two plots in 0.25-m^2 quadrats showing a) site scores and b) species scores in two plots montane grasslands at Pukaki, New Zealand. This study took place in a site that was burnt in a wildfire in spring 2020. Large symbols represent the centroids of 16, 0.25-m^2 quadrats in each of plot 1 (green) and plot 2 (orange). Ellipses represent 95% confidence intervals for centroids. Point shapes represent the number of months the measurement taken after the wildfire: 1 month (rectangle), 4 months (circle), and 16 months (triangle). Species' scores represent exotic (filled) and native (hollow) and species categorised as forbs (circle), graminoids (rectangle), and woody (triangle)

Recovery by biostatus and growth form

Between 1-16 months post-fire, both natives and exotics recovered at same rate in quadrat richness in both plots (Figure 2.6; Table S2.3, Appendix A). Richness of native and exotic forbs significantly increased 4-16 months after fire but not 1-4 months after fire. Richness of native graminoids significantly increased 4-16 months post-fire on plot 2 but it did not increase 1-4 after fire. Richness of both exotic and native graminoids did not increase on plot 1 both 1-4 and 4-16 months after fire. Native woody species richness significantly increased 4-16 months after fire on plot 1 (where there were no exotic woody species), but native woody species richness did not increase both 1-4 and 4-16 months after fire on plot 2. There were a few woody exotic species on plot 2 and these did not change significantly in richness over time.

2.3.4 Probability of plants recovering from seed at Pukaki

We destructively sampled 37 individual plants across 15 species (biostatus: 10 natives and 5 exotics; meristem height: 5 high and 10 low) (Table S2.2 & Table S2.4, Appendix A). A total of seven plants were recovering from seed compared to 30 plants that survived the fire. All species were survived in fire but of them three species were also recovering from seed. All species were survived fire but of them ten species were also recovering from seed. Among, 19 species, *Pilosella officinarum* Vaill. and *Agrostis capillaris* L. were dominant species that survived fire. *Wahlenbergia* species was dominant species recovering from seed too. At four months post-fire, the probability of recovering from seed was not significant in any of three predictors biostatus, substrate and meristem height (Table 2.3). One-month post-fire, all excavated plants had survived and all of them had low meristems.

2.4 Discussion

Our study using repeated measurements shows there were substantial changes in vascular plant community structure in the months following fire at these two sites in montane grasslands of the South Island of New Zealand. At both sites, most species that were present 1-2 months after fire were present at later months. Moreover, most species we excavated 1-4 months after fire had survived. Together, these results suggests that temporal dynamics in community structure in these tussock grasslands were driven by resprouting of surviving species rather than colonization of new species. As plants recovered, species richness increased and plant community composition became more similar within fire histories (Deep Stream) or plots (Pukaki), *i.e.*, composition somewhat converged. While there were differences in composition associated with different recent fire histories at Deep Stream in terms of reburnt or not that were close to each other in the same habitat, these differences became less apparent in the later period of the study (13-26 months after fire). While species richness increased over time, rates of increase differed according to growth form and biostatus. Graminoids had high species richness immediately after fire at both sites; at Deep Stream they were predominantly native, while at Pukaki they were predominantly exotic. In contrast, native woody species had low richness 1-2 months after fire and increased significantly in later time periods. Overall, our study demonstrates the value of understanding short-term changes in plant community structure after fire to elucidate patterns of recovery in the face of increased fire activity with climate change.

Most of the individual plants we dug up were not from seed (85 % at Deep Stream, 81% at Pukaki), showing that most of species appeared to survive the fires. *Pilosella officinarum* Vaill. and *Agrostis capillaris* L. were dominant species that survived fire. *Wahlenbergia* species was dominant species recovering from seed. Over time, some of the species that survived fire started flowering and new individuals were coming from seed at each site. We were surprised by the high survival of plants at both sites, and an increase in species richness, particularly native species because the New Zealand flora is generally considered to be poorly adapted to fire (Bond, 2008; Gitay et al., 1992). Our results are comparable to other grasslands and savannahs that have experienced greater historical fire activity (Bond & Keeley, 2005; Bowman, 2022; Dairel & Fidelis, 2020). For example, a short-term post-fire study showed that many plants rapidly recovered from fires in savannahs in Brazil where the authors were able to categorise species into five fire-response groups Pilon et al.(2021). Future studies in New Zealand’s montane grasslands using finer categories for species (such as those described by Pilon et al. 2021) would provide further knowledge of flora responses in plants that are thought to have evolved in low fire activity but may still have adaptations to recover from fires (Antonelli et al., 2011).

Convergence in species composition and increase in species richness is likely is due to resprouting of surviving plants. This suggests that plant community in these montane grasslands recover from fire rapidly. Past studies in these grasslands demonstrated that tussock species (*Chionochloa*) are long lived and take 15-20 years to recover in their biomass after fire (Gitay et al., 1992; Payton & Pearce, 2009); however, this represents only one species at each of our sites. Our measurements did not allow us to assess changes in biomass of plants, but this would be a useful addition for future studies. A detailed study at Deep Stream assessing populations of soil amphipods for 15 years pre- and post-fire shows most species can recover to pre-fire abundance within three years (Barratt et al., 2019). Pre-fire plant data is desperately needed to be able to directly assess fire impacts and directly assess resilience in these grasslands, which is currently lacking.

The effect of fire history on community structure was detectable among areas that had either burnt only once or twice in 18 years at Deep Stream. Composition in reburnt quadrats differed from those that had only burnt once although all of them were close to each other in the same the habitat. Richness of forbs tended to be lower on quadrats that had not burnt in 2001 (unburnt 2001) compared to those that had reburnt, but this was only significant 13 months after fire. However, we did not detect a strong effect of the season of the first fire in 2001 (spring or summer). We may have expected to see a season effect given that losses of tussock biomass and mortality were greater in the summer fire in the prescribed burns, due to drier conditions and greater biomass in summer increasing vegetation flammability (Payton & Pearce, 2009). Therefore, while overall our results suggest there is rapid recovery and general convergence of community after fire, the legacy effects of fire from 18 years ago, regardless of season, have clearly left a signal that is still detectable through an additional fire event. This suggests that more frequent fires that are predicted in these areas will impact plant community structure through multiple fire cycles and over the long term. The implications of these changes are yet unknown.

Both our sites contained more native species than exotics. We had expected exotic forbs, which have lower flammability than other species in this system (Padullés Cubino et al., 2018), to potentially benefit from the fire by surviving and outcompeting native species, which was not the case at either site at a community level. This suggests that, at this time scale, fire will not cause dramatic shifts towards exotic species at a community level (although there may be changes in biomass). Graminoids and some forbs have low meristems, so they may be less impacted by the heat of the fire and recover rapidly (Araújo et al., 2013; Simpson et al., 2021). Forb richness did not change significantly after fire at Deep Stream. This further suggests that, at this time scale, fire will not cause dramatic shifts towards exotic species at a community level. Graminoids also have protected buds and a storage reserve that allow them to resprout immediately after fire (Pausas & Paula, 2020; Simpson et al., 2021). An experimental study on comparison of native and exotic graminoids' fuel moisture content in northwestern California, USA showed that exotic species such as *Anthoxanthum odoratum* contain high moisture content so cannot be easily burnt and thus recover after fire (Livingston & Varner, 2016). This may explain why in our study *Anthoxanthum odoratum* and *Agrostis capillaris* recovered well after the fire (Figure S2.9 & Figure S2.10, Appendix A). At the individual level, we found exotics were more likely to be growing from seed than natives at Deep Stream 2 months after fire. Most of the native species in this montane environment are clonal and have a low meristem so they can recover after fire(Ladwig et al., 2018). These results suggest that seed dispersal from exotic species could cause dramatic changes in plant community if fires become very frequent or severe.

Woody species took longer to recover than forbs and graminoids; they had relatively low richness 1-2 months after fire and increased over time. A study conducted after grassland fires in Central Great Plains of North America reported woody cover replaced herbaceous cover one to five- or 10-years post-fire (Ratajczak et al., 2014). Another study conducted in páramo grasslands in Ecuador, which are similar in structure to the montane grasslands in our study, showed that woody species outcompeted forbs and graminoids 15 years after fire (Zomer & Ramsay, 2021). Woody plants generally recover by resprouting even in ecosystems that have evolved in low fire frequency (Bond & Midgley, 2003; Del Tredici, 2001; Teixeira et al., 2020). This shows that woody species are slow growing, and they would likely be the group most adversely affected by increased fire frequency.

Plants coming back from seed were less likely be on moss than other substrates at Deep Stream. Germination of seed on moss could limited due to competition for light or exhibit allelopathic effects (Michel et al., 2011). However, all the mosses we excavated plants from were dead so may not have been able to retain much water for seed germination. Instead, the greater moisture holding capacity in mosses may have facilitated survival of plants that were rooted in them or plants themselves might have high moisture content thereby reducing fire intensity during wildfire. In a grassland ecosystem study in Namibia the probability of seedling surviving was higher in irrigated areas (Zimmermann et al., 2008). Further studies on the role of mosses in seed germination and water retention in post-fire environments are warranted.

Community recovery after fire was broadly similar at both Deep Stream and Pukaki despite the sites differing in location, vegetation types, fire history and wildfires burning at different times. Although we saw signs of browsing by hares at both sites, Pukaki was more disturbed by being closer to farmland and a highway, while Deep Stream relatively isolated and undisturbed by human activity. This may explain why there were more exotics species at Pukaki compared to Deep Stream. The fire at Pukaki was in early spring but at Deep Stream it was in late spring. Measurements at Deep Stream were taken in mid-summer (2 and 26 months post-fire) and early summer (13 months). In contrast, measurements at Pukaki were in late spring (1 month post-fire) and summer (1 and 16 months). Previous research on the effect of fire history on vegetation dynamics has shown that past fire seasons can affect post-fire plant population responses and that these effects can vary across plant trait values and growth forms (Fill & Crandall, 2020; Miller et al., 2020).

2.5 Conclusions

Our study shows that increases in richness and dynamics (*i.e.* divergence at the initial measurement and convergence over time) in composition can occur in within 16 or 26 months after fire in New Zealand’s montane grasslands. Repeated short-term measurements enabled us to determine that, surprisingly, most plants survived the fires. Many native species were able to survive post-fire and these natives were relatively unaffected at both the sites. In addition, historical fires had a lasting effect on species composition and richness. This suggests that we expect more frequent fires projected in this system will lead to further observable changes in plant community structure. Our study contributes unique knowledge of plant recovery in montane grasslands of New Zealand, an area with few ecological studies on the effects of fire.

Chapter 3 **Short-term response of New Zealand tussock grasslands to fire is predictable despite long-term community dynamics**

3.1 Introduction

Understanding long-term community dynamics is critical for characterising and measuring the relative importance of short-term responses of community to ecological disturbances. This is particularly important for distinguishing dynamics from community resilience in response to disturbance (Abrahamson et al., 2021; Kimball et al., 2018). Community resilience is where, after disturbance, a community returns rapidly to pre-disturbance structure and function (Holling, 1973; Walker et al., 2004). Dynamics in plant community structure, i.e., changes in species richness and composition over time, occur continuously in all community, but at different rates. Rates of change are affected by changes in environmental factors (Avolio et al., 2015; De Laender, 2018; Sousa-Silva et al., 2018), including anthropogenic and natural disturbances (Blackhall et al., 2017; Dantas et al., 2013; Day & Buckley, 2013; Lindenmayer et al., 2017; Lloret et al., 2009; Shinneman et al., 2021; Tsafrir et al., 2019). Predicting future changes in community structure due to these processes therefore relies on observations at the appropriate temporal scales.

Predicting plant community resilience requires understanding pre-disturbance 'legacies' that could influence subsequent trajectories (Blackhall et al., 2017; Johnstone et al., 2016). Such legacies include the functional traits of species present and available plant propagules, such as the seed bank (Johnstone et al., 2016; Lewis et al., 2010; Speed et al., 2010). Plant species that can survive or tolerate certain disturbance types can be identified based on their functional traits. For example, species that can survive and recover quickly after fire may be clonal (Clarke et al., 2015) and/ or have a meristem that is near or below the soil surface (Clarke et al., 2013; Ladwig et al., 2018; Lipoma et al., 2016). Weedy plants can have fire-tolerant traits that enable them to germinate and outcompete native perennials in post-fire environments (Balshor et al., 2017; Wainwright et al., 2012). In contrast, plants lacking such functional traits are less likely to survive and/ or recover after disturbance. Such legacy effects of pre-disturbance community thus impact post-disturbance dynamics in community structure as species that have fire-resilient traits are retained in the community and those without are more prone to be lost (Bond & Midgley, 1995; MacDermott et al., 2017; Wright et al., 2019). Where functional traits are related to plant flammability, these legacy effects may influence community flammability and fire behaviour (Keeley et al., 2011; Schertzer & Staver, 2018). Thus, environmental variability, including disturbance regimes, anthropogenic influences such as dynamics in invasive plant and animal populations or changes in land management practices, may influence plant community resilience by altering the functional traits present in the resident community (Abella et al., 2021; Jäger & Kowarik, 2010; Kimball et al., 2018; Steel et al., 2021).

Ecosystems subjected to frequent fires are predicted to contain species that have evolved adaptations to survive or tolerate fire; in some cases, such ecosystems have many fire-adapted species that rely on fire to reproduce (Furlaud et al., 2021; Paritsis et al., 2015; Rogers et al., 2015). These adaptations may include serotiny, lignotubers, bud banks and thick barks (Bond et al., 2004; Clarke et al., 2013). However, in ecosystems that experience few fires, species are less likely to be tolerant to fire (Ogden et al., 1998). Wildfires are now increasing in frequency and intensity in many parts of the world due to climatic and land use change (Duane et al., 2021; Jain et al., 2022; Vilar et al., 2021). Furthermore, changes in post-fire community composition and fuel loads are thought to further affect these future fire regimes for instance fire frequency, and intensity due to change in plant traits (Bowd et al., 2021; McLauchlan et al., 2020; Xu et al., 2022). Plant life histories and growth forms will likely influence and be influenced by fire (Arnoldi et al., 2018; Bowd et al., 2021). Therefore, fires are likely to become increasingly important driver of community dynamics, depending on inherent levels of community resilience.

Monitoring pre- and post-fire community dynamics is critical to understanding dynamics and resilience of community exposed to wildfire (Bowd et al., 2021). This is because the spatial and temporal scales of pre-fire (background) community dynamics determine the detectability of changes induced in response to fire. Comparing pre- and post-fire dynamics for the same location will provide the most reliable conclusions on the response of a community to fire (Arnoldi et al., 2018; Steel et al., 2021), in contrast to space for time comparisons (Paudel et al., 2022; Rodhouse et al., 2020). Such understanding is essential to inform biodiversity conservation and ecosystem management (Tolhurst, 2012). Wildfires that burn pre-existing vegetation monitoring locations are a ‘natural experiment’ allowing repeated measurements in community before and after fire that can be used to predict successional temporal changes in ecosystems (Bowd et al., 2021; Springer et al., 2022).

New Zealand native plant species have evolved in environments where fires were not a prominent component of the disturbance regime, and few native plants are characterised as fire tolerant (Perry et al., 2010; Perry et al., 2012). However, with human settlement approximately 800 years ago, widespread burning occurred, leading to vast areas undergoing a transition from forest to grassland ecosystems, particularly in southern and eastern parts of the South Island (Mark & Dickinson, 2003; McGlone et al., 1997, 2014; Perry et al., 2014). In recent years fires have become more frequent and intense due to increased temperatures and drought conditions (McGlone et al., 2014; Perry et al., 2014); this pattern is predicted to continue (Melia et al., 2022; Simpson, et al., 2014). Parts of the eastern South Island, which are dominated by native tussock grasslands, are expected to experience some of the greatest increases in wildfires in the coming decades (Melia et al., 2022).

Tussock grasslands are dominated by long-lived, perennial, native species that provide a wide range of ecosystem services, including provisioning biodiversity values, regulating water sources, supporting soil conservation and carbon sequestration (Mark et al., 2013; Yeates & Lee, 1997). However, increasing weed invasion, natural disturbances, such as fire, and introduced mammalian grazing and browsing pressure all pose threats to the integrity of these grassland ecosystems (Cruz et al., 2017; Day & Buckley, 2013). Predicting post-fire successional trajectories in tussock grasslands is complicated by high abundances of exotic plant species and, despite fire being regularly used as a land management tool in pastoral farming in these grasslands, relatively little is known about potential resilience of grasslands to fire (McGlone et al., 2014; Rogers et al., 2007). Many New Zealand native plant species are thought to be fire-sensitive (McGlone, 2001; McGlone et al., 1997; Perry et al., 2014) and, therefore, potentially susceptible to competition with more fire-tolerant exotic species. Fire promotes vegetative growth, flowering and seed germination in *Chionochloa* spp., but grazing by introduced mammals after fire causes elevated mortality (Dickinson et al., 1992; Gitay & Wilson, 1995; Mark, 1994; O’Connor & Alison, 1963). In contrast, exotic invasive hawkweeds (*Pilosella* spp.) can easily re-establish following fire (Mark et al., 2010).

This study aimed to quantify plant community responses to fire disturbance and to test for community resilience in tussock-dominated areas of montane grasslands in the South Island of New Zealand. This was achieved by comparing pre-fire and post-fire changes in plant community structure. I used repeated measurements of plant community before and after wildfire over long (35 years) to short (two weeks) timescales to quantify the response to fire disturbance by (1) testing for community resilience to wildfire disturbance and 2) comparing response of changes in species of different biostatus (native and exotic species) and growth forms (forbs, graminoids and woody). I used long-term data from vegetation surveys over four decades from four, permanently marked transects (Buckley & Freckleton, 2010; Day & Buckley, 2013), three of which were burnt in an accidental wildfire in October 2020 and one nearby transect that did not burn.

3.2 Methods

3.2.1 Study location

This study was conducted in an area which until 1950 was grazed pastoral land (McMillan, 2012), but now is a part of the Ruataniwha Conservation Park on the western shore of Lake Ōhau at the foothills of the Ben Ōhau mountain range (elevation ca. 670-850 m a.s.l.) in the Canterbury region of South Island, New Zealand (Figure S3.1, Appendix A). This area features a diverse range of vegetation types including tussock grasslands, mountain beech forest, and subalpine shrublands. In drier areas, including the tall tussock grasslands, prominent invasive species are wilding pines (*Pinus* spp.) and hawkweeds (*Pilosella officinarum* Vaill, *Pilosella piloselloides* subsp. *praealta* (Gochnat) S.Bräut. & Greuter, *Hypochaeris radicata* L.), which continue to spread (The Ōhau Conservation Trust, 2017). Mean annual precipitation, mean summer temperature and mean winter temperature were 906 mm, 13.67°C and 1.96 °C respectively (Wratt et al., 2006). In October 2020 (early spring) a wildfire started accidently by an electric short circuit and about 5,000 ha was burnt (Fire and Emergency New Zealand, 2020).

3.2.2 Vegetation surveys

Four, permanent, 100-m vegetation monitoring transects were established in 1983 in tussock grassland habitat within this area (Figure 3.1; Figure S3.1, Appendix A). They were subsequently remeasured in 1993 and 2006. In the October 2020 wildfire, two of the transects (OHAT043 and OHAT044) and approximately one-third of a third transect (OHAT042) was burnt. A fourth transect (OHAT045) was unburnt (Figure S3.2., Appendix A). In late October 2020, two weeks after the wildfire, I remeasured all four transects. I remeasured the burnt transects again in January 2021 (3 months post-fire) and in January 2022 (15 months post-fire). According to previous literature, communities in these grasslands are perennial and do not undergo drastic changes within a short period of time unless there are natural disturbances

(Mark, 1969). Therefore, I did not remeasure unburnt transects in the following short-term measurements.

Figure 3.1. Photo plates showing changes in pre- and post-fire vegetation change on 100-m, permanent transects at Lake Ōhau, Canterbury, South Island, New Zealand measured between 1983 and 2022. Each transect comprises 50, 0.25-m^2 quadrats, spaced 2 m apart. (*Photo source*: photos from 15 and 29 prior fire were taken from Day et al., unpublished).

At each transect, I recorded vegetation in fifty, 0.5 × 0.5-m (0.25-m^2) quadrats positioned every two metres on the right side along the 100-m permanently marked transects running from the south to the north direction. A consistent sampling protocol was followed at all times to record the presence of all species in each quadrat at each measurement (Buckley & Freckleton, 2010; Day & Buckley, 2013; Duncan et al., 2001). In 1983 and 1993, the presence of each species was recorded in each quadrat including species that were overhanging, but not rooted in, the quadrats. From 2006 to 2022 the percent cover of each species was estimated within each quadrat and recorded as one of six cover classes: (1 = <1 %, 2 = 1-5 %, 3 = 6-25 %, 4 = 26-50 %, 5 = 51=75 %, and 6 = 76-100 %). Overlapping percent cover values were recorded, thus, the total percent cover of quadrats can be greater than 100 %.

Plant trait data

I obtained data on traits of all species from published databases (Breitwieser et al., 2010; *Ecological Traits of New Zealand Flora Online*, 2022; *New Zealand Plant Conservation Network*, 2022). I recorded biostatus (native or exotic), growth form (forb, graminoid, or woody), clonality (non-clonal or clonal), meristem height (high or low) (Table S3.1, Appendix A) for all 88 plant species recorded on the permanent transects over the four decades. Clonality was determined based on the presence of buds and meristem height were based on Raunkiær's life form (Raunkiaer, 1934; Raunkiaer, 1905).

Fire severity

Field sampling was undertaken at the three burnt transects to compare three methods for assessing fire severity: minimum branch diameters of woody plants and percent covers of burnt and live vegetation and litter (Appendix B). The results were inconclusive and so these data are not presented in this chapter.

3.2.3 Data analysis

I categorised the four, 100-m permanent transects into two groups: three burnt transects (OHAT042.burnt, OHAT043.burnt, OHAT044.burnt) and two unburnt transects (OHAT042.unburnt and OHAT045.unburnt). Due to the uncertainty in precisely relocating 0.25-m^2 quadrats at each measurement time, I calculated the frequency of species in sections of five quadrats on each transect for both primary data collected during study period and secondary data collected previously (Buckley & Freckleton, 2010; Day & Buckley, 2013; Duncan et al., 2001). I did this by dividing each transect into ten sections of 10 m, each comprising five quadrats. The partially burnt transect, OHAT042, contained three burnt 10-m sections and six unburnt 10-m sections. Two quadrats were in the trail so three unburnt quadrats measured were excluded hence, 10th 10-m section was excluded. I created matrices for subsequent analyses of (1) species' frequencies in transect sections at all measurement times and (2) species' mean quadrat percent cover in quadrats within each 10-m transect section for measurements from 2006 to 2022; percent cover of species in quadrats was not recorded at the

1980s and 1990s measurements. These matrices, both at the 10-m transect section scale, were used to investigate community dynamics across pre-fire (1980 – 2006) and post-fire (2020 – 2022) measurements. The burnt and unburnt sections of OHAT042 were treated separately in all analyses.

To visualise changes in plant community composition over time for each transect, I used a Bray-Curtis dissimilarity matrix calculated from the matrix of species' frequencies in 10-m transect sections at all measurement times in a principal coordinate analysis (PCoA) implemented using 'labdsv' (Roberts, 2019) in R v.4.2.1 (R Core Team, 2022) for both pre (1980 – 2006) and post-fire (2020 – 2022) measurements. This was repeated using the matrix of species' covers for the 2006 – 2022 measurements to evaluate short-term community dynamics immediately following fire.

Following methods in Avolio et al. (2019) and Buckley et al. (2021) for characterising temporal community dynamics, I tested the significance of the change in mean composition (i.e., the 10-m transect section centroids) and change in compositional variance for each transect section at each post-fire measurement specifying 2006 (the most recent pre-burn measurement) as the baseline. Differences among measurement times were tested for significance using the 'pairwise.adonis2' function within the 'vegan' for change in mean composition (Oksanen, 2021) and the 'permutest' function within 'vegan' for change in variance (Anderson, 2006). For these tests, transect was used as a grouping variable to account for the spatial non-independence of the temporal measurements, i.e., OHAT042.burnt, OHAT042.unburnt, OHAT043, OHAT044, and OHAT045.

To characterise community dynamics over four decades (1980 – 2022), I calculated several measures of community structure that could be compared over time (Avolio et al., 2019) using 'codyn' (Hallett et al., 2020): (1) species' rank abundance within transects at each measurement, calculated as the number of quadrats that each species occurred in at each time, (2) total species richness within each 10-m transect section, (3) mean percent cover of species per quadrat within each 10-m transect section, (4) relative change in total transect section species richness between measurements (change in the number of species divided by the total number of unique species), and (5) relative number of species gained or lost from transect sections between measurements (gains or losses divided by the total number of unique species). Species richness variables and gains and losses were computed for all species and for species subsets including natives, exotics, forbs, graminoids and woody species.

Venn diagrams of transect species lists at each measurement were made to show the number of species present from 1983 to 2022 and the number of colonisations and extinctions. Rank abundance curves were generated for transects at each measurement to determine which species were driving the community dynamics at a transect scale (Avolio et al., 2019).

To assess community-scale changes in the relative frequency of disturbance-related plant traits over time, I calculated relative ratio of species in two groups: clonality and meristem height for the sections on each transect at each measurement. For the clonality ratio, the total number of clonal species was divided by number of non-clonal species. For the meristem height ratio, the total number of species whose meristem is close to the ground was divided by total number of all other plant morphologies.

I used generalized linear mixed models implemented using the ‘glmmTMB’ function in R (Brooks et al., 2017) for the post-fire change comparison of total species richness, mean quadrat percent cover, relative change in species richness, gains and losses in transect sections. For richness (count data) models assumed a Conway-Maxwell-Poisson error distribution and for all other dependent variables (continuous data), models assumed a gaussian error distribution. For all models, transect was included as a random effect to account for the spatial non-independence of 10-m transect sections. Models were applied to datasets containing all species and to species subsets: natives, exotics, forbs, graminoids and woody species. *Post-hoc* comparisons among measurement times were performed for all models using ‘emmeans’ (Lenth, 2022). All statistical analyses were performed in R v.4.2.1 (R Core Team, 2022) and data visualisations were conducted using the packages ‘tidyverse’ (Wickham et al., 2019), ‘ggreppel’ (Slowikowski et al., 2021), ‘ggVennDiagram’ (Gao, 2022), ‘gghighlight’ (Yutani, 2022), and ‘egg’ (Auguie, 2019).

3.3 Results

I recorded 88 species (64 native species and 24 exotic species) on the four transects across all five measurement times (Table S3.1, Appendix A). Species composition within the 10-m transect sections varied over time (1983 – 2022) on all transects (Figure 3.2 & 3.3). Composition changed more in locations that were burnt compared to unburnt locations. Change in composition and change in variance were significantly different between the pre-fire 2006 measurement and the initial post-fire measurement in 2020 (Table 3.1; Figure 3.4). Changes in the mean and variance in species composition were significant after fire on OHAT043.burnt

(2006 – 2020) and OHAT044.burnt (2006 – 2021). On the unburnt transect, OHAT045.unburnt, mean composition changed significantly, but variance did not; however, change in the mean was not as large as those caused by the fire on other transects. On the unburnt section of OHAT042 (*n* = 3), the mean composition and variance did not change significantly.

Table 3.1. Short-term patterns of change in community structure on both burnt and unburnt permanent 100-m transects at Lake Ōhau, Canterbury, South Island, New Zealand measured before and after the October 2020 wildfire between 1983 and 2022. Species composition was quantified using a Bray-Curtis dissimilarity matrix based on mean percent covers of species in 0.25-m^2 quadrats for 10-m transect sections on 100-m permanent transects. The significance of changes in mean composition (10-m transect centroids ± one standard error) and variation in composition (among 10-m transect sections ± one standard error) were compared among measurements. Means were either not significantly different (=mean) or significantly different (Δmean) between measurement times. Variance in composition either significantly decreased (↓variance) or significantly increased (↑variance) or no change (=variance) between measurement times

Multivariate community pattern	**Transect**	**Years compared**	***n***	**Change in composition**	**Change in variance**	**Species gains**	**Species losses**
=mean, =variance	OHAT042.burnt	2006 – 2020	3	0.95 ± 0.02	-0.02 ± 0.02	0	22
	OHAT042.burnt	2006 – 2021	3	0.75 ± 0.05	-0.04 ± 0.04	3	14
	OHAT042.unburnt	2006 – 2022	6	0.42 ± 0.09	0.05 ± 0.04	0	4
=mean, ↓variance	OHAT042.burnt	2006 – 2022	3	0.60 ± 0.06	-0.04 ± 0.02	1	14
Δmean, =variance	OHAT042.unburnt	2006 – 2020	6	0.43 ± 0.05	0.01 ± 0.03	1	12
	OHAT043.burnt	2006 – 2021	10	0.73 ± 0.09	-0.02 ± 0.03	5	2
	OHAT043.burnt	2006 – 2022	10	0.50 ± 0.08	0.04 ± 0.02	7	0
	OHAT044.burnt	2006 – 2020	10	0.62 ± 0.08	-0.02 ± 0.02	6	5
	OHAT044.burnt	2006 – 2022	10	0.47 ± 0.07	0.04 ± 0.02	9	0
	OHAT045.unburnt	2006 – 2022	10	0.55 ± 0.09	0.02 ± 0.02	6	5
Δmean, ↑variance	OHAT043.burnt	2006 – 2020	10	0.91 ± 0.13	0.23 ± 0.04	1	14
	OHAT044.burnt	2006 – 2021	10	0.55 ± 0.1	0.01 ± 0.03	6	1

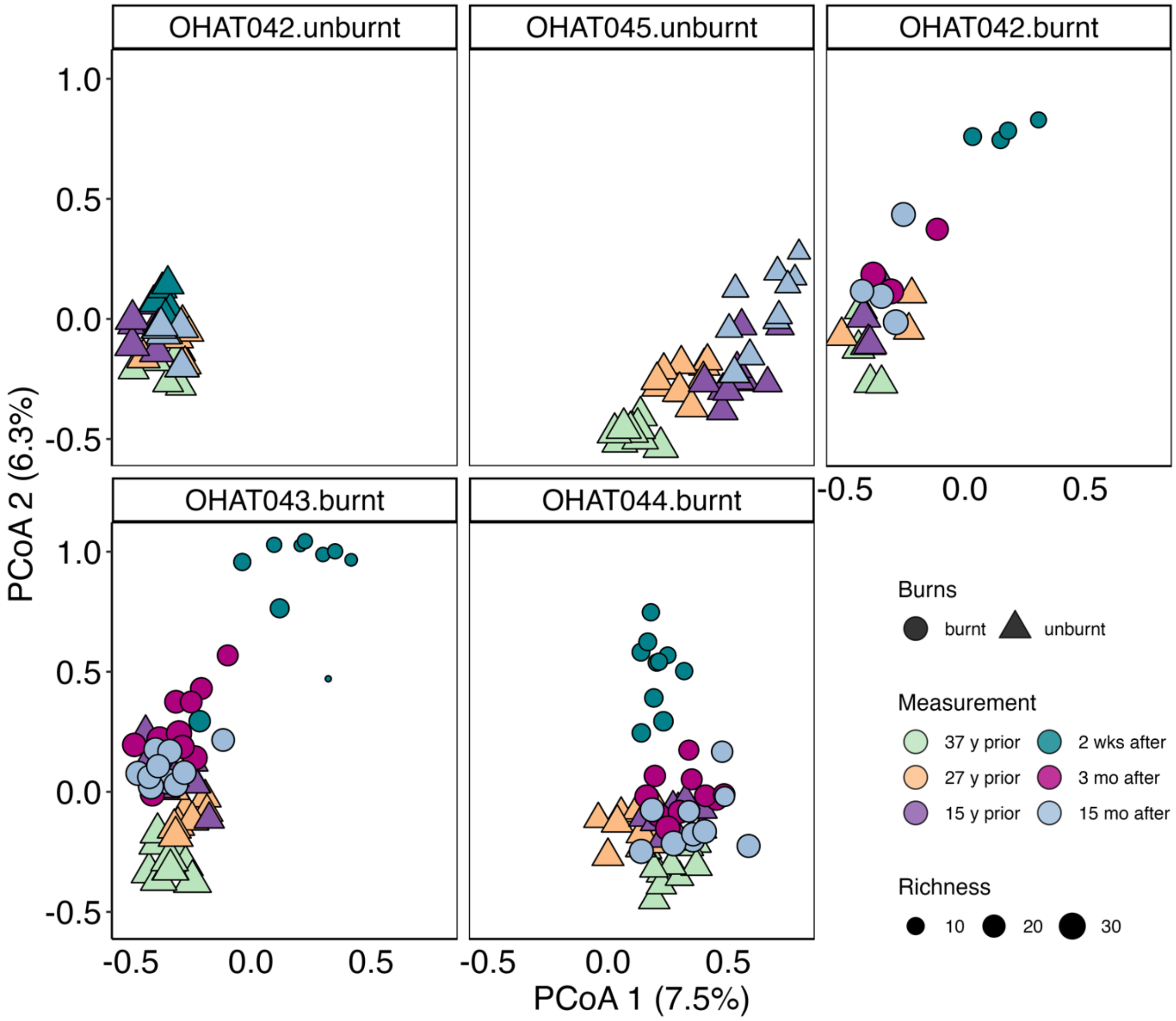

Figure 3.2. Principal coordinate analysis (PCoA) of a Bray-Curtis dissimilarity matrix of species' frequencies, measured as number of occupied 0.25-m^2 quadrats in 10-m transect sections across time on 100-m permanent transects at Lake Ōhau, Canterbury, South Island, New Zealand measured between 1983 and 2022. Each section comprised five quadrats. The shapes of points represent burnt (circles) and unburnt (triangles) transect sections. The colours of points represent measurement times in relation to the October 2020 wildfire. Point sizes are proportional to species richness. The transect sections were analysed in the same PCoA but are plotted separately

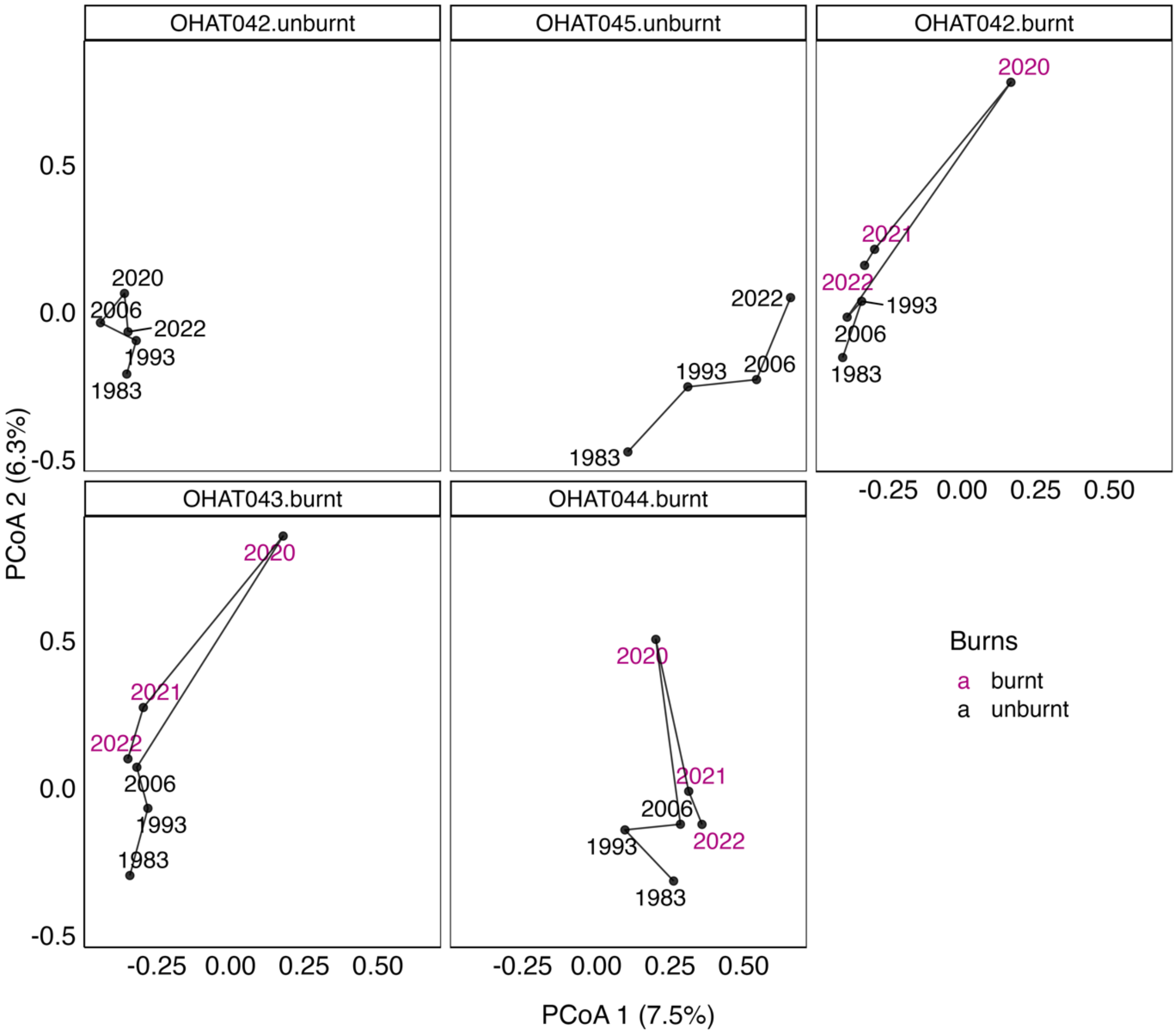

Figure 3.3. Principal coordinate analysis (PCoA) of a Bray-Curtis dissimilarity matrix of species' frequencies, measured as number of occupied 0.25-m^2 quadrats in 10-m transect sections across time on 100-m permanent transects at Lake Ōhau, Canterbury, South Island, New Zealand measured between 1983 and 2022. Each section comprised five quadrats. Points represent transect centroids in species space for each measurement time. Lines show the trajectories of change in species composition over time from the initial survey in 1983 to the final survey in 2022. The text colour indicates unburnt (black) or burnt (purple) measurement times. The transect sections were analysed in the same PCoA but are plotted separately

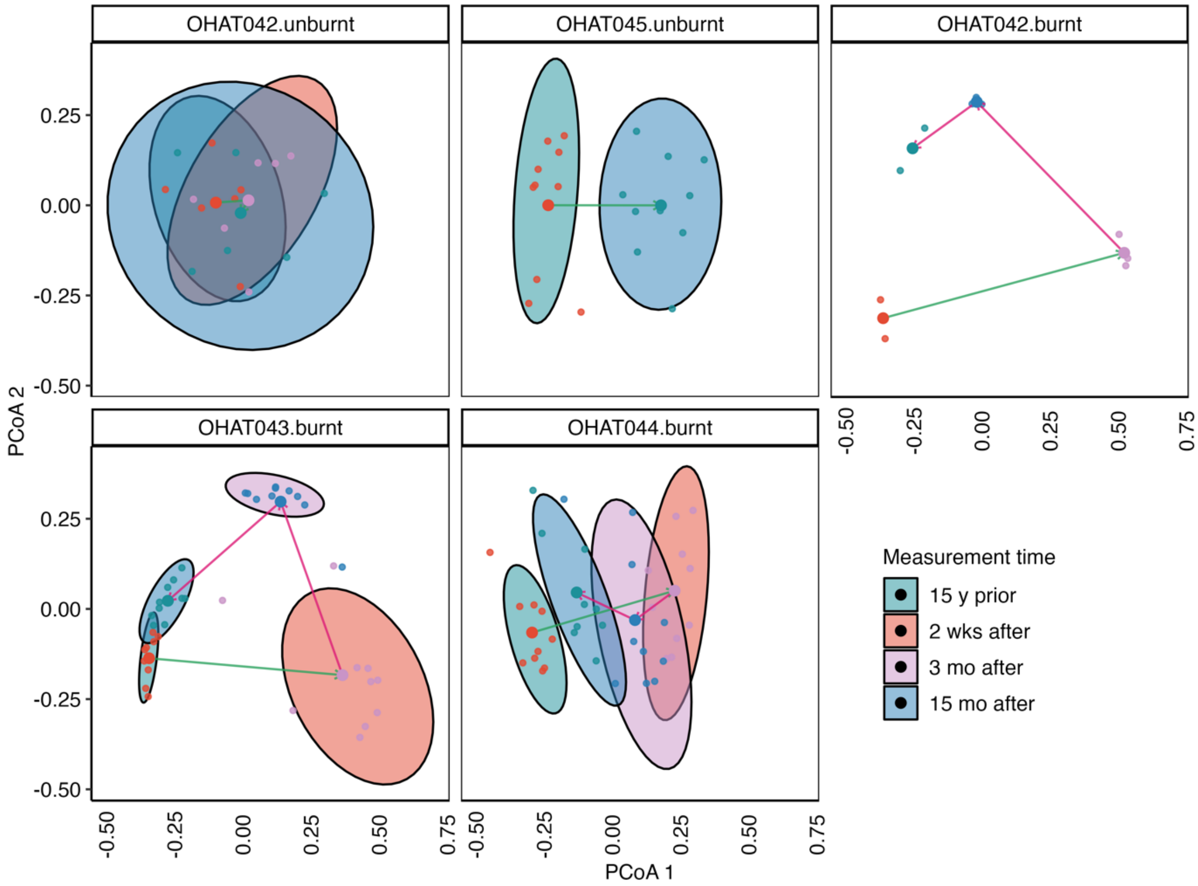

Figure 3.4. Principal coordinate analysis (PCoA) of a Bray-Curtis dissimilarity matrix of species' percent cover, measured as the mean % cover in 0.25-m^2 quadrats within 10-m transect sections (small-coloured dots) within 100-m permanent transects at Lake Ōhau, Canterbury, South Island, New Zealand measured between 2006 and 2022. Each 10-m transect section comprised five quadrats. Large, coloured dots represent the centroids for each measurement time encompassing all transects connected by lines. Ellipses represent the 95% confidence envelope for a multivariate t–distribution for transect centroids and thus represent the relative variance of each transect at each measurement time. The ellipse colour represents measurement time. Ellipses could not be calculated for measurements on OHAT042.burnt due to the low number of transect sections that were burnt within that transect (*n* = 3)

Most of the species were present across all the measurements (Figure 3.5). Six native species on each of three burnt transects and two exotic species on two of the burnt transects (but not on one burnt transect OHAT043.burnt) colonised after the fire (2020 – 2022). The highest number of local extinctions of native species across the entire study period occurred on

OHAT042.burnt (*n* = 9) and the lowest on OHAT044.burnt (*n* = 5). In contrast, local extinction of exotic species was the lowest on OHAT042.burnt (*n* = 1) and the highest on OHAT043.burnt (*n* = 4*)*. Local extinction of species was higher than colonisation on the unburnt transect OHAT045. On this transect, 17 species extinct and only seven species colonised between 1983 to 2022.

Rank abundance curves showed compositional changes were driven by a drop in the richness and evenness of the community after the fire as well as reordering of species' ranks, which occurred in all growth forms (Figure 3.6). The recovery of transects after the fire was characterised by increases in transect richness and evenness, and further reordering of species. Some native species which had high frequency pre-fire, such as *Festuca novae-zelandiae*, became locally extinct (OHAT042.burnt) post-fire (Figure S3.3, Appendix A). Some exotic forbs, such as *Pilosella* spp., had high percent cover both pre- and post-fire (2006 – 2022) on both burnt and unburnt transects (Figure S3.4, Appendix A).

Species richness of native and exotic species in 10-m transect sections decreased between the most recent pre-fire measurement (2006) and two weeks post-fire (2020), then recovered on all burnt transects within three months (2021), except for exotic species on OHAT042.burnt, where there was no significant decrease due to fire (Figure 3.7). However, on all burnt transects, natives decreased more than exotics post-fire and increased more three months post-fire (Figure 3.8). When growth forms were considered separately, native forbs and graminoids responded more strongly to fire than exotic species (Figure 3.9). The exception was exotic graminoids on OHAT044.burnt, where they significantly recovered three months post-fire. The number of woody exotic species in general was lower than natives and they were relatively unchanged by fire except on OHAT044.burnt, where there was a significant increase in mean species richness three months post-fire. The unburnt transect OHAT045 showed long-term losses in native and exotic species from 1983 to 2022 (Figure 3.7); these changes were largely due to a decrease in richness of native and exotic forbs and native graminoids (Figure 3.8 & 3.9).

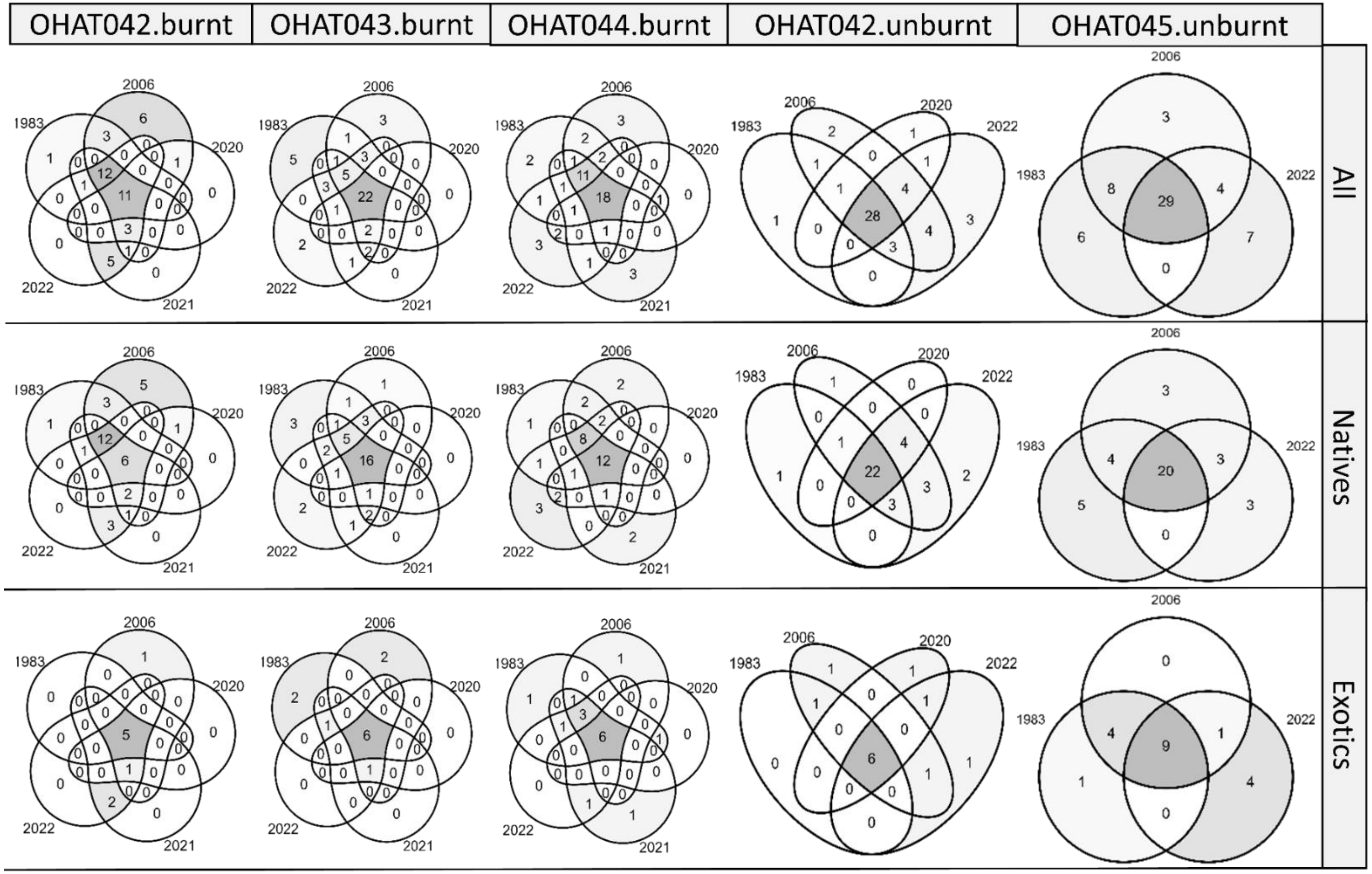

Figure 3.5. Venn diagrams of all species, natives and exotics recorded between 1983 and 2022 in 0.25-m^2 quadrats within burnt and unburnt, permanent 100-m transects at Lake Ōhau, Canterbury, South Island, New Zealand

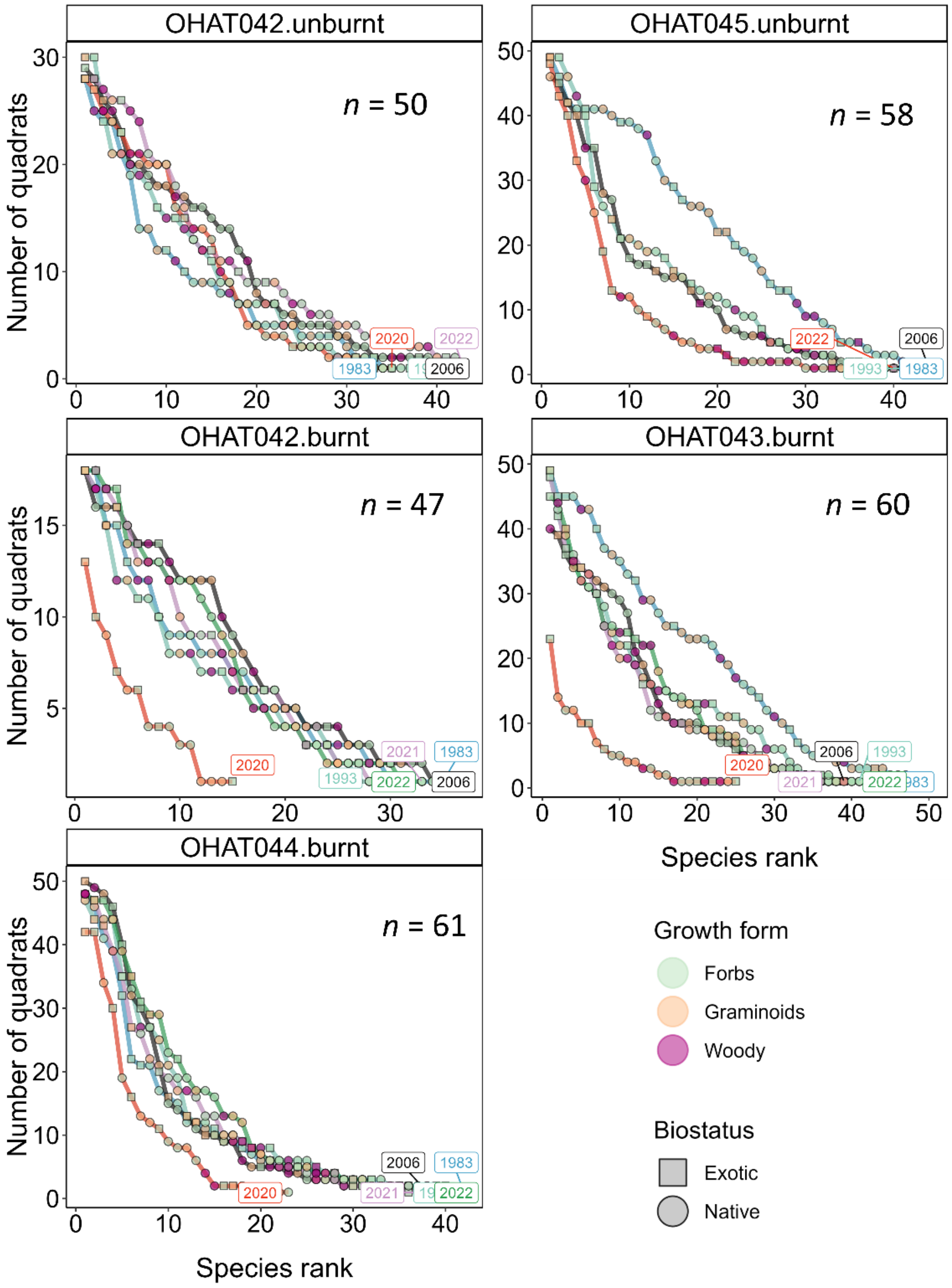

Figure 3.6. Rank abundance curves showing the number of 0.25-m2 quadrats each species occurred in on 100-m permanent transects at Lake Ōhau, Canterbury, South Island, New Zealand measured between 1983 and 2022. All other transects comprised 50 quadrats. Species occurring on the burnt portion of OHAT042 could only occur in a maximum of 18 quadrats and on the unburnt portion of that transect, species could occur in a maximum of 30 quadrats. *n* = represents total number of species of the transect. Shape of points represent either exotic (squares) or native species (circles). Point colours represent forbs (green), graminoids (orange) or woody (purple) species. Line colours distinguish measurement times

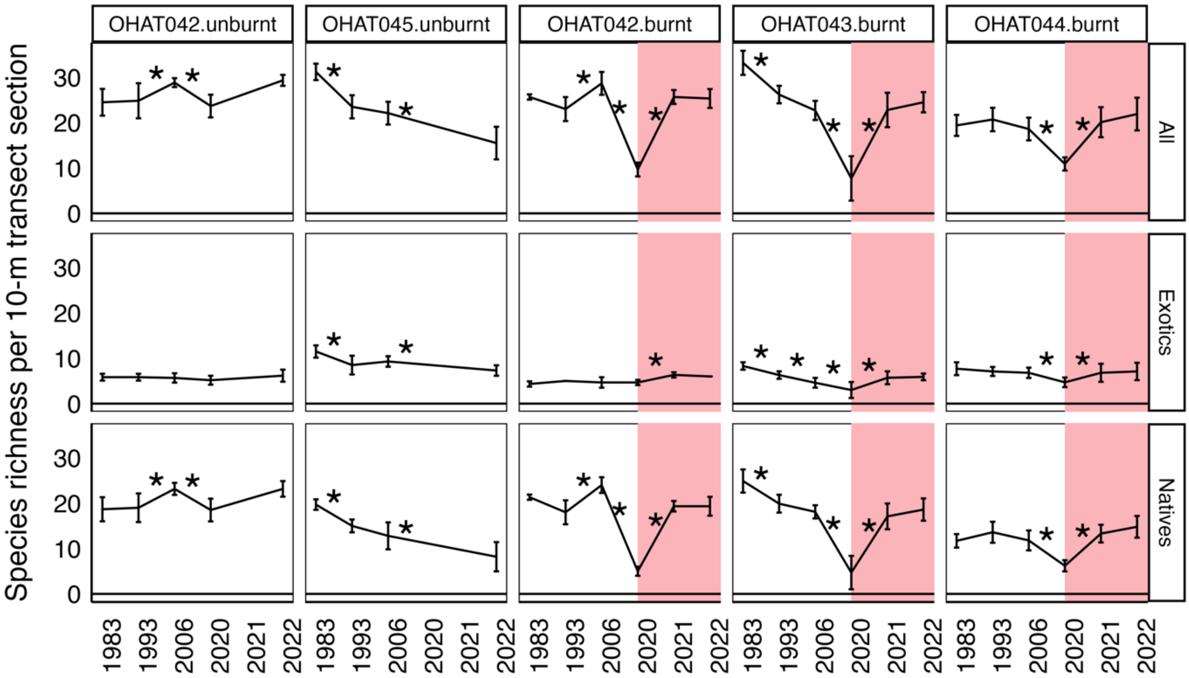

Figure 3.7. Species richness (± one standard error) for all species, natives and exotics recorded in 10-m transect sections comprising five, 0.25-m^2 quadrats on 100-m, permanent transects at Lake Ōhau, Canterbury, South Island, New Zealand measured between 1983 and 2022. The background colour represents before (white) and after (red) the October 2020 wildfire. Asterisks represent significant differences in richness between measurements determined by generalised linear mixed-effects modelling ($P < 0.05$)

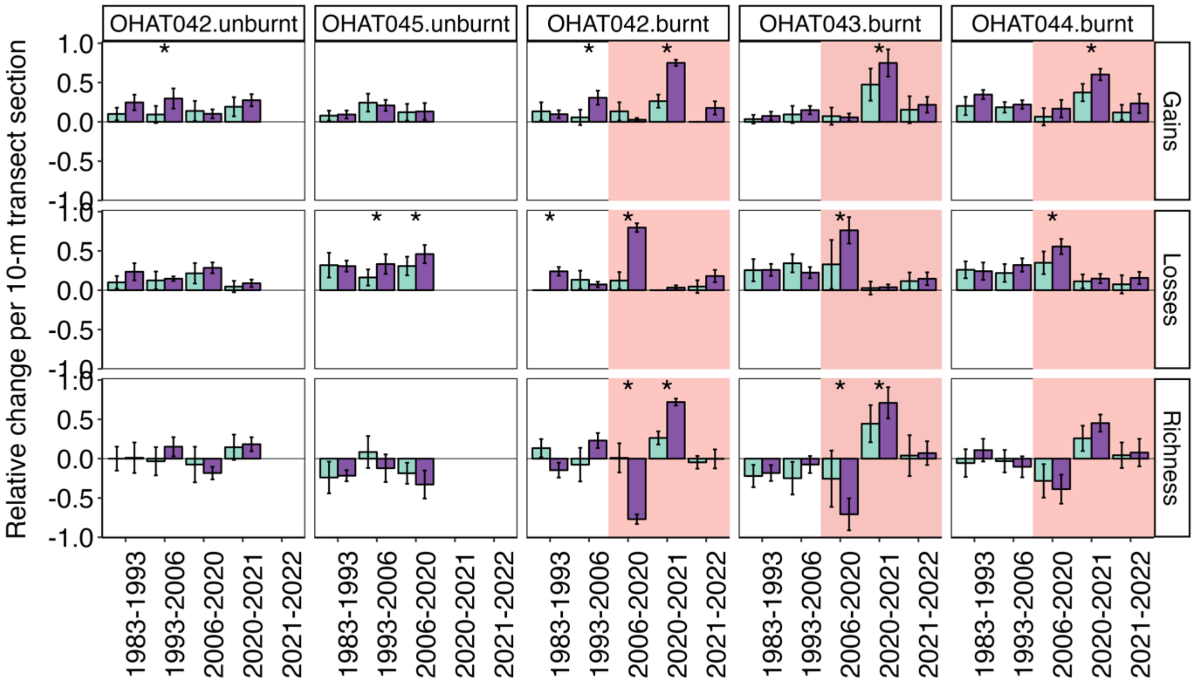

Figure 3.8. Comparisons of native (purple) and exotic (green) species community dynamics (± one standard error) showing changes in relative change in species gains, losses, and richness per 10-m transect sections on 100-m permanent transects at Lake Ōhau, Canterbury, South Island, New Zealand measured between 1983 and 2022. Each section comprised five quadrats. Species presence was recorded in 0.25-m^2 quadrats spaced every 2 m on each transect. The background colour represents before (white) and after (red) the October 2020 wildfire. Asterisks represent significant differences in species gains, losses, and richness between changes in native and exotic species determined by generalised linear mixed-effects modelling ($P < 0.05$)

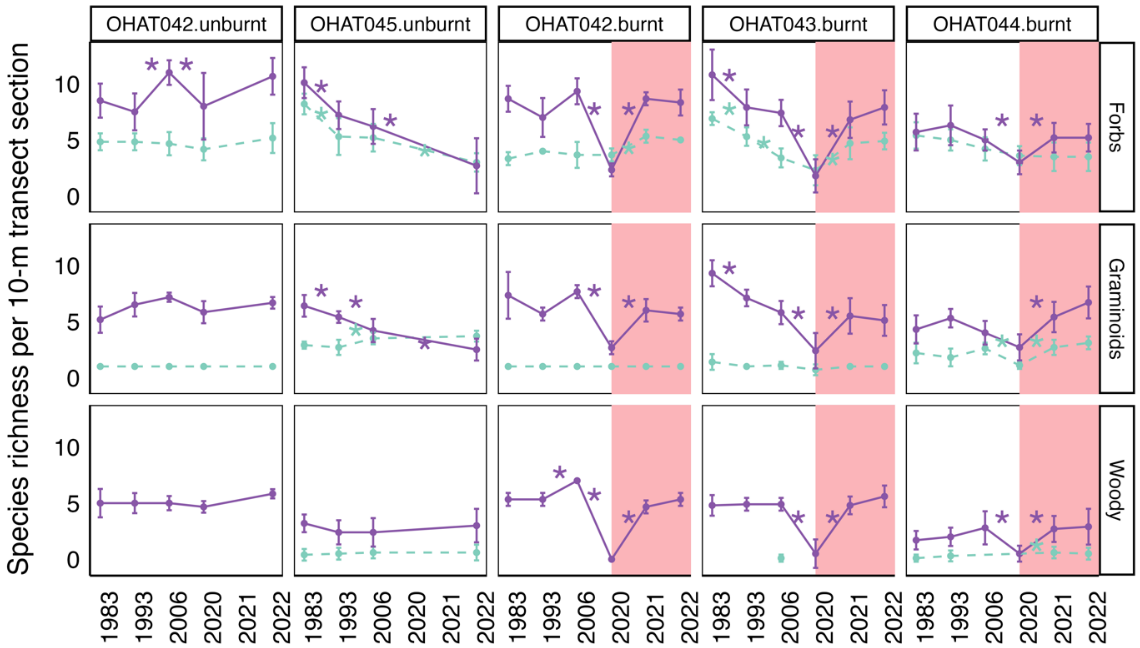

Figure 3.9. Species richness (± one standard error) of native (purple, solid) and exotic (green, dashed) species categorised as either forbs, graminoids or woody within 10-m transect sections on 100-m permanent transects at Lake Ōhau, Canterbury, South Island, New Zealand measured between 1983 and 2022. The background colour represents before (white) and after (red) the October 2020 wildfire. Asterisks represent significant differences in richness between measurements determined by generalised linear mixed-effects modelling ($P < 0.05$)

Changes in mean quadrat percent cover of all species showed a dramatic decrease due to fire followed by recovery over 15 months (2022) post-fire (Figure 3.10; Figure S3.5, Appendix A), which was slower than the recovery of species richness (Figure 3.7). These changes were similar for native species and exotic species, except exotics had lower overall mean quadrat percent cover. Mean quadrat cover only partially recovered for native species within 15 months post-fire, whereas exotic species cover fully recovered within 3 to 15 months post-fire. The cover of woody species decreased to zero right after fire but partially recovered in the three months post-fire (Figure 3.11). The unburnt portion of OHAT042 decreased in cover of exotic species but not in natives. In contrast, the unburnt transect OHAT045.unburnt decreased in native species cover, whereas exotic cover did not change significantly. OHAT044.burnt had a relatively high cover of exotic forbs compared to the other transects (except OHAT045.unburnt) and the cover of these species did not significantly increase in post-fire in contrast to the other burnt transects (OHAT043.burnt). On OHAT045.unburnt, forbs decreased and exotic graminoids increased between 2006 and 2022.

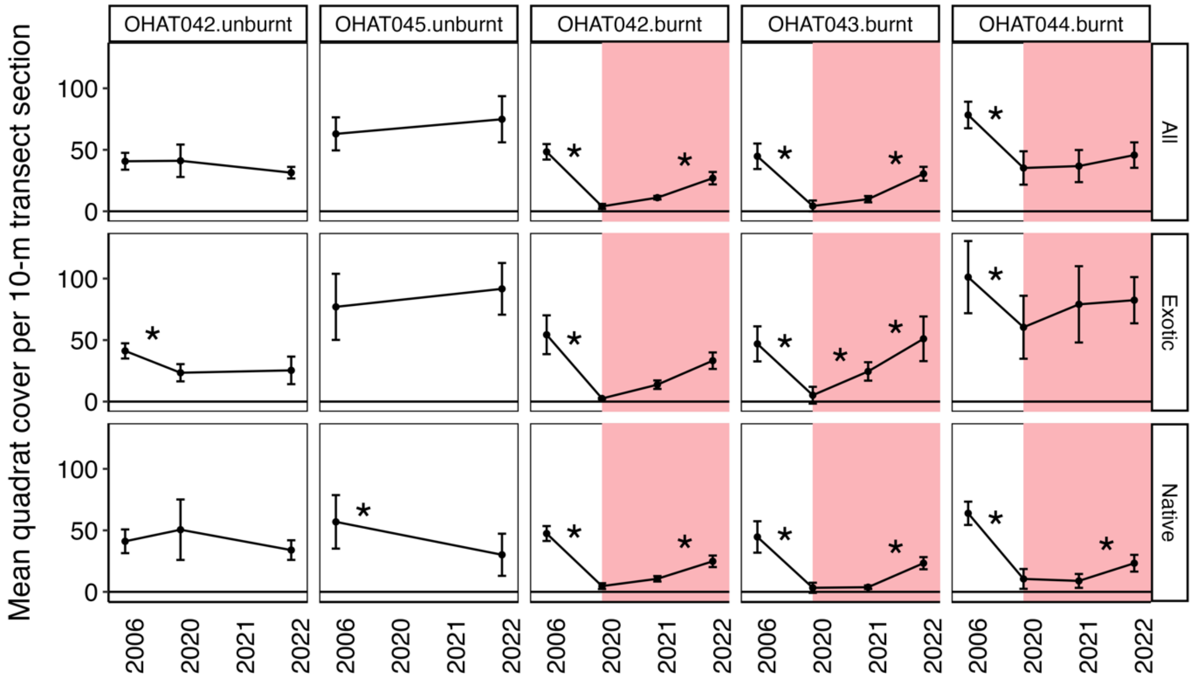

Figure 3.10. Sum of mean percent cover (± one standard error) for all species, natives and exotics within 0.25-m^2 quadrats within 10-m sections on 100-m permanent transects at Lake Ōhau, Canterbury, South Island, New Zealand measured between 1983 and 2022. Total quadrat cover can sum to more than 100% because percent covers for species could overlap. The background colour represents before (white) and after (red) the October 2020 wildfire. Asterisks represent significant differences in quadrat cover between measurements determined by generalised linear mixed-effects modelling ($P < 0.05$)

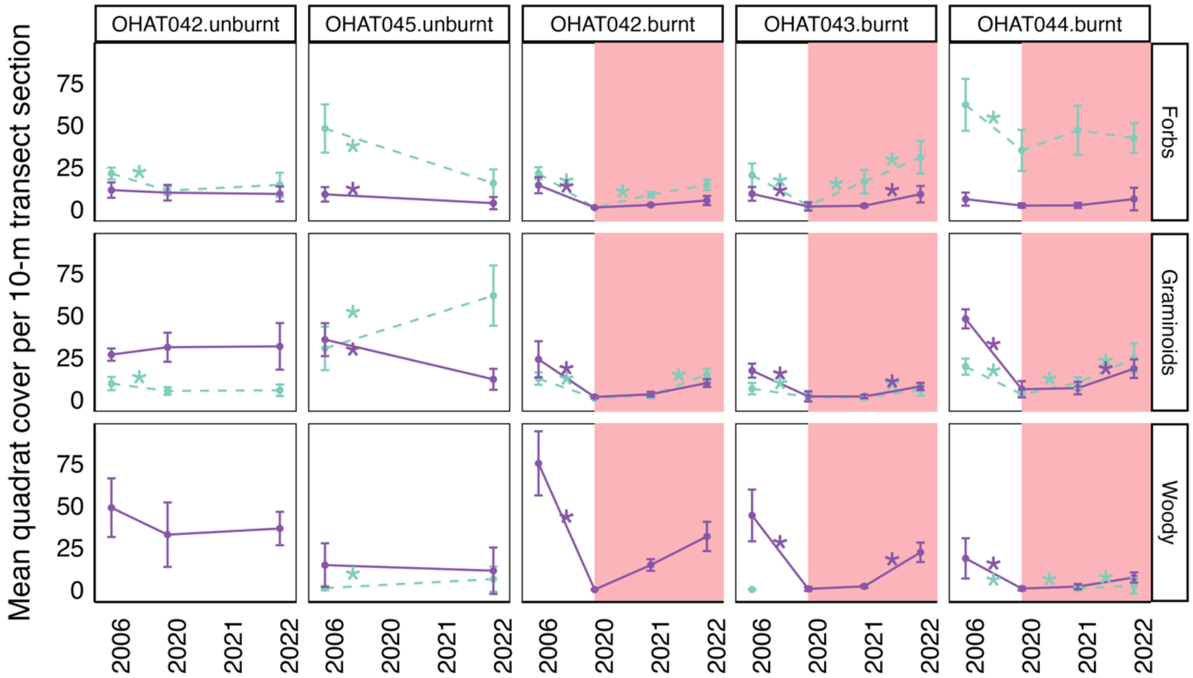

Figure 3.11. Mean percent cover (± one standard error) for native (purple, solid) and exotic (green, dashed) species categorised as either forbs, graminoids or woody in 0.25-m^2 quadrats for 10-m transect sections on 100-m permanent transects at Lake Ōhau, Canterbury, South Island, New Zealand measured between 2006 and 2022. The background colour represents before (white) and after (red) the October 2020 wildfire. Asterisks represent significant differences in quadrat cover between measurements determined by generalised linear mixed-effects modelling ($P < 0.05$)

The ratio of plant species that were clonal and had low meristems changed with change in community structure (Figure 3.12). The ratio of clonal plant species was significantly higher two weeks after fire on two of the burnt transects than at subsequent pre-and post-fire measurements, but not on OHAT044.burnt, where it was significantly lower. On the unburnt transect OHAT042.unburnt, there was no significant change in the ratio of clonal species, but it significantly increased on OHAT045.unburnt. The ratio of plants with their meristem close to ground was high on all the transects and significantly increased two weeks after fire (2020) and was significantly higher than at subsequent pre-and post-fire measurements on burnt transects. On the unburnt transect OHAT045.unburnt, the ratio of plants with their meristem close to the ground significantly decreased, except on OHAT042.unburnt.

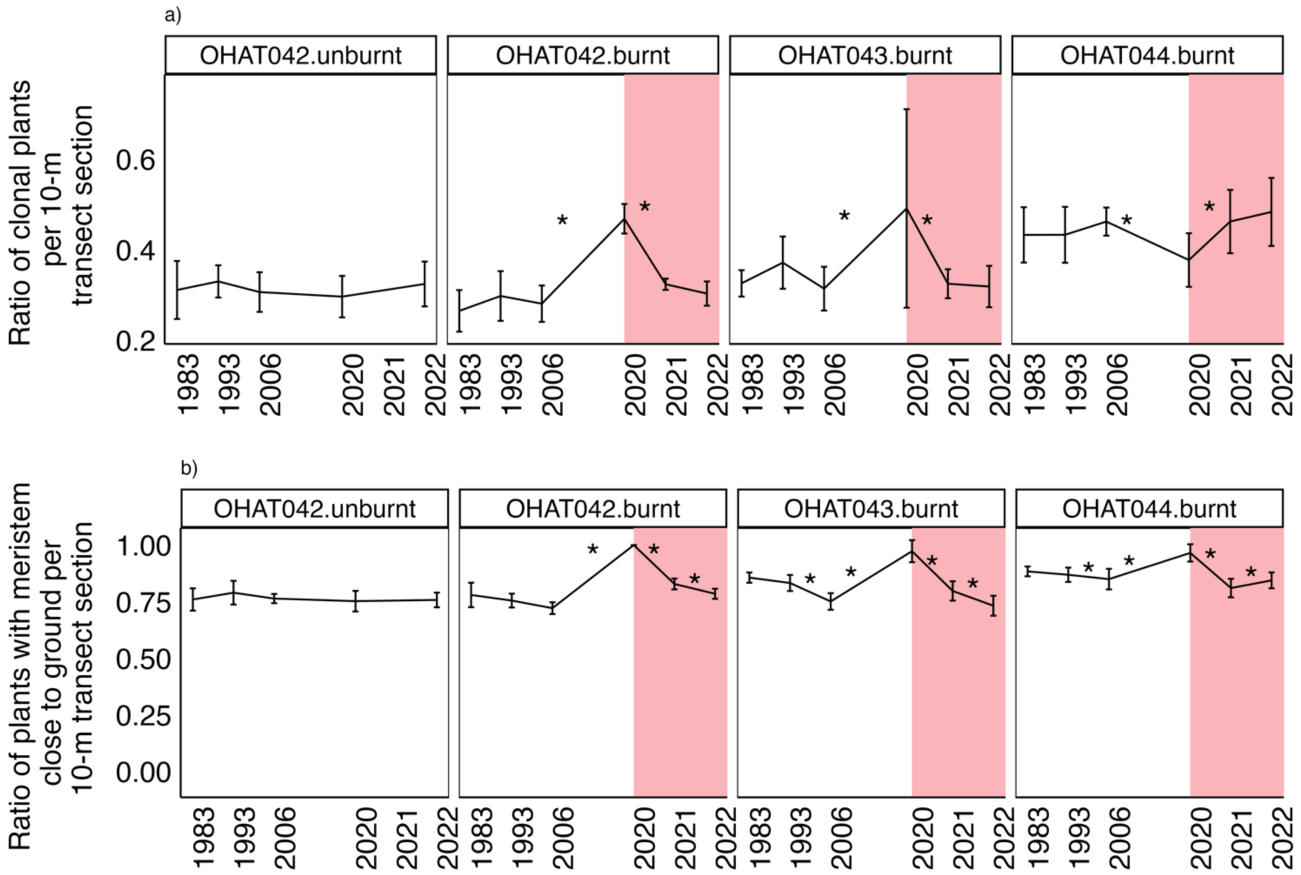

Figure 3.12. Ratio of species (± one standard error) that were (a) clonal and (b) had their meristem close to the ground recorded within 0.25-m^2 quadrats within 10-m transect sections on 100-m permanent transects at Lake Ōhau, Canterbury, South Island, New Zealand measured between 1983 and 2022. Each 10-m transect section comprised five quadrats. The background colour represents before (white) and after (red) the October 2020 wildfire. Asterisks indicate a significant change in ratio, determined using generalised linear modelling ($P < 0.01$).

3.4 Discussion

This observational study comprising both long-term and short-term repeated vegetation measurements on unburnt and burnt transects before and after wildfire demonstrates that grassland community, even those from a historically low-fire frequency environment, show a significant, but mostly short-term response and, thus, resilience to wildfire. Community structure (species composition and richness) diverged with fire then converged over a short timescale. Changes in community structure were primarily driven by gains and losses in native species because they were dominant in the community (native species comprised 77% of all species). However, both natives and exotics showed similar responses to the fire on burnt transects. When growth forms were considered separately, species richness of native forbs and graminoids were generally more affected by fire than exotic species in those growth forms. Species cover recovered slower than richness; this is because fire-affected plant community take time to increase biomass. Comparison with unburnt transects showed that these changes were relatively strong compared to the long-term dynamics of these grasslands.

I demonstrated that plant communities in tussock-dominated montane grasslands are resilient to fire. There was a predictable short-term response to fire of divergence followed by convergence in plant community structure (species composition, richness, relative abundance, gains, losses and mean quadrat cover) that reflects recovery of plant communities. However, generally, these community did not return exactly to their state 15 years prior (2006) to the fire in terms of species richness or cover. Composition was not significantly different between pre- and post-fire samples on the partially burnt transect, likely due to the small sample sizes. Species richness returned close to pre-fire levels within three to 15 months suggesting that most individual plants survived the fire and subsequently recovered. Species' survival and recovery rates were affected by fire based on their traits. Most of these plants were perennial, have tightly clustered leaf primordia and leaf bases of the mature leaves that could protect apical meristems from burning during a fire (Clarke et al., 2013; Lamont et al., 2004). Plants with such traits are resilient to fire as previously shown in fire-prone ecosystems (Clarke et al., 2015; Lipoma et al., 2016; Pausas & Paula, 2020).

In contrast to other studies that have shown a general trend for exotic species to pre-empt space after to fire disturbance (D’Antonio & Vitousek, 1992), I did not find any evidence that exotics species increased at the expense of native species (in terms of cover or richness) within 15 months post-fire. In fact, both natives and exotics showed a broadly similar response to the fire, including the recovery of individuals after fire (Appendix C). This is further evident in my results where there was similar community recovery in both native and exotic species richness and species cover on burnt transects. This further suggests that exotics in these grasslands are not limited by space (Day and Buckley 2011).

Plant species of different growth forms responded differently. For example, species richness of native forbs and graminoids were generally more affected by fire than exotic species in those growth forms. These short-term changes are large compared to pre-fire long-term dynamics, with the exception of one unburnt transect (OHAT045) where all forbs and native graminoids had significantly declined, while exotic species had remained stable over the four decades of sampling except exotic graminoids. Unburnt transects showed that some components of these communities were gradually changing over longer timescales. These changes were characterised by ongoing increases in the cover of exotic graminoids and woody invasion on OHAT045, and decreases in native species in those growth forms, including forb species. This suggests that this unburnt transect will be dominated by exotic graminoids. This is consistent with the finding that tussock-dominated grasslands are dynamic and an important component of these changes is ongoing invasion (Day & Buckley, 2011, 2013).

Plant traits are important for understanding community resilience to fire (Lipoma et al., 2016; Speed et al., 2010). For example, ratio of plants that are clonal and had low meristem generally increased immediately after fire and returned back to pre-fire levels in three, and 15 months post-fire (Figure 3.12). Similarly, I can infer that individual woody plants died back resulting in decreased observed richness immediately after the fire, but subsequently recovered their living biomass. Detailed natural history observations of individual plants after fire, especially to determine resprouting ability and seed production for a wide range of species, will assist future research that seeks to predict community response to fire.

Finally, both long- and short-term plant community responses to fire must be viewed in the context of land use history, grazing, drought, weed invasion and climate change (Baillie & Bayne, 2019; D’Antonio & Vitousek, 1992; Duncan et al., 2001; Karavani et al., 2018; Mandle et al., 2011). This is because the effect of fire in these grasslands will change over time due to global change drivers such as increasing temperatures, and decreasing rainfall and humidity and hence, more extreme fire weather conditions (Jones et al., 2022). Monitoring community dynamics at burnt and unburnt locations both in short-term and long-term using a combination of experimental burning and long-term sampling would be useful for testing specific hypotheses of individual species and community level drivers of post-fire community changes.

3.5 Conclusion

Repeated measurements of these pre-existing, vegetation monitoring transects has enabled us to compare before and after disturbance measurements for characterising the community response to fire and the effect of fire on species' recovery. Our results show that these community were relatively resilient to this single wildfire event. However, the observed long-term dynamics, including ongoing plant invasions, combined with the predicted increase in droughts and wildfires are likely to put native species in these community at risk. Further, in most areas, these grasslands are subjected to heavy grazing and browsing from both stock and invasive mammals. The synergistic effects of environmental changes and such negative interactions is likely to cause further community changes. To generate recommendations for land managers, we require increased research effort in both vegetation monitoring and experimental studies to tease apart the effects of these interacting factors.

Chapter 4 Dynamics of plant community flammability in Arthur’s Pass over nine decades

4.1 Introduction

Due to global climate change, fire frequency, intensity and severity are forecasted to increase in many parts of the world beyond historical norms (Clarke Smith, & Pitman, 2011; Environment, 2022; Keeley & Syphard, 2019) and are expected to affect spatial and temporal patterns in vegetation and ecosystem function (Armenteras et al., 2021; Bond & Keeley, 2005; Bowman et al., 2020). In particular, fires are predicted to become more intense in temperate and alpine regions (Environment, 2022; Melia et al., 2022) leading to increases in more flammable plant species or vegetation types (Cardoso et al., 2018; Landesmann et al., 2021; Schwilk, 2003). Thus, it is imperative for predicting impacts of global change that research focuses on understanding the drivers of plant community flammability.

Plant community flammability reflects the combined effects of flammability traits of the constituent species of the community (Keeley et al., 2011; Landesmann et al., 2021; Simpson et al., 2016). Temporally, community change in their community structure over time through succession and this change can influence change in amount and condition of fuels, and therefore, community flammability (McColl-Gausden & Penman, 2019; Tiribelli et al., 2018). Exploring post-fire successional changes in plant community are ’natural experiments’ where relationships between fire and plant flammability can be determined and are important to determine future community flammability (Blackhall et al., 2017; Tiribelli et al., 2018). The patterns of post-fire community flammability can be determined by determining successional changes in both plant traits and community structure (Plucinski & Anderson, 2008; Uyehara & Pacala, 2018). Other environmental factors such as solar radiation and rainfall can indirectly affect plant community flammability (Gomes et al., 2020). For instance, solar radiation and precipitation have been shown to influence species composition and community type abundances (Cadiz et al., 2020). So, if there was increase in the abundance of low flammability species in a community, e.g., forbs, I would expect that community flammability would decrease.

Plant traits represents variation in ecological strategies and determine how plants respond to environmental factors and influence ecosystems (Palmquist et al., 2017; Pérez-

Harguindeguy et al., 2013). They are shown to be strongly related to plant flammability and phylogenetically conserved (Cui et al., 2020). Plant traits can be directly measured at various scales by experimentally burning plants or plant parts: e.g., leaf flammability and shoot flammability (Alam et al., 2020; Padullés Cubino et al., 2018; Pérez-Harguindeguy et al., 2013). From such experiments, various studies have reported that high leaf dry matter content, shoot dry matter content and amount of retained dead material enhance plant flammability, whereas high specific leaf area and leaf moisture content negatively influence plant flammability (Alam et al., 2020; Mason et al., 2016; Murray et al., 2013; Wyse et al., 2016). Furthermore, plants with thin, dry leaves and branching patterns can generate fine and well-aerated fuel beds and are highly flammable (Fernandes & Cruz, 2012; Schwilk, 2003). In contrast, other studies have found that traits including thick, fleshy leaves, and high moisture content are low flammable (Ganteaume et al., 2021; McDaniel et al., 2021).

Under similar environmental conditions some plants burn better than others due to the intrinsic morphological traits of a plant (Fuentes-Ramirez et al., 2016), suggesting the effect of individual traits accumulates within a plant community (Engber & Varner, 2012; Tumino et al., 2019). Traits can evolve with changing environmental condition and this change can change plant flammability (Bond & Keeley, 2005; Keeley et al., 2011) as well as whole community flammability (Magalhães & Schwilk, 2012; Uyehara & Pacala, 2018). Furthermore, plant flammability is phylogenetically conserved among family and higher taxonomic level (Cui et al., 2020). Thus, understanding patterns of change in traits related to plant flammability and how these are affected by vegetation change may be one way to predict the effects of fire and dynamics of flammability at landscapes under changing fire regimes (Pausas et al., 2017). Such studies are crucial to elucidate the relationships among plant species' morphological traits, flammability, and fire behaviour. A first step in this understanding is to observe the relationship between species' traits and their flammability, such as shoot-level flammability. Secondly, it is important to explore the changing community composition over time. These can help to understand changes in traits and community that can influence community flammability. For instance, an increases in the dominance of small leaved woody plant species can increase community flammability (Calitz et al., 2015; Fraser et al., 2016).

New Zealand's vegetation mostly evolved with low fire frequency (McGlone, 2001; Perry et al., 2012). However, some vegetation types were dominated by highly fire-susceptible plant species (Perry et al., 2012, 2014) and some New Zealand native plant species are inherently flammable (Mason et al., 2016; Wyse et al., 2016). In subalpine ecosystems, flammable vegetation types are prevalent, including native grasslands dominated by *Chionochloa* spp., *Festuca novae-zelandiae* (Payton & Pearce, 2009; Perry et al., 2014), bracken (McGlone, 2001), and shrublands dominated by *Dracophyllum* spp. (Johnson, 2001; McGlone & Topping, 1983). In succession, a highly flammable woody species *Dracophyllum* spp. can easily invade and regenerate after fire in areas previously dominated by *Chionochloa* spp., *Festuca novae-zelandiae* and *Pteridium esculentum* (Johnson, 2001). With predicted future increases in the fire weather index in New Zealand (Pearce et al., 2011; Simpson et al., 2014), an increase in fire frequency is expected (Pearce & Clifford, 2008). Further research is needed on how these predicted changes in vegetation may interact with the effects of other global change drivers. For example, the invasion of low statured forbs into the tussock grasslands of New Zealand's South Island has led to a probable decrease in the flammability of these invaded community (Padullés Cubino et al., 2018). Studies in fire-prone ecosystems including Australia, South Africa, Europe and America (Gill & Zylstra, 2005; McColl-Gausden & Penman, 2019; Raubenheimer et al., 2021; Tiribelli et al., 2018; Zylstra, 2018) have predicted that plant community flammability will change over time (Moreira et al., 2014; Pausas et al., 2017; Schertzer & Staver, 2018) due to effect of global climate change (H. G. Clarke et al., 2011). One study conducted in New Zealand found that community flammability declined in tussock grassland, based on an assessment of community-weighted mean flammability from permanent transects remeasured of a 25 year period (Padullés Cubino et al., 2018). Long-term plots provide a unique window into how community flammability has changed over decadal scales.

In this study, I aimed to quantify community flammability over nine decades of post-fire vegetation change in one of the world's oldest permanent transect dataset, the 'Cockayne Plots'. These transects were set up in the early 1930s in a range of vegetation types (grassland, shrubland and forest) within the low nutrient, perennial-dominated, sub-alpine ecosystem at Arthur's Pass, New Zealand (Burge et al., 2020; Calder & Wardle, 1969; Cockayne, 1898; Cockayne & Calder, 1932). The transects were burnt in 1890, 42 years prior to the first vegetation measurement. They were burnt three times after the initial fire in 1921, 1930 and 1932. A recent analysis has shown that with succession, the richness and abundance of native woody species have increased to three times than that of the initial vegetation measurement; however, there were no any exotic woody species at this site over nine decades of vegetation measurement (Burge et al., 2020).

Here, I combine these plot data with data from laboratory burns to estimate community flammability in these transects during each census period (Jaureguiberry et al., 2011; Padullés Cubino et al., 2018; Wyse et al., 2016). These estimates were then used to examine the changes in relative community flammability over the 90 years of post-fire succession. I predicted that community flammability in grassland vegetation would be relatively higher early in the post-fire vegetation change due to an initial increase in fine fuels (grasses) or species such as bracken (*Pteridium esculentum* (G. Forst.) Cockayne) and *Dracophyllum* spp. (Johnson, 2001; McGlone & Topping, 1983; McWethy et al., 2013). I predicted that community flammability would subsequently decline in grassland vegetation due to an increase in species that contain higher leaf moisture content (Padullés Cubino et al., 2018). In forested vegetation and shrubland, where there is an increase in biomass and woody community, I predict community flammability will increase over time, due to the prevalence of high flammability forest species, such as mountain beech *Fuscospora cliffortioides*. Specifically, for this dataset quantifying post-fire vegetation change of over 90 years I asked: (1) Which measured morphological traits predict variation in shoot flammability and (2) How has community flammability changed over time?

4.2 Methods

4.2.1 Study area

Arthur's Pass is the highest pass across the Southern Alps in South Island, New Zealand (Figure S4.1, Appendix A). Geographically, this location is 920 m a.s.l. with latitude 42˚54'19.2' S and longitude 171˚33'56.0' E. Arthur's Pass is a markedly wet zone (Leathwick et al., 2002); climate data from the last 49 years show that Arthurs Pass has a mean annual maximum temperature of 17.13 ± 0.60 ˚C and a mean annual minimum temperature of 1.7 ± 0.45˚C (NIWA, 2021). Rainfall data from the past 115 years (1906 to 2021) show that the site has a mean total annual rainfall of 4080.565 ± 59.89 mm (Figure S4.2, Appendix A).

When Cockayne first established nine permanent vegetation monitoring transects in 1932, the vegetation was predominantly subalpine scrub (Calder & Wardle, 1969). In the first (1932) and second (1965) measurements, the common species at Transects 1 and 2 were *Chionochloa* sp. (Calder & Wardle, 1969; Cockayne & Calder, 1932) (Table 4.1). Transects 3 and 4 were in beech forest and remained stable in composition across all four (1932, 1965, 2001 and 2018) vegetation measurements (Burge et al., 2020). Common species were *Phyllocladus alpinus* and *Fuscospora cliffortioides* and understory species *Coprosma* spp., *Olearia* spp., and *Pseudopanax colensoi*. At Transect 5, in subalpine scrub, the common species were *Dracophyllum longifolium*, and *Veronica subalpina* in the first and second measurements, but later in 2018 *Dracophyllum uniflorum* was more common. At Transect 6, in subalpine scrub, the relatively more common species from 1932 to 2018 were *Dracophyllum longifolium*, *Dracophyllum uniflorum*, *Gaultheria rupestris*, *Pentachondara pumila*, and *Celmisia discolor*. At Transect 7, in subalpine scrub, the common species were *Astelia nervosa, Phormium cookianum*, *Blechnum penna-marina* and *Chionochloa* sp. in 1932 to 2018 (Burge et al., 2020; Calder & Wardle, 1969; Cockayne & Calder, 1932). At Transect 9, in subalpine scrub, the relatively more common species at the first measurement were *Ozothamnus leptophyllus* and *Veronica subalpina*, but later, in 2018, *Dracophyllum longifolium*, *Dracophyllum uniflorum*, *Brachyglottis elaeagnifolia, Coprosma colensoi*, *Blechnum minus, Phormium cookianum* and *Astelia nervosa* were more common. In subalpine low forest at Transect 10, the common species were *Dracophyllum longifolium* and *Astelia nervosa, Phormium cookianum* at the first and second measurements. In 2018, *Coprosma dumosa* and *Coprosma pseudocuneata* had become co-dominant.

There have been no fires in Arthur's Pass since 1932. The 1890 fire burnt a large area that encompassed all nine of the transects locations, except Transect 10, which was burnt in a fire in 1878 (Cockayne 1898). Small fires occurred at Transects 9, 7 and 2 in 1921, 1930 and 1932, respectively (Burge et al., 2020; Calder & Wardle, 1969). Transect 8, which was originally established with all other nine transects was abandoned in 2001 because it lacked permanent markers and was not drawn to scale. These transects were located with a geographical positioning system (GPS) and the guidance of previous researcher who worked on the plant species composition at this site.

Table 4.1. Description of nine permanent transects established at Arthur's Pass in 1932 and remeasured in 1969, 2001 and 2018. Width (m) and length (m) are the dimensions of the transects. Area is the total area sampled within each of the belt transects. Vegetation type was based on a classification by Calder & Wardle (1969)) and observations made during data collection. Dominant species on each transect were those that had greater than 30% mean relative percent frequency in each transect across all measurement times. 'Years since last fire' is the number of years between 2018 and the last fire at each transect. The relative percent frequency was calculated by dividing the total number of grid cells (each was 1 foot square, or 0.093 m^2) on a transect by the total number of grid cells

Transect	Width (m)	Length (m)	**Area (m^2)**	**Vegetation type**	**Dominant species**	**Aspect**	**Elevation (m a.s.l.)**	**Years since last fire**
T1	1.2	8.8	10.78	Beech forest edge	*Fuscospora cliffortioides*, *Chionochloa* spp.	97˚ E	880	128
T2	1.2	5.2	6.32	Tussock grassland	*Chionochloa* spp.	80˚ NE	901	86
T3	2.4	19.8	48.31	Beech forest	*Phyllocladus alpinus*, *Fuscospora cliffortioides*, *Brachyglottis elaeagnifolia*, *Coprosma pseudocuneata*	100˚ E	906	128
T4	2.4	19.7	47.92	Beech forest	*Phyllocladus alpinus*, *Fuscospora cliffortioides*, *Brachyglottis elaeagnifolia*, *Coprosma pseudocuneata*	100˚ E	929	128
T5	2.4	10.7	26.01	Subalpine scrub	*Dracophyllum* spp., *Brachyglottis elaeagnifolia*	132˚ SE	920	128
T6	1.8	3.4	6.13	Subalpine scrub	*Dracophyllum* spp., *Pentachondra pumila*, *Celmisia discolor*	340˚ NW	909	128
T7	1.2	8.1	9.85	Subalpine scrub	*Astelia nervosa*, *Phormium cookianum*, *Blechnum minus*, *Chionochloa* spp.	250˚ SW	919	88
T9	1.2	5.5	6.69	Subalpine scrub	*Dracophyllum* spp., *Brachyglottis elaeagnifolia*, *Blechnum minus*, *Phormium cookianum*, *Astelia nervosa*	239˚ SW	909	79
T10	1.2	11.6	14.12	Subalpine low forest	*Dracophyllum* spp., *Coprosma dumosa*, *Coprosma pseudocuneata*	260˚ SW	841	140

4.2.2 Data collection

Long-term plant community data

I used plant community composition data from the nine transects that were of variable size compiled by Burge et al., (2020) to estimate how changes in plant community structure were related to community flammability over time. The data comprised relative percent frequency of plant species within the nine permanently marked transects from 1932 to 2018. These long-term data were used to determine which species were relatively more common across all time points, to direct sample collection for trait and flammability measurements, and how estimated as the relative percent frequency of each species had changed on the transects over time. The alpha diversity of plant community at each of the four vegetation measurement times was computed as total species richness per transect.

Plant morphological and flammability trait measurement

Field sampling

Shoots were collected from the 50 most abundant species for the nine transects. To achieve this, species with greater than or equal to 30% relative percent frequency on at least one transect in 2018 were sampled. Sample collection followed methods described in previous plant trait and flammability studies (Alam et al., 2020; Jaureguiberry et al., 2011; Padullés Cubino et al., 2018; Pérez-Harguindeguy et al., 2013). Shoots, or, if smaller than 70 cm, the entire plant, were sampled to measure a range of morphological and plant flammability traits (Alam et al., 2020; Cui et al., 2020; Padullés Cubino et al., 2018). To avoid any impact of destructive sampling on the permanent transects, the plant samples were collected outside the permanently marked transects, but within approximately 50 m. For trees and shrubs, 70-cm long terminal branches were cut from healthy, reproductively mature, plants with sun-exposed shoots, where possible. For grasses and forbs, whole tillers were collected including roots, then the roots were cut to a minimum length to preserve the aboveground plant architecture. In cases where the grasses and forbs were longer than 70 cm, the lower 70 cm was sampled and material above that length was trimmed. For ferns, fronds of up to 70 cm were collected. One shoot sample was collected from each of six different individuals of each species. Additionally, from those same individual plants, shoot subsamples of approximately 10-cm long were collected to measure moisture content, and leaf samples were collected for morphological, and moisture content measurements. Shoot samples were stored in black polythene bags and leaf samples were collected in plastic zip lock bags and stored chilled for a maximum of five days before trait measurements were taken.

Morphological trait measurements

Both leaves and shoots were measured to assess morphological trait variation among species. At the leaf level, the dimensions of leaves, including the length, width and thickness, were measured. Leaf length and width were measured using a ruler and thickness was measured using a micrometre (size 3202-25A of measuring range 0-25 mm). Leaf samples were also scanned to create digital images from which the leaf surface area of each individual was computed using ImageJ (version 1.53E). At the shoot level, two sub-samples of approximately 10 cm in length were used for dehydration and saturation. One of the subsamples was air dried for 24 hours and the other was soaked in water for 7 hours. The biomass of each water-soaked and air-dried samples were measured. Then both samples were oven dried for 48 hours at 65˚C. Similarly, at the leaf level, the leaves were soaked in water for 7 hours and then oven dried for 48 hours at 65˚C. Samples were then weighed to obtain a leaf fresh mass and an oven dried biomass for both leaves and shoots.

Plant flammability trait measurements

Shoot- or plant-level flammability for the 50 sampled species was quantified as four flammability components (see detail in Padullés Cubino et al., 2018): 1) ignition score, time to ignition (0-10 s) subtracted from 10 (Padullés Cubino et al., 2018); 2) the maximum temperature measured using an infrared thermometer; 3) burning time, the time of flaming duration; and 4) burnt biomass, the visually-estimated percent biomass consumed. The relative flammability of species was estimated by burning shoot and above-ground plant samples using a specially designed device by Jaureguiberry et al. (2011) and modified by Wyse et al. (2016)). The device consists of a vertically half cut barrel of size 85 × 60 cm placed horizontally on four metal legs of 100 cm in length with a gas grill and connected to gas cylinder. Prior to burning, samples were air dried at room temperature for 24 hours. Then were measured for length, width, and height. Percent of dead material present on each sample was visually estimated just before burning. Then, each sample was laid horizontally on the grill for two minutes, then ignited it with a blowtorch flame for 10 s. The time to ignition (if it occurred) and the length of time the sample burnt for were recorded. The maximum temperature attained during burning was recorded using an infrared thermometer (Fluke 572, Fluke Corp., Everett, WA, USA). Finally, the percent biomass consumed in the fire was visually estimated. Samples that did not ignite were assigned zero percent consumed and the maximum temperature was recorded as the initial temperature of the grill, 150 °C (Cui et al., 2020, 2020; Padullés Cubino et al., 2018).

Long-term climate data

To determine how climate variables relate to changes in community flammability, climate data for 10-35 year were collated. Daily climate data was downloaded from National Institute of Water and Atmospheric Research Ltd (https://cliflo.niwa.co.nz): rainfall, maximum and minimum temperature, wind speed, solar radiation, relative humidity, potential evapotranspiration, moisture, and soil moisture from 1906 to 2021 (NIWA, 2021). Daily temperature, rainfall, relative humidity, soil moisture, vapour pressure, potential evapotranspiration, wind speed and moisture deficit data were used to calculate annual mean values. Means of these annual means were then calculated for separate periods (four periods for rainfall: 115 year and two periods for wind speed: 24 years) to create a climate window of minimum 10 to 35 years relating to vegetation measurement. For instance, to correlate 1932 vegetation measurement with rainfall, a climate window of 26 year was created from the mean annual rainfall from 1906 to 1932. These climate windows for each variable were plotted across the vegetation measurement time to correlate climate change variables with relative community flammability using the'ggplot2' package, v.3.3.2 (The R Core Team, 2020).

4.2.3 Data analysis

Variation in plant community structure and morphological traits

A detrended correspondence analysis (DCA) was used to explore changes in plant community over time using R function 'decorana' in 'vegan' (Oksanen, 2021). DCA is an iterative algorithm used to explore gradients among species in community and is particularly useful with long gradients in species composition, as in this case where several different vegetation types were analysed (Hill & Gauch, 1980). Species richness and Pielou's evenness (E) were calculated using function 'specnumber' and index 'Shannon' in base R. The number of colonized and locally extinct species were computed from the species composition data.

To explore variation in morphological plant traits among species, principal component analysis (PCA) was implemented using the function 'pca' in 'FactoMineR' v.2.3 in R (R Core Team, 2022). Morphological trait composition was calculated as the community weighted mean of each morphological trait at the transect level (see formula in Appendix D) based on plant life form, clonality and height (see detail in next section and Table S4.1, Appendix A). Trajectories were plotted from the first vegetation measurement to the most recent measurement to show the relative changes over time of transects in species space and in trait space (Buckley et al., 2021).

Species flammability-trait relationships

To investigate relationships among species flammability and morphological traits, leaf area, leaf dry matter content, leaf specific leaf area, and leaf moisture content were calculated at the individual sample level, following previous studies (Appendix D; Alam et al., 2020; Padullés Cubino et al.; Pérez-Harguindeguy et al., 2013). Species-level values for each flammability, and morphological trait were estimated by taking the mean values for individual samples within species. For species that were not sampled, data from existing sources were collated (Alam et al., 2020; Cui et al., 2020; Padullés Cubino et al., 2018; Wyse et al., 2016), resulting in flammability data and at least partial trait data for 67 species. Linear regression of ignitability on burnt biomass was used to replace one missing value for *Aristotelia fruticosa*, where time to ignition was not recorded.

A principal component analysis (PCA) was performed at the species level to quantify the relative flammability for the 67 species for which I had data (species' flammability rankings; raw data in Table S4.2, Appendix A). The first flammability component (PC1) was further used to calculate community-level flammability as per Padullés Cubino et al. (2018). Data for the morphological traits of leaf length, leaf thickness, leaf area, leaf dry matter content, specific leaf area, bulk density, moisture content and dead material were log transformed prior to analysis. A second PCA was performed using species' morphological trait data for the 57 species for which I had morphology data (Table S4.3,Appendix A). A third PCA was performed using both the flammability and morphological traits for these 57 species to understand relationships among flammability and morphological traits. This was executed to visualise relationships among these all the plant traits used in this study. Pairwise relationships among all trait values were quantified using Pearson's correlation coefficient in base R v.4.2.1 (R Core Team, 2022).

Phylogenetic species flammability PC1 and morphological trait relationship

To determine the phylogenetic signal of plant flammability (PC1) among species, phylogeny of 57 species was assessed using function 'phylo.maker' that quantifies the phylogenetic properties (e.g. phylogenetic diversity and phylogenetic relatedness) of vascular plants (Qian & Jin, 2016). To visualize species flammability (PC1) pattern across the phylogeny, a circular diagram was made using function ‘ggtree’ (Yu et al., 2017). The phylogenetic signal was evaluated using Pagel’s labda (λ) correlation structure using function ‘corPagel’ (Freckleton et al., 2002). Pagel’s λ varies from zero to unity. A value of $\lambda = 0$ indicates that there is no phylogenetic signal in the trait, that is, that the trait has evolved independently of phylogeny and thus close relatives are not more similar on average than distant relatives; $\lambda = 1$ indicates a strong phylogenetic signal, and that the trait has evolved according to the evolutionary model of Brownian motion model structure. But values in between 0 and 1 indicate that there is phylogenetic signal in the traits, and also evolved according to other stochastic ecological pressures rather than linear increase in divergence among the species with time (Freckleton et al., 2002). Eight candidate models were set up where species flammability (PC1) as a response variable and morphological traits (PC1_morph, PC2_morph and PC3_morph) as predictor in phylogenetic generalized least squared (pgls) to evaluate phylogenetic pattern of species flammability and morphological traits association.

Estimation of community flammability

All 134 species recorded in the transect vegetation measurements were categorised into fourteen classes based on their life history traits (Table S4.4, Appendix A). The life history traits were derived from life form (perennials, annuals, ferns, woody species, then within graminoid: tufted grass, grass-like sedge, iridoform, junciform, other petalous monocots; within dicots: mat forming, rosette, erect, ascending, tall shrubs, prostrate shrubs, spreading to erect small shrub, stem climbers and small tree), clonality (non-clonal, clonal above ground: stolon, gemmiparous, other vegetative buds or plant fragments and clonal below ground: rhizomes, tubers, bulbs, adventitious root buds) and mean plant height. The 67 species’ flammability scores on PC1 of the flammability PCA (for species that I had flammability measurements for) were assigned to those that did not have flammability measurements for ($n = 67$), making the assumption that species that were in the same genus and life history class would have similar flammability (Padullés Cubino et al., 2018; Table S4.4 Appendix A). To estimate the relative community flammability for each transect at each measurement time, the transect community matrix of species composition data was multiplied by the vectorised flammability component PC1 (Padullés Cubino et al., 2018). Subsequently, a community flammability weighted mean value for each transect measurement dataset was calculated as the ratio of the sum of the flammability community matrix and the community composition matrix (Padullés Cubino et al., 2018).

Change in community flammability

Community weighted mean flammability for each of the nine transects was used as response variable in a simple linear regression against measurement time across the 86 years (1932-2018). Then a post-hoc TukeyHSD test was implemented using ‘agricolae’ (De Mendiburu Delgado & De Mendiburu Delgado, 2009) in R v.4.2.1 (R Core Team, 2022) to test for significant change variation in community flammability over time.

4.3 Results

4.3.1 Change in community composition over time

The patterns revealed in the DCA of plant community composition for all transects at all measurement times were consistent with results presented in Burge et al. (2020), showing full turnover of species composition and a strong compositional gradient from forest to grassland vegetation types on the first DCA axis (Table 4.2; Figure 4.1 & 4.2). The second DCA axis reflected variation among transects in relative dominance by shrubs. Transects on which high shrub dominance were at the bottom of ordination space, whereas transects on which shrubs were low were moved to upward in DCA ordination plot. Trajectories for each transect showed that the transects differed in the extent to which species composition changed over time, some being more stable than others (Figure 4.2). Specifically, T1 and T7 changed markedly in composition (shown by large trajectories in ordination space), while T2, T4 and T5 changed very little. Changes for individual transects also varied among the time periods.

Table 4.2. Results from detrended correspondence analysis (DCA) on species composition of all nine transects at all measurement times 1932-2018. Eigenvalues and axis lengths are given for four DCA axes

	DCA1	**DCA2**	**DCA3**	**DCA4**
Eigenvalues	0.6501	0.3288	0.1356	0.14892
Axis lengths	4.3853	2.7533	1.8345	1.73873

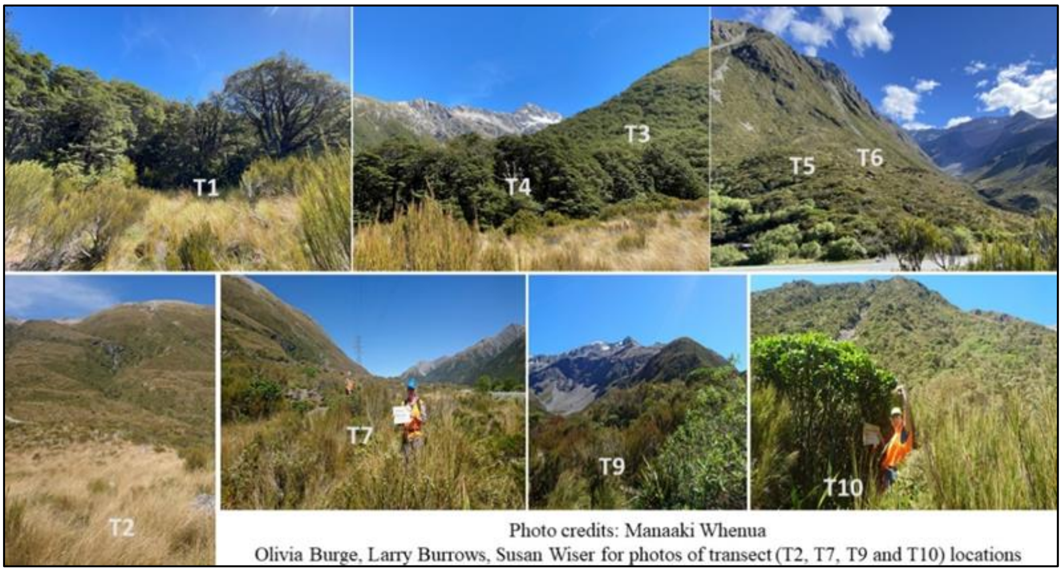

Photo credits: Manaaki Whenua
Olivia Burge, Larry Burrows, Susan Wiser for photos of transect (T2, T7, T9 and T10) locations

Figure 4.1. Photos of permanent transect locations in different vegetation types including beech forest edge (T1), tussock grassland (T2), beech forest (T3 & T4), subalpine scrub (T5, T6, T7 &T9) and subalpine low forest (T10)

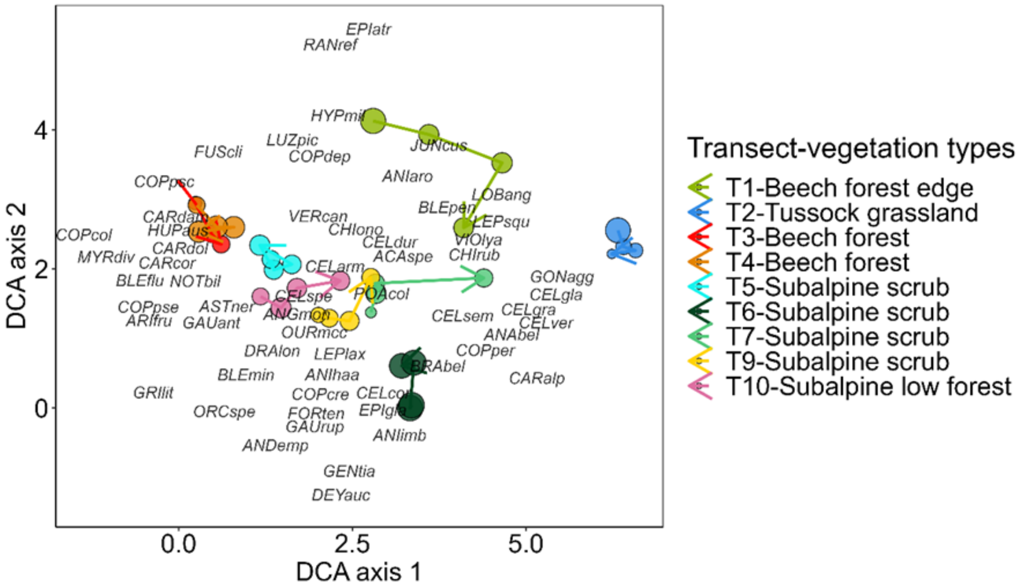

Figure 4.2. Detrended correspondence analysis (DCA) diagram showing variation in species composition among transects and closely associated species. Species labels are shown for those with greater than 30 percent frequency in 2018. Each point represents the composition of a transect at a particular measurement time. Measurements for each transect are joined by a trajectory arrow starting from the first vegetation measurement year (1932) to the most recent measurement (2018). The size of points is proportional to the value from the community flammability weighted mean. Full species names represented by the abbreviations are given in Table S4.1, Appendix A

Beech forest edge (T1)

Transect T1 was at the edge of beech forest where the vegetation was a mix of grassland and forest edge species (Figure 4.1). In this vegetation type, in 1932, two tall, prostrate shrubs were relatively common (i.e., had a relative percent frequency of more than 30): *Coprosma depressa* and *Dracophyllum uniflorum* (Table 4.3). *Chionochloa rubra* was the most common species (i.e., a relative percent frequency more than 30). In 1965, the shrubs *Coprosma cheesmani, Dracophyllum uniflorum, Veronica canterburiensis* were relatively abundant, but no trees had more than 30 relative percent frequency. *Chionochloa rubra* was still the most common species in 1965 too. In 2001 and 2018, species having more than 30 percent relative frequency were the tall trees and shrubs *Fuscospora cliffortioides* and *Coprosma depressa*, and the rosette *Anisotome aromatica*. Transect species richness and evenness fluctuated, but richness increased by 10 species across all time periods, as did Pielou's evenness (E) by 0.03; these changes were driven by colonisations and extinctions of predominantly native species (Table 4.4 & Table 4.5).

Tussock grassland (T2)

Transect T2 was in tussock grassland, dominated by grasses and other low stature species. The most common species having more than 30 relative percent frequency were grasses, rosettes, and cushion species (Figure 4.1). The common grass species were *Chionochloa rubra* and *Carpha alpina*, rosette species were *Ourisia macrocarpa* and *Brachyglottis bellidioides* (Table 4.3). There were no shrubs and trees occurring at more than 30 relative percent frequency in 1932. In 1965, the most common species were *Blechnum penna-marina*, *Chionochloa rubra*, *Schoenus pauciflorus*, *Viola lyallii*, *Dolichoglottis lyallii*, *Celmisia gracilenta*, *Celmisia verbascifolia* and *Craspedia* spp. In 2001, common species having greater than 30 relative percent frequency were *Chionochloa rubra*, *Schoenus pauciflorus*, *Viola lyallii*, *Celmisia gracilenta, Ourisia macrocarpa* and *Craspedia* spp. In 2018, the most common species were *Chionochloa rubra*, *Viola lyallii*, *Schoenus pauciflorus*, *Poa colensoi*, *Blechnum penna-marina* and *Gonocarpus aggregatus*. Previously dominant species *Carpha alpina*, and *Dolichoglottis lyallii* were no longer recorded. Overall, despite fluctuations in species colonisations and extinctions, species richness on this transect doubled between 1932 and 2018 and evenness increased (Table 4.4 & Table 4.5).

Table 4.3. Species in each growth form class that had a relative percent frequency of greater than 30% at each of the four measurement times 1932-2018. The '-' symbol indicates where no species met the 30% threshold at a given time. Growth forms are based on 14 life history category

Transect	**Life form**	**1932**	**1965**	**2001**	**2018**
T1	Trees	-	-	*Fuscospora cliffortioides*	*Fuscospora cliffortioides*
	Shrubs	*Coprosma depressa,* *Dracophyllum uniflorum*	*Coprosma cheesmani,* *Dracophyllum uniflorum,* *Veronica canterburiensis*	*Coprosma depressa*	*Coprosma depressa*
	Graminoids	*Chionochloa rubra*	*Chionochloa rubra*	*Chionochloa rubra,* *Chionochloa* spp.	*Chionochloa* spp.
	Forbs	-	*Aporostylis bifolia*	*Aporostylis biflora*	*Anisotome aromatica*
	Fern	-	-	*Blechnum penna-marina*	-
T2	Trees	-	-	-	-
	Shrubs	-	-	-	-
	Graminoids	*Chionochloa rubra,* *Carpha alpina*	*Chionochloa rubra,* *Schoenus pauciflorus,*	*Chionochloa rubra,* *Schoenus pauciflorus*	*Chionochloa rubra,* *Poa colensoi,* *Schoenus pauciflorus*
	Forbs	*Ourisia macrocarpa,* *Brachyglottis bellidioides*	*Anisotome aromatica,* *Blechnum penna-marina,* *Celmisia gracilenta,* *Celmisia verbascifolia,* *Crasepedia* spp., *Dollichoglottis lyalli,* *Viola lyali*	*Celmisia gracilenta,* *Craspedia* spp., *Dollichoglottis lyalli,* *Ourisia macrocapa,* *Viola lyalli*	*Blechnum penna-marina,* *Celmisia gracilenta,* *Celmisia verbascifolia,* *Gonocarpus aggregatus,* *Ourisia macrocapa,* *Viola lyalli*
T3	Trees	-	-	*Fuscospora cliffortioides*	*Fuscospora cliffortioides,* *Myrsine divaricata,* *Phylocladus alpinus*
	Shrubs	*Brachyglottis elaeagnifolia*	*Brachyglottis elaeagnifolia,* *Coprosma pseudocuneata*	*Coprosma pseudocuneata*	*Coprosma pseudocuneata,* *Coprosma foetidissima*

Transect	**Life form**	**1932**	**1965**	**2001**	**2018**
T4	Graminoids	-	-	-	-
	Forbs	-	-	*Astelia nervosa,*	*Astelia nervosa*
	Trees	-	*Olearia ilicifolia,* *Phylocladus alpinus*	*Olearia ilicifolia,* *Phylocladus alpinus*	*Phyllocladus alpinus*
	Shrubs	-	*Coprosma dumosa,* *Coprosma pseudocuneata*	*Coprosma pseudocuneata*	*Coprosma pseudocuneata*
T5	Graminoids	-	-	-	-
	Forbs	-	*Phormium cookianum,* *Polystichum vestitum*	-	-
	Trees	-	-	-	-
	Shrubs	*Brachyglottis elaeagnifolia*	*Brachyglottis elaeagnifolia,* *Dracophyllum longifolium*	*Brachyglottis elaeagnifolia,* *Coprosma serrulata,* *Dracophyllum longifolium*	*Brachyglottis elaeagnifolia,* *Coprosma depressa,* *Coprosma serrulata,* *Dracophyllum longifolium*
T6	Graminoids	-	-	-	-
	Forbs	-	-	-	-
	Fern	-	*Blechnum minus*	*Blechnum minus*	*Blechnum minus*
	Trees	-	-	-	-
	Shrubs	-	-	*Gaultheria rupestris,* *Myrsine nummularia,* *Pentachondra pumila*	*Myrsine nummularia,* *Pentachondra pumila*
T7	Graminoids	-	*Chionochloa* spp., *Schoenus pauciflorus*	*Chionochloa* spp., *Schoenus pauciflorus*	*Chionochloa* spp., *Schoenus pauciflorus*
	Forbs	*Celmisia discolor*	*Celmisia discolor,* *Phormium cookianum*	*Celmisia discolor*	*Celmisia discolor*
	Fern	-	-	*Blechnum minus,* *Lycopodium scariosum*	*Blechnum minus,* *Lycopodium scariosum*
	Trees	-	-	-	-

Transect	Life form	1932	1965	2001	2018
	Shrubs	-	*Coprosma serrulata, Gaultheria rupestris, Veronica canterburiensis*	*Coprosma serrulata, Dracophyllum longifolium*	*Coprosma serrulata, Gaultheria rupestris, Dracophyllum longifolium, Brachyglottis elaeagnifolia, Lepidothamnus laxifolius, Myrsine nummularia*
	Graminoids	-	-	*Chionochloa rubra*	-
	Forbs	*Phormium cookianum*	*Astelia nervosa, Celmisia armstrongii, Phormium cookianum*	*Astelia nervosa, Phormium cookianum*	*Astelia nervosa, Phormium cookianum*
	Fern	-	-	*Blechnum minus*	*Blechnum minus*
T9	Trees	-	-	-	*Pseudopanax colensoi*
	Shrubs	*Ozothamnus leptophyllus, Veronica subalpina,*	*Brachyglottis elaeagnifolia, Coprosma serrulata, Dracophyllum uniflorum*	*Coprosma serrulata, Dracophyllum longifolium, Dracophyllum uniflorum*	*Coprosma serrulata, Dracophyllum longifolium, Dracophyllum uniflorum, Brachyglottis elaeagnifolia, Gaultheria rupestris,*
	Graminoids	-	-	-	-
	Forbs	*Ourisia macrocarpa*	*Ourisia macrocarpa*	-	-
	Fern	*Blechnum minus*	*Blechnum minus*	*Blechnum minus*	*Blechnum minus*
T10	Trees	-	-	-	-
	Shrubs	-	*Dracophyllum longifolium,*	*Dracophyllum longifolium, Coprosma dumosa, Coprosma pseudocuneata*	*Dracophyllum longifolium, Coprosma dumosa, Coprosma pseudocuneata*
	Graminoids	-	-	-	-
	Forbs	-	*Astelia nervosa, Phormium cookianum*	*Astelia nervosa, Phormium cookianum*	*Astelia nervosa, Phormium cookianum*
	Fern	-	*Blechnum minus*	*Blechnum minus*	*Blechnum minus*

Table 4.4. Transect species richness (S) and Pielou's evenness (E) over time

Transect	**1932**		**1965**		**2001**		**2018**	
	S	E	S	E	S	E	S	E
T1	26	0.02	30	0.03	42	0.03	36	0.05
T2	16	0.04	34	0.03	38	0.04	34	0.05
T3	15	0.04	30	0.03	35	0.04	32	0.06
T4	20	0.03	50	0.02	41	0.03	38	0.05
T5	20	0.03	35	0.03	41	0.03	38	0.05
T6	18	0.03	20	0.06	24	0.06	26	0.07
T7	28	0.02	37	0.03	42	0.03	42	0.04
T9	24	0.02	20	0.06	19	0.08	21	0.09
T10	24	0.02	27	0.04	25	0.06	28	0.07

Beech forest (T3 and T4)

Woody species were relatively more common on the two transects in this vegetation type; however, in 1932 and 1965, shrubs were relatively more common (greater than 30 relative percent frequency) on T3 than beech trees, including *Brachyglottis elaeagnifolia* and *Coprosma pseudocuneata* (Figure 4.1). In 2001, mountain beech (*Fuscospora cliffortioides*), the shrub *Coprosma pseudocuneata*, and the forb *Astelia nervosa* were at greater than 30 relative percent frequency (Table 4.3). In 2018, the tall shrubs *Coprosma pseudocuneata*, *Myrsine divaricata*, *Coprosma foetidissima*, the trees *Fuscospora cliffortioides* and *Phyllocladus alpinus*, and the rosettes *Astelia nervosa*, had greater than 30 relative percent frequency on T4. In 1932, no species had more than 30 relative percent frequency. By 1965, the trees *Phyllocladus alpinus* and *Olearia ilicifolia*, the shrubs *Coprosma pseudocuneata*, *Brachyglottis elaeagnifolia*, *Coprosma dumosa*, *the* forb *Phormium cookianum*, and the fern *Polystichum vestitum* had greater than 30 relative percent frequency. In 2001, the shrub species *Coprosma pseudocuneata* and the trees *Phyllocladus alpinus*, *Fuscospora cliffortioides*, *Olearia ilicifolia* and the forb *Astelia nervosa* were common. In 2018, the relatively common species were the trees *Phyllocladus alpinus* and *Fuscospora cliffortioides* and the shrub species *Coprosma pseudocuneata*, *Myrsine divaricata*, and *Coprosma foetidissima* were common (Table 4.3). Species richness and evenness increased over time on both transects, reflecting many colonisations and extinctions, especially on T4 (Table 4.4 & Table 4.5).

Table 4.5. The number of native (exotic) species that became extinct or colonised each transect across each of the three measurement periods

Transect	**Colonisations**			**Extinctions**		
	1932-1965	**1965-2001**	**2001-2018**	**1932-1965**	**1965-2001**	**2001-2018**
T1	13	18	5	10	8	12
T2	19	9	4	1	6	8
T3	17	9	4	2	5	7
T4	31	5	0	1	14	3
T5	16	10 (2)	7	1	6	8 (2)
T6	5	7	5	3	3	3
T7	21	15	8 (1)	11 (1)	10	10
T9	3	3	6	7	4	4
T10	10 (1)	2	6 (1)	7 (1)	4	3

Subalpine shrubland (T5, T6, T7, T9)

Four transects T5, T6, T7 and T9 were classified as subalpine shrubland. On T5, in 1932, the only woody species with greater than 30 relative percent frequency was the shrub *Brachyglottis elaeagnifolia*. In 1965, the shrubs *Dracophyllum longifolium* and *Brachyglottis elaeagnifolia*, and the fern *Blechnum minus*, were common. In 2001, in addition to those previous three species, the shrub species *Coprosma serrulata* was relatively common, and in 2018, the shrub *Coprosma depressa* had also increased to more than 30 relative percent frequency (Table 4.3).

On T6, in 1932, there was single common species having more than 30 relative percent frequency, the forb *Celmisia discolor*. In 1965, in addition to *Celmisia discolor*, the graminoids, *Schoenus pauciflorus*, a tussock *Chionochloa* spp., and a rosette *Phormium cookianum* had more than 30 relative percent frequency. In 2001, in addition to the above species, the ferns *Lycopodium scariosum* and *Blechnum minus*, and the shrubs *Pentachondra pumila*, *Myrsine nummularia* and *Gaultheria rupestris* had become common. In 2018, there was little change from 2001 except *Gaultheria rupestris*, which was no longer recorded (Table 4.3).

On T7 in 1932, the only species with greater than 30 relative percent frequency was the *Phormium cookianum*. In 1965, there were three common forb species *Phormium cookianum*, *Astelia nervosa* and *Celmisia armstrongii* and three shrubs *Coprosma serrulata*, *Veronica canterburiensis* and *Gaultheria rupestris.* In 2001, the two shrubs *Dracophyllum longifolium* and *Coprosma serrulata*, one graminoid, *Chionochloa rubra*, two forbs, *Astelia nervosa* and

Phormium cookianum, and the fern, *Blechnum minus*, were common. In 2018, the fern *Blechnum minus*, shrubs *Lepidothamnus laxifolius*. *Coprosma serrulata*, *Veronica canterburiensis*, and *Myrsine nummularia* and the forbs *Astelia nervosa* and *Phormium cookianum* were common (Table 4.3).

On T9 in 1932, the shrubs *Veronica subalpina* and *Ozothamnus leptophyllus*, the rosette *Ourisia macrocarpa* and the fern *Blechnum minus* were common having more than 30 relative percent frequency. In 1965, the shrubs *Coprosma serrulata*, *Brachyglottis elaeagnifolia* and *Dracophyllum uniflorum*, rosette *Ourisia macrocarpa* and the fern *Blechnum minus* were common. The previously common species *Veronica subalpina* and *Ozothamnus leptophyllus* were extinct. In 2001 and 2018, the fern *Blechnum minus* and the shrubs *Dracophyllum longifolium*, *Dracophyllum uniflorum* and *Coprosma serrulata* were common. In addition, in 2001 and 2018 two woody species, *Brachyglottis elaeagnifolia*, and *Gaultheria rupestris* had become common and in 2018, *Pseudopanax colensoi* had also become common (Table 4.3).

Species richness increased overall on all of the subalpine shrubland transects, except T9, which decreased by three species in total; evenness also increased on all transects (Table 4.4). Relatively more colonisations and extinctions occurred on T7 and relatively fewer occurred on T6 (Table 4.5).

Low subalpine forest (T10)

In 1932, the low subalpine forest transect T10 did not contain any species that had more than 30 relative percent frequency. By 1965, common species were the fern *Blechnum minus*, forbs *Astelia nervosa* and *Phormium cookianum*, and the shrub *Dracophyllum longifolium* (Table 4.3). In 2001 and 2018, these species remained common and in addition, the shrubs *Coprosma dumosa* and *Coprosma pseudocuneata* had also become common. Species richness increased overall only by four species and was relatively stable over the measurement periods (Table 4.4), despite numerous colonisations and extinctions (Table 4.5).

4.3.2 Community weighted means of morphological trait composition across transects

At community level, changes over time in morphological trait composition varied among transects (Figure 4.3; Table S4.5, Appendix A). The first two principal components of community weighted mean trait values explained 41.73% and 27.10%, respectively (Figure 4.3). First axis (PC1) represents the transects in beech and scrub vegetation from left to the transects located in the grassland in the right of the ordination space. Second axis represent trait variation of the transects where community with high bulk density and leaf dry matter content at the bottom and transects with high specific leaf area and moisture content at the top. This shows that transects changed across the time with change in their trait composition. Simple linear regression showed that most changes in community weighted trait mean values over 86 years (1932-2018) were non-significant (Figure S4.3, Appendix A). However, community weighted means of leaf specific area significantly decreased on all the transects of the nine transects except on T6 and T7)

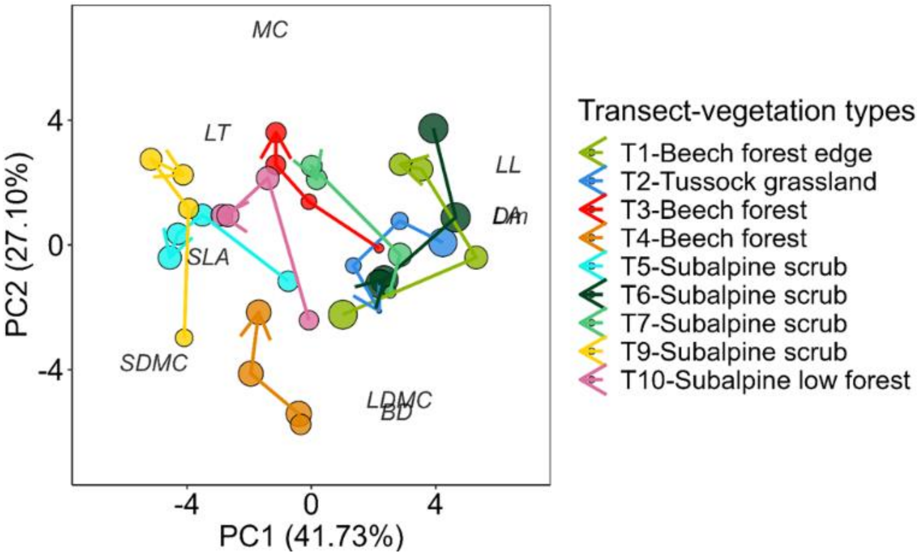

Figure 4.3. Principal component analysis of the community weighted means of nine morphological traits for each of the nine transects based on the trait values for the 57 species for which I had measurements. Each point represents a transect at a particular measurement time. Measurements for each transect are joined by a trajectory arrow starting from the first vegetation measurement year (1932) to the most recent measurement (2018). The size of points is proportional to the weighted mean community flammability. The morphological traits included were leaf length (LL), leaf thickness (LT), leaf area (LA), leaf dry matter content (LDMC), specific leaf area (SLA), shoot dry matter content (SDMC), bulk density (BD), moisture content (MC), and percent dead mass (Dm). Dm and LA are overlapped in figure due to high correlation to each other

4.3.3 Species-level flammability

Shoot-level flammability varied widely among species; the variance explained by the first and second principal components were 56.68% and 21.26%, respectively, for the individual-level analysis (Figure 4.4a) and 66.55% and 20.08% for the species-level analysis (Figure 4.4b). At both the individual and species levels, all the four of the flammability traits were strongly associated with each other and had high positive loadings on the first principal component; ignition score: 0.81, burnt biomass: 0.82, maximum temperature: 0.93, and burning time: 0.65. There was species variation within each of flammability components (Figure S4.4, Appendix A). Some species (e.g., *Phormium cookianum*) burnt for longer time than others. High biomass was consumed in some species and high maximum temperatures were also recorded. The tussock growth form was the most flammable (Figure S4.5, Appendix A). The most flammable species were *Phormium cookianum*, *Phyllocladus alpinus*, *Chionochloa rubra*, *Celmisia discolor*, *Lycopodium scariosum* and the least flammable species were *Anisotome haastii*, *Anisotome aromatica*, *Aporostylis bifolia*, *Brachyglottis bellidioides*, *Ourisia macrophylla* and *Viola lyalli* (Figure S4.6, Appendix A). Community flammability was significantly negatively associated to the community weighted means of specific leaf area (Figure 4.5).

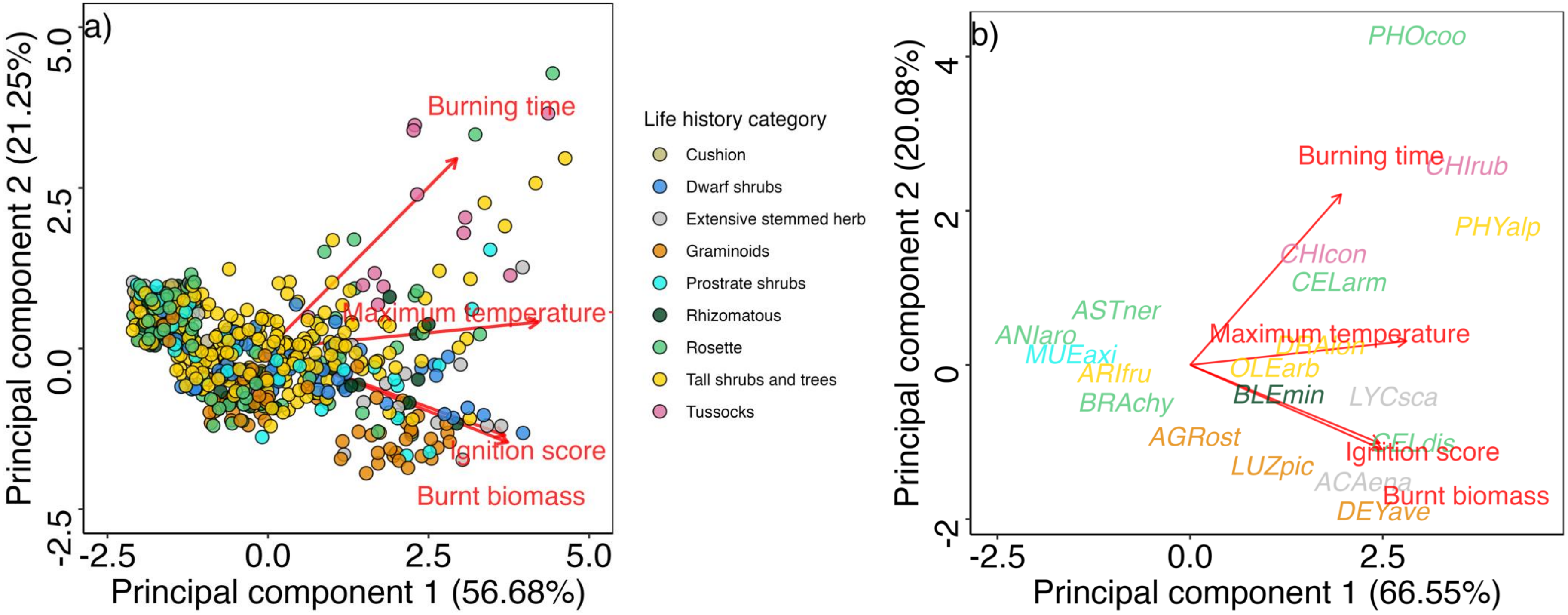

Figure 4.4. Principal component analysis of (a) the four flammability measurements for the 578 individual samples of 67 species for which I had flammability measurements and (b) the mean values of the four flammability measurements for the 67 species. The *x* – axis and *y* – axis represent first and second axes of the principal component analysis. Points in (a) and text in (b) are coloured according to their nine life history category (simplified from fourteen category for visualization; see detail in Table S4.4). Ignition score is an inverse of time to ignition: the high the ignitability represents high shoot flammable and zero value was of those samples that did not ignite after the blowtorch was applied for 10 s. Plant names represented by abbreviations based on first three letters of the genus and the specific epithet

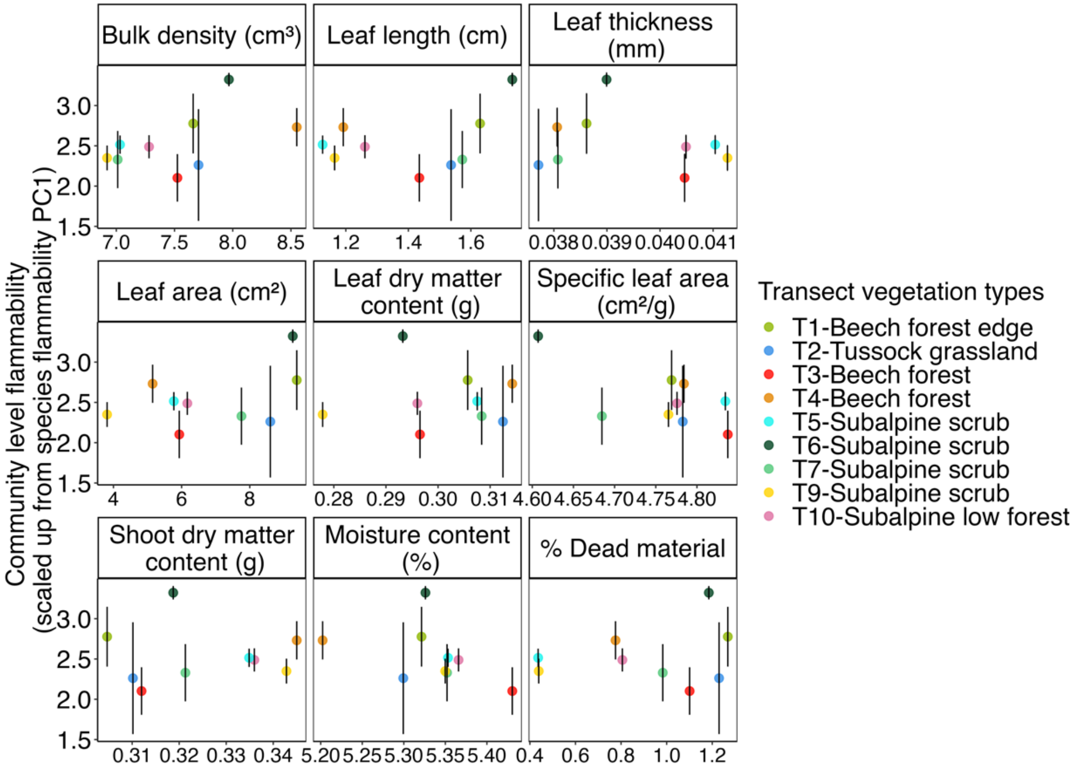

Figure 4.5. Relationship between changes in community flammability and community weighted means of morphological traits. Point colours represent the vegetation types on the transect. Community flammability and community weighted trait mean relationships (blue lines) and their standard errors (grey envelopes) based on the linear regression are shown for significant relationships between plant taxon flammability (PC1) and leaf and shoot morphology ($P < 0.05$). Error bars of points represent standard error around mean

4.3.4 Relationships among species flammability and morphological traits

The first two components of the PCA of morphological trait variables for the 57 species explained 32.95% and 27.88%, respectively (Figure 4.6a; Table S4.6, Appendix A). In PCA of both the flammability and morphological trait variables for the 57 species, the first two principal components explained 38.98 % and 21.63 % of the total variance (Figure 4.6b). Shoot dry matter content, bulk density, leaf area, leaf length and dead material were positively associated with the four flammability traits (ignition score, maximum temperature, burning time and burnt bioimass). In contrast, specific leaf area and moisture content were negatively associated with four flammability components. Shoot and leaf dry matter content and dead material were strongly associated with three components ignition score, maximum temperature and burnt biomass. Burning time was strongly associated with bulk density, and leaf dimensions (leaf area, leaf length and leaf thickness) Figure 4.6a). Species' flammability (PC1) was strongly negatively associated with specific leaf area, moisture content, and rosette species (Table 4.6; Figure 4.6b). Only shoot dry matter content and dead material were significantly positively associated with species flammability PC1 (Figure 4.7).

Table 4.6. Correlation matrix of species' flammability and morphological (shoot and leaf) traits at the species level. Values in bold fonts were significant (*P* < 0.05). Trait values are shoot dry matter content (SDMC), bulk density (BD), moisture content (MC), and percent dead mass (Dm), leaf length (LL), leaf thickness (LT), leaf area (LA), leaf dry matter content (LDMC), and specific leaf area (SLA)

Flammability components and first two axes of PCA	**Shoot traits**				**Leaf morphological traits**				
	SDMC	BD	MC	Dm	LA	LL	LT	LDMC	SLA
Ignition score	0.70	0.18	-0.68	0.51	-0.08	-0.15	-0.05	0.42	-0.29
Maximum temperature	0.55	0.35	-0.57	0.39	0.08	0.10	0.17	0.05	-0.49
Burning time	0.34	0.37	-0.35	0.38	0.55	0.50	0.43	-0.06	-0.65
Burnt biomass	0.55	-0.07	-0.53	0.47	-0.13	-0.12	-0.07	0.24	-0.23
PC1-flammability	0.66	0.25	-0.66	0.53	0.1	0.07	0.13	0.2	-0.49
PC2-flammability	-0.14	0.35	0.12	-0.02	0.61	0.60	0.47	-0.33	-0.44

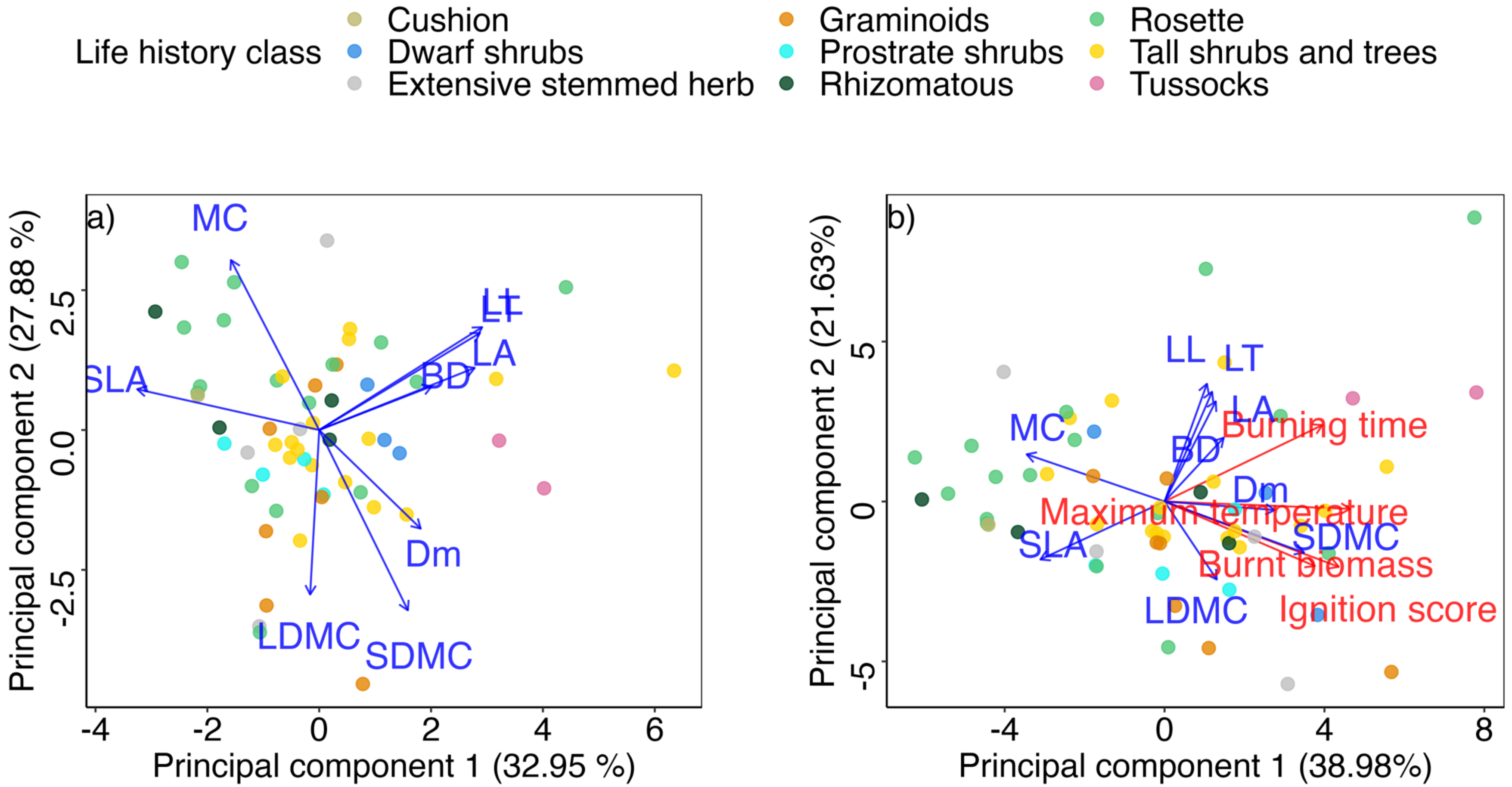

Figure 4.6. Principal component biplots of 57 species a) morphological traits and b) species' flammability traits (red text and arrow line; ignitability, burning time, maximum temperature and burnt biomass) and morphological traits (blue text and arrow line) for which had morphological trait measurements. Point colours represent their nine life history category (simplified from fourteen category for visualization; see detail in Table S4.4). Abbreviations of the morphological traits are leaf length (LL), leaf thickness (LT), leaf area (LA), leaf dry matter content (LDMC), specific leaf area (SLA), shoot dry matter content (SDMC), bulk density (BD), moisture content (MC), and percent dead mass (Dm)

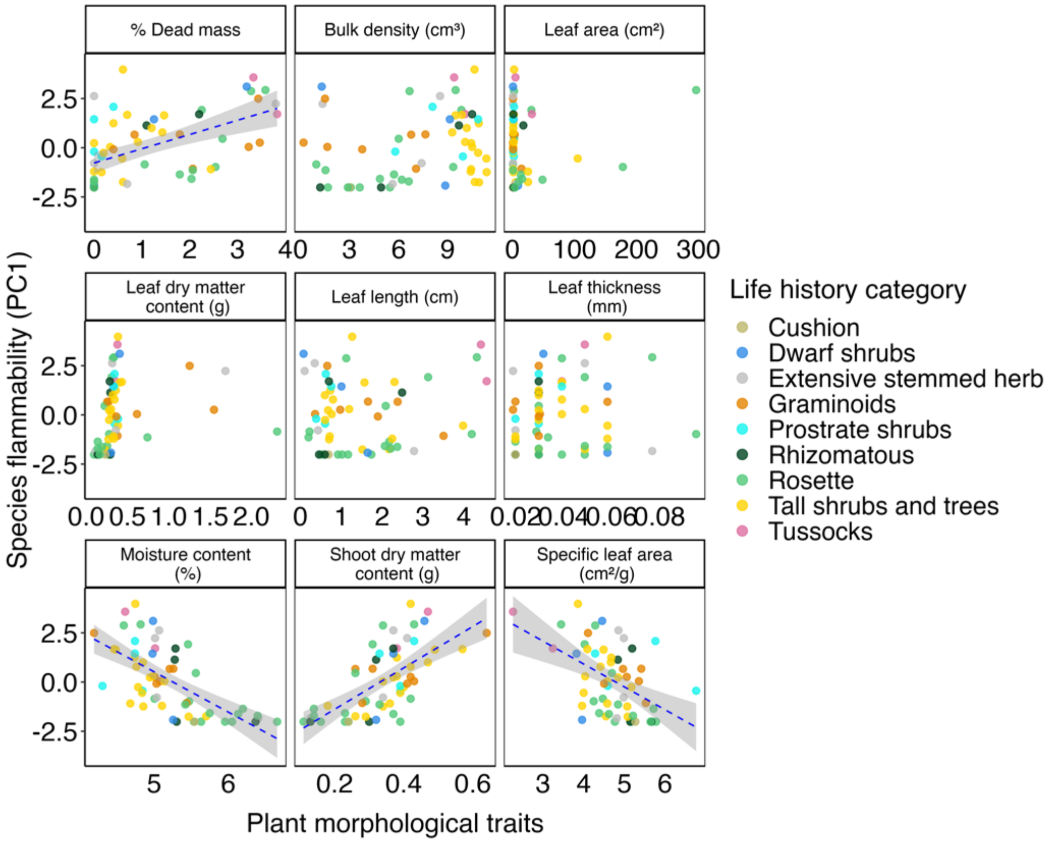

Figure 4.7. Relationship between species flammability and morphological traits. Point colours represent their nine life history category (simplified from fourteen category for visualization; see detail in Table S4.4). Species flammability and trait relationships (black lines) and their standard errors (grey envelopes) based on the linear regression are shown for significant relationships between plant taxon flammability (PC1) and leaf and shoot morphology (*P* < 0.05)

4.3.5 Phylogenetic pattern

Species flammability (PC1) integrated with plant phylogeny showed that closely related taxa tend to have similar flammability (Figure 4.8). In contrast, some of the closely related species had variation in their flammability. For instance, *Celmisia armostrongii* and *Celmisia discolor* were highly flammable but *Celmisia gracilenta* was low flammable within family Asteraceae. Pagel's λ under Brownian motion structure was statistically significant for the relationship between flammability and all the first three axes components of morphological traits (PC1_morph, PC2_morph and PC3_morph) in generalised least square (gls) candidate modelling (Figure 4.9) showing their relationship is phylogenetically conserved. Species flammability (PC1) was increased with increase in first axis of principal component of morphological traits (PC1_morph). The PC1_morph represents leaf dry matter content, shoot dry matter content and retained dead material. In contrast, species flammability (PC1) decreased when second and third axes component of PCA increase. They are represented by the morphological traits, specific leaf area, moisture content, leaf thickness and bulk density.

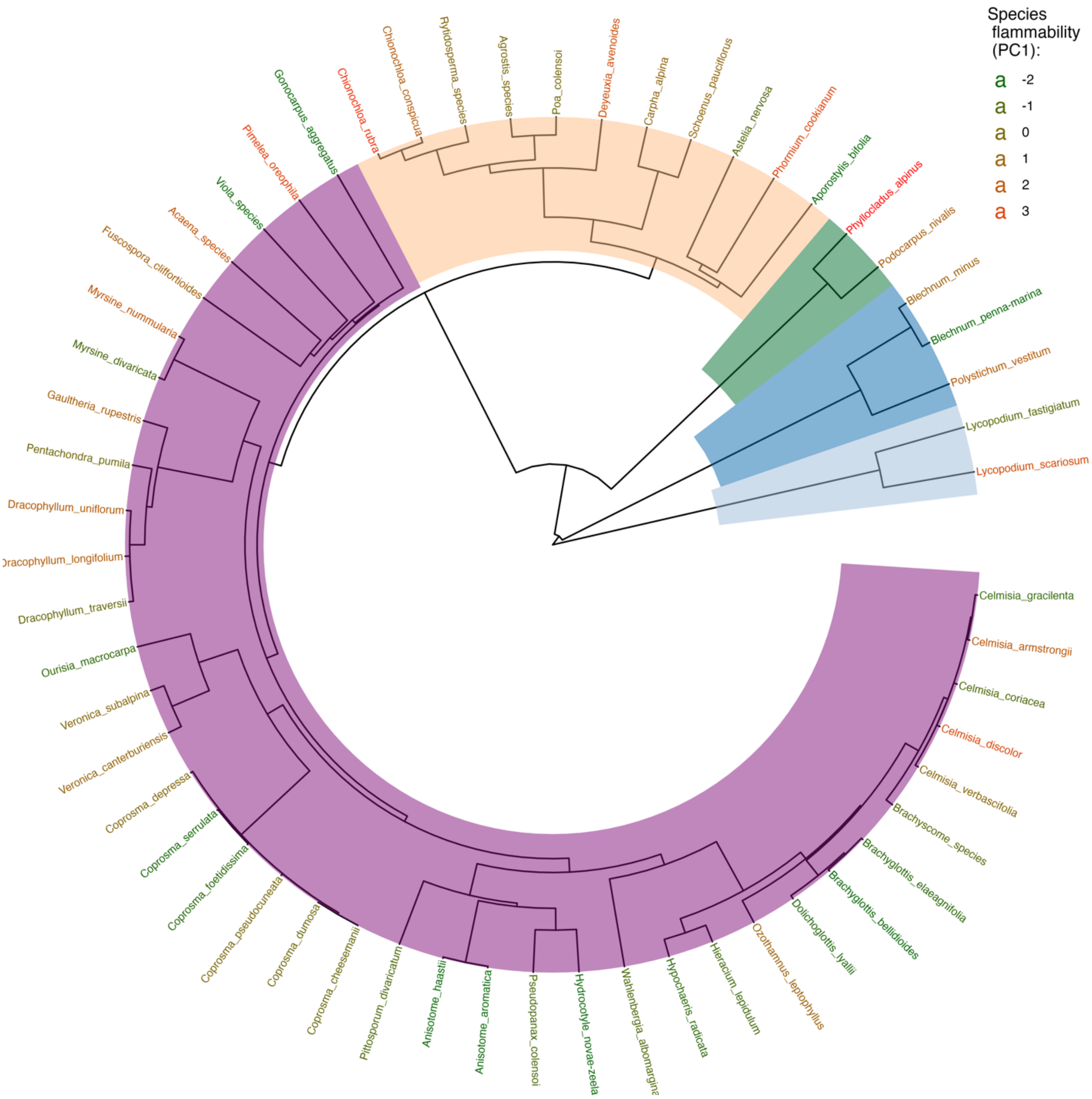

Figure 4.8. The phylogenetic tree obtained from an R package ‘ggtree’ showing evolution of species flammability across the 57 vascular plants species at Arthur’s Pass, South Island, New Zealand. Text colours show the species flammability (PC1) gradient from low (green) to high (red). Box colour on the branch shows the different clades; Lycopodiophyta (grey), Fern (blue), Gymnosperm (green), Monocots (orange) and Eudicots (purple) adopted from Cui et al. 2020.

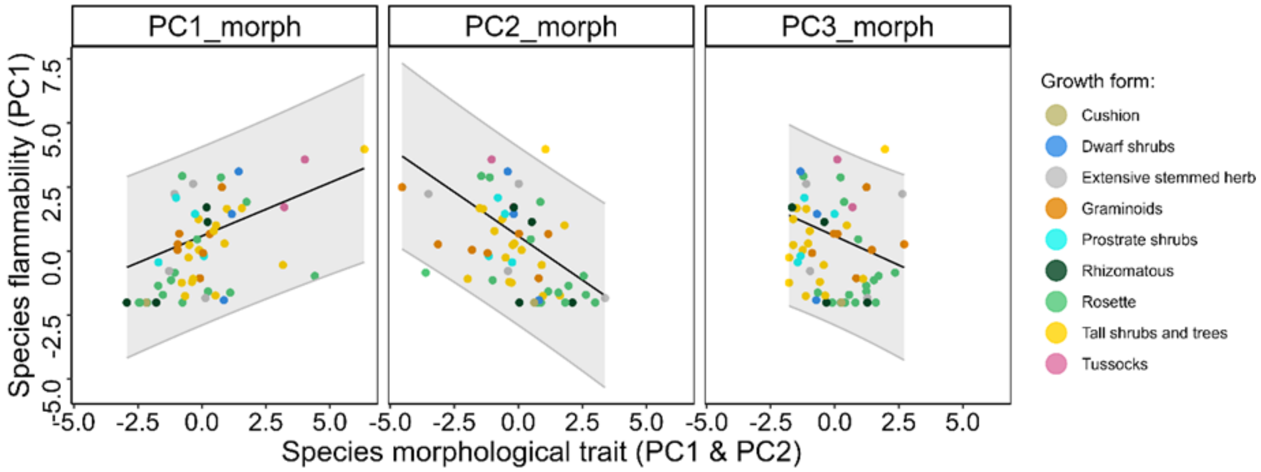

Figure 4.9. Phylogenetic relationship between species flammability (PC1) and morphological traits (PC1_morph, PC2_morph and PC3_morph: represents the first three axis of principal component) across the vascular plants at Arthur's Pass, South Island, New Zealand. Model average predictions (black lines) and their standard errors (grey envelopes) based on the candidate model set are shown for significant relationships between plant taxon flammability (PC1) and morphological traits ($P < 0.05$)

4.3.6 Community flammability dynamics

Overall, community flammability did not change significantly across time or transects (Table 4.7; Figure 4.10; Figure S4.7,Appendix A). It increased significantly over the time only on transect T3. On the remaining transects (T4, T5, T6, T9 and T10), community flammability changed very little and were not significant. For example, on one transect (T7), flammability initially increased, but then levelled off. There was a sharp, but non-significant decrease in community flammability between 1932 and 1965 at two transects from relatively very high flammability (T1 and T2). On T1, community flammability remained stable from 1965 to 2018. On T2, it continued to decline between 1965 and 2018.

Table 4.7. Analysis of variance results from a comparison of community flammability (Mean CF), quantified as community weighted mean flammability, among measurement times for each transect separately

Transect	**Mean CF**	***F*-value**	***P*-value**
T1	0.47 ± 0.03	5.71	0.14
T2	0.39 ± 0.06	11.53	0.08
T3	0.34 ± 0.03	110.3	**0.01**
T4	0.44 ± 0.03	2.45	0.26
T5	0.41 ± 0.01	5.06	0.15

Transect	**Mean CF**	***F*-value**	***P*-value**
T6	0.55 ± 0.01	13.47	0.07
T7	0.39 ± 0.03	1.10	0.41
T9	0.39 ± 0.01	4.21	0.18
T10	0.41 ± 0.01	0.88	0.45

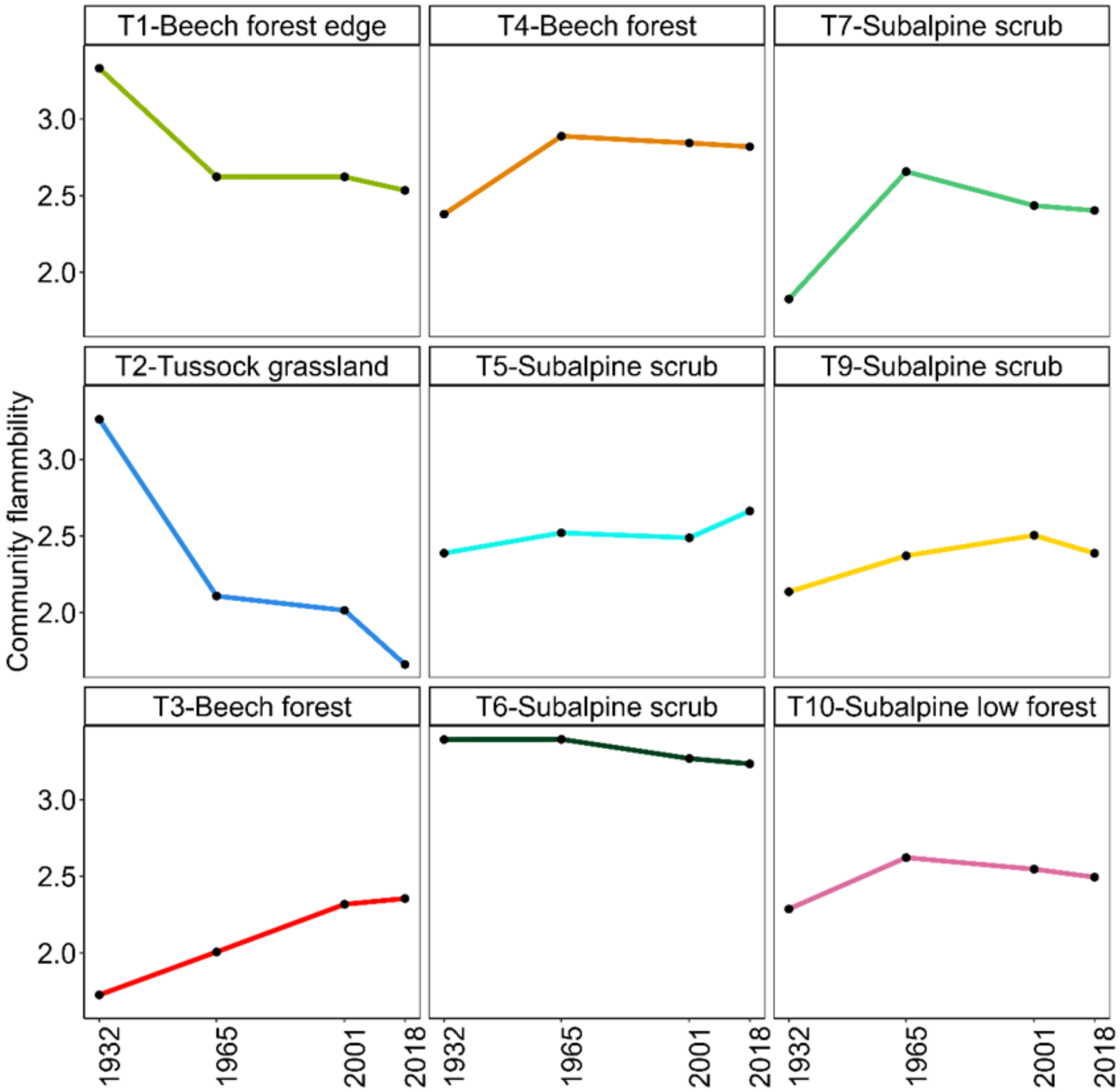

Figure 4.10. Change in the community weighted mean flammability over time for each transect over time (1932-2018). The first component of the species flammability PCA was used to calculate community flammability (see mathematical expression in Appendix D). There was significant change ($P < 0.01$, based on simple linear regression) in community flammability across the sampled period on T3. Line colours represent the vegetation type on the transect

4.4 Discussion

Plant community flammability, as quantified in this study of the Arthur's Pass subalpine environment, did not vary over the 86 years (1932-2018) of vegetation monitoring. This stability necessarily depends on the species present and their relative flammability, due to the community weighted means approach to estimating community flammability. Changes in community flammability over time for the nine transects were mostly non-significant, which is likely because the transects were established 40 years after the fire, meaning I have missed the most dramatic community changes caused by the fire, and in part likely due to the small number of time measurements for each transect ($n = 4$). There was no consistency among the different vegetation types in how community flammability changed over the study period; this is because species composition was highly variable among transects, even those classed as the same structural vegetation type (grassland, shrubland, forest). In contrast, clear relationships are shown between plant and community flammability traits and plant morphological traits. In particular, flammability was significantly related to morphological traits (shoot dry matter content, dead material, leaf specific area, and moisture content). Flammability was found to be phylogenetically conserved, showing the influence of evolutionary history on this variable. Plant traits related to flammability were also attributable to differences in growth forms. This research shows that relationships between plant and shoot level flammability and morphological traits can allow predictions to be made about how community flammability should change under future vegetation change.

4.4.1 Community flammability dynamics varied among transects

Community flammability had an overall increasing trend on the transect T3 over the 86 years (1932-2018). The increase in community flammability on these transects was due to presence of relatively more flammable species becoming more dominant over time, for example *Phyllocladus alpinus*, *Phormium cookianum*, *Chionochloa rubra*, *Dracophyllum longifolia*, *Dracophyllum uniflorum* and *Dracophyllum traversi* (Figure 4.2). These species possess traits that are shown here, and in other studies (Cui et al., 2020; Fogarthy, 2002; Wyse et al., 2016), to be significantly and positively related to community flammability: leaf length and bulk density, which showed decreasing trends on transects T3. Leaf dry matter content showed an increasing trend on T3. On the other transects (T2, T4, T5, T6, T7, T9, and T10) community flammability was stable due to relatively small changes in species composition over time.

In summary, I show that relative community flammability exhibited an increasing trend in woody-dominated plant community types, but in overall it remailed stable both in woody and in grassland-dominated community types. These patterns are linked with changes in species composition and plant community traits. For instance, an increase of the highly flammable tree species *Phyllocladus alpinus* and *Fuscospora cliffortioides* in more recent measurements (2001 and 2018) in one transect was related to flammability increase. In contrast an increase in low flammable species such as *Ourisia macrocarpa*, *Brachyglottis bellidioides*, *Celmisia gracilenta*, *Celmisia verbascifolia*, and *Gonocarpus aggregatus* was associated with decreases in grassland community flammability. Overall, these results confirm prior research showing relationships between key morphological traits and plant flammability (Cui et al., 2020; Padullés Cubino et al., 2018; Wyse et al., 2016). But in our study, the link to changes in community level flammability is weaker due to high variability among transects in species composition, low temporal sample sizes and inconsistent changes in transect species composition over time since fire.

These plant flammability and morphological trait relationship results were in contrast to what I predicted for post-fire changes in flammability for these transects, based on the previously reported increase in the abundance of woody species (Calitz et al., 2015; Fraser et al., 2016). It is possible that major shifts in species composition that would have resulted in the predicted dramatic changes in community flammability may have occurred with plant community succession after fire occurred in the 40 years between the largest fire in 1893 where most of the transects were burnt and before Cockayne set up the transects in 1932. It is also possible that climatic changes during the study period created the observed variability in community flammability and morphological traits by driving some of the post-fire compositional change in ways that are inconsistent with predicted successional patterns (Figure 4.10; Figure S4.2 & Figure S4.3, Appendix A). Studies have shown that solar radiation and precipitation influence species' abundances and community composition (Cadiz et al., 2020). Drought can increase plant ignitability, which increases community flammability (Ormeño et al., 2020). In contrast, the increasing precipitation in this study period, which may have led to improved conditions for forbs that tend to be of relatively lower flammability, rather than woody community, which tend to have higher flammability (Figure 4.10; Figure S4.2, Appendix A).

4.4.2 Plant morphological traits strongly relate to community flammability

Previous research shows that plant traits are related to flammability at shoot and plant levels (Alam et al., 2020; Cui et al., 2020; Wyse et al., 2016). In this study, I show mean trait values for species were significantly positively correlated with shoot dry matter content and dead material and negatively correlated with specific leaf area and moisture content. Life history categories represent well the variation in key traits that are closely related to plant flammability. Thus, broad changes in the dominance of different growth forms in community over time correlates with changes in community flammability. For example, on transects where rosette plants increased in abundance over time, the community weighted mean moisture content also increased, a pattern that has previously been demonstrated in New Zealand tussock grassland vegetation (Padullés Cubino et al., 2018). Other studies have also shown that species that contain high moisture, such as forbs, have lower flammability (Cui et al., 2020; Padullés Cubino et al., 2018). Specific leaf area was negatively associated with shoot dry matter content and bulk density, which is supported by previous studies where it has been shown that shoot flammability is positively correlated with dry matter content (Alam et al., 2020; Wyse et al., 2016). On our transects, where there was an increase in abundance of prostrate shrubs, tall shrubs and trees on transects, community flammability showed an increasing trend. This means that if woody frequency increases in alpine ecosystems, flammability will increase (Fraser et al., 2016). Thus, results of our study are confirmatory links between plant traits, especially leaf traits, and community flammability. This shows that it is possible to use plant traits to make generalisations about community flammability.

4.5 Conclusion

I showed that plant community flammability varied among transects in one of New Zealand's longest permanent subalpine vegetation datasets; however, community flammability was relatively stable over time in most vegetation types, despite overall increases in woodiness. Community flammability was strongly related to variation in plant traits and community structure. Consistent with previous studies, vegetation changes changed the trait profile of the community and had a predictable impact on community flammability. For example, an increase in rosette plants with higher leaf moisture content and lower biomass were associated with decreases in flammability over time. In contrast an increase in dwarf shrubs and tussocks with high dry matter content, larger leaves and greater dead biomass were associated with an increase in community flammability. It is possible that most of the vegetation change that would have caused the largest post-fire disturbance shift in community flammability at these sites that may have occurred in the 40 years after the initial fire, which occurred before Cockayne established these plots. This research emphasises the importance of measuring species' trait variation as part of understanding community flammability dynamics. Understanding the temporal changes in traits and community composition is vital to determine the change in community flammability and to managing future ecosystem fire risk. These results underscore the importance of understanding trait-composition relationships for predicting how fire regimes in native vegetation may change with changing environmental conditions and emphasises the value of long-term vegetation and plant trait datasets.

Chapter 5 **Leaf morphological and nutrient traits are associated with plant flammability in sub-alpine vegetation, New Zealand**

5.1 Introduction

Leaf nutrient concentrations are key plant functional traits (Domínguez et al., 2012; Wright & Westoby, 2003). Leaf nutrient concentrations, such as nitrogen (N), phosphorus (P), magnesium (Mg), potassium (K), calcium (Ca), and sulphur (S) form part of the leaf economic spectrum, which describes the life history strategy of plants along a continuum from slow-growing and disturbance tolerant, to fast-growing and short-lived (Lichstein et al., 2021; Reich, 2014; Sun et al., 2015; Wright et al., 2004). Leaf nutrient concentrations are also important effect traits (Lavorel & Garnier, 2002), in that they can influence ecosystem processes, such as decomposition, nutrient cycling, and disturbance regimes; such as fire.

Leaf nutrient traits are most likely to influence fire regimes via their influence on plant flammability. Several studies have examined the relationship between flammability and leaf nutrients; such as [P] and [N]. Variation in [P] indirectly influences fire behaviour at both individual species and community levels (Scarff et al., 2012; Scarff & Westoby, 2008), with lower [P] generally associated with higher flammability (but see Mason et al., 2016). In 32 evergreen tree and shrub species from eastern Australia, when leaf [P] and [N] were high, leaf flammability, particularly flame duration, was low (Grootemaat et al., 2015). Further evidence for the potential direct influence of plant [P] on flammability comes from fire management. For example, salts of phosphorus have been widely used as flame retardants even in fires that have burnt at high temperatures (Chukwunwike & Okafor, 2019; Scarff et al., 2012; Scarff & Westoby, 2008; Schafer & Mack, 2018). The use of compounds containing other leaf nutrients as fire retardants suggests that Mg, K, S and Ca could also influence plant flammability, though no studies have examined direct relationships between these leaf nutrient traits and flammability. For example, sulphur-based flame retardants with low phosphate content are used in the commercial wood industry (Gebke et al., 2020). Magnesium and potassium phosphate composites are used as fire-resistant compounds to coat substrates to protect against fire, such as birch plywood (Fang et al., 2021; Guo et al., 2021; Yan et al., 2019), and calcium hydrogen phosphate dihydrate is a potential fire retardant for bonding wood-based materials (Ozyhar et al., 2022). It is therefore worth exploring whether other nutrients influence plant flammability.

Multiple leaf and canopy traits influence the flammability of live fuels (Alam et al., 2020; Murray et al., 2013; Schwilk, 2003). Such traits include shoot biomass, shoot bulk density, moisture content, retention of dead material, specific leaf area, leaf size (area, length and thickness), and leaf and shoot dry matter content (dry mass: saturated mass) (Alam et al., 2020; Grootemaat et al., 2015). Leaf dry matter content, shoot dry matter content and the amount of retained dead material are positively related to plant flammability, whereas other traits, including specific leaf area and moisture content, are often negatively related to plant flammability (Alam et al., 2020; Mason et al., 2016; Wyse et al., 2016). Whether these morphological traits are as important, or more important than leaf nutrient traits have rarely been explored.

In some taxa, plant flammability has evolved as a result of fire regime changes (Moreira et al., 2014; Pausas et al., 2012; Schwilk & Kerr, 2002). Understanding how flammability evolves would facilitate our understanding of how fire interacts with plants over time, and may help us to prepare for anticipated wildfires in many regions. Few studies have examined variation in flammability using phylogenetic approaches in order to identify evolutionary patterns of plant flammability (Cui et al., 2020). These previous studies focused on morphological traits for measuring evolutionary patterns of flammability but nutrient trait relationship remain unclear.

While several studies have examined the role of leaf nutrients (mainly phosphorus and nitrogen) affecting plant flammability, almost all of these studies have focussed on flammability at the leaf scale (Grootemaat et al., 2015; Scarff et al., 2012), or as part of litter fuel mixes (Scarff & Westoby, 2008). Leaf flammability is a poor predictor of shoot flammability. The latter should better approximate whole plant flammability because burning entire shoots maintains any effects of plant architecture (Alam et al., 2020). However, despite the importance of shoot flammability, and its recognised links to some leaf nutrient traits, such as tannins, lignin and terpenes (Alam et al., 2020), few studies have examined the association between leaf nutrient traits and shoot flammability. The one exception to this was Alam et al. (2020), who found that P was not correlated with shoot flammability. Here, for the first time, we examined the association between several leaf nutrient concentrations (P, Mg, K, Ca, S) and shoot or whole-plant flammability, using 29 taxa from subalpine plant community in 90-year-old permanently-marked transects in New Zealand (Burge et al., 2020).

5.2 Methods

Samples of 29 plant taxa (Table S5. 1, Appendix A) were collected in Arthur's Pass National Park adjacent to nine permanent transects established in 1932 (Burge et al., 2020), South Island, New Zealand (920 m asl; 42°54′19.2″ S, 171°33′56.0″ E). These taxa were the most abundant (≥30 relative percent frequency in at least one of the transects in 2018) and had ≥15 g fresh weight of leaf material that could be readily collected for leaf nutrient concentration analysis. Samples of ca. 70 cm in length were collected from each of six individual plants by stratified random sampling of each taxon from each transect. Shoot and whole plant flammability testing and trait sampling followed Alam et al. (2020) and Pérez-Harguindeguy et al. (2013). Shoot or whole plant-level flammability for each sample was quantified as four flammability variables: 1) ignition score, time to ignition (0-10 s) subtracted from 10 (Padullés Cubino et al., 2018); 2) the maximum temperature measured using an infrared thermometer; 3) burning time, the time of flaming duration; and 4) burnt biomass, the visually-estimated percent biomass consumed.

To measure leaf nutrient concentrations, we oven-dried leaf samples of ca. 15 g for 72 hours at 65˚C, following previous methods (Habte et al., 2016; Pérez-Harguindeguy et al., 2013). A leaf sample of ca. 5 g dry weight was then ground, and leaf nutrient concentrations (Ca, Mg, P, K and S) were analysed using an Inductively Coupled Plasma – Optical Emission Spectroscopy (Agilent 5110 ICP-OES) technique in a microwave digester (CEM MARS Xpress, CEM Corporation, North Carolina, USA). A dried, ground, and well-mixed 0.2 g dry weight sample was placed in a microwave vessel for element extraction. We added 2.0 ml trace element grade Nitric acid (69%) and 2.0 ml of 30% hydrogen peroxide (modified EPA method 3050B) to the sample (USEPA, 1996), sealed the vessel and vortexed it. We digested plant samples following a heating program consisting of a heating ramp up to 90°C for 15 minutes and a heating plateau for five minutes (Liberato et al., 2017). This was followed by a heating ramp up to 180°C for 10 minutes and a heating plateau for 15 minutes. Finally, we recorded the amount of digested sample (mg/kg) obtained after plant digestion. We directly measured 156 samples of 26 taxa for flammability and 87 samples of 23 of these same taxa for nutrient concentration data and we obtained flammability and morphological traits of three taxa (Curran et al. unpublished data; Padullés Cubino et al., 2018) and nutrient data of six taxa (Richardson et al. unpublished data) from different locations in New Zealand.

We measured morphological traits (shoot dry matter content (i.e., both twigs and leaves), shoot bulk density, shoot moisture content, percent dead material, leaf length, leaf thickness, leaf area, leaf dry matter content and specific leaf area; following previous methods (Alam et al., 2020 and SI, Appendix E). To determine shoot moisture content, we air-dried sample for 24 hours before oven-drying for 48 hours at 65˚C.

All statistical analyses were conducted using taxon-level values for variables, which were calculated as the mean of the individual sample measurements for each taxon. All analyses were performed in R v.4.2.1 (R Core Team, 2022). We computed pairwise Pearson's correlation coefficients among all measured leaf nutrient concentration, and leaf morphology and shoot traits. To reduce variables for modelling, we performed separate principal component analyses (PCA) for three sets of trait variables (1) flammability components, (2) leaf nutrient concentrations, (3) leaf morphology and shoot traits. PCAs were implemented using the 'pca' function in 'FactoMineR' v.2.3 (Lê et al., 2008). The first plant flammability component (PC1) was used a response variable against the other three PC components (leaf nutrients and leaf and shoot morphology) as predictors by constructing a set of eight, candidate generalised linear models (Table 5.1) implemented using 'lme4' (Bates et al., 2015). We calculated AICc (small-sample-size-corrected Akaike's information criterion) for each candidate model and used model averaging to estimate the effects of plant traits on relative shoot flammability using 'AICmodavg' (Mazerolle, 2020). To determine which of the predictors are most influencing flammability, we calculated the relative importance of each predictor using function 'importance' (Mazerolle, 2020). We performed phylogenetic generalised least squares (PGLS) means using 'ape' (Paradis & Schliep, 2019) for Pagel's lamda (λ) under Brownian motion correlation structure to determine phylogenetic signals in between flammability PC1 and leaf nutrients and morphological traits in the candidate modelling (Díaz-Uriarte & Garland, 1996; Revell, 2010; Revell et al., 2008) (

Table **S5.2**, Appendix A). Before modelling, we created a 'megatree' phylogeny (Webb, 2000) of 29 taxa (Figure S5.1, Appendix A) using function 'V.PhyloMaker2' (Qian & Jin, 2016) which derives the resulting phylogeny from two large vascular plant phylogenies (Smith & Brown, 2018; Zanne et al., 2014).

5.3 Results

Plant flammability varied widely among taxa (Figure 5.1a). The first principal component (hereafter, flammability PC1) of the four flammability variables (ignition score, maximum temperature, burning time and burnt biomass) explained 66.15% of the variation and was therefore used as the modelled response variable (Table S5.3; Figure S5.2, Appendix A). PC1 of plant nutrient concentrations explained 52.56% of the total variation and was positively associated with [Mg], [K], [P], and [S]; PC2 was positively associated with [Ca] (Figure S5.3, Appendix A). The first component of the PCA on leaf morphology and shoot traits explained 29.27% of the total variation and was positively associated with percent dead material, leaf length, leaf thickness and leaf area, and negatively related to leaf specific area (Figure S5.4, Appendix A). The second component explained 23.86% of the total variation and was positively associated with percent dead material, shoot dry matter content, leaf dry matter content, and negatively related to moisture content.

Table 5.1. Comparisons based on AICc among candidate generalised linear models assessing the relationships between relative plant taxon flammability (response variable), leaf nutrient concentration, and leaf morphology and shoot traits, based on principal components from PCAs. Principal components (PC) used as predictors in the models were either leaf nutrient content (PC1_nutrient) or leaf morphology (PC1_morph) and shoot traits (PC2_morph). For each model, K is the number of parameters, AICc is the sample size corrected Akaike information criterion, DAICc is difference in AICc of each model from the top model, W is the relative weight of each model in the model set, and LL is the model log-likelihood. R^2 is the proportion of variation of flammability PC1 explained by predictors.

Model	***K***	**AICc**	**DAICc**	***W***	***LL***	***R^2***
PC1_nutrients + PC2_morphology	4	101.23	0	0.66	0.66	0.48
PC1_nutrients + PC1_morphology + PC2_morphology	5	104.16	2.93	0.15	0.82	0.48
PC2_morphology	3	104.58	3.36	0.12	0.94	0.35
PC1_morphology +PC2_morphology	4	106.44	5.21	0.05	0.99	0.37
PC1_nutrients	3	110.37	9.15	0.01	1	0.21
PC1_nutrients+PC1_morphology	4	112.94	11.72	0	1	0.19
Null model (intercept)	2	114.98	13.75	0	1	0
PC1_morphology	3	116.93	15.71	0	1	0.02

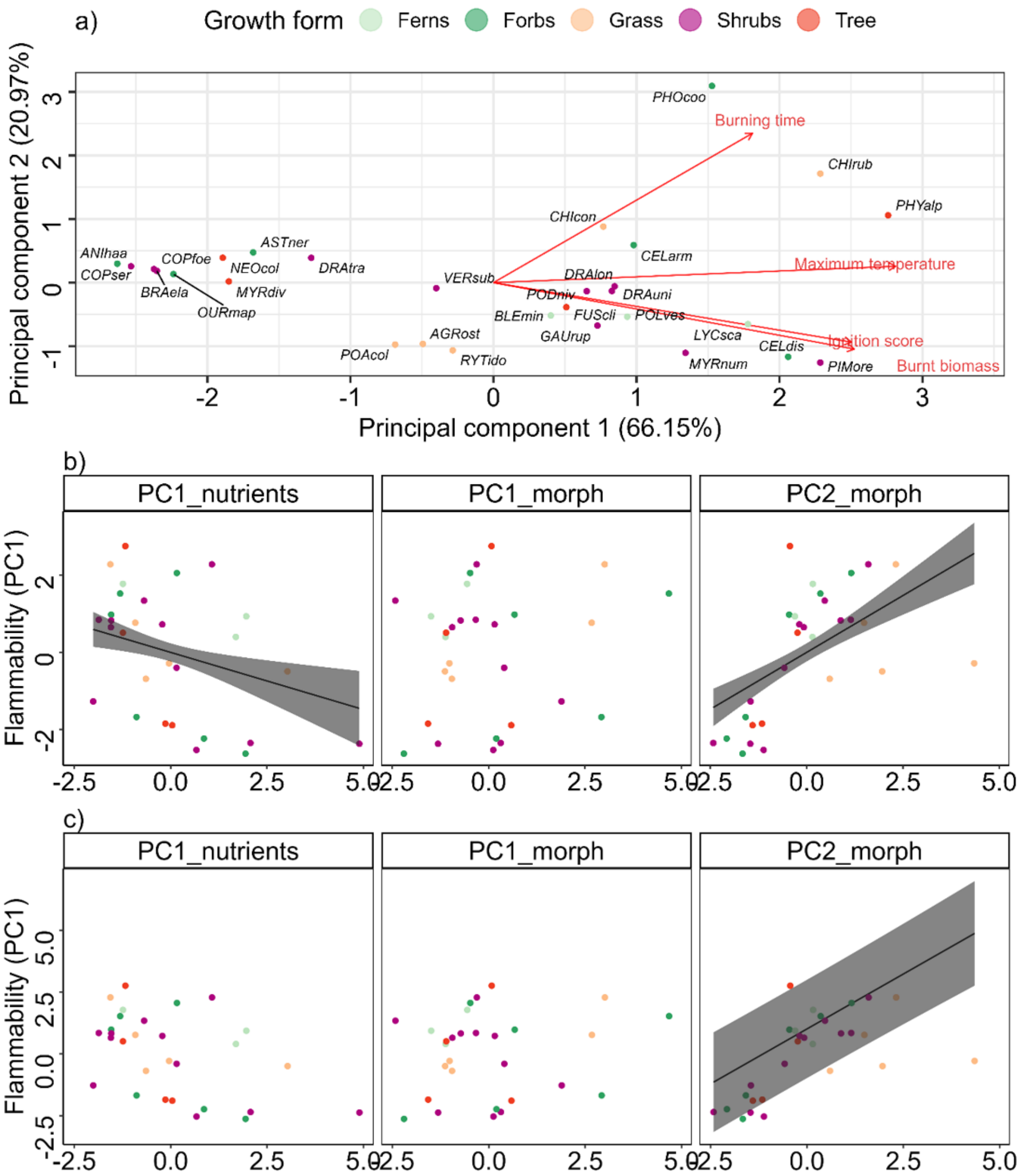

Figure 5.1. a) Principal component analysis biplot of relative taxon flammability for the 29 taxa. Taxon codes are the first three letters of each of genus and species epithet (see full species list in Table S5. 1, Appendix A). Plant flammability (PC1) relationship with leaf nutrient traits (PC1_nutrients), leaf morphology and shoot trait (PC1_morph and PC2_morph) for testing b) phylogenetic independence and c) phylogenetic dependence using Pagel's λ under Brownian motion structure. Model average predictions (black lines) and their standard errors (grey envelopes) based on the candidate model set are shown for significant relationships between plant taxon flammability (PC1) and leaf nutrients ($P < 0.05$) and leaf and shoot morphology ($P < 0.001$).

Principal components that were correlated with each other were excluded from the models of relative flammability (Figure 5.2). PC2 of the leaf nutrient (represents calcium) concentrations PCA was excluded as this was strongly positively correlated with the PC1 of the leaf morphology and shoot trait PCA (Figure 5.2; Table S5.4, Appendix A). PC3 of the leaf morphology and shoot trait PCA (which explained 14.45 %) was excluded because it was positively correlated with PC1 of leaf nutrient concentration (Figure 5.2).

Flammability of the 29 taxa was best explained by leaf morphology and shoot traits, and leaf nutrient concentrations (Figure 5.1b; Table 5.1; Table S5.5 & S5.6, Appendix A). However, when phylogenetic corrections were used, shoot flammability retained its strong significant relationship with leaf morphology (PC2_morph), while the significant relationship with leaf nutrients (PC1_nutrients) was lost (Figure 5.1c; Table S5.7, Appendix A). Taxa with higher flammability had higher percent dead material, higher leaf and shoot dry matter content and thicker leaves, and lower specific leaf area, and lower moisture content (Figure 5.2; Table S5.4, Appendix A). Flammability was negatively associated with higher leaf nutrient concentrations of [Mg], [K], [P], and [S] when phylogenetic corrections were not applied.

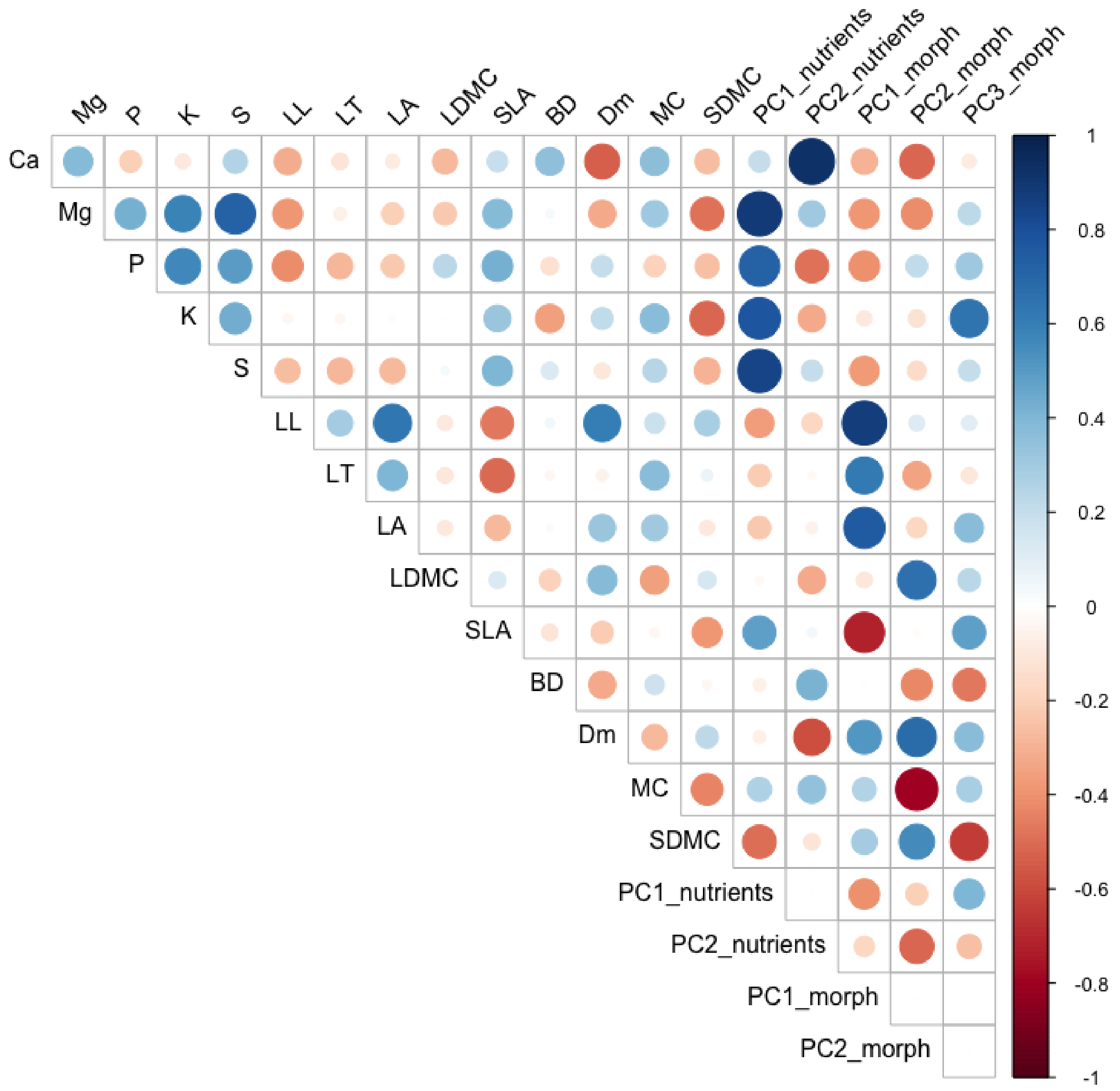

Figure 5.2. Pearson correlation coefficients for pairwise comparisons of measured leaf nutrient concentrations and leaf morphology and shoot traits for the 29 plant taxa, in addition to their correlations with principal components from PCA of each variable set. Variables are calcium concentration (Ca), magnesium (Mg), phosphorus (P), potassium (K), sulphur (S), leaf length (LL), leaf thickness (LT), leaf area (LA), leaf dry matter content (LDMC), specific leaf area (SLA), bulk density (BD), % dead material (Dm), % moisture content (MC), and shoot dry matter content (SDMC). PC1_nutrients explained 52.56 % of the variation among taxa in leaf nutrient concentrations, and PC2_nutrient explained 26.64 %. PC1_morph explained 29.27 % of the variation among taxa in leaf and shoot morphological traits, PC2_morph explained 23.86 %, and PC3_morph explained 14.45 %.

5.4 Discussion

Our study is one of the few to examine relationships between leaf nutrient traits and plant flammability (Alam et al., 2020; Grootemaat et al., 2015; Mason et al., 2016; Scarff et al., 2012), and the first to test the relationships between plant flammability and Mg, P, K, S, and Ca. We show that flammability, estimated using shoot or whole plant flammability, was related to a range of morphological traits, and that this relationship is so strong that it persisted with or without phylogenetic correction. In contrast, flammability was negatively associated with leaf nutrient traits (([Mg], [K], [P], and [S]),), but only when there was no phylogenetic correction, showing that flammability-nutrient relationships are driven by evolutionary history of our study taxa. While this means that there may be limited generality of our findings on flammability-nutrient relationships, there are still important proximal implications. For instance, if a fire occurs in this community, we expect taxa to burn differently, and that variation in nutrients will likely contribute to that, but not in a way that can be disentangled from the evolutionary history of the taxa sampled. Our work provides tentative confirmation that leaf nutrients are important in predicting plant flammability and that this may be so for a wider range of nutrient traits. This hints that leaf nutrients could play a role in determining fire behaviour, and therefore, may influence ecosystem processes such as fire.

Our finding that leaf concentrations of Mg, K, P, and S were negatively associated with plant flammability in this vegetation community was consistent with the use of compounds of these elements as fire retardants in fire management and the wood industry (Braun et al., 2006; Chukwunwike & Okafor, 2019; Scarff et al., 2012; Scarff & Westoby, 2006, 2008; Schafer & Mack, 2018). For example, magnesium and potassium phosphate composites were used as fire retardants to protect birch plywood substrate from fire (Fang et al., 2021; Guo et al., 2021), and sulphur-based flame retardants with low phosphate content have reduced flammability of modified wheat starch and wood fibre (Gebke et al., 2020; Yang & Steinberg, 1977). Compounds of potassium combined with nitrogen have been used as a fire suppressant (Pei et al., 2021). Plant phosphate has been shown to reduce plant flammability in several studies (Grootemaat et al., 2015; Scarff et al., 2012; Scarff & Westoby, 2006, 2008), and a phosphate compound, magnesium potassium phosphate cement, is widely used as a fire retardant (Fang et al., 2021; Gaan & Sun, 2007; Green, 1992). One previous study examining the relationship of phosphorus with shoot flammability found no association between the two (Alam et al. 2020).

While further research is required to test relationships between leaf nutrient traits and plant flammability, this should include phylogenetic corrections. Our study suggests that such work will clarify the nature of the relationships between flammability and morphological and nutrient traits, particularly for measurements at different plant scales (leaves, shoots, wood, whole plants) (Cornwell et al., 2008; Zhang et al., 2008). Relationships between morphological and nutrient traits and flammability are likely to underpin key trade-offs in ecosystem functioning, as recent studies have found that leaf nutrients are correlated positively with plant digestibility, and hence palatability, but negatively with plant flammability (Archibald et al., 2019; Gowda et al., 2022; Hempson et al., 2019).

The association between plant flammability and plant traits other than leaf nutrients found in our study are consistent with other research. The morphological traits: moisture content, shoot dry matter content, and dead material (Alam et al., 2020; Dent et al., 2019; Wyse et al., 2016) and leaf size (area and length) were correlated with shoot flammability (Padullés Cubino et al., 2018). This further demonstrates that it is suites of traits, rather than single traits, which influence flammability (Alam et al., 2020), reinforcing the need to consider morphological, physiological, architectural, and nutrient concentration traits when examining drivers of flammability. While nutrient concentration assays are time-consuming, costly, and require specialized equipment, this could be a worthwhile addition to plant flammability.

5.5 Conclusion

Leaf nutrient traits (K, Mg, P, and S) were negatively related to plant flammability in this vegetation community but were not as informative as morphological traits nor as robust to phylogenetic corrections. Leaf nutrients should be considered when investigating relationships between plant flammability and traits, when feasible, though evolutionary relationships need to be accounted for. There is still much to learn about relationships between leaf nutrient, leaf and shoot morphological traits and plant flammability, especially regarding the relative importance of different plant nutrients, how tightly coupled these are with phylogeny, and how well these relationships scale up to affect fire behaviour and fire regimes, for instance via trade-offs between palatability and flammability.

Chapter 6 **General discussion**

The main theme of my thesis was to investigate plant community responses to fire using different datasets on timescales ranging from two weeks to nine decades at different locations in montane environments in New Zealand's South Island. The most interesting result of this thesis is that native plant community are resilient to fire. Most of the plants in recently burnt sites were able to survive the fires, suggesting that plants in these environments can recover quickly. For example. the plant community studied at three different locations in the recent fire in the Lake Ōhau area (Chapter 3) appeared relatively resilient to fire as they recovered close to their pre-fire condition within a short period of time. A strength of some of this thesis research was being able to compare pre- and post-fire vegetation data to understand patterns in community dynamics over the long-term and short-term. No prior fire ecology studies in New Zealand have observed post-fire recovery while comparing to pre-fire data. The plant traits that are important in this community-level resilience need further research to examine the relative effects of ecological and evolutionary processes in trait variation and the causes and effects of within-species trait variability.

Generally, native plants in New Zealand are thought not adapted to fire due to historically low fire frequencies (McGlone et al., 2014; Ogden et al., 1998; Perry et al., 2014). So, there has been apprehension among ecologists in how native New Zealand community may respond to increasing fire regimes. This concern was warranted by previous findings which have demonstrated that only a few species, such as *Chionochloa* spp., are able to survive and resprout after fire (Gitay et al., 1992; Gitay & Wilson, 1995; Payton & Pearce, 2009); however, to date, there was little research on many other species in grasslands, e.g., *Pteridium esculentum* (McGlone, 2001)*, Dracophyllum* spp. (McGlone & Topping, 1983), *Discaria toumatou* (Perry et al., 2014), and *Aciphylla* spp. (Yeates & Lee, 1997). However, my thesis (Chapters 2 & 3) has shown that many other species can survive, including both native and exotic species, across different growth forms. The most surprising result was that many woody species with meristems that are quite high on the plant, and hence prone to fire damage, were able to survive these wildfires, e.g., *Acrothamnus colensoi*, *Leucopogon fraserii*, *Gaultheria* spp. and *Coprosma* spp. McGlone et al. (2014) and Mark (1994) suggested that *Festuca novae-zealandiae* survive fires; however, my research showed that it did not come back after the Ōhau fire over 15 months. However, this result is only from one site and one fire, so it would be worthwhile to conduct further research on this important native species in short tussock grasslands. Some New Zealand native species adaptations to fire, such as serotiny in *Leptospermum scoparium,* and it has been suggested this is evidence for natural selection via fire (Bond et al., 2004; Battersby et al., 2017). This thesis provides evidence of other species that also can regenerate by seed after fire, e.g., *Deyuexia avenoides, Brachyglottis lagopus, Carex* spp., and *Anaphalioides bellidioides.* Together, this suggests that New Zealand's flora is potentially not as susceptible to losses of native species due to fire as we initially thought. However, more studies are needed that incorporate more species and greater trait variation across environmental gradients, particularly with pre-fire data.

In Chapter two on plant community at Deep Stream, I showed that there was a significant effect of fire on plant community structure almost two decades later. This suggests that although individual plants were able to rapidly recover after fire, there are community level-effects of fire that are evident on longer time scales. Overall, richness of forbs and graminoids were significantly higher in the plots that had burnt only once or reburnt compared to the plots that had never burnt. This suggests that if fire occurs frequently at least annually, it could lead to a very different plant community with unknown consequences for ecosystem functioning. So, we should not be complacent about fire effects on native plant biodiversity in New Zealand.

From a long-term dataset over nine decades (1932-2018), my thesis showed that there is not complete transition of vegetation types over the long fire free periods. In both nine decades post-fire (Arthur's Pass) and four decades unburnt plots (Ōhau) were dynamics in community compositional changes but there were not complete shifts. Plots that were in shrublands and grasslands over the nine decades of sampling were still dominated by shrubs and grasses, respectively; however, these sites showed increases in woody species (Burge et al., 2020). Community-level flammability did not change in a predictable manner across all community types; it was associated with the high degree of spatial variation in community composition. For instance, mountain beech forest was dominated by relatively flammable woody species and community flammability significant increased over time. This was not the pattern in other community types. However, there is a lack of pre-fire community data and information about the extent and severity of the fires in the area over that time period. Future research in New Zealand should target fires of differing extent, frequency and severity to better understand the influence of these factors on plant community.

Plant traits that were shown to have a positive effect on shoot flammability were the retention of plant dead material and leaf dry matter content, confirming previous research that shows when material is dead it is dry and can ignite quickly and burn well. Other plant traits are negatively associated with shoot flammability. Species with high leaf specific area that have thick leaves tend to have more moisture in their tissues, making them harder to ignite and burn. The nutrient contents of leaves, i.e., phosphorus, magnesium, calcium, and potassium, were negatively related to flammability. This is consistent with previous research, for instance, phosphorus is used in fire retardants to fight wildfires and composites of sulphur and phosphorus are used as fire retardants in sawmills (Gebke et al., 2020). Calcium, was not significantly associated with flammability but was highly correlated with SLA, reflecting the complex interrelationships among leaf traits, leaf tissue composition, and flammability-related traits. The combination of these traits impacts the flammability of individual shoots, which can be used to scale up to estimate community-level flammability. Morphological traits have been measured in plants in New Zealand previously (e.g. Alam et al., 2020; Cui et al., 2020; Wyse et al., 2016). However, this thesis research is the first time that these nutrients have been assessed in terms of their relationships with flammability of plants in New Zealand. Including a larger number of species would likely have made understanding the phylogenetic patterns in morphological traits, leaf nutrients and flammability components clearer; however, there are clear evolutionary patterns that affect the interrelationships among these variables, which is consistent with other research (e.g., Cui et al. 2020). Therefore, I highly recommend incorporating more leaf nutrient analysis in future flammability studies in New Zealand to clarify these patterns. This will help to confirm if nutrient and flammability associations are phylogenetically conserved as flammability and morphological traits are (Cui et al., 2020). This may lead to recommendations for the use of particular species with particular leaf nutrient concentrations landscape fire risk management. For example, in replanting after fire, restoration projects, and green fire breaks around pine plantations (Clarke et al., 2011).

This study demonstrates how wildfires can affect New Zealand montane plant community over short and longer timescales. This thesis provides evidence of the critical importance of understanding the roles of response and effect of traits in determining community dynamics in predicting plant community flammability and future community structure. The logical next step in this line of research inquiry is to therefore conduct experimental studies to tease out these patterns. In particular, making the link between community structure, including trait composition and diversity at the community level, and how fires burn in plant community is required. Experimental burning in the field is the best way to address this research gap (this was part of the originally proposed research plan, but it was not able to be completed due to the covid-19 pandemic). I detail below a protocol for conducting this research.

A. **Pre-fire measurements**

   a. Community structure (species composition and diversity, trait composition and diversity) in addition to the physical structure of the vegetation using height frequency method and the spatial distribution of individual plants of key species, e.g., *Chionochloa* tussocks will determine spatial variation in fuel loads, which affect fire intensity, speed, and other aspects of fire behaviour.

   b. Individual plants should be tagged and measured so they can be remeasured after the fire. This can be used to monitor the survival of individuals after the fire. Individual variation in traits such as size, amount of dead material, clonality, and meristem position, can then be related to survival, plant-level patterns of burning and recovery**.**

   c. Microhabitat characteristics for tagged plants, including variables such as humidity, substrate type, soil moisture, and proximity to surrounding plants, can be used to determine the role of environmental conditions at fine scales in plant survival, fire behaviour and plant recovery.

   d. Soil physico-chemistry and microbial community structure can be measured by taking small soil samples throughout the area to be burnt, i.e., 10-cm soil cores. This will enable quantification of changes in soil properties that may occur due to the fire.

B. Destructive sampling outside the burnt area

   a. The traits of plants can be measured by taking measurements and samples of plants outside, but adjacent to, the burnt area. Traits measured should include seed viability, leaf nutrient concentrations, leaf and plant-level morphological traits, including those traits related to fuel type and loads and regeneration strategies.

C. During the experimental fire

   a. Measuring both air and soil temperatures during the experimental fire using thermocouples and heat mapping using drones to take aerial video footage can be used to measure fire intensity.

b. The rate of fire spread can be estimated by timing the movement of the fire front as it moves past pre-placed reference markers at set distances.
c. Drone or ground imagery can be used to record other characteristics of fire behaviour such as flame depth, height and angle.
d. Measuring the evaporation from pre-placed cans of water in different parts of the experimentally burnt area can be used to quantify variation in fire intensity.

D. Post-fire sampling

a. Repeated measurements of community structure and individually-tagged plants (including seed viability) to determine survival rates and community dynamics due to fire.
b. Repeated surveys of individual plants recovering and re-colonising the burnt site and recording their traits can be used to determine the most successful reproductive strategies in post-fire community recovery.
c. Re-measuring soil properties such as pH, gravimetric moisture and soil microbial community of pre- and post-fire will help to identify by how much amount fire modifies soil and underground soil microbial community and in turn they that can influence post-fire recovery of vegetation.

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Appendices

Appendix A: Supplementary figures and tables

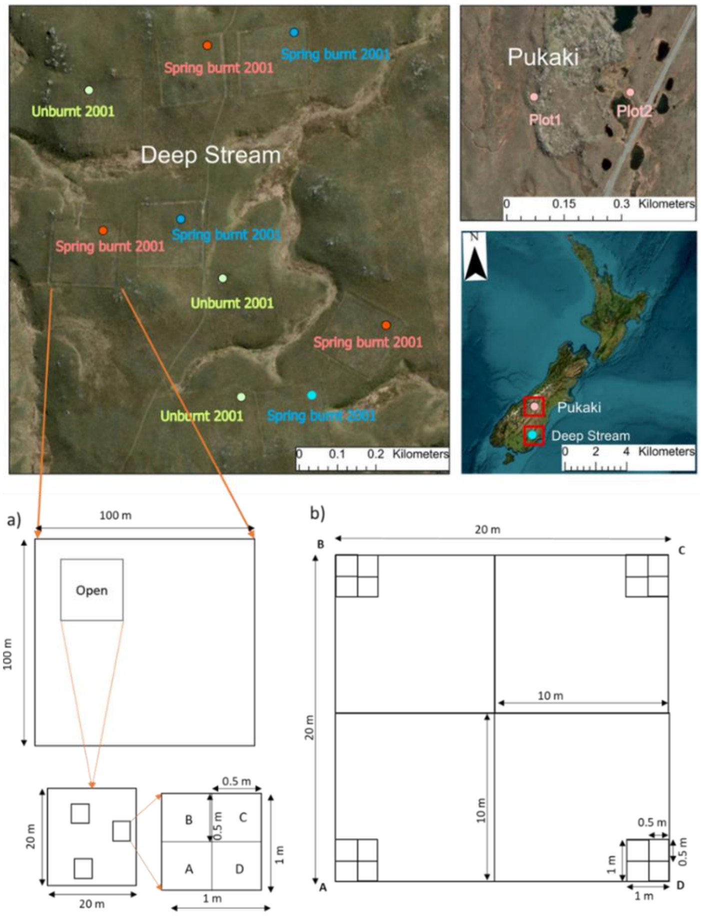


Figure S2.1. Map of study area showing locations of burns in montane grasslands (in rectangle) for the wildfire of November 2019 at Deep Stream, and August 2020 at Pukaki, South Island, New Zealand. Colour of texts and points in the map represent plots that had different fire history treatments of 2001 (circle: light green, red and blue) in addition to 2019 wildfire at Deep Stream (source: Eagle Technology, Land Information New Zealand). Plot layout for vegetation surveys to assess post-fire plant community response at a) Deep Stream and b) Pukaki. At Deep Stream, there were nine 1 hectare permanent plots that has inside it two 20-m plots, one open (used in this study) and one closed. Inside those 20-m plots were three 1 m subplots that was then divided by 4, 0.25-m^2 quadrats. In unburnt area, 3, 20-m plots were made approximately 1 kilometre from this permanent transects but not shown in this map. At Pukaki, two 20-m plots (modified Whitaker's nested sampling) were set up at the first measurement. Within plot, four 1 m subplots were made on each corner and was then divided into 4, 0.25-m^2 quadrats

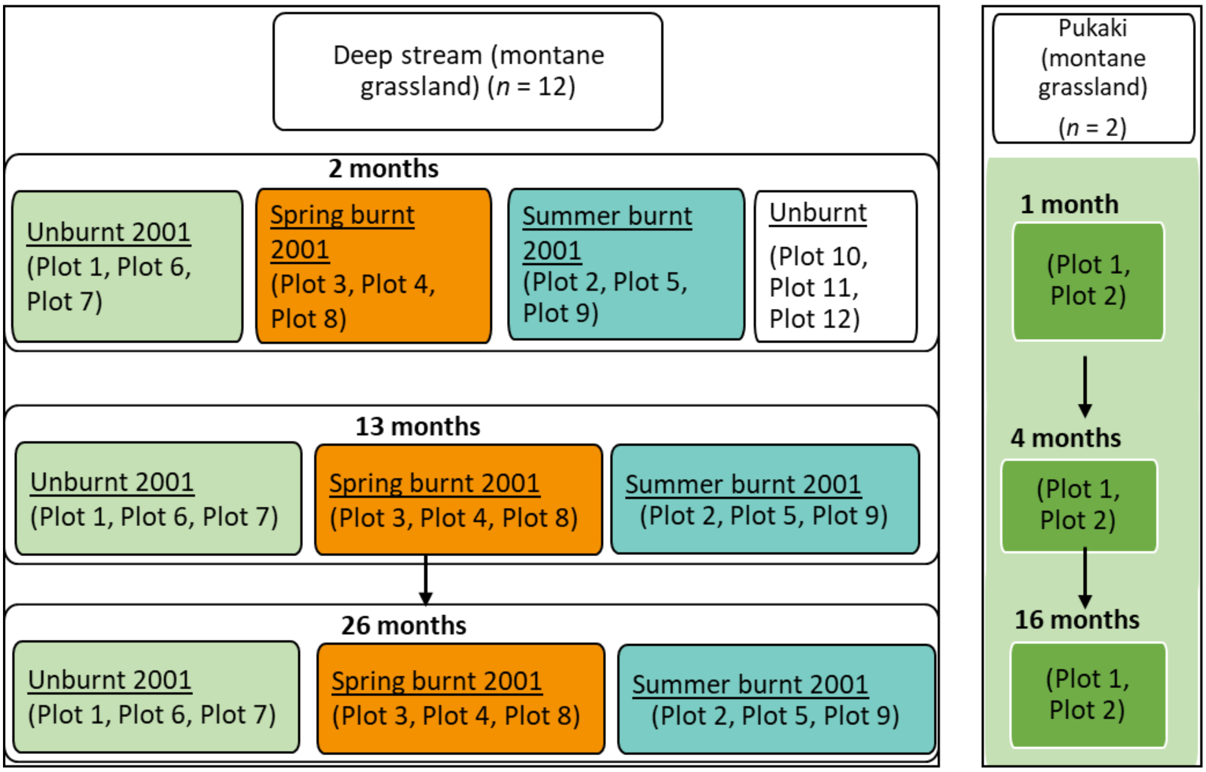


Figure S2.2. Flow chart of vegetation measurements in montane grasslands relative to wildfire of November 2019 at Deep Stream and August 2020 at Pukaki, New Zealand. At Deep Stream, colour of rectangles represents the plots that had different fire history treatments of 2001 (rectangle: light green, red, blue and grey) in addition to 2019 wildfire at Deep Stream. Plots in those fire history treatments were measured three times following 2019 wildfire. At Pukaki, there was no fire history. In the initial measurement, two plots were set up in montane grasslands at one month post-fire and remeasured twice at 4 and 16 months. n represents the number of 400-m^2 plots measured at each site across the time (and fire history treatments at Deep Stream). In each of 400-m^2 plots, 12, 0.25-m^2 quadrats were made to record vascular plant species in each measurement at both the sites

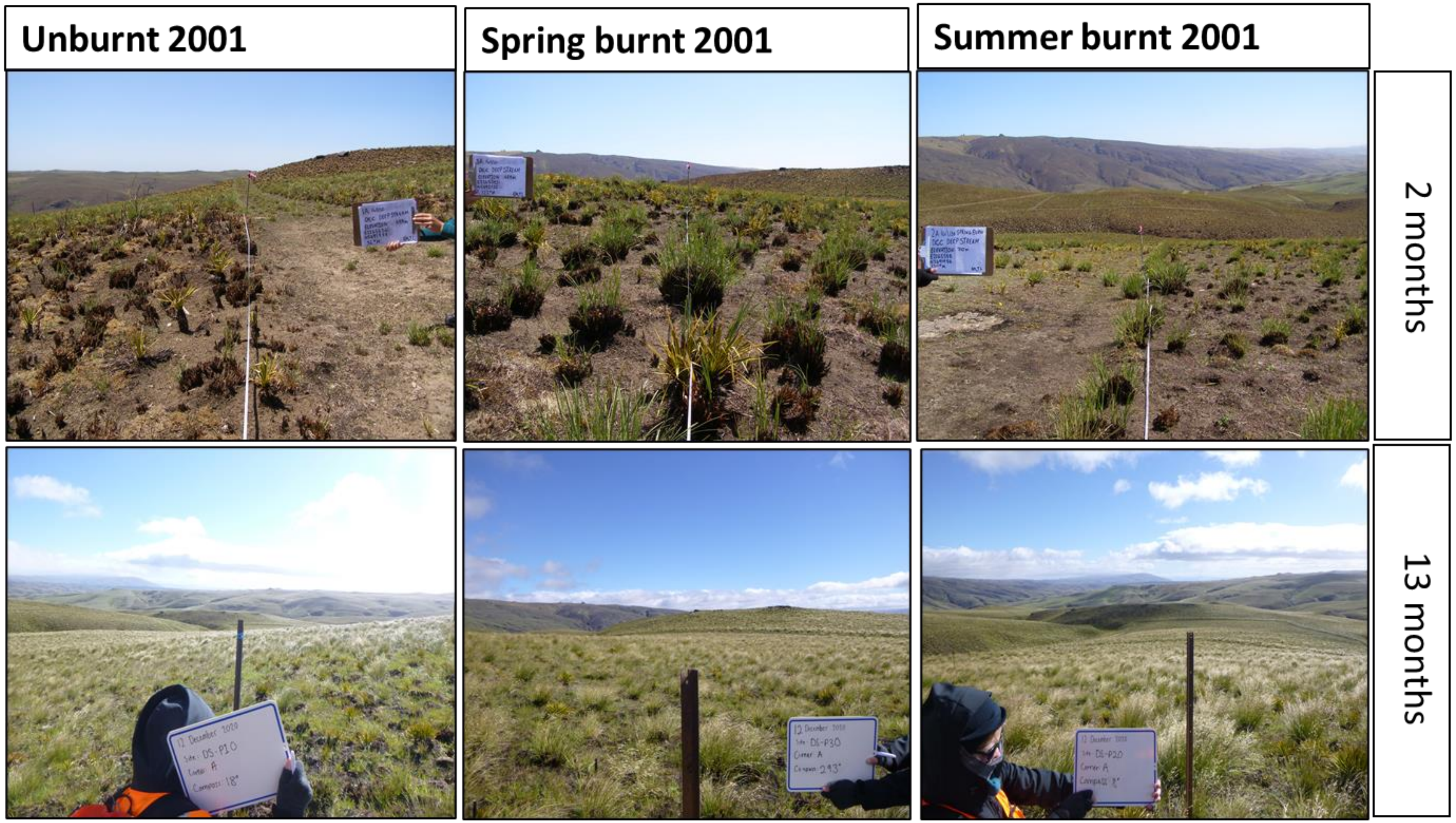


Figure S2.3. Photos of 400-m^2 plots at 2 and 13 months after wildfire of spring (November) 2019 in three different fire history treatments in montane grasslands at Deep Stream, New Zealand. Photos were not taken at 26 months. Note these photos were taken in different locations at each time. There were no photos taken at third measurement time

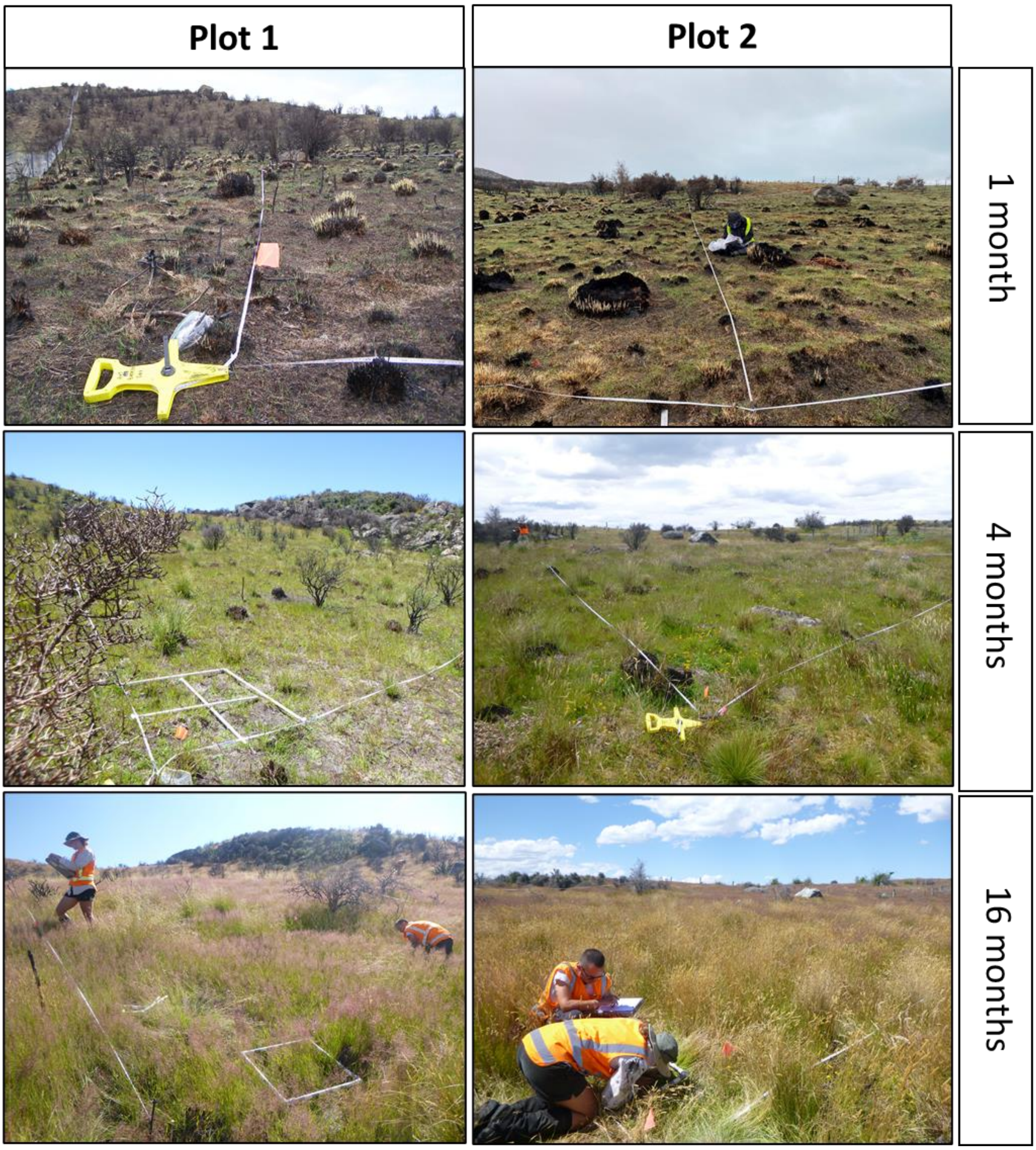


Figure S2.4. Photos of 400-m^2 plots taken at one, four, and 16 months post-fire in which vegetation was measured at Pukaki, New Zealand. *Note these photos were taken in different locations at each time*

Table S2.1.Species recorded in post-fire in 0.25-m^2 quadrats in 12, 400-m^2 plots within 26 months in montane grasslands at Deep Stream, New Zealand. All 42 species were categorised into fourteen groups (bold in colour) based on plant life form, clonality (Day at al. unpublished; Padullés Cubino et al., 2018; Pérez-Harguindeguy et al., 2013) and meristem height based on apical bud position (Raunkiaer, 1934; Raunkiaer, 1905); https://www.nzflora.info). Species names and biostatus were taken from Flora of New Zealand the (https://www.nzflora.info) and New Zealand Plant Conservation Network (https://www.nzpcn.org.nz). Asterisk (*) at the species end represents those species that were excavated to assess proportion of seed germination in the post-fire. Code represents first three letters each from genus and species epithet. Growth forms basically are summarised from fourteen groups and biostatus represents origin of the species.

Life history category and botanical name	**Code**	**Growth form**	**Meristem height**	**Biostatus**
Herbaceous, rosette plants (a1a1) < 20 cm				
Aciphylla aurea	ACIAUR	Forb	High	Native
Anisotome aromatica	ANIARO	Forb	Low	Native
Anisotome flexuosa	ANIFLE	Forb	Low	Native
Aporostylis bifolia	APOBIF	Forb	Low	Native
*Brachyglottis lagopus**	BRALAG	Forb	Low	Native
*Celmisia gracilenta**	CELGRA	Forb	Low	Native
Chaerophyllum ramosum	CHARAM	Forb	Low	Native
Craspedia uniflora	CRAUNI	Forb	Low	Native
Epilobium species	EPILOB	Forb	Low	Native
Gentianella grisebachii	GENGRI	Forb	Low	Native
*Pilosella officinarum**	PILOFF	Forb	Low	Exotic
Plantago lanceolata	PLALAN	Forb	Low	Exotic
Prasophyllum colensoi	PRACOL	Forb	Low	Native
Viola cunninghamii	VIOCUN	Forb	Low	Native
Wahlenbergia albomarginata	WAHALB	Forb	Low	Native
Herbaceous, rosette plants (a1a2) >20 cm				
Hieracium lepidulum	HIELEP	Forb	Low	Exotic
*Hypochaeris radicata**	HYPRAD	Forb	Low	Exotic
Herbaceous, elongated, leaf-bearing rhizomatous (a1b1) < 8 cm				
Geranium microphyllum	GERMIC	Forb	Low	Native
Herbaceous, elongated, leaf-bearing rhizomatous (a1b2) > 8 cm				
Pterostylis venosa	PTEVEN	Forb	Low	Native
Thelymitra nervosa	THENER	Forb	Low	Native
Thelymitra species	THELYM	Forb	Low	Native

Life history category and botanical name	**Code**	**Growth form**	**Meristem height**	**Biostatus**
Herbaceous, cushion plants (a1c1)				
Colobanthus strictus	COLSTR	Forb	Low	Native
*Gonocarpus montanus**	GONMON	Forb	Low	Native
Herbaceous, extensive-stemmed herbs (a1d1) < 20 cm				
*Helichrysum filicaule**	HELFIL	Forb	Low	Native
Stackhousia minima	STAMIN	Forb	Low	Native
Herbaceous, extensive-stemmed herbs (a1d2) > 20 cm				
Cirsium vulgare	CIRVUL	Forb	Low	Exotic
*Lycopodium fastigiatum**	LYCFAS	Forb	Low	Native
Tussocks (a1e1)				
Chionochloa rigida	CHIRIG	Graminoid	Low	Native
Graminoids (a1f1) > 15 cm				
*Carex species**	CAREX	Graminoid	Low	Native
*Herpolirion novae-zelandiae**	HERNOV	Graminoid	Low	Native
Luzula rufa	LUZRUF	Graminoid	Low	Native
Rytidosperma gracile	RYTGRA	Graminoid	Low	Native
Graminoids (a1f2) < 15				
*Agrostis capillaris**	AGRCAP	Graminoid	Low	Exotic
Anthoxanthum odoratum	ANTODO	Graminoid	Low	Exotic
*Deyeuxia avenoides**	DEYAVE	Graminoid	Low	Native
*Poa colensoi**	POACOL	Graminoid	Low	Native
Woody, prostrate shrubs (a3a1)				
Acrothamnus colensoi	ACRCOL	Woody	High	Native
Leucopogon fraseri	LEUFRA	Woody	High	Native
Pentachondra pumila	PENPUM	Woody	High	Native
Woody, dwarf shrub (subshrub) (a3b1)				
*Gaultheria macrostigma**	GAUMAC	Woody	High	Native
*Pimelea oreophila**	PIMORE	Woody	High	Native
Woody, shrub and trees (a3c1)				
Coprosma species	COPROS	Woody	High	Native

Table S2.2. Species recorded in post-fire in 0.25-m^2 quadrats in 2, 400-m^2 plots within 16 months in montane grasslands at Pukaki, New Zealand. All 48 species were categorised into fourteen groups and data collated from online sources same as at Deep Stream (see details in Table S1). Asterisks * at the end of the species represent those species that were excavated four months post-fire respectively to assess proportion of seed germination. *Geranium microphyllum* excavated at four months was not present on vegetation survey plot.

Life history category and botanical name	**Code**	**Growth form**	**Meristem height**	**Bio - status**
Herbaceous, rossette plants (a1a1) < 20 cm				
Brachyglottis lagopus (Raoul) B.Nord.	BRALAG	Forb	Low	Native
Celmisia gracilenta Hook.f. *	CELGRA	Forb	Low	Native
Hypochaeris radicata L.*	HYPRAD	Forb	Low	Exotic
Pilosella aurantiaca (L.) F.W.Schultz & Sch.Bip.*	*PILAUR*	Forb	Low	Exotic
Pilosella officinarum Vaill.*	PILOFF	Forb	Low	Exotic
Pilosella piloselloides subsp. *praealta* (Gochnat) S.Bräut. & Greuter	PILPIL	Forb	Low	Exotic
Prasophyllum colensoi Hook.f.	*PRACOL*	Forb	Low	Native
Wahlenbergia albomarginata Hook.	WAHALB	Forb	Low	Native
Wahlenbergia Schrad. ex Roth *	WAHLEN	Forb	Low	Native
Herbaceous, rossette plants (a1a2) > 20 cm				
Anisotome aromatica Hook.f.*	ANIARO	Forb	Low	Native
Herbaceous, elongated, leaf-bearing rhizomatous (a1b1) < 8 cm				
Hydrocotyle novae-zeelandiae DC.	HYDNOV	Forb	Low	Native
Viola cunninghamii Hook.f.*	VIOCUN	Forb	Low	Native
Herbaceous, elongated, leaf-bearing rhizomatous (a1b2) > 8 cm				
Blechnum penna-marina (Poir.) Kuhn	BLEPEN	Fern	Low	Native
Pteridium esculentum (G.Forst.) Cockayne *	*PTEESC*	Fern	Low	Native
Thelymitra longifolia J.R.Forst. & G.Forst.	THELON	Forb	Low	Native
Herbaceous, extensive-stemmed herbs (a1d1) < 20 cm				
Anaphalioides bellidioides (G.Forst.) Glenny	ANABEL	Forb	Low	Native
Cirsium arvense (L.) Scop.	CIRARV	Forb	Low	Exotic
Cuscuta epithymum (L.) L.	CUSEPI	Forb	Low	Exotic
Dianthus armeria L.	DIAARM	Forb	High	Exotic
Epilobium ciliatum Raf.	*EPICIL*	Forb	Low	Exotic
Gonocarpus micranthus Thunb.	GONMIC	Forb	Low	Native

Life history category and botanical name	Code	Growth form	Meristem height	Bio - status
Helichrysum filicaule Hook.f.	HELFIL	Forb	Low	Native
Stellaria elatinoides Benth. ex Hook.f.	STEELA	Forb	Low	Unknown
Stellaria L.	STELLA	Forb	Low	Native
Herbaceous, extensive-stemmed herbs (a1d2) > 20 cm				
Bellardia viscosa (L.) Fisch. & C.A.Mey.	BELVIS	Forb	High	Exotic
Cerastium fontanum Baumg.	CERFON	Forb	Low	Exotic
Lotus pedunculatus Cav.	LOTPED	Forb	Low	Exotic
Microtis unifolia (G.Forst.) Rchb.f.	MICUNI	Forb	Low	Native
Trifolium repens L.	TRIREP	Forb	Low	Exotic
Verbascum thapsus L.	*VERTHA*	Forb	Low	Exotic
Tussocks (a1e1)				
Chionochloa rigida (Raoul) Zotov	CHIRIG	Graminoid	Low	Native
Festuca novae-zelandiae(Hack.) Cockayne	FESNOV	Graminoid	Low	Native
Graminoids (a1f1) >15 cm				
Carex L.	CAREX	Graminoid	Low	Native
Juncus articulatus L.	JUNART	Graminoid	Low	Exotic
Juncus conglomeratus L.	JUNCON	Graminoid	Low	Exotic
Luzula rufa Edgar	LUZRUF	Graminoid	Low	Native
Graminoids (a1f2) < 15 cm				
Agrostis capillaris L.*	AGRCAP	Graminoid	Low	Exotic
Anthosachne solandri (Steud.) Barkworth & S.W.L.Jacobs	ANTSOL	Graminoid	Low	Exotic
Anthoxanthum odoratum L.*	ANTODO	Graminoid	Low	Native
Deyeuxia avenoides (Hook.f.) Buchanan	DEYAVE	Graminoid	Low	Native
Festuca rubra L.	FESRUB	Graminoid	Low	Exotic
Poa colensoi Hook.f.	POACOL	Graminoid	Low	Native
Schoenus pauciflorus (Hook.f.) Hook.f.	SCHPAU	Graminoid	Low	Native
Woody, prostrate shrubs (a3a1)				
Coprosma petriei Cheeseman	COPPET	Woody	High	Native
Leucopogon fraseri A.Cunn.	LEUFRA	Woody	High	Native
Woody, dwarf shrub (subshrub) (a3b1)				
Gaultheria parvula Heenan	GAUPAR	Woody	High	Native
Pimelea prostrata (J.R.Forst. & G.Forst.)	PIMPRO	Woody	High	Native
Woody, shrub and trees (a3c1)				

Life history category and botanical name	**Code**	**Growth form**	**Meristem height**	**Bio - status**
Acrothamnus colensoi (Hook.f.) Quinn *	ACRCOL	Woody	High	Native
Corokia cotoneaster Raoul *	CORCOT	Woody	High	Native
Discaria toumatou Raoul *	DISTOU	Woody	High	Native
Gaultheria depressa Hook.f.*	GAUDEP	Woody	High	Native
Pinus contorta Loudon	PINCON	Woody	High	Exotic
Rosa rubiginosa L.	ROSRUB	Woody	High	Exotic

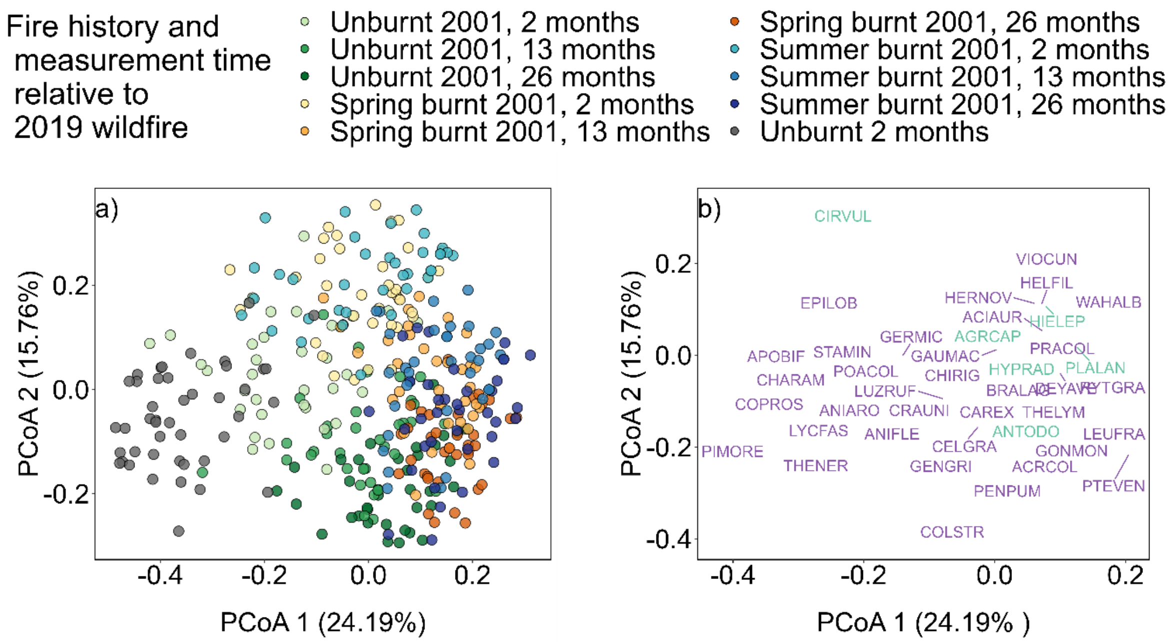


Figure S2.5. Ordination diagrams for a PCoA for Jaccard dissimilarity of plant species presence in 0.25-m^2 quadrats in 12, 400-m^2 plots showing a) site scores and b) species at Deep Stream, New Zealand. Colour of the points represents fire history treatments and colour gradient shows vegetation measurement time relative to November 2019 fire. Colours of text represents the biostatus of species: exotics (green) and natives (purple)

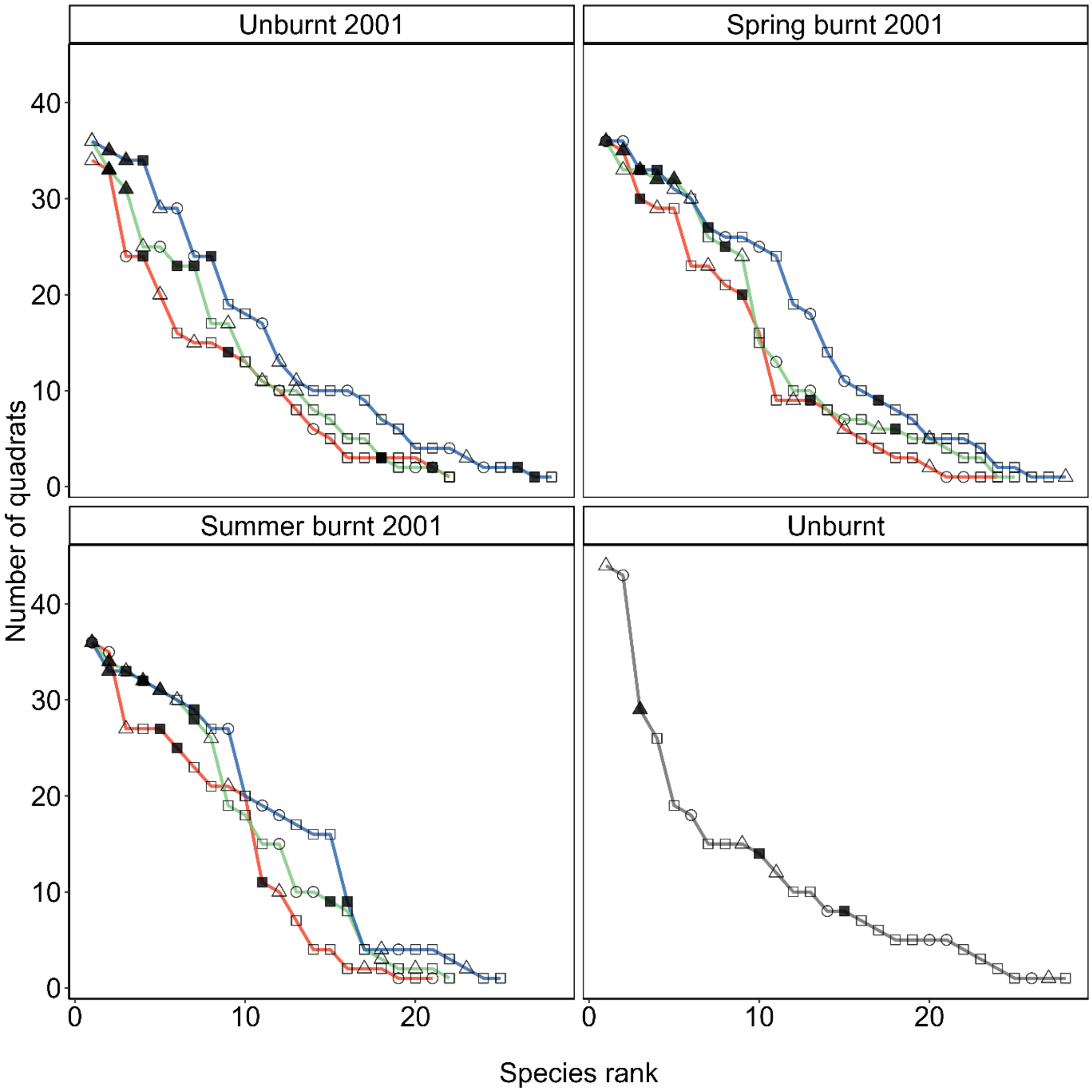


Figure S2.6. Rank abundance curves based on number of quadrats 0.5 × 0.5-m each species occurred in each fire history treatment which were measured three times in 400-m^2 plots after November 2019 wildfire in montane grasslands at Deep Stream, New Zealand. The *x*- axis represents species rank determined from the number of quadrats in which species occurred. Shapes represent growth forms classified as forb (circle), graminoid (rectangle) and woody (triangle). Ferns were included in forbs. Point colours represent plant biostatus: native (hollow) or exotics (black). Line colours represent post-fire 2 (orange), 13 (green), 26 (blue) and 2 unburnt (grey) months

Table S2.3. Result of Post-hoc test after generalised linear mixed effect model (glmmTMB) for comparison of post-fire species richness over time (in months). Mean quadrat species richness was compared in between post-fire measurement months for growth forms: forb, graminoid and woody within biostatus (natives and exotics) across the fire history treatments at Deep Stream and plots at Pukaki. Significant post-fire months contrasts (*P* < 0.05) are presented in bold.

Site	**Post-fire months contrast**	**Category**	**Fire history/ plot**	**Growth form**	**Estimate**	**S.E.**	***df***	***t* - ratio**	***P* - value**
Deep Stream	2 - 13	Natives	Unburnt 2001	Forb	0.15	0.16	104.00	0.90	0.64
	13 - 26	Natives	Unburnt 2001	Forb	-0.27	0.16	104.00	-1.66	0.23
	2 - 26	Natives	Unburnt 2001	Forb	-0.12	0.15	104.00	-0.77	0.72
	2 - 13	Natives	Unburnt 2001	Graminoid	-0.10	0.15	104.00	-0.62	0.81
	13 - 26	Natives	Unburnt 2001	Graminoid	-0.04	0.15	104.00	-0.30	0.95
	2 - 26	Natives	Unburnt 2001	Graminoid	-0.14	0.15	104.00	-0.91	0.63
	2 - 13	Natives	Unburnt 2001	Woody	-0.26	0.24	104.00	-1.08	0.53
	13 - 26	**Natives**	**Unburnt 2001**	**Woody**	**-0.79**	**0.19**	**104.00**	**-4.10**	**< 0.001**
	2 - 26	**Natives**	**Unburnt 2001**	**Woody**	**-1.05**	**0.21**	**104.00**	**-4.97**	**< 0.001**
	2 - 13	Natives	Spring burnt 2001	Forb	0.04	0.13	104.00	0.32	0.94
	13 - 26	Natives	Spring burnt 2001	Forb	-0.08	0.13	104.00	-0.64	0.80
	2 - 26	Natives	Spring burnt 2001	Forb	-0.04	0.13	104.00	-0.32	0.95
	2 - 13	Natives	Spring burnt 2001	Graminoid	0.09	0.17	104.00	0.52	0.86
	13 - 26	Natives	Spring burnt 2001	Graminoid	-0.06	0.18	104.00	-0.35	0.93
	2 - 26	Natives	Spring burnt 2001	Graminoid	0.03	0.17	104.00	0.17	0.98
	2 - 13	**Natives**	**Spring burnt 2001**	**Woody**	**-0.55**	**0.20**	**104.00**	**-2.71**	**< 0.05**
	13 - 26	**Natives**	**Spring burnt 2001**	**Woody**	**-0.56**	**0.15**	**104.00**	**-3.66**	**< 0.01**
	2 - 26	**Natives**	**Spring burnt 2001**	**Woody**	**-1.12**	**0.19**	**104.00**	**-5.97**	**< 0.001**
	2 - 13	Natives	Summer burnt 2001	Forb	0.11	0.14	104.00	0.83	0.69

Site	**Post-fire months contrast**	**Category**	**Fire history/ plot**	**Growth form**	**Estimate**	**S.E.**	***df***	***t* - ratio**	***P* - value**
	13 - 26	Natives	Summer burnt 2001	Forb	-0.13	0.14	104.00	-0.96	0.60
	2 - 26	Natives	Summer burnt 2001	Forb	-0.02	0.13	104.00	-0.13	0.99
	2 - 13	Natives	Summer burnt 2001	Graminoid	-0.06	0.18	104.00	-0.36	0.93
	13 - 26	Natives	Summer burnt 2001	Graminoid	-0.11	0.18	104.00	-0.62	0.81
	2 - 26	Natives	Summer burnt 2001	Graminoid	-0.05	0.17	104.00	-0.26	0.96
	2 - 13	**Natives**	**Summer burnt 2001**	**Woody**	**-0.65**	**0.20**	**104.00**	**-3.21**	**< 0.01**
	13 - 26	**Natives**	**Summer burnt 2001**	**Woody**	**-0.38**	**0.15**	**104.00**	**-2.48**	**< 0.05**
	2 - 26	**Exotics**	**Summer burnt 2001**	**Woody**	**-1.03**	**0.19**	**104.00**	**-5.40**	**< 0.001**
	2 - 13	Exotics	Unburnt 2001	Forb	-0.13	0.21	104.00	-0.63	0.81
	13 - 26	Exotics	Unburnt 2001	Forb	-0.22	0.19	104.00	-1.14	0.49
	2 - 26	Exotics	Unburnt 2001	Forb	-0.35	0.20	104.00	-1.76	0.19
	2 - 13	**Exotics**	**Unburnt 2001**	**Graminoid**	**-0.66**	**0.21**	**104.00**	**-3.09**	**< 0.01**
	13 - 26	Exotics	Unburnt 2001	Graminoid	-0.08	0.17	104.00	-0.43	0.90
	2 - 26	**Exotics**	**Unburnt 2001**	**Graminoid**	**-0.74**	**0.21**	**104.00**	**-3.49**	**< 0.01**
	2 - 13	Exotics	Spring burnt 2001	Forb	-0.08	0.18	104.00	-0.45	0.89
	13 - 26	Exotics	Spring burnt 2001	Forb	-0.08	0.17	104.00	-0.43	0.90
	2 - 26	Exotics	Spring burnt 2001	Forb	-0.16	0.18	104.00	-0.88	0.65
	2 - 13	**Exotics**	**Spring burnt 2001**	**Graminoid**	**-0.60**	**0.21**	**104.00**	**-2.87**	**< 0.05**
	13 - 26	Exotics	Spring burnt 2001	Graminoid	-0.08	0.17	104.00	-0.43	0.90
	2 - 26	**Exotics**	**Spring burnt 2001**	**Graminoid**	**-0.68**	**0.21**	**104.00**	**-3.27**	**< 0.01**
	2 - 13	Exotics	Summer burnt 2001	Forb	-0.09	0.17	104.00	-0.52	0.86
	13 - 26	Exotics	Summer burnt 2001	Forb	-0.03	0.17	104.00	-0.17	0.98
	2 - 26	Exotics	Summer burnt 2001	Forb	-0.12	0.17	104.00	-0.69	0.77
	2 - 13	**Exotics**	**Summer burnt 2001**	**Graminoid**	**-0.59**	**0.21**	**104.00**	**-2.84**	**< 0.05**

Site	**Post-fire months contrast**	**Category**	**Fire history/ plot**	**Growth form**	**Estimate**	**S.E.**	***df***	***t* - ratio**	***P* - value**
	13 - 26	Exotics	Summer burnt 2001	Graminoid	0.00	0.18	104.00	0.00	1.00
	2 - 26	**Exotics**	**Summer burnt 2001**	**Graminoid**	**-0.59**	**0.21**	**104.00**	**-2.84**	**< 0.05**
Pukaki	1 - 4	Natives	Puk-1	Forb	-1.04	0.47	44.00	-2.19	0.08
	16 - 4	**Natives**	**Plot 1**	**Forb**	**0.86**	**0.29**	**44.00**	**2.96**	**< 0.05**
	1 - 16	**Natives**	**Plot 1**	**Forb**	**-1.90**	**0.44**	**44.00**	**-4.33**	**< 0.001**
	1 - 4	Natives	Puk-1	Graminoid	-0.56	0.63	44.00	-0.89	0.65
	16 - 4	Natives	Plot 1	Graminoid	0.89	0.45	44.00	1.98	0.13
	1 - 16	**Natives**	**Plot 1**	**Graminoid**	**-1.45**	**0.56**	**44.00**	**-2.60**	**< 0.05**
	1 - 4	Natives	Plot 1	Woody	-21.89	13335.17	44.00	0.00	1.00
	16 - 4	**Natives**	**Plot 1**	**Woody**	**0.85**	**0.28**	**44.00**	**3.01**	**< 0.05**
	1 - 16	Natives	Plot 1	Woody	-22.73	13335.17	44.00	0.00	1.00
	1 - 4	Natives	Plot 2	Forb	-0.89	0.45	44.00	-1.98	0.13
	16 - 4	**Natives**	**Plot 2**	**Forb**	**0.75**	**0.29**	**44.00**	**2.55**	**< 0.05**
	1 - 16	**Natives**	**Plot 2**	**Forb**	**-1.64**	**0.41**	**44.00**	**-3.96**	**< 0.001**
	1 - 4	Natives	Plot 2	Graminoid	-0.36	0.49	44.00	-0.72	0.75
	16 - 4	**Natives**	**Plot 2**	**Graminoid**	**1.06**	**0.37**	**44.00**	**2.90**	**< 0.05**
	1 - 16	**Natives**	**Plot 2**	**Graminoid**	**-1.42**	**0.42**	**44.00**	**-3.38**	**< 0.05**
	1 - 4	Natives	Plot 2	Woody	-0.41	0.91	44.00	-0.44	0.90
	16 - 4	Natives	Plot 2	Woody	1.10	0.67	44.00	1.65	0.24
	1 - 16	Natives	Plot 2	Woody	-1.50	0.78	44.00	-1.92	0.14
	1 - 4	**Exotics**	**Plot 1**	**Forb**	**-1.79**	**0.62**	**44.00**	**-2.87**	**< 0.05**
	16 - 4	Exotics	Plot 1	Forb	0.67	0.29	44.00	2.29	0.07
	1 - 16	**Exotics**	**Plot 1**	**Forb**	**-2.46**	**0.60**	**44.00**	**-4.08**	**< 0.001**
	1 - 4	Exotics	Plot 1	Graminoid	-0.39	0.31	44.00	-1.23	0.44

Site	**Post-fire months contrast**	**Category**	**Fire history/ plot**	**Growth form**	**Estimate**	**S.E.**	***df***	***t* - ratio**	***P* - value**
	16 - 4	Exotics	Plot 1	Graminoid	0.22	0.27	44.00	0.80	0.70
	1 - 16	Exotics	Plot 1	Graminoid	-0.60	0.30	44.00	-1.99	0.13
	1 - 4	Exotics	Plot 2	Forb	-0.21	0.37	44.00	-0.56	0.84
	16 - 4	**Exotics**	**Plot 2**	**Forb**	**0.78**	**0.30**	**44.00**	**2.59**	**< 0.05**
	1 - 16	**Exotics**	**Plot 2**	**Forb**	**-0.99**	**0.32**	**44.00**	**-3.05**	**< 0.05**
	1 - 4	Exotics	Plot 2	Graminoid	-0.69	0.33	44.00	-2.12	0.10
	16 - 4	Exotics	Plot 2	Graminoid	0.13	0.26	44.00	0.52	0.86
	1 - 16	**Exotics**	**Plot 2**	**Graminoid**	**-0.83**	**0.32**	**44.00**	**-2.58**	**< 0.05**
	1 - 4	Exotics	Plot 2	Woody	24.34	136383.45	44.00	0.00	1.00
	16 - 4	Exotics	Plot 2	Woody	24.75	136383.45	44.00	0.00	1.00
	1 - 16	Exotics	Plot 2	Woody	-0.41	0.91	44.00	-0.44	0.90

Table S2.4.Number of individual plants excavated that were survived or germinated from seed in relation to three predictors biostatus (native vs. exotics), substrate type (moss vs. not on moss) and meristem height (low vs. high meristem) in the post-fire in montane grasslands at two months at Deep Stream, and four months at Pukaki, New Zealand. *n* represents the total number of individuals excavated after wildfire.

Site and time	**Fixed effect category**	**Predictors**	**Survived**	**Germinated from seed**
Deep Stream (n = 360) at 2 months	Biostatus	Native	165	15
		Exotics	137	43
	Substrate	Not on moss	181	53
		moss	121	5
	Meristem height	Low	267	0
		High	35	58
Pukaki (n = 37) at 4 months	Biostatus	Native	15	5
		Exotics	15	2
	Substrate	Not on moss	30	7
	Meristem height	Low	21	0
		High	9	7

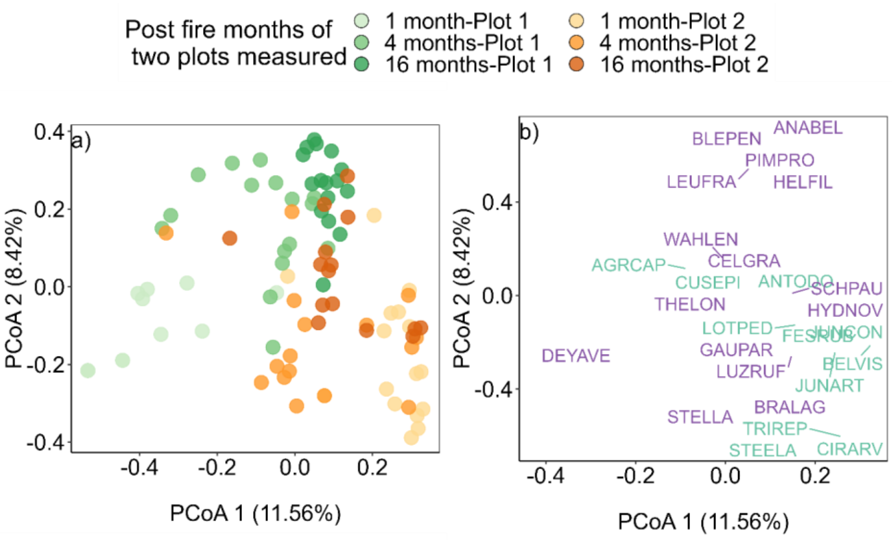


Figure S2.7. Ordination diagrams for a PCoA of Jaccard dissimilarity of plant species presence in 0.25-m^2 quadrats in 2, 400-m^2 plots showing a) site scores and b) species in post-fire at Pukaki, New Zealand. Colour of the points represent vegetation measurement time relative to August 2020 fire and plots. Colours of texts represent the biostatus of species: exotics (green) and natives (purple)

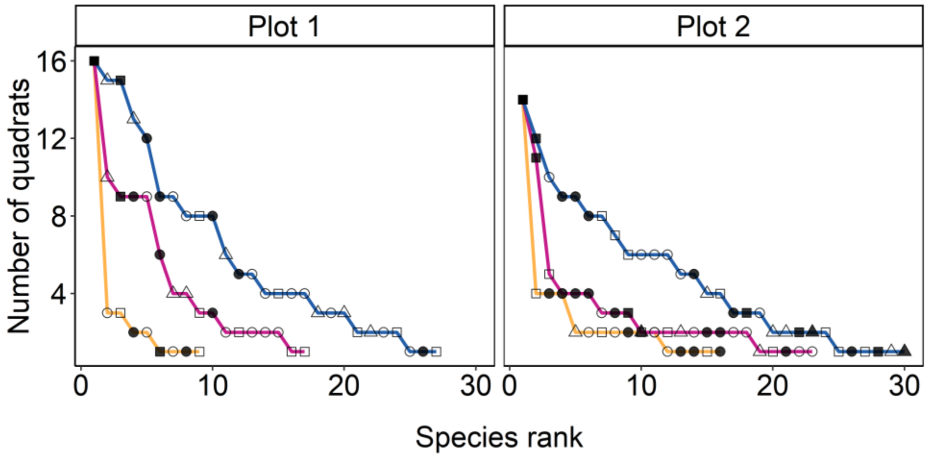


Figure S2.8. Rank abundance curves based on number of quadrats 0.5 × 0.5-m each species occurred in on the two 400-m^2 plots measured three times (until 16 months) after August 2020 wildfire in montane grasslands at Pukaki, New Zealand. The *x* - axis represents species rank determined from the number of quadrats in which species occurred. Shapes represent growth forms classified as forbs (circle), graminoids (rectangle) and woody (triangle). Ferns were included in forbs. Point colour represents plant biostatus: native (hollow) or exotics (black). Line colours represent measurement time relative to August 2020 fire: one month (orange), 4 months (pink) and 16 months (blue) post-fire.

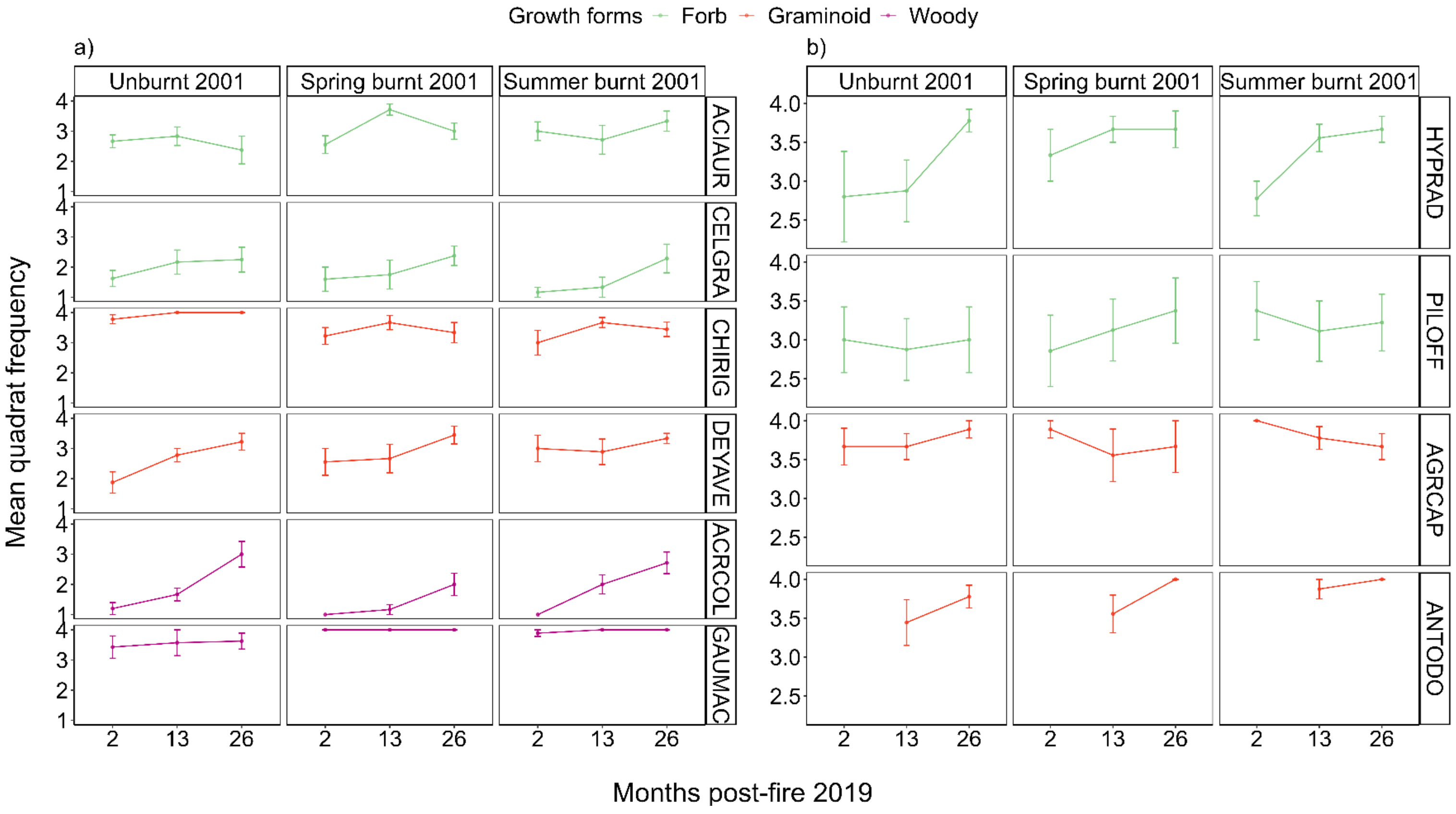


Figure S2.9. Post-fire short-term occurrence (number of 0.25-m^2 quadrats in three 400-m^2 plots in each of the fire history) of ten species (most common species on the plot) a) six native species and b) four exotic species relative to wildfire of November 2019 across different fire history treatments within 26 months in montane grasslands at Deep Stream, New Zealand. The *x* - axis represents post-fire months and *y* – axis represents the total number of occurrences in 0.25-m^2 quadrats for each measurement time and fire history treatments. Colour of lines represent growth forms: forbs (green), graminoids (blue), and woody (orange). Species codes can be found in (Table S2.1, Appendix A)

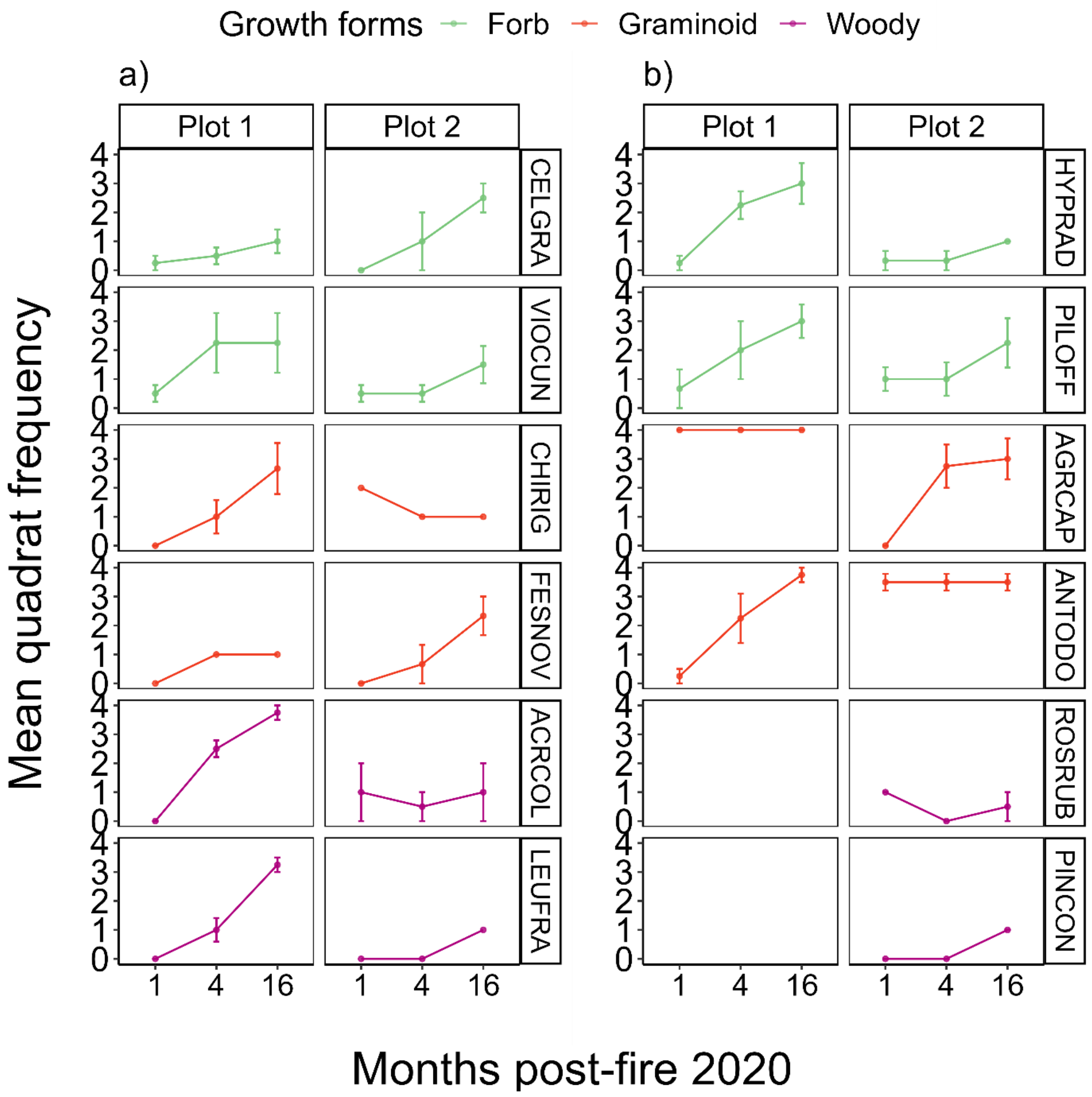


Figure S2.10. Post-fire species occurrence (based on number of 0.25-m^2 quadrats in each 400-m^2 plot) of 12 most common species a) six native species and b) six exotic species relative to August 2020 wildfire in montane grasslands at Pukaki, New Zealand. The *x* - axis represents months post-fire and y – axis represents the total number of occurrences in 0.25-m^2 quadrats for each measurement time on each plot. Generalised linear model (GLM) showed that *Acrothamnus colensoi* (ACRCOL), was significantly (*P* < 0.01) in post-fire. Line colours represent growth forms: forbs (green), graminoids (blue) and woody (orange). Species codes can be found in Table S5.3, Appendix A

Figure S3.1. Map of the study area showing the locations of the four permanent 100-m transects that were burnt (red dots; OHAT042, OHAT043, OHAT044) and not burnt (black dots; OHAT042, OHAT045) in the October 2020 wildfire (source: Eagle Technology, LINZ and Earthstar Geographics) at Lake Ōhau, Canterbury, South Island, New Zealand. The blue polygon with a red outline approximately represents the boundary of the area that was burnt

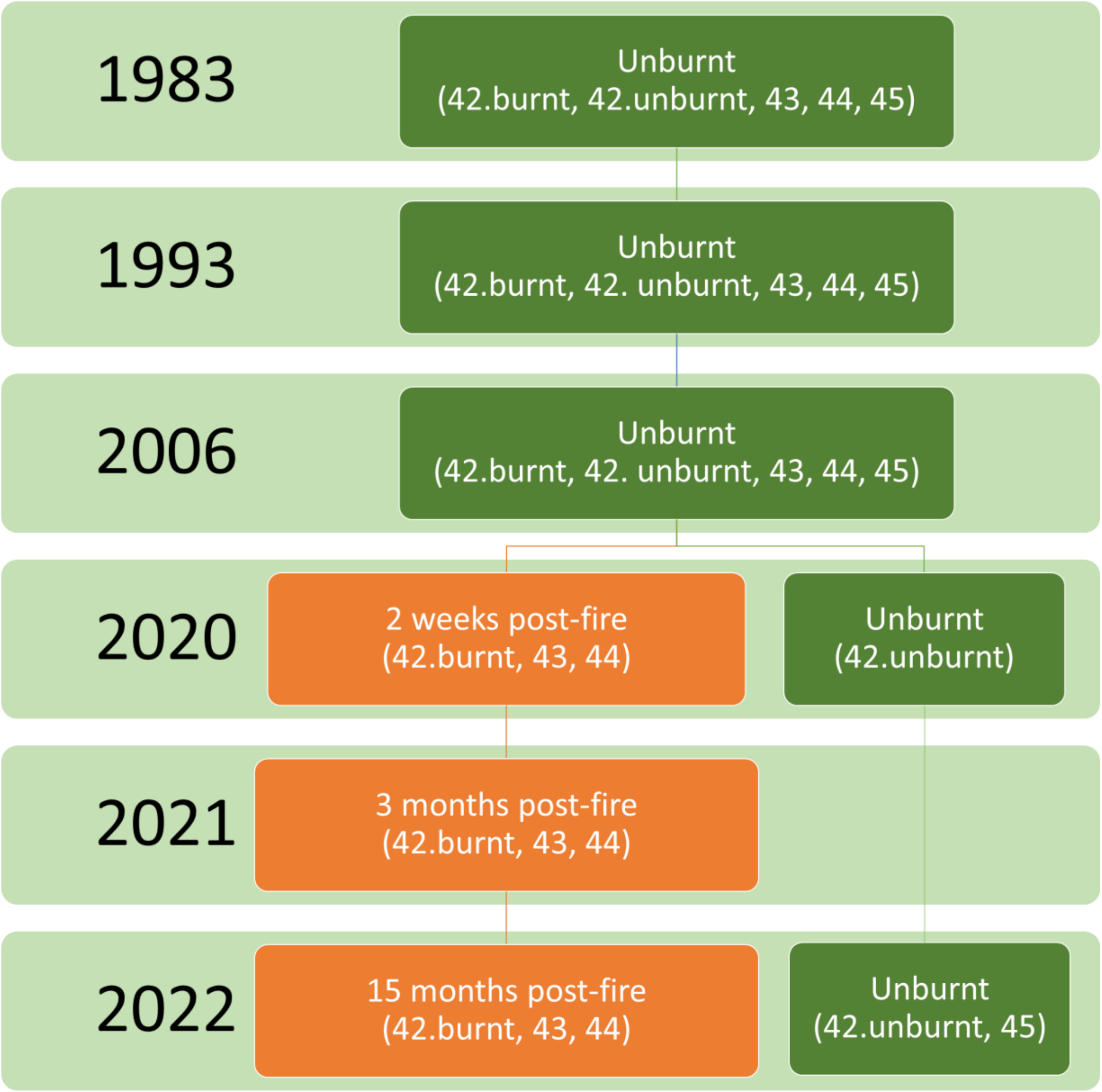


Figure S3.2. Diagram showing the study design and data collection at Lake Ōhau, Canterbury, South Island, New Zealand. Measurements of plant community structure were taken over time within 0.25-m^2 quadrats on four permanent transects (OHAT042, OHAT043, OHAT044, and OHAT045), measured repeatedly between 1983 and 2022. A wildfire in October 2020 burnt all of two transects (OHAT043 and OHAT044), partially burnt a third transect (OHAT042) and the fourth transect (OHAT045) remained entirely unburnt. Three post-burn measurements were conducted, two weeks after fire, three months after fire, and fifteen months after fire. Transect OHAT042 was split into two sections prior to analysis: OHAT042.1 (burnt quadrats 1-35 m) and OHAT042.2 (unburnt 41-99 m); quadrats at 37 m and 39 m were excluded from all analysis as a walking trail was put over them prior to the 2020 measurement, destroying the vegetation

Table S3.1. Species recorded in 0.25-m^2 quadrats on 100-m permanent transects sampled between 1983 and 2022 at Lake Ōhau, Canterbury, South Island, New Zealand. All 88 species were categorised into 13 groups based on plant life form, clonality (Day at al. unpublished; Padullés Cubino et al., 2018; Pérez-Harguindeguy et al., 2013) and meristem height based on apical bud position (Raunkiaer, 1934; Raunkiaer, 1905); https://www.nzflora.info). Species names and codes were taken from Flora of New Zealand the (https://www.nzflora.info) and New Zealand Plant Conservation Network (https://www.nzpcn.org.nz). Meristem type is based on the bud position according to Raunkier's life form classification (Raunkiaer, 1934). Clonality is recorded as either non-clonal, clonal belowground or clonal aboveground. Asterisks (*) represent species for which flammability data from experimental burning exist (Curran et al. unpublished; this thesis).

Life history category and botanical name	Code	Biostatus	Clonality	Meristem type
Herbaceous, rosette plants < 20 cm				
Brachyglottis lagopus (Raoul) B.Nord.	BRAlag	Native	Non-clonal	Low
Brachyscome longiscapa G.Simpson & J.S.Thomson	BRAlon	Native	Non-clonal	Low
Celmisia gracilenta Hook.f.	CELgra	Native	Non-clonal	Low
Cotula L.	COTULA	Exotic	Non-clonal	High
Craspedia incana Allan	CRAinc	Native	Non-clonal	Low
Hieracium lepidulum (Stenstr.) Omang	HIElep	Exotic	Non-clonal	Low
Hypochaeris radicata L.	HYPrad	Exotic	Non-clonal	Low
Lagenophora cuneata Petrie	LAGcun	Native	Clonal	Low
Leptinella pectinata (Hook.f.) D.G.Lloyd & C.J.Webb	LEPpec	Native	Clonal	Low
Microseris scapigera (Sol. ex A.Cunn.) Sch.Bip.	MICsca	Native	Non-clonal	Low
Pilosella aurantiaca (L.) F.W.Schultz & Sch.Bip.	PILaur	Exotic	Clonal	Low
Pilosella officinarum Vaill.	PILoff	Exotic	Clonal	Low
Pilosella piloselloides subsp. *praealta* (Gochnat) S.Bräut. & Greuter	PILpsp	Exotic	Clonal	Low

Life history category and botanical name	Code	Biostatus	Clonality	Meristem type
Plantago lanigera Hook.f.	PLAlng	Native	Non-clonal	Low
Taraxacum officinale F.H.Wigg.	TARoff	Exotic	Non-clonal	Low
Wahlenbergia albomarginata Hook.	WAHalb	Native	Clonal	Low
Herbaceous, rosette plants < 20 cm				Low
Anisotome aromatica Hook.f.	ANIaro	Native	Clonal	Low
Anisotome flexuosa J.W.Dawson	APIsp	Native	Clonal	Low
Chaerophyllum colensoi (Hook.f.) K.F.Chung	CHAcol	Native	Non-clonal	Low
Crepis capillaris (L.) Wallr.	CREcap	Exotic	Non-clonal	High
Ophioglossum coriaceum A.Cunn.	OPHcor	Native	Clonal	Low
Ranunculus foliosus Kirk	RANfol	Native	Clonal	Low
Herbaceous, elongated, leaf-bearing rhizomatous < 8 cm				
Hydrocotyle novae-zeelandiae DC.	HYDnov	Native	Clonal	Low
Viola cunninghamii Hook.f.	VIOcun	Native	Non-clonal	Low
Herbaceous, elongated, leaf-bearing rhizomatous > 8 cm				
Geranium sessiliflorum Cav.	GERses	Native	Non-clonal	Low
Pteridium esculentum (G.Forst.) Cockayne	PTEesc	Native	Clonal	Low
Thelymitra longifolia J.R.Forst. & G.Forst.	THElon	Native	Clonal	Low
Herbaceous, cushion plants				
Colobanthus strictus Cheeseman	COLstr	Native	Non-clonal	Low
Galium perpusillum (Hook.f.) Allan	GALper	Native	Clonal	Low
Gonocarpus Thunb.	GONOCA	Native	Non-clonal	Low
Nertera balfouriana Cockayne	NERbal	Native	Clonal	Low
Raoulia subsericea Hook.f.	RAOsbs	Native	Clonal	Low
Scleranthus biflorus (J.R.Forst. & G.Forst.) Hook.f.	SCLbif	Native	Non-clonal	Low
Herbaceous, extensive-stemmed herbs < 20 cm				

Life history category and botanical name	Code	Biostatus	Clonality	Meristem type
Anaphalioides bellidioides (G.Forst.) Glenny	ANAbel	Native	Non-clonal	Low
Cerastium fontanum Baumg.	CERfon	Exotic	Clonal	Low
Epilobium L.	EPILOB	Native	Non-clonal	Low
Euchiton audax (D.G.Drury) Holub	EUCaud	Native	Clonal	Low
Euphrasia zelandica Wettst.	EUPzel	Native	Non-clonal	High
Helichrysum filicaule Hook.f.	HELfil	Native	Clonal	Low
Prunella vulgaris L.	PRUvul	Exotic	Clonal	Low
Rumex acetosella L.	RUMace	Exotic	Clonal	Low
Trifolium dubium Sibth.	TRIdub	Exotic	Non-clonal	High
Herbaceous, extensive-stemmed herbs > 20 cm				
Acaena Mutis ex L.	ACAENA	Native	Clonal	Low
Achillea millefolium L.	ACHmil	Exotic	Clonal	Low
Centaurium erythraea Rafn.	CENery	Native	Clonal	Low
Dianthus armeria L.	DIAarm	Exotic	Non-clonal	High
Linum catharticum L.	LINcat	Exotic	Non-clonal	Low
Microtis unifolia (G.Forst.) Rchb.f.	MICuni	Native	Clonal	Low
Trifolium repens L.	TRIrep	Exotic	Clonal	Low
Verbascum thapsus L.	VERtha	Exotic	Non-clonal	Low
Herbaceous, tussocks				
Aciphylla aurea W.R.B.Oliv.	ACIaur	Native	Non-clonal	Low
Chionochloa rigida (Raoul) Zotov	CHIrig	Native	Non-clonal	Low
Festuca novae-zelandiae (Hack.) Cockayne	FESnov	Native	Non-clonal	Low
Herbaceous, graminoids < 15 cm				
Agrostis petriei Hack.	AGRpet	Native	Non-clonal	Low
Carex L.	CAREX	Native	Clonal	Low

Life history category and botanical name	**Code**	**Biostatus**	**Clonality**	**Meristem type**
Luzula rufa Edgar	LUZruf	Native	Non-clonal	Low
Herbaceous, graminoids < 15				
Agrostis capillaris L.	AGRcap	Exotic	Clonal	Low
Agrostis muelleriana Vickery	AGRmue	Native	Non-clonal	Low
Anthosachne solandri (Steud.) Barkworth & S.W.L.Jacobs	ANTsol	Native	Non-clonal	Low
Anthoxanthum odoratum L.	ANTodo	Exotic	Non-clonal	Low
Bromus diandrus Roth	BROdia	Native	Non-clonal	Others
Deyeuxia avenoides (Hook.f.) Buchanan	DEYave	Native	Non-clonal	Low
Dichelachne crinita (L.f.) Hook.f.	DICcri	Native	Non-clonal	Low
Festuca rubra L.	FESrub	Exotic	Clonal	Low
Holcus lanatus L.	HOLlan	Exotic	Clonal	Low
Lachnagrostis filiformis (G.Forst.) Trin.	LACfil	Native	Non-clonal	High
Poa colensoi Hook.f.	POAcol	Native	Non-clonal	Low
Poa lindsayi Hook.f.	POAlin	Native	Non-clonal	Low
Poa pratensis L.	POApra	Exotic	Clonal	Low
Rytidosperma Steud.	RYTIDO	Native	Clonal	Low
Schoenus pauciflorus (Hook.f.) Hook.f.	SCHpau	Native	Clonal	Low
Woody, prostrate shrubs				
Acrothamnus colensoi (Hook.f.) Quinn	ACRcol	Native	Non-clonal	High
Androstoma empetrifolium Hook.f.	ANDemp	Native	Non-clonal	High
Coprosma atropurpurea (Cockayne & Allan) L.B.Moore	COPatr	Native	Non-clonal	High
Gaultheria nubicola D.J.Middleton	GAUnub	Native	Non-clonal	High
Leucopogon fraseri A.Cunn.	LEUfra	Native	Non-clonal	High
Muehlenbeckia axillaris (Hook.f.) Endl.	MUEaxi	Native	Clonal	High

Life history category and botanical name	**Code**	**Biostatus**	**Clonality**	**Meristem type**
Pentachondra pumila (J.R.Forst. & G.Forst.) R.Br.	PENpum	Native	Non-clonal	High
Podocarpus nivalis Hook.	PODniv	Native	Non-clonal	High
Woody, dwarf shrub (subshrub)				
Gaultheria depressa Hook.f.	GAUdep	Native	Non-clonal	High
Lupinus polyphyllus Lindl.	LUPpol	Exotic	Clonal	Low
Pimelea oreophila C.J.Burrows	PIMore	Native	Clonal	Low
Woody, shrub and trees				
Aristotelia fruticosa Hook.f.	ARIfru	Native	Non-clonal	High
Coprosma propinqua A.Cunn.	COPpro	Native	Non-clonal	High
Discaria toumatou Raoul	DIStou	Native	non-clonal	High
Dracophyllum longifolium (J.R.Forst. & G.Forst.) R.Br. ex Roemer & Schult.	DRAlon	Native	Non-clonal	High
Leptospermum scoparium J.R.Forst. & G.Forst.	LEPsco	Native	Non-clonal	High
Cytisus scoparius (L.) Link	CYTsco	Exotic	Non-clonal	High
Rosa rubiginosa L.	ROSrub	Exotic	Clonal	High

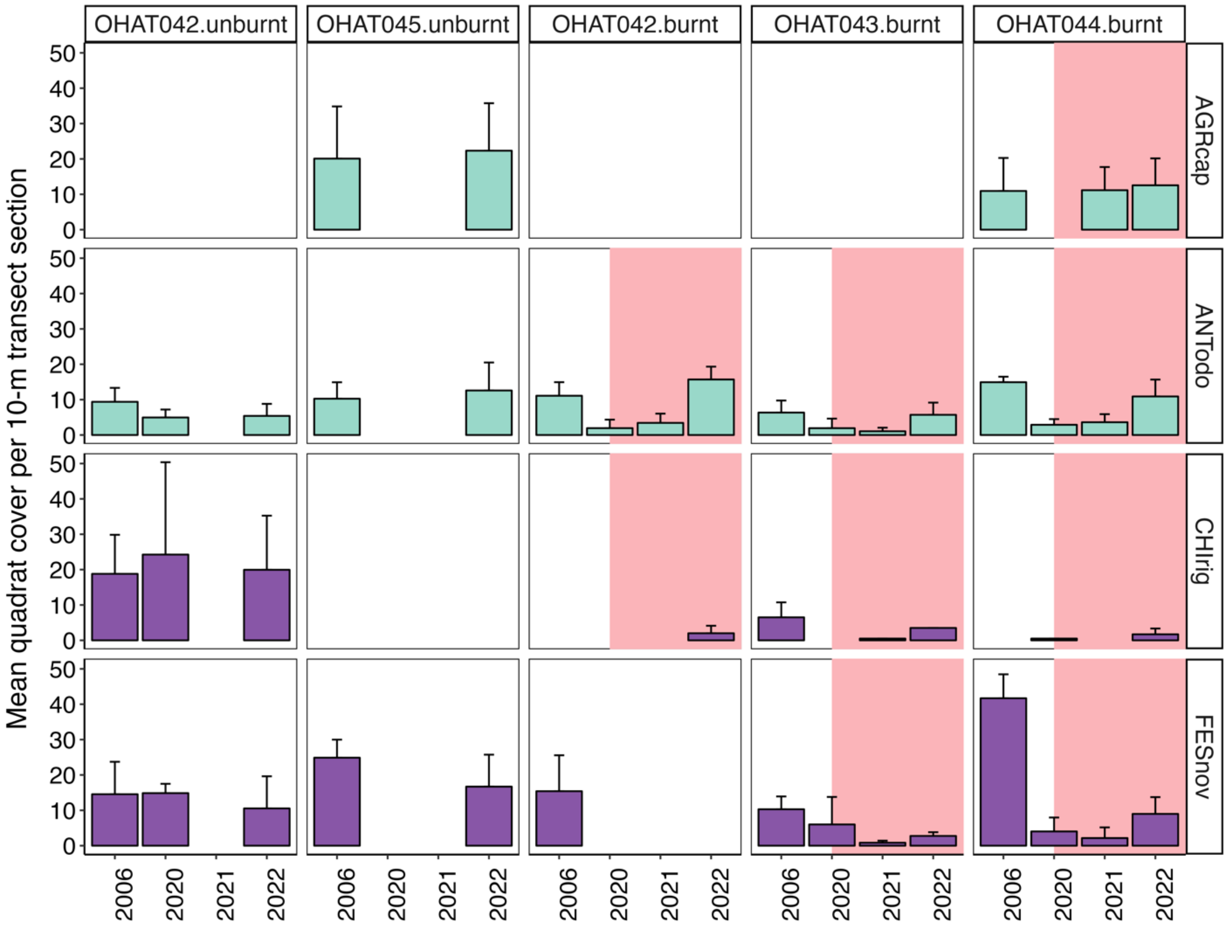


Figure S3.3. Bar graph showing mean percent cover (± one standard error) of four native (purple) and exotic (green) graminoid species recorded in 0.25-m^2 quadrats ($n = 5$) on 10-m sections of 100-m permanent transects at Lake Ōhau, Canterbury, South Island, New Zealand measured between 2006 and 2022. The background colour represents before (white) and after (red) the October 2020 wildfire. For *Chionochloa rigida* on OHAT043.burnt and OHAT044.burnt where it was present in only a single quadrat there are no error bars. *AGRcap* = *Agrostis capillaris*; *ANTodo* = *Anthoxanthum odoratum*; *CHIrig* = *Chionochloa rigida*; *FESnov* = *Festuca novae-zelandiae*

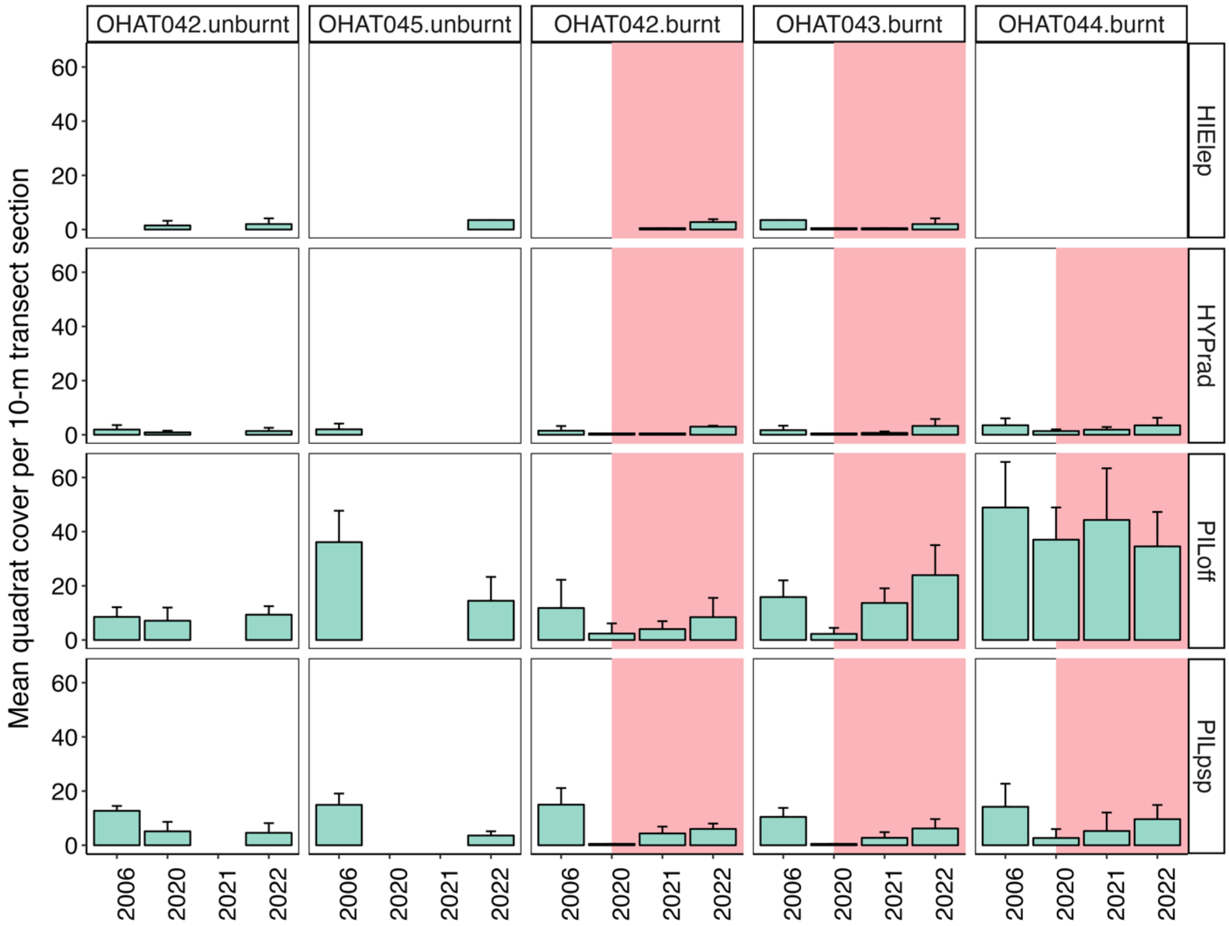


Figure S3.4. Bar graph showing mean percent cover (± one standard error) of four exotic forb species recorded in 0.25-m^2 quadrats (n = 5) on 10-m sections of 100-m permanent transects at Lake Ōhau, Canterbury, South Island, New Zealand measured between 2006 and 2022. The background colour represents before (white) and after (red) the October 2020 wildfire. For HIElep where it was present in only single quadrat has no error bars. *HIElep* = *Hieracium lepidulum*; *HYPrad* = *Hypochaeris radicata*; *PILoff* = *Pilosella officinarum*; *PILsp.* = *Pilosella piloselloides* subsp. *praealta*

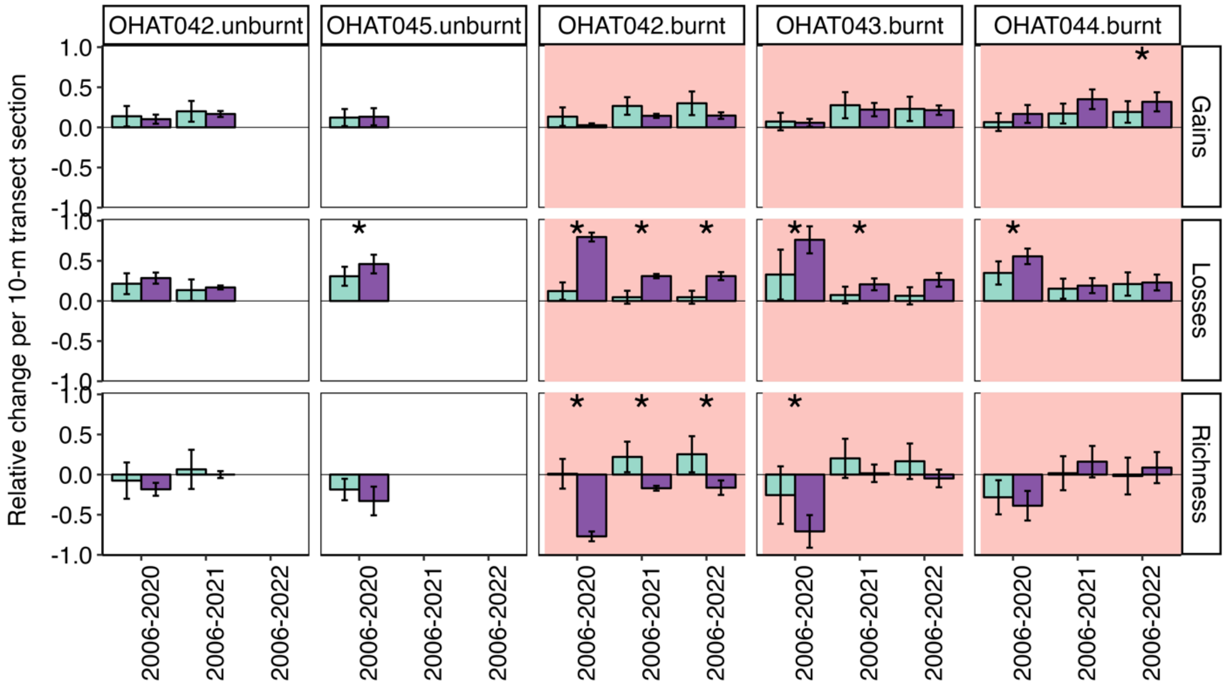


Figure S3.5. Comparisons between native (purple) and exotic (green) species in their relative community dynamics (± one standard error) within 0.25-m^2 quadrats within 10-m transect sections on 100-m transects at Lake Ōhau, Canterbury, South Island, New Zealand measured between 2006 and 2022. Each 10-m transect section comprised five quadrats. Relative changes in species gains, species losses, and species richness were calculated for each 10-m transect section on 100-m transects. The background colour represents before (white) and after (red) the October 2020 wildfire. Asterisks indicate significant differences between native and exotic changes, determined using generalised linear mixed-effects modelling ($P < 0.05$)

Figure S4.1. Map of the study area with transect locations at Arthur's Pass, New Zealand shown as labelled, coloured points (source: Eagle Technology, LINZ and Earthstar Geographics)

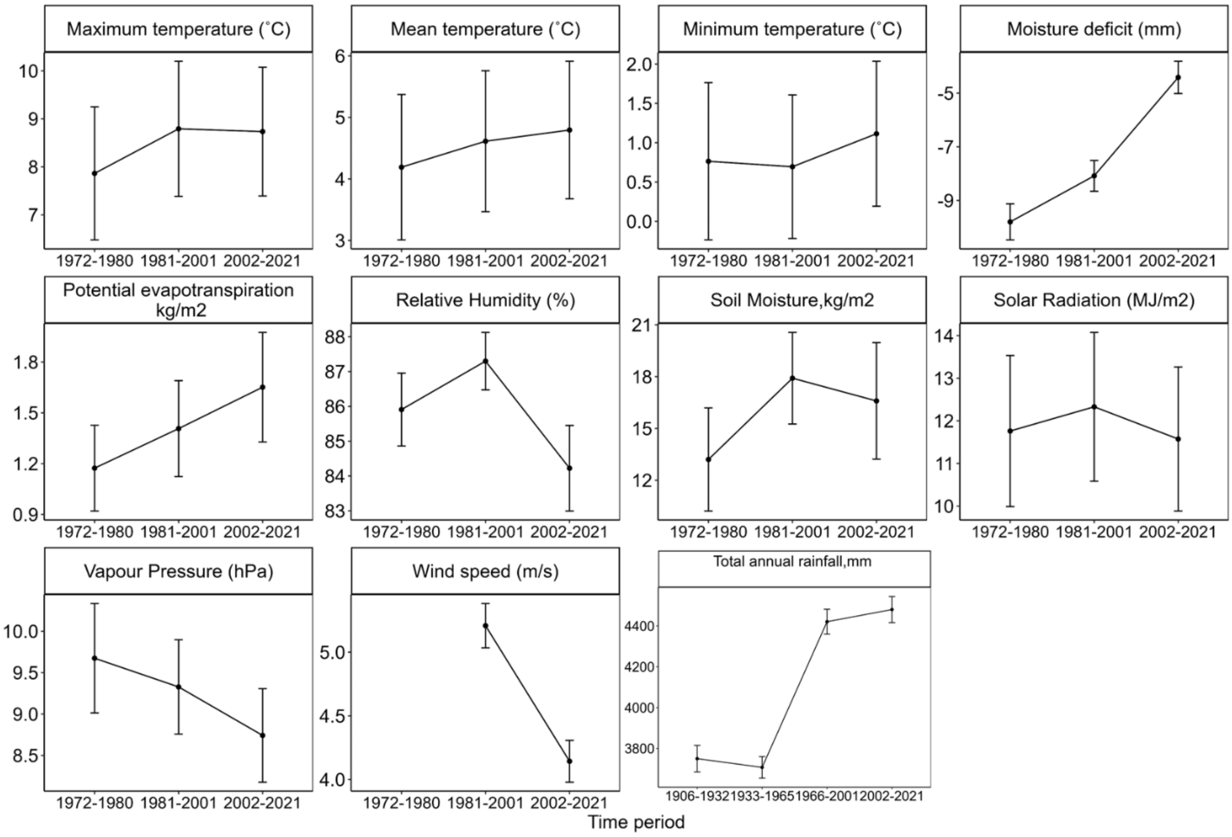


Figure S4.2. Climate variables recorded at Arthur’s Pass at Arthur’s Pass, New Zealand between 1906 and 2021. Total annual rainfall was recorded over the longest time period (115 y). In contrast, average annual wind speed was recorded for only 24 y. Other recorded variables covered 49 years and include annual potential evapotranspiration, annual relative humidity, annual solar radiation, annual vapour pressure, annual moisture deficit, annual maximum, minimum and mean temperatures. Relative soil moisture was recorded as the moisture in the soil at an average depth (cm), expressed as a percentage by volume

Table S4.1. Species recorded in transects at Arthur's Pass, New Zealand sampled between 1932 and 2018. All 134 species were categorised into thirteen groups based on plant life form, clonality (Padullés Cubino et al., 2018; Pérez-Harguindeguy et al., 2013) and height (http://nzflora.info)). Species names and codes were taken from Flora of New Zealand the (http://nzflora.info) and New Zealand Plant Conservation Network (https://www.nzpcn.org.nz). Species without * are those for which flammability data were not collected, * represents species with flammability data and burnt during this study, and ** represents species with flammability data collated from prior research

Species name and growth form:	**Code**
Herbaceous, rosette plants < 20 cm	
Anisotome imbricata (Hook.f.) Cockayne	ANIimb
Aporostylis bifolia (Hook.f.) Rupp & Hatch*	APObif
Brachyglottis bellidioides (Hook.f.) B.Nord.*	BRAbel
Brachyscome Cass.**	BRAchy
Cardamine dolichostyla Heenan	CARdlc
Cardamine L.	CARdam
Celmisia discolor Hook.f.*	CELdis
Celmisia glandulosa Hook.f.	CELgla
Craspedia G.Forst.**	CRAspe
Gentiana Moench	GENtia
Lagenophora strangulata Colenso	LAGstr
Leptinella squalida Hook.f.**	LEPsqu
Microseris D.Don	MICros
Orchid	ORChid
Oreomyrrhis Hook.f.	OREomy
Ourisia macrocarpa Hook.f.*	OURmcc
Ourisia macrophylla Hook.	OURmap
Plantago L.	PLAnta
Viola lyallii Hook.f.*	VIOla
Wahlenbergia albomarginata Hook.**	WAHalb
Wahlenbergia gracilis (G.Forst.) A.DC.	WAHgra
Herbaceous, rossette plants < 20 cm	
Anisotome aromatica Hook.f.*	ANIaro
Anisotome haastii (F.Muell.) Cockayne & Laing*	ANIhaa
Astelia nervosa Hook.f.*	ASTner
Celmisia armstrongii Petrie*	CELarm
Celmisia coriacea (G.Forst.) Hook.f.	CELcor
Celmisia durietzii Cockayne & Allan	CELdur

Species name and growth form:	**Code**
Celmisia gracilenta Hook.f.*	CELgra
Celmisia semicordata Petrie	CELsem
Celmisia spectabilis Hook.f.	CELspe
Celmisia verbascifolia Hook.f.*	CELver
Gingidia montana (J.R.Forst. & G.Forst.) J.W.Dawson	ANGmon
Hieracium lepidulum (Stenstr.) Omang*	HIElep
Mycelis muralis (L.) Dumort.	MYCmur
Phormium cookianum Le Jol.*	PHOcoo
Ranunculus lyallii Hook.f.	RANhir
Ranunculus reflexus Garn.-Jones	RANlya
Hypochaeris radicata L.*	HYPrad
Herbaceous, elongated, leaf-bearing rhizomatous < 8 cm	
Hydrocotyle novae-zeelandiae DC.*	HYDnov
Herbaceous, elongated, leaf-bearing rhizomatous > 8 cm	
Hypolepis millefolium Hook.	HYPmil
Blechnum fluviatile (R.Br.) Lowe ex Salomon	BLEflu
Blechnum minus (R.Br.) Ettingsh.*	BLEmin
Blechnum penna-marina (Poir.) Kuhn*	BLEpen
Geranium L.**	GERani
Notogrammitis billardierei (Willd.) Parris	NOTbil
Polystichum vestitum (G.Forst.) C.Presl	POLves
Growth form: Herbaceous, cushion plants	
Gonocarpus aggregatus (Buchanan) Orchard*	GONagg
Galium perpusillum (Hook.f.) Allan	GALper
Herbaceous, extensive-stemmed herbs < 20 cm	
Anaphalioides bellidioides (G.Forst.) Glenny	ANAbel
Epilobium alsinoides subsp. *atriplicifolium* (A.Cunn.) P.H.Raven & Engelhorn	EPIatr
Epilobium glabellum G.Forst.	EPIgla
Epilobium L.	EPIlob
Epilobium nerteroides A.Cunn.	EPIner
Epilobium nummulariifolium R.Cunn.	EPInum
Epilobium pedunculare A.Cunn.	EPIped
Euphrasia cockayneana Petrie	EUPcoc
Forstera tenella Hook.f.	FORten
Lycopodium scariosum G.Forst.*	LYCsca

Species name and growth form:	Code
Herbaceous, extensive-stemmed herbs > 20 cm	
Acaena Mutis ex L.**	ACAena
Cirsium vulgare (Savi) Ten.	CIRlan
Dolichoglottis lyallii (Hook.f.) B.Nord.*	DOLlya
Huperzia australiana (Herter) Holub	HUPaus
Lobelia angulata G.Forst.	LOBang
Luzuriaga parviflora (Hook.f.) Kunth	LUZpar
Lycopodium fastigiatum R.Br.*	LYCfas
Phlegmariurus varius (R.Br.) A.R.Field & Bostock	PHLvar
Tussocks	
Chionochloa conspicua (G.Forst.) Zotov*	CHIcon
Chionochloa rubra Zotov*	CHIrub
Chionochloa Zotov**	CHIono
Festuca matthewsii (Hack.) Cheeseman	FESmat
Graminoids > 15 cm	
Juncus L.	JUNcus
Graminoids < 15 cm	
Agrostis L.**	AGRost
Carex corynoidea K.A.Ford*	CARex
Carpha alpina R.Br.*	CARalp
Deyeuxia aucklandica (Hook.f.) Zotov	DEYauc
Deyeuxia avenoides (Hook.f.) Buchanan*	DEYave
Koeleria cheesemanii (Hack.) Petrie	KOEche
Luzula picta A.Rich.	LUZpic
Oreobolus strictus Berggr.	OREstr
Poa colensoi Hook.f.*	POAcol
Rytidosperma Steud.	RYTido
Zotovia colensoi (Hook.f.) Edgar & Connor	ZOTcol
Graminoids < 15-90 cm	
Hierochloe R.Br.	HIEroc
Holcus lanatus L.	HOLlan
Microlaena avenacea (Raoul) Hook.f.	MICave
Schoenus pauciflorus (Hook.f.) Hook.f.*	SCHpau
Woody, prostrate shrubs	

Species name and growth form:	**Code**
Androstoma empetrifolium Hook.f.	ANDemp
Coprosma cheesemanii W.R.B.Oliv.*	COPche
Coprosma perpusilla Colenso	COPper
Lepidothamnus laxifolius (Hook.f.) Quinn	LEPlax
Muehlenbeckia axillaris (Hook.f.) Endl.**	MUEaxi
Myrsine nummularia (Hook.f.) Hook.f.*	MYRnum
Pentachondra pumila (J.R.Forst. & G.Forst.) R.Br.*	PENpum
Podocarpus nivalis Hook.*	PODniv
Woody, dwarf shrub (subshrub)	
Coprosma serrulata Hook.f. ex Buchanan*	COPser
Gaultheria antipoda G.Forst.	GAUant
Gaultheria rupestris (L.f.) D.Don*	GAUrup
Pimelea lyallii Hook.f.	PIMlya
Pimelea oreophila C.J.Burrows**	PIMore
Woody, shrub and trees	
Aristotelia fruticosa Hook.f.**	ARIfru
Brachyglottis elaeagnifolia (Hook.f.) B.Nord.*	BRAela
Clematis paniculata J.F.Gmel.	CLEpan
Coprosma ciliata Hook.f.	COPcil
Coprosma colensoi Hook.f.	COPcol
Coprosma crenulata W.R.B.Oliv.	COPcre
Coprosma depressa Colenso ex Hook.f.*	COPdep
Coprosma foetidissima J.R.Forst. & G.Forst.*	COPfoe
Coprosma pseudociliata G.T.Jane	COPpsc
Coprosma pseudocuneata W.R.B.Oliv. ex Garn.-Jones & Elder*	COPpse
Coprosma rugosa Cheeseman	COPrug
Coprosma dumosa (Cheeseman) G.T.Jane*	COPdmo
Coprosma J.R.Forst. & G.Forst.	COPros
Dracophyllum longifolium (J.R.Forst. & G.Forst.) R.Br. ex Roemer & Schult.*	DRAlon
Dracophyllum traversii Hook.f.*	DRAtra
Dracophyllum uniflorum Hook.f.*	DRAuni
Fuscospora cliffortioides (Hook.f.) Heenan & Smissen*	FUScli
Griselinia littoralis (Raoul) Raoul**	GRIlit
Hoheria glabrata Sprague & Summerh.**	HOHgla
Melicytus alpinus (Kirk) Garn.-Jones**	MELalp
Myrsine divaricata A.Cunn.*	MYRdiv
Olearia arborescens (G.Forst.) Cockayne & Laing	OLEarb

Species name and growth form:	**Code**
Olearia colensoi Hook.f.	OLEcol
Olearia ilicifolia Hook.f.**	OLEili
Olearia lacunosa Hook.f.	OLElac
Olearia nummulariifolia (Hook.f.) Hook.f.	OLEnum
Ozothamnus leptophyllus (G.Forst.) Breitw. & J.M.Ward*	OZOlep
Phyllocladus alpinus Hook.f.*	PHYalp
Pittosporum divaricatum Cockayne**	PITdiv
Podocarpus laetus Hooibr. ex Endl.	PODlae
Pseudopanax colensoi (Hook.f.) Philipson*	NEOcol
Pseudopanax crassifolius (Sol. ex A.Cunn.) K.Koch**	PSEcra
Raukaua simplex (G.Forst.) A.D.Mitch., Frodin & Heads	RAUsim
Veronica canterburiensis J.B.Armstr.*	VERcan
Veronica subalpina Cockayne*	VERsub

Table S4.2. Mean (± standard error) flammability traits for each of the 67 species. *n* is number of individuals measured for each species. Ignitability a measure of inverse of time taken by the sample to ignite, combustibility a measure of maximum temperature released when a sample burns, sustainability a burning time and consumability a visually estimated burnt biomass. A temperature 150˚C was assigned to those species which did not ignite during experimental burning, which was the temperature of the grill. Life history category is the simplified set of classes based on 14 groups (Table S4.1, Appendix A)

Species code	**Life history category**	***n***	**Ignitability (s)**	**Combustiblity (˚C)**	**Sustainability (s)**	**Consumability (%)**
ACAena	Extensive stemmed herb	8	9.31 ± 0.09	433 ± 79.58	6 ± 2.03	64.38 ± 14.41
AGRost	Graminoids	16	9.47 ± 0.03	198.31 ± 26.48	1.44 ± 1.13	17.5 ± 9.46
ANIaro	Rosette	6	1 ± 0	150 ± 0	0 ± 0	0 ± 0
ANIhaa	Rosette	6	1 ± 0	150 ± 0	0 ± 0	0 ± 0
APObif	Rosette	6	1 ± 0	150 ± 0	0 ± 0	0 ± 0
ARIfru	Tall shrubs and trees	8	4.27 ± NA	200.88 ± 21.04	2.25 ± 0.92	7.88 ± 2.5
ASTner	Rosette	6	3.5 ± 1.59	202.17 ± 34.77	30.33 ± 22.98	2.83 ± 2.46
BLEmin	Rhizomatous	6	6.5 ± 1.31	460.83 ± 74.72	11.17 ± 5.47	29.17 ± 7
BLEpen	Rhizomatous	6	1 ± 0	150 ± 0	0 ± 0	0 ± 0
BRAbel	Rosette	6	1 ± 0	150 ± 0	0 ± 0	0 ± 0
BRAchy	Rosette	8	7.94 ± 1.02	150 ± 0	0 ± 0	0 ± 0
BRAela	Tall shrubs and trees	6	1.5 ± 0.34	166.17 ± 14.26	1 ± 0.68	1.5 ± 1.31
CARalp	Graminoids	6	7.5 ± 1.31	271.5 ± 28.13	6.33 ± 1.78	38.83 ± 10.39
CARcor	Graminoids	8	3 ± 1.31	162.88 ± 9.12	1.38 ± 0.94	22.5 ± 14.73
CELarm	Rosette	6	7.83 ± 0.6	467.67 ± 68.87	79.83 ± 38.59	21.5 ± 6.37
CELdis	Rosette	6	9 ± 0	451.33 ± 20.66	37.67 ± 11.9	75.83 ± 10.12
CELgra	Rosette	6	1.67 ± 0.67	195 ± 45	4 ± 4	2.5 ± 2.5
CELver	Rosette	6	6.17 ± 1.64	235.17 ± 41.13	5.33 ± 1.91	48.33 ± 15.74
CHIcon	Tussocks	6	8.67 ± 0.33	419.33 ± 40.99	93.5 ± 17.99	11.17 ± 5.23

Species code	**Life history category**	***n***	**Ignitability (s)**	**Combustiblity (˚C)**	**Sustainability (s)**	**Consumability (%)**
CHIrub	Tussocks	7	6.43 ± 1.41	553.43 ± 24.8	162.71 ± 24.47	49.71 ± 9.65
COPche	Prostrate shrubs	6	6 ± 1.59	216.33 ± 23.71	6.5 ± 3.16	15 ± 5.16
COPdep	Tall shrubs and trees	6	8 ± 0.77	250.6 ± 44.28	11 ± 4.93	20 ± 6.9
COPdmo	Tall shrubs and trees	9	6 ± 1.26	282.67 ± 35.67	16.89 ± 4.55	6.11 ± 2.51
COPfoe	Tall shrubs and trees	6	1.5 ± 0.5	167.5 ± 11.34	1.33 ± 0.88	0.33 ± 0.21
COPpse	Tall shrubs and trees	5	7 ± 1.05	294.6 ± 32.98	9.6 ± 3.25	10 ± 3.7
COPser	Dwarf shrubs	6	1.17 ± 0.17	152.67 ± 2.67	0.67 ± 0.67	0.33 ± 0.33
DEYave	Graminoids	8	9.5 ± 0	375.88 ± 25.41	8.62 ± 1.73	83.38 ± 3.53
DOLlya	Extensive stemmed herb	6	1.33 ± 0.33	165.33 ± 15.33	0.67 ± 0.67	0.5 ± 0.5
DRAlon	Tall shrubs and trees	6	8.17 ± 0.65	451.17 ± 76.68	48 ± 13.41	26.17 ± 8.89
DRAtra	Tall shrubs and trees	5	2.8 ± 1.11	308.4 ± 42.11	22.8 ± 11.13	3.2 ± 1.77
DRAuni	Tall shrubs and trees	6	8.17 ± 0.54	415.17 ± 94.22	49.83 ± 14.38	30.83 ± 13.86
FUScli	Tall shrubs and trees	6	8.5 ± 0.22	417.5 ± 54.52	26.83 ± 6.86	21.83 ± 9.82
GAUrup	Dwarf shrubs	6	8.67 ± 0.21	433.5 ± 44.13	18.17 ± 6.15	30 ± 7.42
GERani	Rhizomatous	16	5.97 ± 1	186.25 ± 24.81	0.31 ± 0.25	11.56 ± 7.93
GONagg	Cushion	6	1 ± 0	150 ± 0	0 ± 0	0 ± 0
GRIlit	Tall shrubs and trees	36	3.45 ± 0.51	284.01 ± 20.11	5 ± 0.87	5.83 ± 1.66
HIElep	Rosette	6	1.17 ± 0.17	199.17 ± 49.17	3 ± 3	14.17 ± 14.17
HOHgla	Tall shrubs and trees	26	6.4 ± 0.69	285.62 ± 25.5	5.27 ± 1.41	14.88 ± 2.66
HYDnov	Rhizomatous	6	1 ± 0	150 ± 0	0 ± 0	0 ± 0
HYPrad	Rosette	6	2.17 ± 1.17	166.17 ± 16.17	1 ± 1	0.83 ± 0.83
LEPsqu	Rosette	8	9.12 ± 0.18	150 ± 0	0 ± 0	0 ± 0
LUZpic	Graminoids	16	9.25 ± 0.1	291.75 ± 41.81	2.12 ± 0.77	43.12 ± 12.63
LYCfas	Extensive stemmed herb	6	3.83 ± 1.64	201.17 ± 35.39	3.67 ± 2.54	18.83 ± 10.74
LYCsca	Extensive stemmed herb	6	8.83 ± 0.17	497.33 ± 35.95	44.33 ± 15.71	55.17 ± 14.2

Species code	**Life history category**	***n***	**Ignitability (s)**	**Combustiblity (˚C)**	**Sustainability (s)**	**Consumability (%)**
MELalp	Dwarf shrubs	39	5.5 ± 0.09	280.72 ± 23.75	5.54 ± 1.2	9.1 ± 2.01
MUEaxi	Prostrate shrubs	12	2.17 ± 0.47	158.83 ± 7.21	1.83 ± 0.79	4.17 ± 1.61
MYRdiv	Tall shrubs and trees	6	3.67 ± 1.69	201 ± 31.61	3.5 ± 2.06	0.83 ± 0.4
MYRnum	Prostrate shrubs	6	8.33 ± 0.21	465.67 ± 40.25	14.17 ± 2.2	54.17 ± 15.41
NEOcol	Tall shrubs and trees	26	5.75 ± 0.12	478.5 ± 23	18.81 ± 3.03	22.69 ± 2.73
OLEarb	Tall shrubs and trees	6	2.33 ± 1.33	170 ± 20	1.67 ± 1.67	2.5 ± 2.5
OURmap	Rosette	6	8.83 ± 0.17	348 ± 43.05	31.33 ± 9.55	20.67 ± 4.67
OZOlep	Tall shrubs and trees	6	3.5 ± 1.59	270.17 ± 76.58	7.5 ± 5.74	32.5 ± 20.56
PENpum	Prostrate-shrubs	6	5.67 ± 1.8	443.83 ± 73.37	218.33 ± 128.52	20 ± 9.75
PHOcoo	Rosette	6	7.83 ± 0.48	625 ± 61.47	136 ± 38.39	53.83 ± 11.97
PHYalp	Tall shrubs and trees	9	8.39 ± 0.23	609.22 ± 39.73	15.78 ± 3.24	69.44 ± 7.61
PIMore	Dwarf shrubs	6	4.83 ± 1.3	185.17 ± 15.2	5.83 ± 2.12	0.67 ± 0.49
PITdiv	Tall shrubs and trees	6	5 ± 1.79	159.17 ± 4.78	3.33 ± 1.74	49.17 ± 22
POAcol	Graminoids	6	8 ± 0.63	428.33 ± 88.88	41.67 ± 22.4	24.67 ± 11.36
PODniv	Prostrate shrubs	6	8.5 ± 0.22	429 ± 58.17	32.5 ± 13.08	36.33 ± 10.02
POLves	Rhizomatous	6	1.83 ± 0.65	253.83 ± 66.42	11.67 ± 7.74	1.17 ± 0.83
PSEcra	Tall shrubs and trees	23	0.8 ± 0.09	170.13 ± 12.78	0.87 ± 0.48	0.83 ± 0.48
RYTido	Graminoids	8	9.5 ± 0	215 ± 42.74	1.12 ± 0.87	23.5 ± 15.4
SCHpau	Graminoids	6	8.83 ± 0.17	338.17 ± 37.73	9.67 ± 2.64	18.33 ± 5.27
VERcan	Tall shrubs and trees	6	6.5 ± 0.22	344.17 ± 33.26	18.17 ± 6.28	30.83 ± 12.16
VERsub	Tall shrubs and trees	6	7.5 ± 0.43	277.5 ± 29.47	33 ± 17.61	10.83 ± 3.16
VIOlya	Rosette	6	1 ± 0	150 ± 0	0 ± 0	0 ± 0
WAHalb	Rosette	8	6.25 ± 1.54	150 ± 0	0 ± 0	0 ± 0

Table S4.3. Mean (± standard error) morphological trait values for the 57 species for which I had measured trait data. Names of traits are based on abbreviations of the morphological traits are leaf length (LL cm), leaf thickness (LT mm), leaf area (LA cm^2), specific leaf area (SLA, cm^2/g), leaf dry matter content (LDMC g), bulk density (BD) cm^3, % moisture content (MC), shoot dry matter content (SDMC g), % dead material mass (Dm). Code represents species abbreviations based on first three letter from the genus and specific epithet (Table S4.1, Appendix A)

Code	**LA**	**LL**	**LT**	**LDMC**	**SLA**	**SDMC**	**BD**	**MC**	**Dm**
ACAena	0.01 ± 0	0.11 ± 0	0.19 ± 0	4.4 ± NA	145.67 ± NA	0.41 ± 0	2.84 ± 1.3	149.16 ± 11.9	43.75 ± 7.1
AGRost	0 ± 0	0.43 ± 0	0.3 ± 0	0.85 ± 0	211.36 ± 28	0.43 ± 0	4.14 ± 1.6	160.07 ± 26.9	24.38 ± 3.5
ANIaro	0.25 ± 0	0.68 ± 0.1	0.02 ± 0	0.31 ± 0	175.15 ± 10.6	0.23 ± 0	36.33 ± 10.5	278.77 ± 8.7	0 ± 0
ANIhaa	1.41 ± 0.4	1.51 ± 0.1	0.02 ± 0	0.31 ± 0	289.42 ± 37.2	0.24 ± 0	235.33 ± 61.9	252.86 ± 13.4	0 ± 0
APObif	3.35 ± 0.9	4.68 ± 0.7	0.04 ± 0	0.1 ± 0	322.31 ± 72.1	0.11 ± 0	4.33 ± 1	781.5 ± 86	0 ± 0
ASTner	176.87 ± 42.6	65.27 ± 8.4	0.1 ± 0	0.32 ± 0	68.89 ± 10.8	0.29 ± 0	11354.33 ± 3206.5	236.9 ± 25.7	11.67 ± 7.5
BLEmin	16.58 ± 1.3	11.04 ± 0.3	0.03 ± 0	0.34 ± 0	125.35 ± 18.9	0.32 ± 0	16056.67 ± 1614.2	194.85 ± 23.2	2 ± 1.6
BLEpen	0.25 ± 0	0.58 ± 0.1	0.02 ± 0	0.34 ± 0	170.87 ± 15.1	0.3 ± 0	137 ± 25.2	200.01 ± 6.4	0 ± 0
BRAbel	2.24 ± 0.3	2.21 ± 0.2	0.05 ± 0	0.17 ± 0	116.57 ± 9.3	0.39 ± 0.2	20.5 ± 5	386.03 ± 32.3	0 ± 0
BRAchy	0.01 ± 0	0.25 ± 0	0.29 ± 0	9.1 ± NA	86.5 ± NA	0.42 ± 0	1.62 ± 0.3	148.17 ± 21.6	1.88 ± 1.3
BRAela	24.2 ± 1.6	7.75 ± 0.4	0.05 ± 0	0.26 ± 0	93.37 ± 15.2	0.26 ± 0	42409 ± 6073.9	298.61 ± 34.7	0.83 ± 0.7
CARalp	2.71 ± 0.3	9.8 ± 0.7	0.06 ± 0	0.29 ± 0	142.72 ± 14.6	0.26 ± 0	864.83 ± 208.5	181.87 ± 24.8	1.33 ± 0.9
CARcor	13.66 ± 3.4	32.2 ± 3	0.03 ± 0	0.46 ± 0.1	251.11 ± 20.3	0.28 ± 0	1166 ± 300.4	229.05 ± 15.4	6.88 ± 4.4
CELarm	29.57 ± 4.3	21.79 ± 1.8	0.05 ± 0	0.36 ± 0	54.89 ± 6.4	0.31 ± 0	18687 ± 3700.8	233.5 ± 88.1	8.5 ± 3.9
CELdis	1.56 ± 0.1	2.07 ± 0.1	0.04 ± 0	0.38 ± 0	71.56 ± 4.2	0.34 ± 0	783.33 ± 187.4	97.3 ± 20	25.67 ± 6.2

Code	LA	LL	LT	LDMC	SLA	SDMC	BD	MC	Dm
CELgra	14.61 ± 2.3	6.9 ± 0.7	0.05 ± 0	0.29 ± 0	79.03 ± 9.1	0.23 ± 0	127.33 ± 38	313.4 ± 35.5	6.67 ± 4.9
CELver	1.62 ± 0.2	7.07 ± 0.7	0.03 ± 0	0.25 ± 0	108.44 ± 9.9	0.26 ± 0	403.17 ± 142.9	259.54 ± 21.7	13.67 ± 7
CHIcon	30.35 ± 5.4	94.42 ± 4.5	0.04 ± 0	0.43 ± 0	24.56 ± 2.3	0.38 ± 0	23496.67 ± 2267.2	149.22 ± 10.2	45 ± 5
CHIrub	3.86 ± 0.4	81.85 ± 5.5	0.05 ± 0	0.46 ± 0	8.61 ± 0.7	0.47 ± 0	11990 ± 1269.3	99.2 ± 5.2	27 ± 8.1
COPche	1.35 ± 0.4	0.83 ± 0.1	0.03 ± 0	0.41 ± 0	866.85 ± 222.1	0.39 ± 0	20474 ± 8123.2	125.66 ± 6.8	0.17 ± 0.2
COPdep	0.28 ± 0	0.97 ± 0.1	0.03 ± 0	0.32 ± 0	126.77 ± 12.5	0.37 ± 0	34154.8 ± 9647.7	139.18 ± 20.6	0 ± 0
COPdmo	0.34 ± 0.1	0.83 ± 0.1	0.03 ± 0	0.32 ± 0	175.94 ± 42.6	0.4 ± 0	52018.89 ± 10505.2	118.31 ± 5.8	0.22 ± 0.1
COPfoe	3.84 ± 0.3	3.56 ± 0.1	0.03 ± 0	0.25 ± 0	159.78 ± 9.4	0.29 ± 0	55195 ± 7311.6	235.49 ± 12.6	0 ± 0
COPpse	0.32 ± 0.1	1.15 ± 0.1	0.04 ± 0	0.36 ± 0	96.7 ± 26	0.34 ± 0	36111.6 ± 13490.4	169.45 ± 17.8	0.4 ± 0.2
COPser	8.08 ± 1.1	4.18 ± 0.3	0.06 ± 0	0.35 ± 0	51.51 ± 2.2	0.32 ± 0	6978.67 ± 975.3	190.69 ± 18.3	0 ± 0
DEYave	0 ± 0	0.93 ± 0	0.3 ± 0	2.5 ± NA	59.74 ± NA	0.64 ± 0.1	3.46 ± 1	64.8 ± 16.5	30 ± 2.8
DOLlya	4.06 ± 0.8	15.13 ± 1.5	0.08 ± 0	0.12 ± 0	122.24 ± 7.3	0.13 ± 0	277.33 ± 130	605.61 ± 38.4	1 ± 0.8
DRAlon	1.31 ± 0.2	9 ± 0.8	0.04 ± 0	0.54 ± 0	58.83 ± 13.8	0.57 ± 0.1	19220 ± 2153	85.1 ± 2.8	1 ± 0.4
DRAtra	104.19 ± 8	52.59 ± 1.7	0.06 ± 0	0.47 ± 0	53.57 ± 2.8	0.39 ± 0	86366 ± 15208.9	124.95 ± 6.3	0.8 ± 0.8
DRAuni	0.48 ± 0.1	3.8 ± 0.1	0.04 ± 0	0.5 ± 0	88.1 ± 25.3	0.49 ± 0	12976.67 ± 1435.8	87.31 ± 9	3.33 ± 1.5
FUScli	0.59 ± 0.1	1.08 ± 0.1	0.03 ± 0	0.43 ± 0	106.67 ± 4.9	0.38 ± 0.1	54110 ± 13681.2	112.87 ± 7	0.5 ± 0.3
GAUrup	0.98 ± 0.1	1.73 ± 0.1	0.06 ± 0	0.39 ± 0	44.73 ± 2.9	0.37 ± 0	9224 ± 1175.3	144.03 ± 8.3	2.5 ± 1.1
GONagg	0.41 ± 0.1	0.99 ± 0.1	0.02 ± 0	0.26 ± 0	193.56 ± 14.4	0.24 ± 0	19 ± 7.2	255.07 ± 43.3	0 ± 0
HIElep	12.32 ± 2.5	7.81 ± 1	0.02 ± 0	0.15 ± 0	303.63 ± 21.1	0.14 ± 0	302.33 ± 81.6	491.45 ± 75.9	5 ± 5
HYDnov	1.33 ± 0.4	0.82 ± 0.1	0.03 ± 0	0.15 ± 0	286.65 ± 40.2	0.13 ± 0	2.33 ± 0.6	583.41 ± 41.6	0 ± 0
HYPrad	9.14 ± 1.1	8.11 ± 0.8	0.03 ± 0	0.15 ± 0	182.7 ± 14.1	0.14 ± 0	746 ± 249.5	599.97 ± 65.4	0 ± 0
LYCfas	0.03 ± 0	0.54 ± 0	0.02 ± 0	0.43 ± 0	144.67 ± 18.8	0.34 ± 0	1639 ± 479.1	152.78 ± 12.7	0 ± 0
LYCsca	0.04 ± 0	0.42 ± 0	0.05 ± 0	0.37 ± 0	127.43 ± 16.5	0.37 ± 0	5063 ± 1932.8	157.73 ± 4.5	0 ± 0

Code	**LA**	**LL**	**LT**	**LDMC**	**SLA**	**SDMC**	**BD**	**MC**	**Dm**
MYRdiv	0.66 ± 0.1	1.02 ± 0	0.02 ± 0	0.31 ± 0	158.52 ± 5.7	0.34 ± 0.1	87608.33 ± 11664.7	127.12 ± 16.3	0.17 ± 0.2
MYRnum	1.57 ± 0.7	0.86 ± 0	0.03 ± 0	0.41 ± 0	317.88 ± 149.9	0.43 ± 0	3203.17 ± 1405.4	113.43 ± 4.3	0.5 ± 0.3
NEOcol	24.07 ± 3.3	8.46 ± 0.6	0.06 ± 0	0.4 ± 0	51.51 ± 4	0.37 ± 0	32990 ± 9693.5	163.89 ± 6.6	0 ± 0
OURmap	47.46 ± 8.2	9.7 ± 0.8	0.06 ± 0	0.21 ± 0	100.64 ± 13.9	0.18 ± 0	487.67 ± 177.9	460 ± 27.1	0 ± 0
OZOlep	0.24 ± 0.1	0.82 ± 0	0.03 ± 0	0.38 ± 0	105.57 ± 25.4	0.37 ± 0	26035.33 ± 5956.7	126.52 ± 7.7	2.33 ± 0.8
PENpum	0.05 ± 0	0.47 ± 0	0.02 ± 0	0.47 ± 0.1	97.76 ± 29.9	0.47 ± 0	326.67 ± 76	72.77 ± 3	0 ± 0
PHOcoo	294.93 ± 69	74.06 ± 5	0.08 ± 0	0.4 ± 0	30.34 ± 4.8	0.39 ± 0	13113.33 ± 2882	122.49 ± 11.2	35 ± 8.5
PHYalp	1.68 ± 0.2	2.55 ± 0.1	0.06 ± 0	0.47 ± 0	46.44 ± 3.8	0.43 ± 0	41736 ± 6820.3	113.99 ± 7.2	0.83 ± 0.3
PIMore	0 ± 0	0.08 ± 0	0.32 ± 0	0.5 ± NA	85 ± NA	0.42 ± 0	2.65 ± 0.7	145.07 ± 17	23.33 ± 4.7
PITdiv	0.25 ± 0	1.05 ± 0.1	0.02 ± 0	0.39 ± 0	96.67 ± 8.2	0.46 ± 0	33833.33 ± 10356.8	106.47 ± 6.7	10.5 ± 9.9
POAcol	0.26 ± 0	5.66 ± 0.4	0.03 ± 0	0.44 ± 0	89.33 ± 9.6	0.36 ± 0	42.33 ± 16	152.13 ± 14.9	0.5 ± 0.3
PODniv	0.21 ± 0	1.13 ± 0.1	0.04 ± 0	0.4 ± 0	71.37 ± 12.1	0.41 ± 0	52130.83 ± 21236.5	113.19 ± 13.5	0 ± 0
POLves	0.43 ± 0.1	1.01 ± 0.1	0.03 ± 0	0.33 ± 0	178.86 ± 45.5	0.33 ± 0	35972 ± 7031.1	196.8 ± 8.3	8 ± 4.6
RYTido	0.01 ± 0	1.65 ± 0	0.19 ± 0	3.7 ± NA	156.43 ± NA	0.42 ± 0	0.2 ± 0.1	148.44 ± 22.4	31 ± 7
SCHpau	0.28 ± 0	4.23 ± 0.6	0.02 ± 0	0.31 ± 0	224.09 ± 55.4	0.31 ± 0	2070 ± 741.7	191.11 ± 12.9	5 ± 2.4
VERcan	0.42 ± 0.1	1.22 ± 0	0.04 ± 0	0.41 ± 0	81.59 ± 24	0.42 ± 0	10676.33 ± 2700.1	115.61 ± 3.5	3.17 ± 1.6
VERsub	0.91 ± 0.1	2.3 ± 0.1	0.05 ± 0	0.35 ± 0	55.68 ± 5.2	0.38 ± 0	23543 ± 12409.5	144.52 ± 11.2	1.5 ± 0.6
VIOlya	2.8 ± 0.5	1.78 ± 0.2	0.03 ± 0	0.18 ± 0	281.89 ± 23.7	0.16 ± 0	17 ± 9.7	424.11 ± 41.2	0 ± 0
WAHalb	0 ± 0	0.22 ± 0	0.34 ± 0	1.1 ± NA	126.13 ± NA	0.33 ± 0	3.6 ± 1	225 ± 32.7	6.88 ± 2.7

Table S4.4. Summary of the sample sizes for species at Arthur's Pass, New Zealand that were burnt (B) and unburnt (UB) by life history class. This life history class was modified to simplified life history category for data visualization. B is the number of species for which I had measured shoot flammability data, UB is the number of unburnt species, *n* is the total number of species and Percent is the percent of species of that life history category for which I had measured shoot flammability data. The total number of species for which I obtained new experimental burn data in this study was 50

Category	**Life history category**	**Simplified life history category**	**B**	**UB**	***n***	**Percent**
a1a1	Terrestrial, herbaceous, rosette plants <20 cm	Rosette	7	13	20	35
a1a2	Terrestrial, herbaceous, rosette plants >20 cm	Rosette	10	8	18	56
a1b1	Terrestrial, herbaceous, elongated, leaf-bearing rhizomatous <8 cm	Rhizomatous	1	0	1	100
a1b2	Terrestrial, herbaceous, elongated, leaf-bearing rhizomatous >8 cm	Rhizomatous	4	3	7	57
a1c1	Terrestrial, herbaceous, cushion plants	Cushion	1	1	2	50
a1d1	Terrestrial, herbaceous, extensive-stemmed herbs <20 cm	Extensive stemmed herbs	1	10	11	9
a1d2	Terrestrial, herbaceous, extensive-stemmed herbs >20 cm	Extensive stemmed herbs	3	4	7	43
a1e1	Terrestrial, tussocks	Tussocks	2	2	4	50
a1f1	Terrestrial, graminoids >15 cm	Graminoids	0	1	1	0
a1f2	Terrestrial, graminoids <15 cm	Graminoids	7	4	11	58
a1f3	Terrestrial, graminoids 15-90 cm	Graminoids	1	3	4	25
a3a1	Terrestrial, woody, prostrate shrubs	Prostrate shrubs	5	3	11	45
a3b1	Terrestrial, woody, dwarf shrub (subshrub)	Dwarf shrubs	4	2	6	67
a3c1	Terrestrial, woody, shrub and trees	Tall shrubs and trees	21	13	31	68
	Totals		67	67	134	50.00

Table S4.5. PCA loadings of community weighted means of morphological traits. Abbreviations of the traits are given in Table S4.3, Appendix A

Community weighted means of traits	**PC1**	**PC2**	**PC3**	**PC4**	**PC5**
LA	0.85	-0.31	-0.11	0.14	-0.24
LL	0.77	-0.14	-0.10	-0.35	0.47
LT	-0.09	0.68	-0.61	0.13	0.00
LDMC	-0.10	0.38	0.47	0.73	0.27
SLA	-0.46	0.03	0.67	-0.52	-0.02
SDMC	-0.81	-0.13	-0.42	-0.13	0.31
BD	-0.42	-0.72	0.18	0.31	0.08
MC	0.41	0.79	0.35	-0.15	0.04
Dm	0.88	-0.29	0.08	0.10	0.15

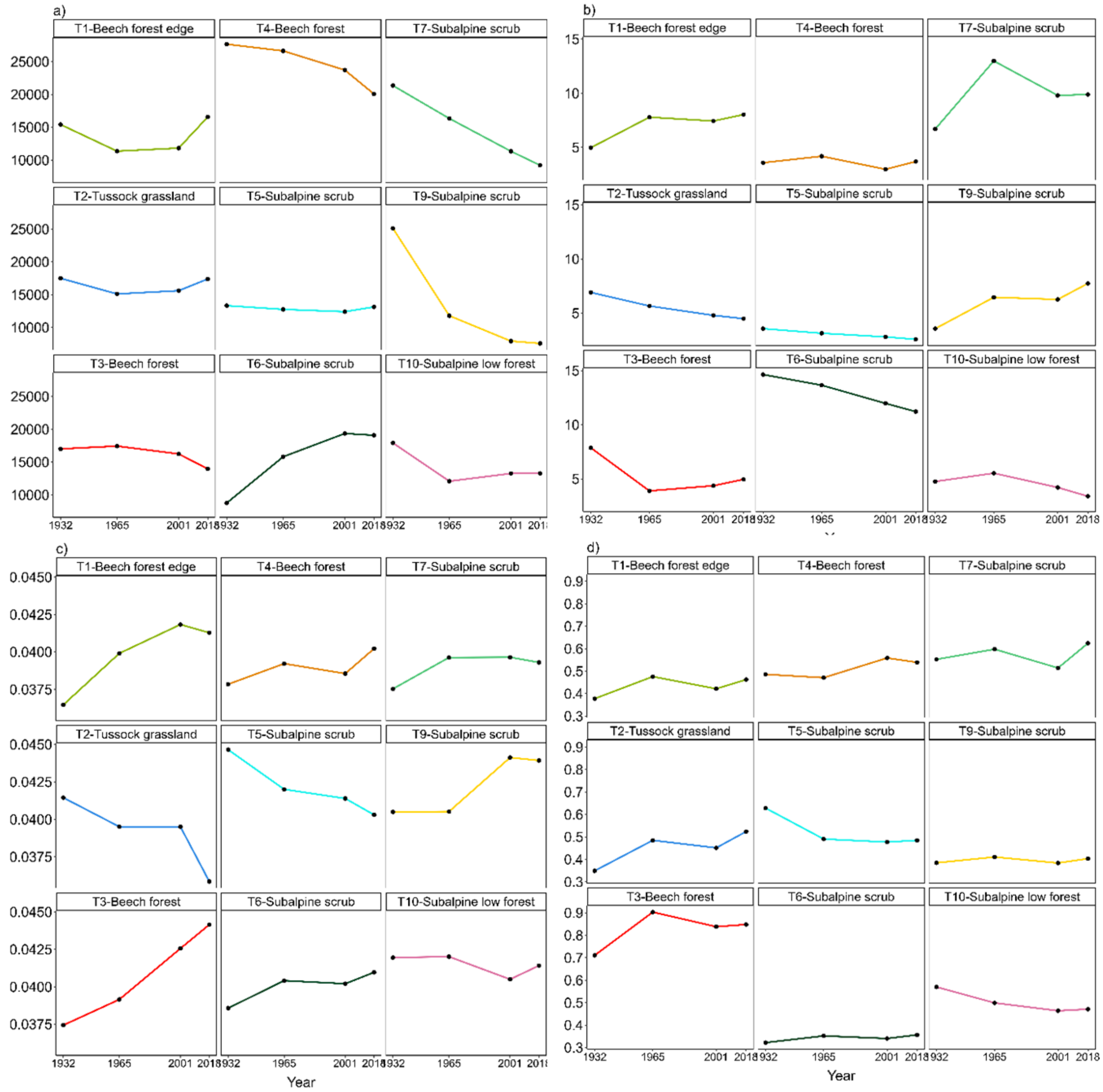


Figure S4.3. Changes in community weighted means of traits over 86 years (1932-2018) of time at Arthur's Pass, New Zealand; a) bulk density, b) leaf length, c) leaf thickness, and d) leaf dry matter content

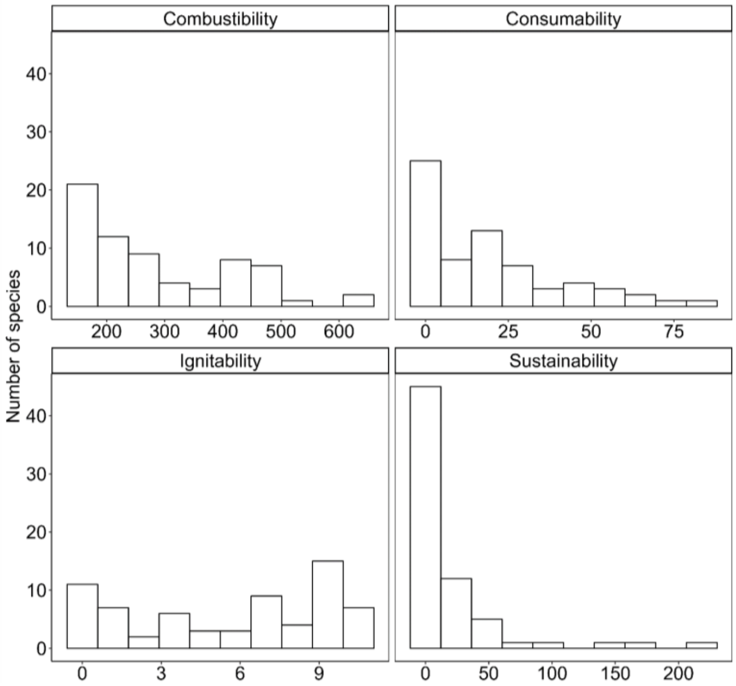


Figure S4.4. Histograms of the mean species level flammability trait values for the 67 species for which I had flammability measurements. The components of flammability are ignitability (s), measured as the time taken for the sample to ignite (samples that did not ignite were recorded as zero), combustibility (˚C), measured as the maximum temperature reached (samples that did not ignite were recorded as the recorded temperature of the grill without ignition with the blowtorch applied, i.e., 150 ˚C), sustainability (s), measured as the total burning time of the sample and consumability (%), measured as the percent biomass burnt out of the total biomass in the sample

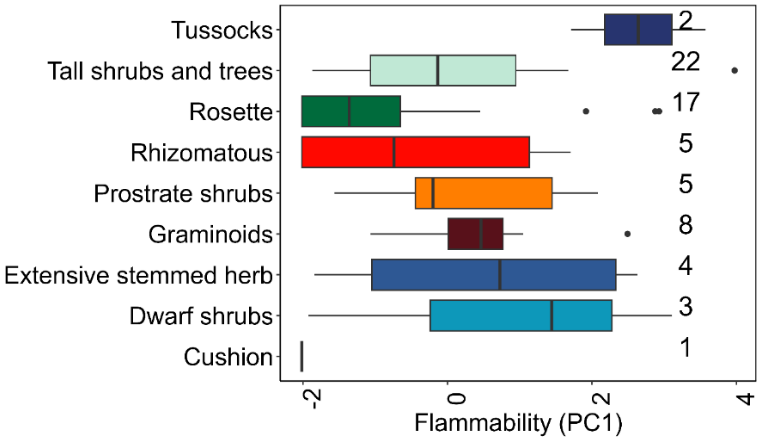


Figure S4.5. Box plot of flammability (PC1) of 67 species across plant history category at Arthur’s Pass, New Zealand

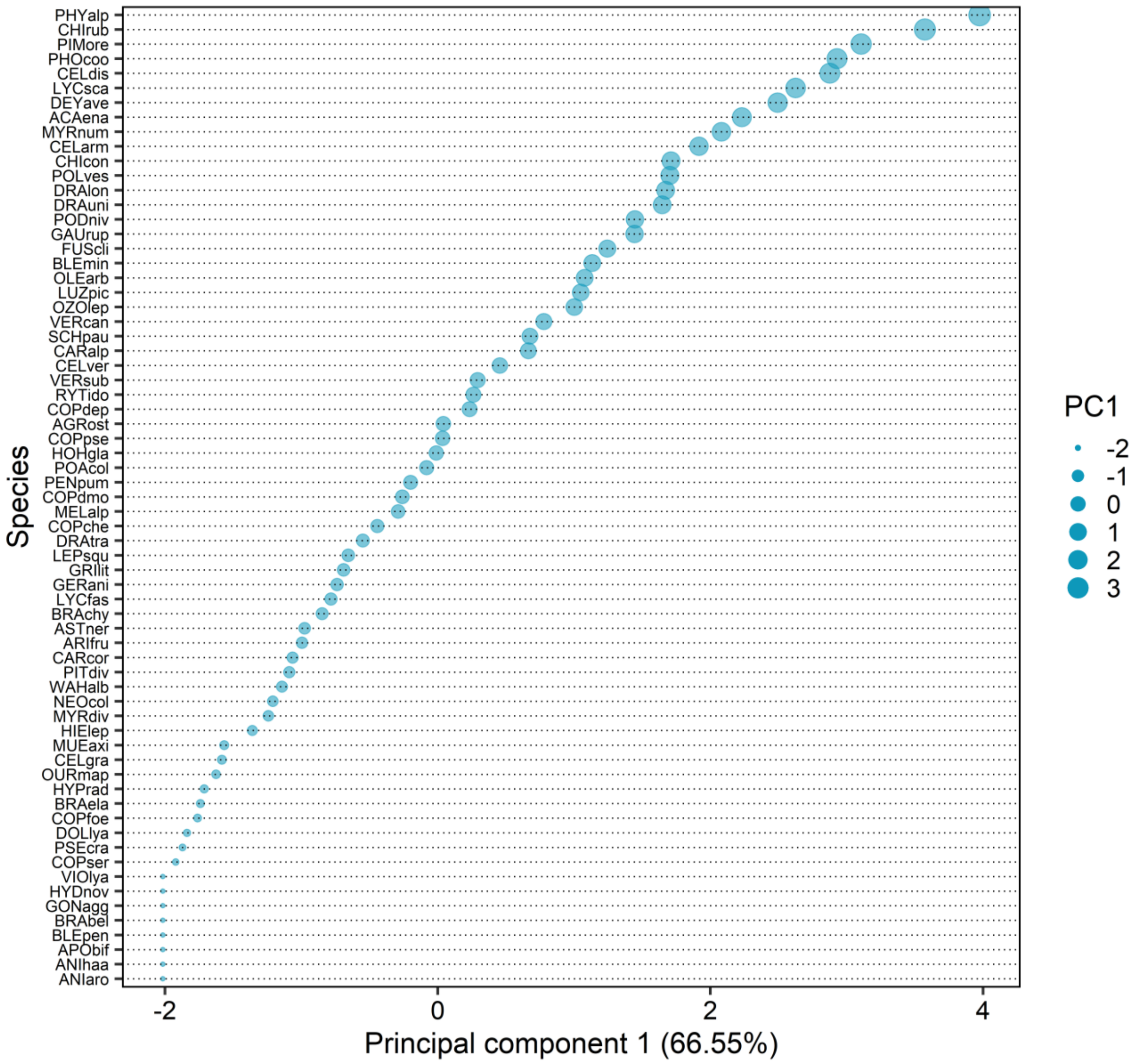


Figure S4.6. Flammability ranking of the 67 species at Arthur's Pass, New Zealand based on their scores on the first component of the species' flammability trait principal component analysis (PC1). Species with high values on PC1 values were relatively more flammable than those with low values on PC1

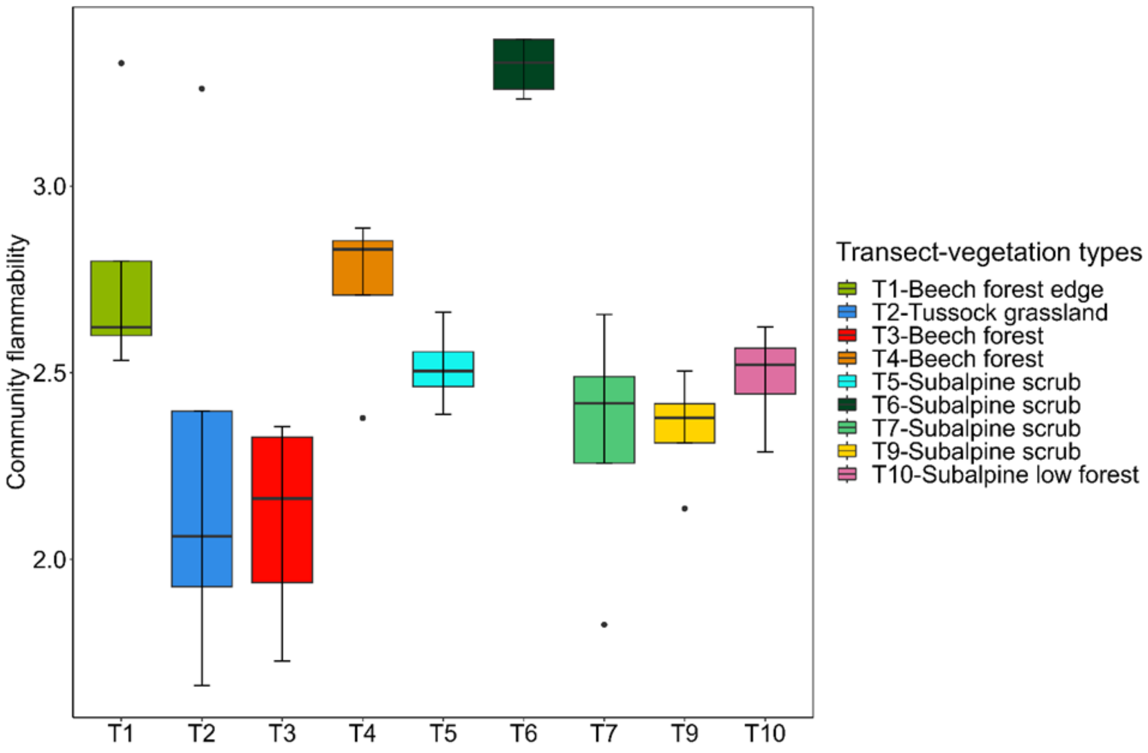


Figure S4.7. Community flammability across different sites in different vegetation types within 86 years (1932-2018) of time at Arthur's Pass, New Zealand. This graph represents mean variation of community flammability on each transect within 86 years

Table S4.6. PCA loadings of species level flammability, and morphological traits. Abbreviations of the traits are given in Table S4.3, Appendix A.

Species traits	**PC1**	**PC2**	**PC3**	**PC4**	**PC5**
Ignitability	0.79	-0.41	-0.07	0.06	0.08
Combustibility	0.84	-0.05	-0.24	0.35	-0.03
Sustainability	0.72	0.48	0.01	0.08	0.14
Consumability	0.68	-0.40	0.02	0.46	-0.08
LA	0.28	0.70	0.32	-0.21	0.40
LL	0.24	0.82	0.22	0.09	0.02
LT	0.26	0.76	0.10	-0.05	-0.33
LDMC	0.29	-0.54	0.56	-0.41	-0.10
SLA	-0.69	-0.40	-0.07	0.16	0.46
SDMC	0.78	-0.36	-0.07	-0.33	0.01
BD	0.33	0.44	-0.73	-0.16	0.15
MC	-0.77	0.33	0.29	0.34	-0.08
Dm	0.61	-0.06	0.60	0.22	0.19

Table S5. 1. List of the 29 plant taxa, for which flammability components ignition score, maximum temperature, burning time and burnt biomass, leaf nutrient concentration, and shoot and leaf morphological traits were measured. All plant samples were burnt as ca. 70 cm shoots, except taxon denoted by *, which were burnt as whole plants (i.e., plants were ≤ 70 cm height), and those denoted by ** were burnt as clump (plant material starting from the bottom centre of each individual and including dead plant biomass and all other branches and stems). Taxon in bold denote those for which leaf nutrient concentration data were obtained from Richardson et al. (unpublished data). Note that some data are presented at the genus level only, consistent with the permanent plot vegetation data (Burge et al., 2020)). Taxon names, family, authority, and growth form were taken from Flora of New Zealand (http://nzflora.info) and New Zealand Plant Conservation Network (https://www.nzpcn.org.nz)

Life history category and botanical name	**Family**	**Code**
Ferns		
**Blechnum minus* (R.Br.) Ettingsh.	Blechnaceae	BLEmin
***Polystichum vestitum* (G.Forst.) C.Presl	Dryopteridaceae	POLves
**Lycopodium scariosum* G.Forst.	Lycopodiaceae	LYCsca
Grasses		
***Poa colensoi* Hook.f.	Poaceae	**POAcol**
**Agrostis* L.	Poaceae	**AGRost**
Rytidosperma Steud.	Poaceae	**RYTido**
***Chionochloa conspicua* (G.Forst.) Zotov	Poaceae	CHIcon
***Chionochloa rubra* Zotov	Poaceae	CHIrub
Forbs		
**Anisotome haastii* (F.Muell.) Cockayne & Laing	Apiaceae	ANIhaa
***Phormium cookianum* Le Jol.	Asphodelaceae	PHOcoo
***Astelia nervosa* Hook.f.	Asteliaceae	ASTner
**Celmisia armstrongii* Petrie	Asteraceae	CELarm
**Celmisia discolor* Hook.f.	Asteraceae	CELdis
**Ourisia macrophylla* Hook.	Plantaginaceae	OURmap
Shrubs		
Brachyglottis elaeagnifolia (Hook.f.) B.Nord.	Asteraceae	BRAela
Dracophyllum longifolium (J.R.Forst. & G.Forst.) R.Br. ex Roemer & Schult.	Ericaceae	DRAlon
Dracophyllum traversii Hook.f.	Ericaceae	DRAtra
Dracophyllum uniflorum Hook.f.	Ericaceae	DRAuni
Gaultheria rupestris (L.f.) D.Don	Ericaceae	GAUrup
Veronica subalpina Cockayne	Plantaginaceae	VERsub

Life history category and botanical name	**Family**	**Code**
Podocarpus nivalis Hook.	Podocarpaceae	PODniv
Myrsine nummularia (Hook.f.) Hook.f.	Primulaceae	**MYRnum**
Coprosma foetidissima J.R.Forst. & G.Forst.	Rubiaceae	**COPfoe**
Coprosma serrulata Hook.f. ex Buchanan	Rubiaceae	COPser
Pimelea oreophila C.J.Burrows	Thymelaeaceae	**PIMore**
Trees		
Pseudopanax colensoi (Hook.f.) Philipson	Araliaceae	NEOcol
Fuscospora cliffortioides (Hook.f.) Heenan & Smissen	Nothofagaceae	FUScli
Phyllocladus alpinus Hook.f.	Podocarpaceae	PHYalp
Myrsine divaricata A.Cunn.	Primulaceae	MYRdiv

Table S5.2. Comparisons based on AICc among candidate phylogenetic generalised least square models assessing the phylogenetic relationships between relative plant taxon flammability (response variable), leaf nutrient concentration, and leaf morphology and shoot traits, based on principal components from PCAs. Principal components (PC) used as predictors in the models were either leaf nutrient content (PC1_nutrients) or leaf morphology (PC1_morph) and shoot traits (PC2_morph). For each model, K is the number of parameters, AICc is the sample size corrected Akaike information criterion, DAICc is difference in AICc of each model from the top model, W is the relative weight of each model in the model set, and LL is the model log-likelihood. A key result of this analysis (Table S5. 1, Appendix A) is that the model with PC1_nutrients alone is no longer a plausible model. R2 is the proportion of variation of flammability PC1 explained by predictors

Model	**K**	**AICc**	**DAICc**	**W**	**LL**	**R2**
PC2_morphology	3	121.09	0	0.53	-57.06	0.48
PC1_nutrients + PC2_morphology	4	123.07	1.99	0.20	-56.70	0.48
PC1_nutrients + PC1_morphology+ PC2_morphology	5	123.73	2.65	0.14	-55.56	0.35
PC1_morphology + PC2_morphology	4	123.79	2.70	0.14	-57.06	0.37
PC1_morphology	3	140.21	19.12	0	-66.63	0.21
PC1_nutrients + PC1_morphology	4	140.54	19.46	0	-65.44	0.19
Null model (intercept)	2	140.58	19.50	0	-68.06	0
PC1_nutrients	3	143.06	21.97	0	-68.05	0.02

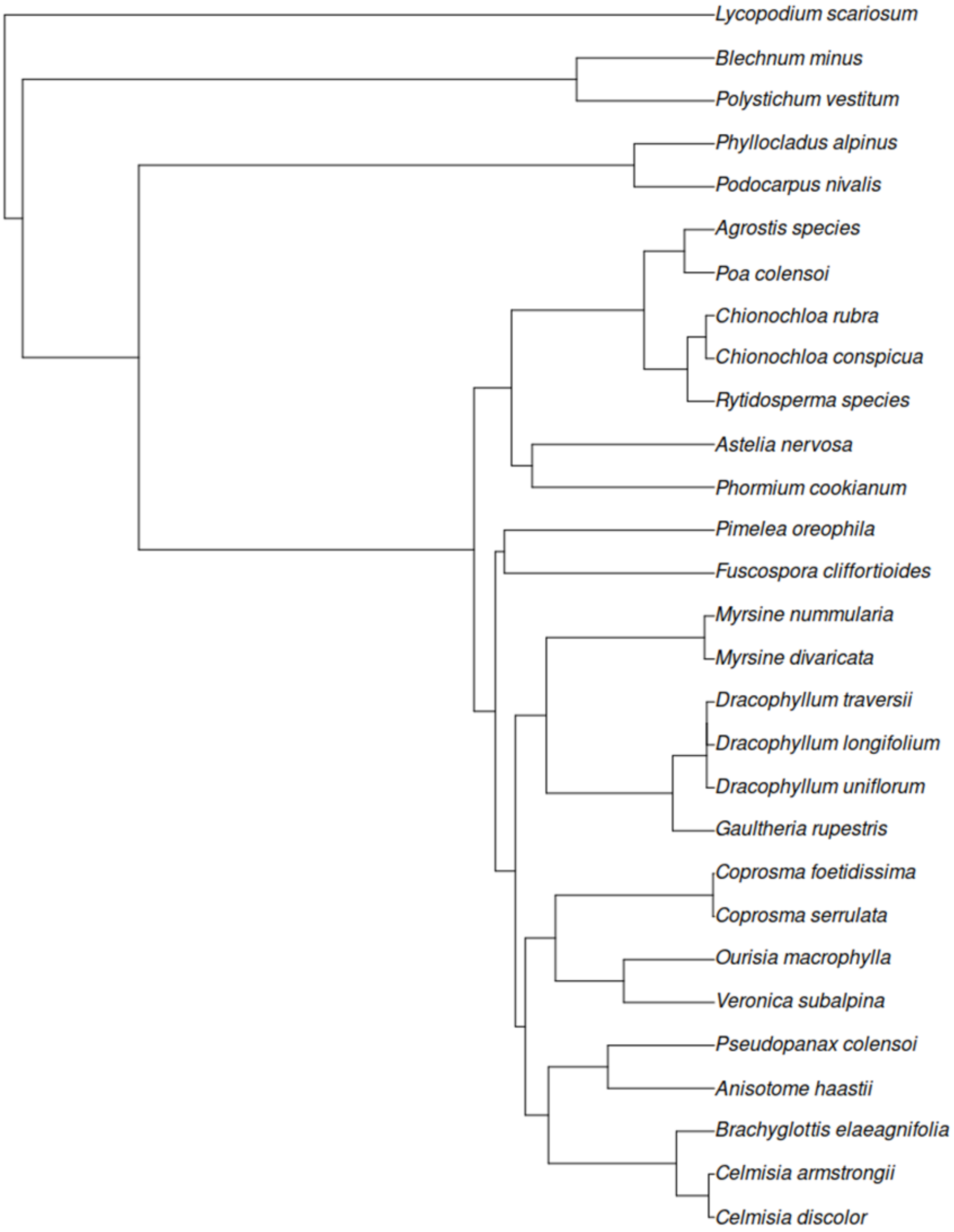


Figure S5.1. Evolution of taxon flammability across the vascular plants at Arthur’s Pass, South Island, New Zealand. The phylogeny of 29 species were obtained from an R package ‘V.PhyloMaker2’

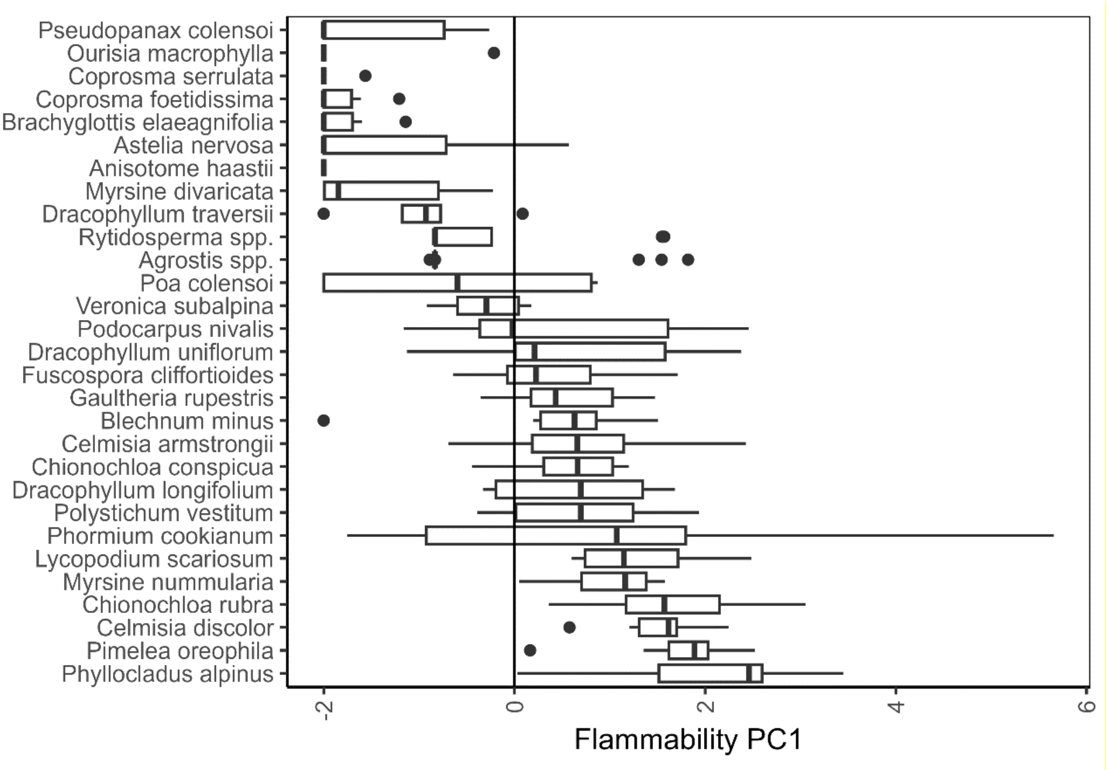


Figure S5.2. Box plot of relative flammability (PC1) for all individual measurements of specimens of the 29 plant taxa. The first and second principal components explained 57.39% and 21.28% of the individual specimen level variation in relative flammability

Table S5.3. Loadings of the four measurements of shoot flammability for the 29 taxa on the first four principal components of PCA on flammability (Figure 5.1a)

Flammability traits	**PC1**	**PC2**
Percent variance explained	**66.15 %**	**20.98 %**
Ignition score	0.83	-0.31
Maximum temperature (˚C)	0.94	0.09
Burnt time (s)	0.60	0.78
Burnt biomass (%)	0.84	-0.35

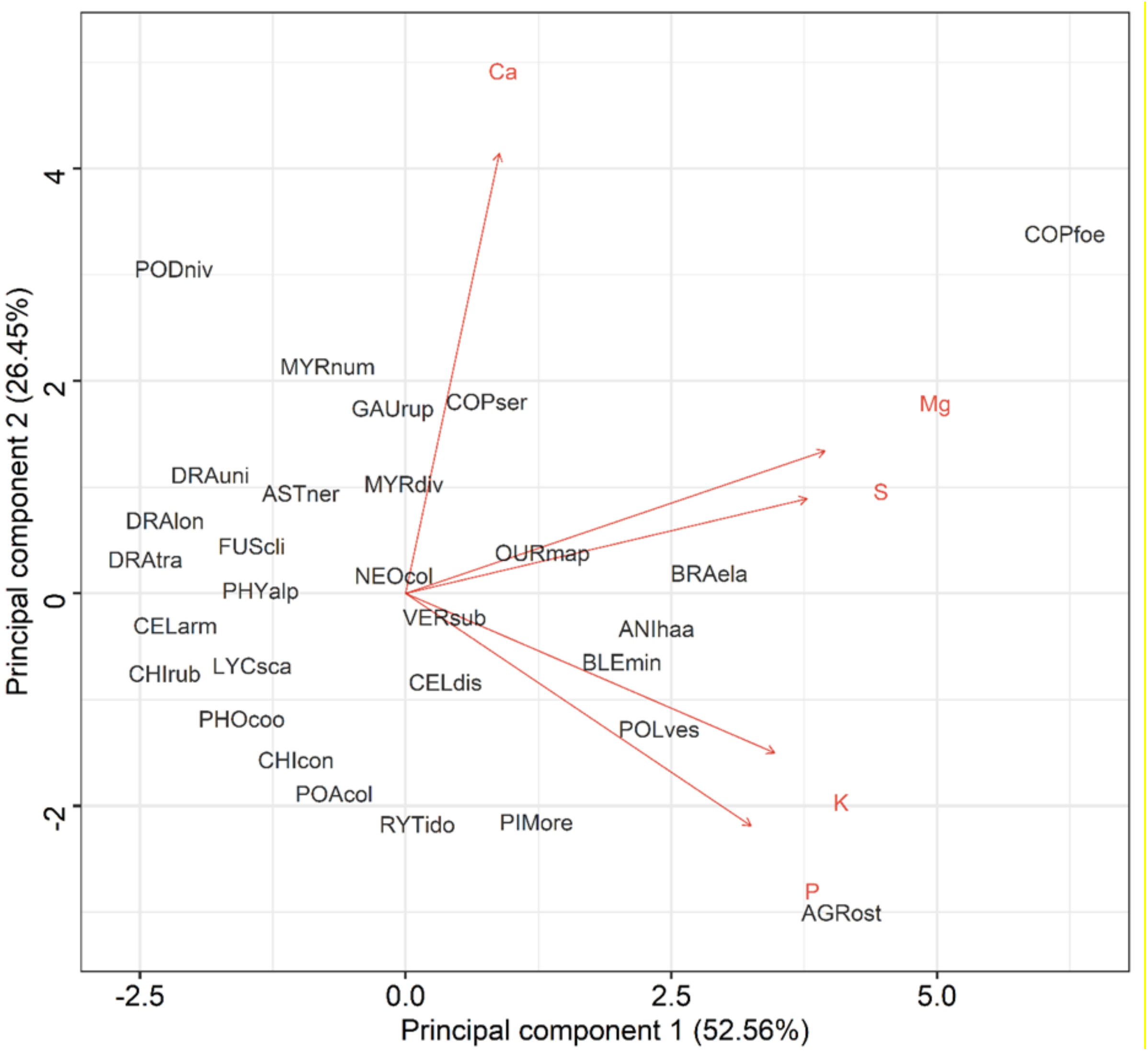


Figure S5.3. Principal component analysis biplot of the mean scores for each taxon based on measurement of leaf nutrient concentration traits (red). Taxon codes are the first three letters of each of genus and species epithet as code (see full species list, Table S5. 1, Appendix A)

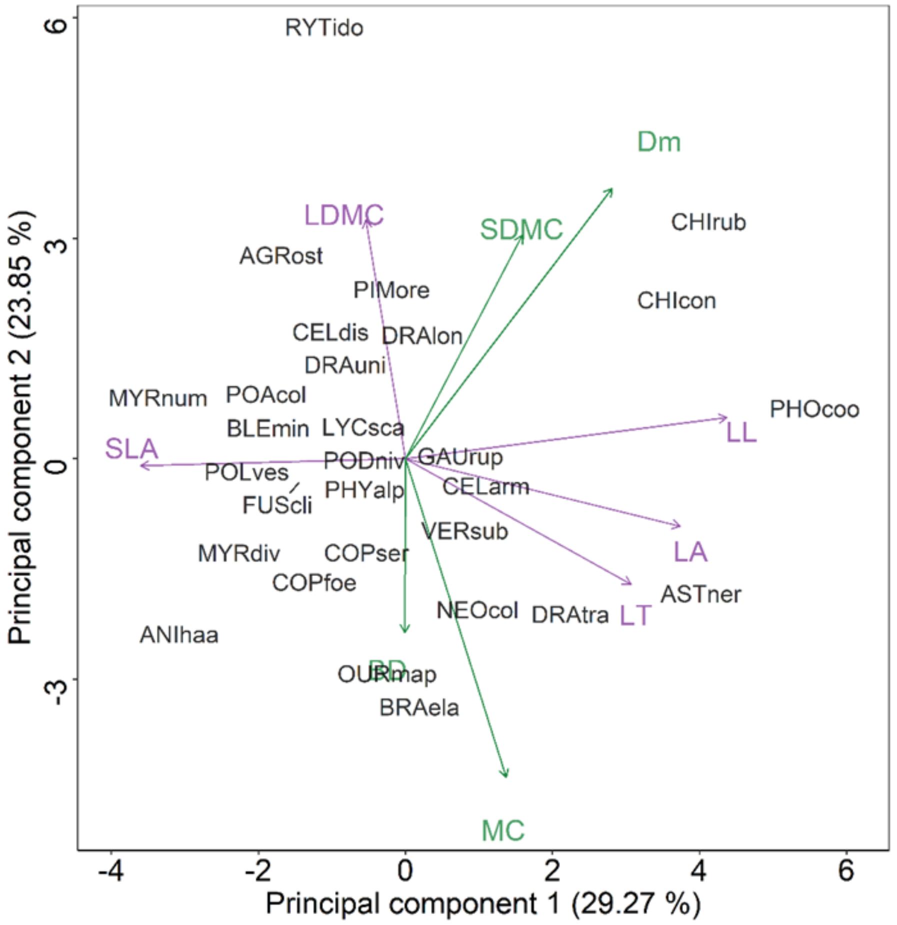


Figure S5.4. Principal component analysis biplot of the mean scores for each taxon based on measurement leaf (green) and shoot (purple) morphological traits for the 29 taxa. Taxon codes are the first three letters of each of genus and species epithet as code (see full species list, Table S5. 1, Appendix A). Abbreviations of morphological traits are shoot dry matter content (SDMC; g/g), bulk density (BD; cm3), % moisture content (MC), % dead material (Dm), leaf length (LL; cm), leaf thickness (LT mm), leaf area (LA; cm^2), leaf dry matter content (LDMC; g/g), specific leaf area (SLA; cm^2/g)

Table S5.4. Correlation among the predictors obtained from dimensional reduction on leaf nutrient concentration PCA and morphological (leaf and shoot) trait for the 29 taxa. These dimensionally reduced variables are used as predictors in generalised linear modelling of relative shoot or whole-plant flammability (PC1)

Traits	**% of variance explained**	**BD**	**Dm**	**MC**	**SDMC**	**LL**	**LT**	**LA**	**LDMC**	**SLA**	**Ca**	**Mg**	**P**	**K**	**S**
PC1_nutrients	52.56	-0.07	-0.07	0.26	-0.5	-0.37	-0.22	-0.23	-0.03	0.48	0.2	0.88	0.72	0.77	0.84
PC2_nutrients	26.64	0.41	-0.59	0.34	-0.12	-0.18	-0.03	-0.06	-0.33	0.04	0.92	0.3	-0.49	-0.33	0.2
PC1_morph	29.27	0.00	0.51	0.25	0.29	0.87	0.61	0.75	-0.11	-0.72	-0.3	-0.39	-0.41	-0.1	-0.38
PC2_morph	23.86	-0.43	0.67	-0.79	0.55	0.11	-0.34	-0.18	0.65	-0.02	-0.52	-0.42	0.21	-0.13	-0.16
PC3_morph	14.45	-0.47	0.37	0.28	-0.64	0.1	-0.11	0.37	0.23	0.48	-0.09	0.22	0.31	0.64	0.2

Table S5.5. Importance value of response variables in the model averaging in simple generalised linear modelling. w+ represents models including the parameter and w- represents models excluding the parameter

Response variables	**Importance values**	
	w+	**w-**
PC1_nutrients	0.83	0.17
PC1_morph	0.20	0.80
PC2_morph	0.99	0.01

Table S5.6. Predictors of plant flammability PC1 based on the model-average result from generalised linear modelling of 29 taxa. Abbreviations: PC1_nutrients represent four leaf nutrient concentration (K, Mg, P and S), PC1_morph represents mixed morphological traits: leaf and shoot (LA, LL, LT, BD, MC) and PC2_morph represents leaf and shoot traits (LL, LDMC, Dm, SDMC, MC)

	Flammability (PC1)	
Predictors	**Estimates**	**Conf. Int (95%)**
(Intercept)	-0.00	-0.48 – 0.48
PC1_nutrients	-0.36 *	-0.67 – -0.05
PC2_morph	0.60 ***	0.26 – 0.94
PC1_morph	0.02	-0.33 – 0.37
Observations	29	
R2	0.477	
* p<0.05 ** p<0.01 *** p<0.001		

Table S5.7. Predictors of plant flammability PC1 based on the model-average result from phylogenetic generalised least square of 29 taxa. Abbreviations: PC1 nutrient represents four leaf nutrient concentration (K, Mg, P and S), PC1 morphology represents mixed morphological traits: leaf and shoot (LA, LL, LT, BD, MC) and PC2 morphology represents leaf and shoot traits (LL, LDMC, Dm, SDMC, MC)

	Flammability (PC1)	
Predictor	**Estimates**	**Conf. Int (95%)**
(Intercept)	1.01	-3.08 – 5.10
PC1 morph	0.13	-0.13 – 0.38
PC2 morph	0.89 ***	0.57 – 1.21
PC1m: PC2 morph	0.21 **	0.08 – 0.35
PC1 nutrients	-0.12	-0.38 – 0.15
PC1 nutrients: PC2 morph	-0.15 *	-0.29 – -0.01
PC1 nutrients: PC1 morph	-0.09	-0.34 – 0.16
PC1 nutrients: PC1 morph: PC2 morph	0.03	-0.12 – 0.19
Observations	29	

* $p<0.05$ ** $p<0.01$ *** $p<0.001$

Appendix B. Fire severity in recent burns in South Island, New Zealand

Introduction

Fire severity is the amount of loss or decomposition of biomass or the organic matter both on the above and below ground and is one of the main characteristics to measure the impacts of a fire (Keeley, 2009). Variations in fire severity within or among sites can create different ecological impacts on ecosystems (Keeley, 2009). When there is high fire severity, this can substantially change the plant community composition and dominant species because many species die or unable to be replaced, so may lead to alternative stable states (Day et al., 2022; Knox & Clarke, 2012). Some studies have shown following fire, short lived and far dispersing species invade the site after fires of high severity (Brodie et al., 2021).

Fire severity could be influenced by many factors such as plant community structure, including plant traits that influence flammability, topography, weather, and fuels (Paudel et al., 2022; Saladyga et al., 2022; Santos et al., 2019), but the degree to which each contributes to the spatial pattern of fire severity under different conditions remains poorly understood. Fire severity can also vary depending on fuel moisture and the relative abundance of particular plant growth forms (Brodie et al., 2021; Estes et al., 2017). For example, grasses produce high amount of fine fuels and promote rapid fires that may be of low severity, while trees have lots of dense fuels and promote severe crown fires (Estes et al., 2017; Pausas et al., 2004; Wragg et al., 2018). Burning conditions and pre-fire vegetation both can influence the severity of fires; therefore, even under extreme fire weather conditions, fuel management treatments can limit fire severity (Viedma et al., 2020; but see Bowman et al., 2021).

Measures of fire severity are not consistent between and within ecosystems Miller & Safford, 2020) in USA and Australia. In some studies, they measure biomass loss to determine fire severity whereas others measure the area burnt during fire (Oliveira et al., 2015; Pascolini-Campbell et al., 2022; Saladyga et al., 2022). Therefore, plant parts combusted during the fire for example branch diameter and cover of live vegetation after the fire can determine fire severity.

Researchers have used a range of measures to estimate fire severity (Kasischke et al., 2008; Keeley, 2006; Nolan et al., 2020). For example sometimes measure the diameter of woody trees and shrubs (Strand et al., 2019). If a remaining branch has a small diameter, then it means the fire is of lower severity because there has been less combustion (Day et al., 2022). The area of burnt vegetation is often measured to determine fire severity both from field studies and remotely sensed satellite data. There are many previous studies where fire severity was assessed based on remotely sensed data basically using NBR (Normalized Burn Ratio) and NDVI (Normalized Difference Vegetation Index) (Escuin et al., 2008; Estes et al., 2017; Fernández-Guisuraga et al., 2021; Garcia et al., 2017; Lentile et al., 2007b; Loboda et al., 2013; R. B. Walker et al., 2018; Whitman et al., 2018). This gives us an idea of very large, burnt areas, but area of burnt in field study could also be estimated at finer spatial scales. We may also be able to estimate community flammability to tell us about fire severity (Cardoso et al., 2018). If there's low fire severity, then we expect greater abundance of low flammable plants. However, this metric would only work best if there is pre-fire vegetation data.

In this pilot study, I aimed to test the methods for estimating fire severity based on field measurements of branch diameter, ground covers and plant community flammability following wildfires in South Island of New Zealand's tussock-dominated montane grasslands. I evaluated these potential fire severity methods by relating the different measurements to each other in recently burnt areas. I expected that in areas of higher fire severity plants would have larger diameter branches and there would be a lower percent cover of live vegetation. I also expected that in areas of lower fire severity, I would observe a higher abundance of less flammable plants.

Methods

Field sampling

This study was conducted in three different sites in Canterbury and Otago regions of South Island, New Zealand. Deep Stream in Otago was burnt in early summer in 2019, while Pukaki and Ōhau, in the Canterbury region, were burnt in spring 2020 (Figure S2.1; Figure S3.1, Appendix A). Deep Stream was within the tussock-dominated grassland (Payton & Pearce, 2009); all of three sites were in montane grasslands. At the Ōhau site, we measured fire severity in 2.5 recently burnt permanent transects set up in 1980s (Buckley & Freckleton, 2010; Day & Buckley, 2013). At all three sites, branch diameter, live vegetation cover were measured in field (Figure S1; a &b) and plant were sampled to burn in laboratory to determine flammability.

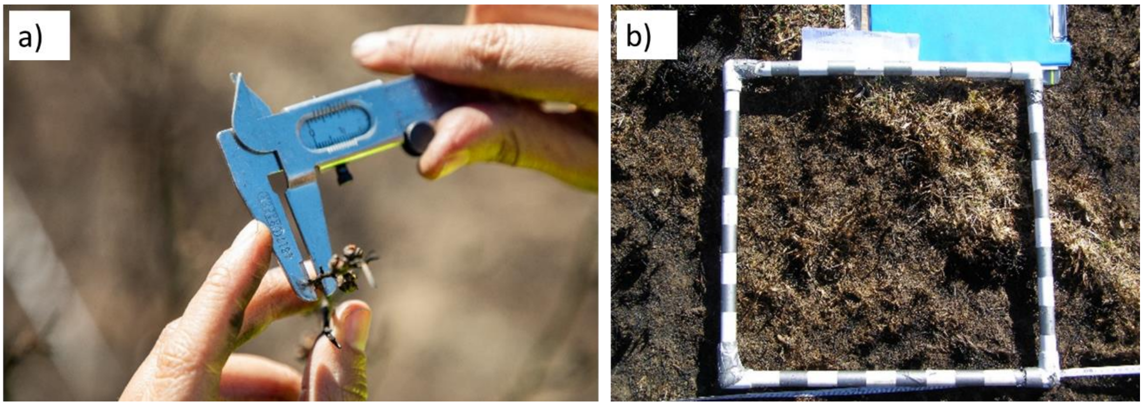


Figure S1. Photos showing a) measurement of branch diameter and b) estimating live vegetation cover in 0.25-m^2 quadrat at on burnt site.

Deep Stream

At Deep Stream, we set up nine 10-m transects away from the experimental burn areas on different aspects: three were north-facing, three were south-facing, and three were on the top of ridgelines (Figure S2a). To estimate woody combustion along each transect, we measured diameters minimum of five branches. Most woody species at this site were prostrate shrubs. To obtain an estimate of area burnt, in each 0.25-m^2 vegetation quadrat in the experimental burns (see detail in Chapter 2), we estimated percent covers of live vegetation.

Pukaki

At Pukaki, we set up seven plots after fire to measure relative fire severity. At this site, representative burnt areas were selected based on plant community types (tussock-dominated and shrubland). Within each 20-m by 20-m plot, three transects were run at 5-m apart (5, 10, 15-m) (Figure S2b). Woody plants were measured for combustion at regular 1-m intervals. Starting from 1-m along the transect, the woody plant (tree, shrub, or ground shrub) nearest to the transect on the right side of the line was measured and identified to species level where possible (but three species could not be identified so named then as unknown, unknown woody 1 and 2). For each individual up to five branches with the thinnest tips had their diameters measured; this gives an indication of fine fuel combustion, where if there are thin branch tips remaining then the fire severity is lower than if only branches with large diameters remain. If the woody plant had leaves remaining this was also recorded. To obtain an estimate of area burnt, in each 0.25-m^2 vegetation quadrat in the corners of the plot, we estimated percent covers of burnt vegetation.

Ōhau

At the Ōhau site, woody combustion was estimated on three 20-m transects running perpendicular to the main 100 m transect at 25-m apart (25, 50, 75-m) except on the half burnt transect OHAT042 (5, 30-m) were made across the permanent transects (Figure S2c). Woody plants were assessed for combustion at regular 1-m intervals. Starting from 1-m along the transect, the woody plant (tree, shrub, or ground shrub) nearest to the transect on the right side of the line was measured and identified to species where possible (but three species could not be identified so named then as unknown, unknown woody 1 and 2). For each individual up to five branches with the thinnest tips had their diameters measured; this gives an indication of fine fuel combustion, where if there are thin branch tips remaining then the fire severity is lower than if only branches with large diameters remain. If the woody plant had leaves remaining this was also recorded. The plant height was measured from ground to tip of the plant; this provides the level of severity, where the shorter the plant height remains the higher the fire severity. In runner species (prostrate) plant height was measured from the ground to the top of the plant. To obtain an estimate of area burned, in each 0.25 m^2 vegetation quadrat along the main 100 m transect, we estimated percent covers of burnt vegetation.

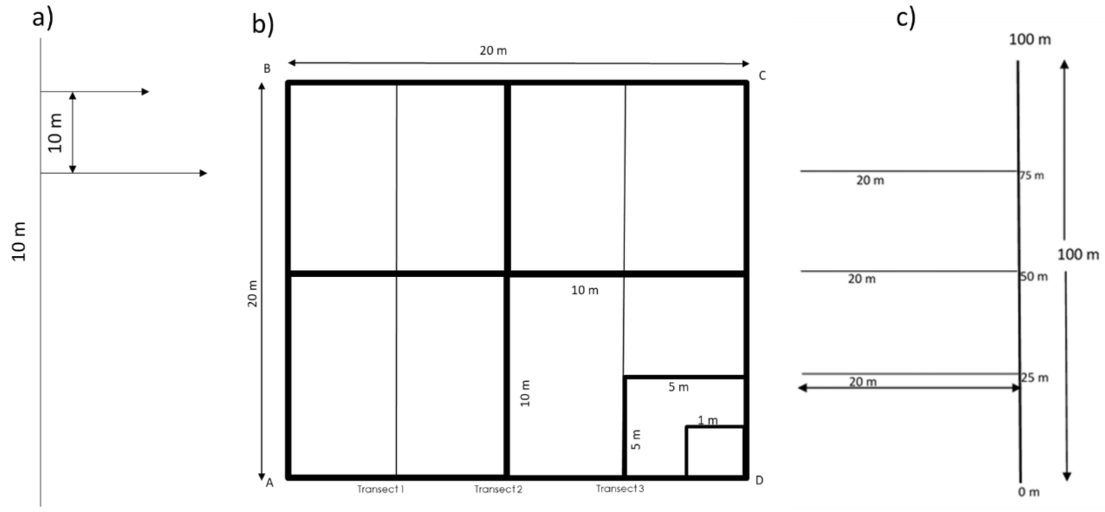


Figure S2. Schematic layout to assess fire severity in relative to branch diameter of woody species in post-fire at a) Deep Stream and b) Pukaki and c) Ōhau. At Deep Stream, nine 10-m transects were made on three different aspects away from 1 hectare experimental plot and branch diameter of woody species were measured at every 1-m on the right side. At Pukaki, three transects were made within 20-m vegetation survey plot at 5, 10 and 15-m and branch diameter of woody species were measured at every 1-m. At Ōhau, three transects were made perpendicular to the 100-m permanent transects at 25, 50 and 75-m and branch diameter of woody species were measured at every one meter distance.

Data analysis

To explore variation in the potential measurements of fire severity among sites I used one-way ANOVA for the branch diameter response variable with site as the predictor. To assess differences in branch diameters within sites I used the transect as the predictor variable. I checked normality of the response variables and since the data were not normally distributed, I log-transformed the branch diameter. I also looked at quadrat percent covers of unburnt (live) vegetation. Here, I considered a low cover score of live vegetation to represent a higher fire severity. As there were large differences between sites at the transect level, we used a post-hoc TukeyHSD test using ‘agricolae’ (De Mendiburu Delgado & De Mendiburu Delgado, 2009) and ‘multcompView’ (Piepho, 2004) in R v.4.2.1 (R Core Team, 2022).

In addition, I compared community flammability (estimated using the weighted means method) among sites. To estimate community flammability, I categorized 114 species present in the study area into fourteen classes based on the following traits: life form, clonality and plant height following Padullés Cubino et al., 2018. Secondly, I combined flammability data with existing flammability data (Curran et al. unpublished). Then, I performed principal component analysis (PCA) using 'FactoMinor' in R v.4.2.1 (R Core Team, 2022) at the species level for flammability component for 44 species. The first flammability component PC1 was further used to calculate community-level flammability (details in chapter one and (Padullés Cubino et al., 2018)). Then, I calculated the abundances of each community types and community flammability weighted means across all the sites in R v.4.2.1 (R Core Team, 2022).

Results

Fire severity in burns measured by branch diameter

Based on branch diameter measurements, fire severity was significantly different ($P < 0.05$) among the sites (Figure S3). The highest fire severity was at Deep stream (with the largest mean minimum branch diameter = 0.53 mm) followed by Pukaki (branch diameter = 0.28 mm) and Ōhau (branch diameter = 0.25 mm). Within Deep Stream, on some transects fire severity was significantly higher than others. For example, on transects RT3 (branch diameter = 0.85 mm) and RN3 (branch diameter = 0.55 mm), fire severity was significantly higher than others (Figure S4a). At Ōhau, the highest fire severity was on the transects OHAT043_75 (branch diameter = 0.40 mm) at transect level (Figure S4b). At Pukaki, fire severity was the highest on the transect Puk-5_T2 (branch diameter = 0.41 m) and Puk-7_T3 (branch diameter = 0.38 mm) (Figure S4c).

Fire severity in burns measured by quadrat covers

I found the highest fire severity was at Pukaki (% of live vegetation cover = 7.44% and organic matter = 82.14%) followed by Deep stream (20.16% and 77.84%) and Ōhau (23.40% and 76.92%) based live vegetation cover occupied in the quadrat (Figure S5). At transect/plot level, the highest severity was on the plot DS_P6O (% of live vegetation cover = 7.66% of burnt vegetation = 45.08% and organic matter = 59%) whereas the lowest fire severity was on the DS_P5O (33.41%, 48.75% and 85.83%) at Deep Stream. At the Pukaki site, there was the highest severity on plots Puk-5 (1.31%, 9.25% and 40.18%) and Puk-7 (1.18%, 26.25% and 89.25%) in terms of live vegetation (Figure S6).

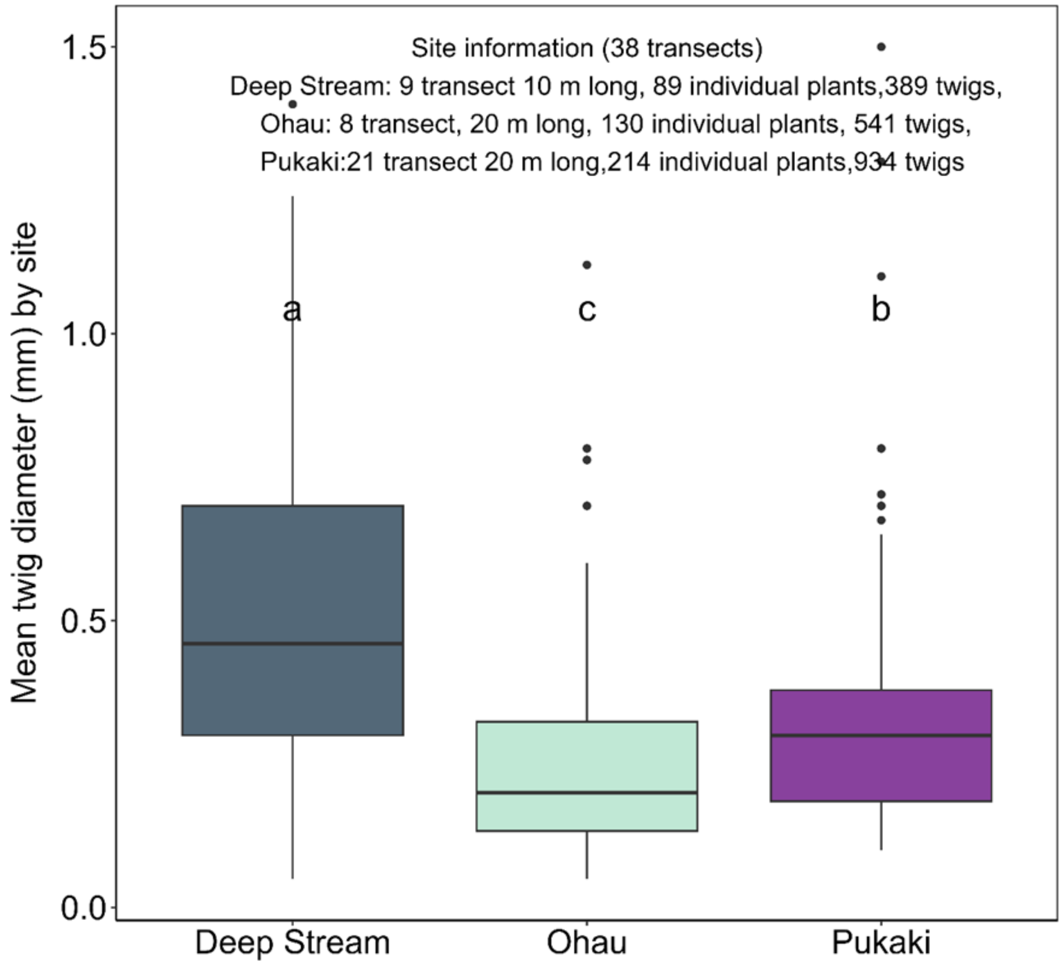


Figure S3: Branch diameters of woody species at three recent wildfire sites. Letters represent significant differences among sites. Letters denote differences in fire severity among sites from one-way ANOVA and Tukey test ($P < 0.05$).

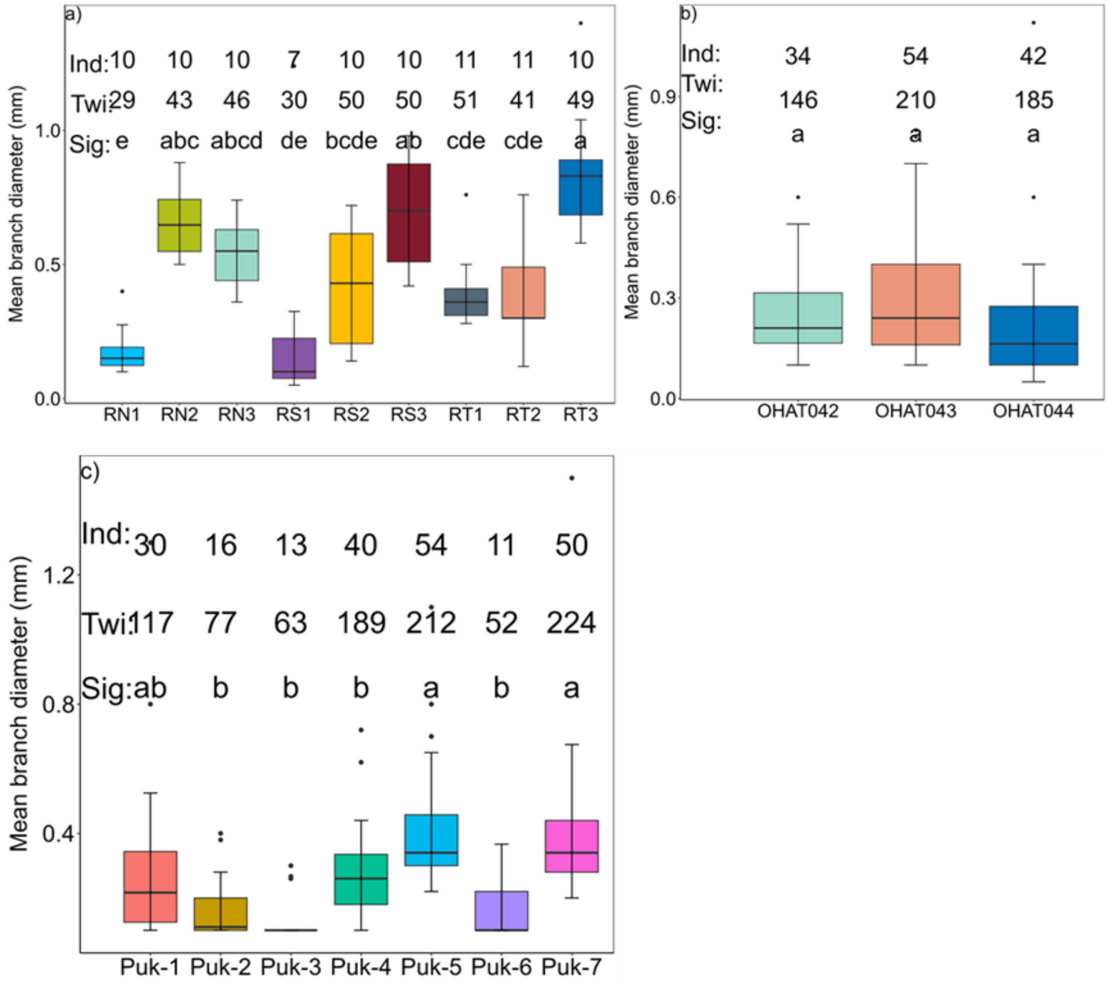
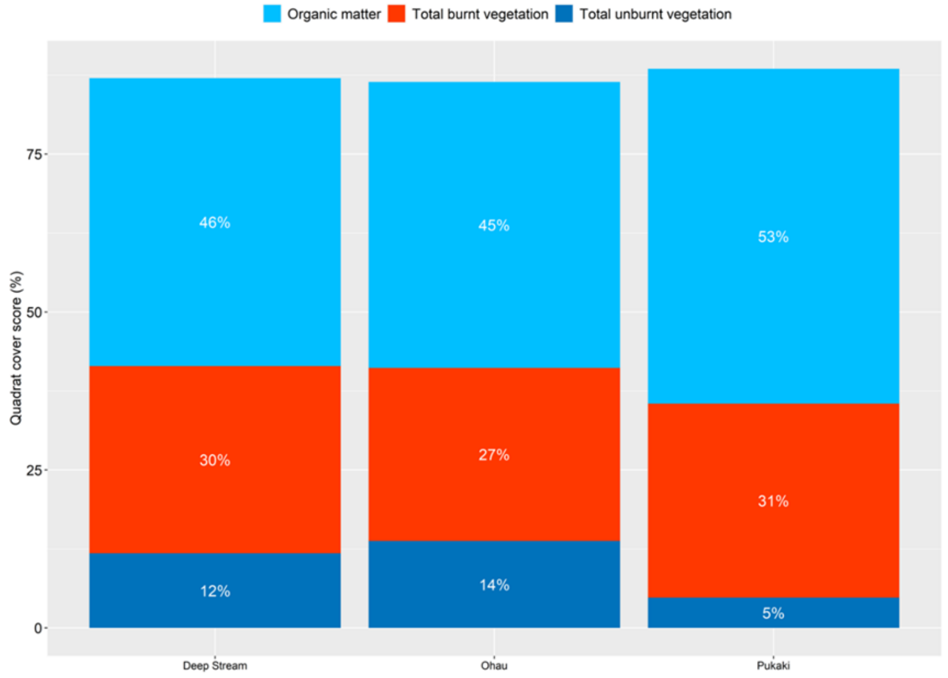
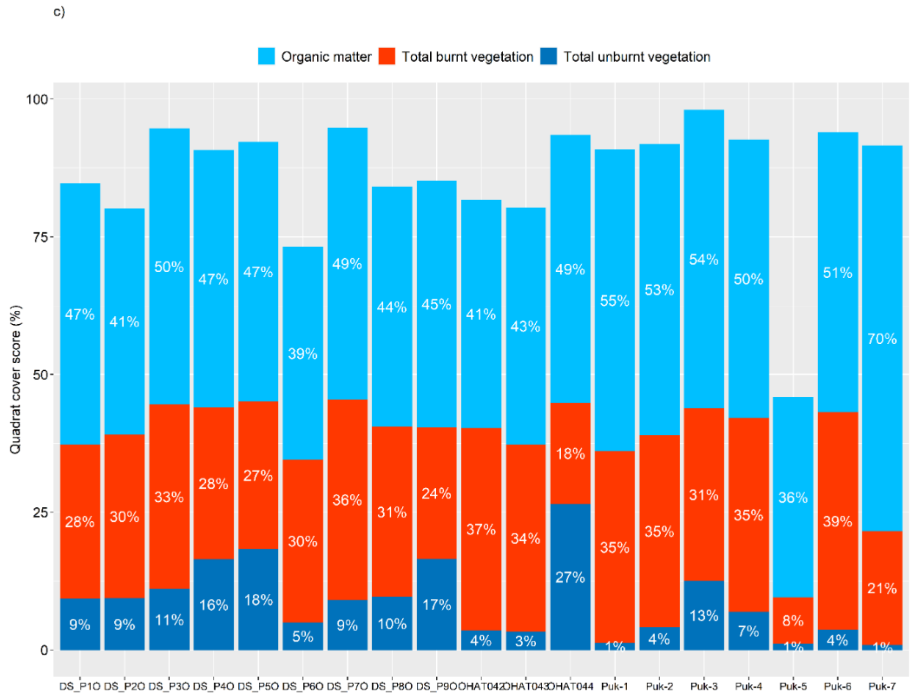


Figure S4. Mean branch diameter as a possible measure of fire severity quantified at the transect level within each of three sites: a) Deep Stream and b) Ōhau and c) Pukaki. Boxes that share letters were not statistically different. Letters denote differences in fire severity among sites from one-way ANOVA and Tukey test (*P* < 0.05). Ind = number of individuals, Twi = total number of branches measured. Sig = significant (*P* < 0.05).



Within quadrat; Organic matter is sum of all the living material,total burnt vegetation is the sum of all the remaining after burns excluding litter and total unburnt vegetation is the sum of living vegetation after burns

Figure S5. Percent quadrat cover comparison to determine fire severity across three recent wildfire sites comparing quadrat percent covers (area burnt) at the recently burnt sites Deep Stream, Ohau and Pukaki.



Within quadrat; Organic matter is sum of all the living material,total burnt vegetation is the sum of all the remaining after burns excluding litter and total unburnt vegetation is the sum of living vegetation after burns

Figure S6. Percent quadrat cover comparison to determine potential fire severity measures across transects and plots within three sites.

Community flammability

Estimated community flammability was highest at Deep Stream, followed by Ōhau and Pukaki. Within Deep Stream, community flammability was highest on P2O followed by P1O and P4O. At the Ōhau site, it was highest was on transect OHAT042 followed by OHAT043 and OHAT044. At the Pukaki site, community flammability was highest on plots Puk-7, Puk-6 and Puk-5 (Figure S7).

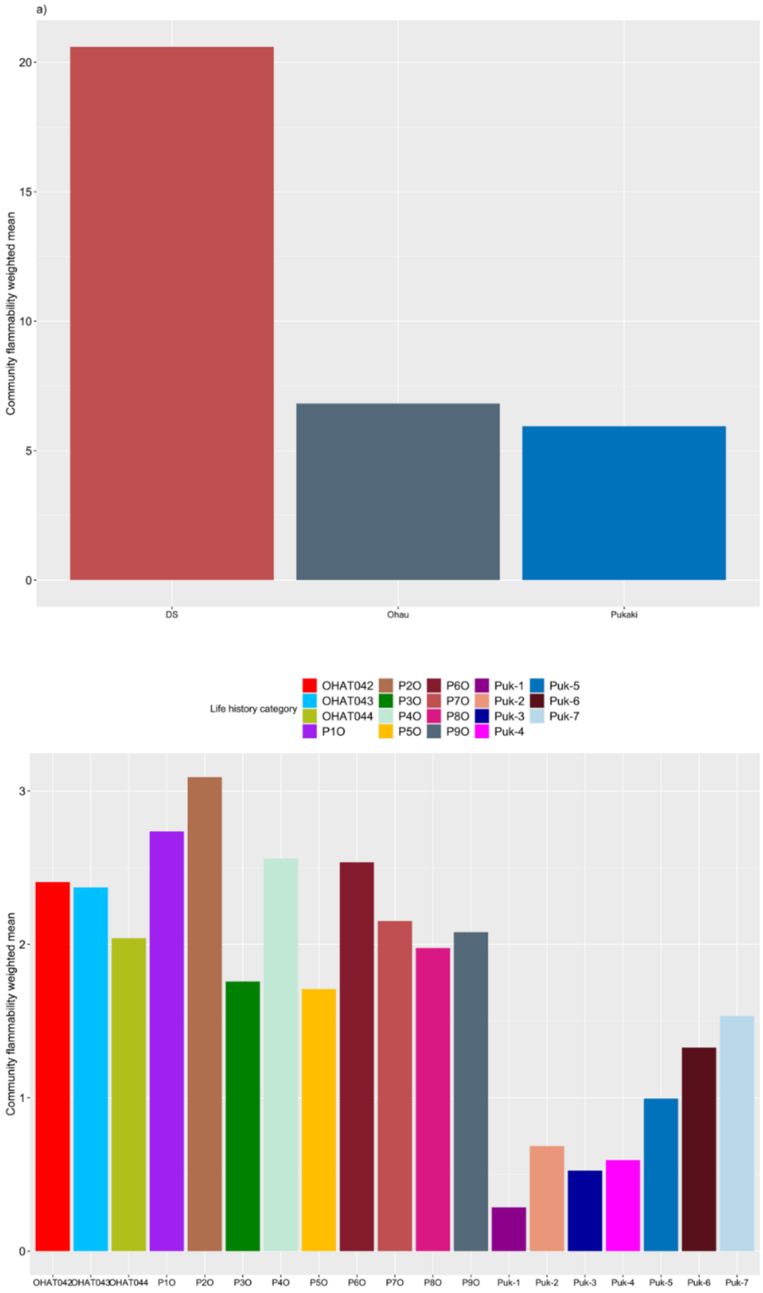


Figure S7. Estimated community flammability weighted means across a) site (Deep Stream, Ohau and Pukaki) and b) plot/transect level within each site.

Discussion and conclusion

I trialled ways to assess fire severity in recent burns in tussock-dominated montane grassland. Measures of branch diameters, quadrat cover of live vegetation and community flammability suggested that Deep Stream fire was had highest severity than the other two sites. However, I was unsure of the ability to directly compare these estimates of fire severity across sites without knowing different pre-fire vegetation. For example, Pukaki had pine trees, which are highly flammable, while Deep Stream had lots of fine prostrate shrubs; these two groups are likely not comparable. In addition, measurements on individuals were taken on a range of woody species and not all species were present at all sampled locations, creating additional variation. I recommend future work tries to assess a good method to measure fire severity in New Zealand's grasslands. Consistency of species measuring at different burnt sites will give more robust and confirmatory fire severity data which is main limitation of my study.

Appendix C. Probability of recovery from seed at Ōhau

I destructively sampled 94 individual plants from 39 species (bio-status: 34 natives and 5 exotics; meristem height: 20 high and 19 low). A total of 9 plants were recovering from seed compared to 85 plants that survived the fire. None of the plants sampled were on moss. Two weeks after fire, the probability of recovering from seed was significantly higher in plants with low meristems compared to high, regardless of whether they were native or exotic (Table S1).

Table S1. Generalised mixed effect modelling results for the probability of individual plants regenerating from seed in relation to three predictors: biostatus (native vs. exotics) and meristem height (low vs. high meristem) in post-fire in montane grasslands at two weeks after fire at Ōhau lake, New Zealand, where *n* = the number of individuals excavated). Significant predictors ($P < 0.001$) are shown in bold.

Model	**Predictor**	**Coefficient**	**S.E.**	***z* - value**	***P* - value**
Bio-status	Exotic (vs. native)	22.34	47864.74	0.00	1
Meristem height	**High (vs. low)**	**-3.75**	**1.197**	**-3.13**	**0.001**

Appendix D: Mathematical expressions used to calculate community flammability and plant morphological traits

a) Community weighted means of traits $= \frac{\sum_p n \times \text{trait}}{\sum_p n}$,

where $\sum_p n \times$ trait represent sum of relative percent frequency of species and trait value and trait represents flammability (PC1) and morphological traits of species measured

b) Leaf area (LA) for broad leaved species $=$ Length (L) $\times$ width (b)

c) Leaf area (LA) for needle leaved species $= 2$ (Length (L) $\times$ thickness (Li))

d) Specific leaf area (SLA)$= \frac{\text{leaf area}}{\text{oven dry mass}}$

e) Dry matter content (DMC) $= \frac{\text{oven dry mass}}{\text{wet mass}}$

f) Moisture content (MC) $= \frac{\text{Fresh mass} - \text{oven dry mass}}{\text{oven dry mass}} \times 100$

Appendix E: Supplementary information (SI) methods

To assess morphological trait variation among taxa, we measured the dimensions of leaves (length, width, and thickness). We measured length and width using a ruler and thickness using a micrometre (size 3202-25A of measuring range 0-25 mm). Also, we scanned leaf samples to create digital images from which we computed the leaf surface area of individual using ImageJ (version 1.53E). At shoot level, we used two sub-samples of approximately 10 cm in length for dehydration and saturation tipping. One of the subsamples was air dried for 24 hours and the other was soaked in water for 7 hours. We measured the biomass of each water-soaked and air-dried samples. Then both samples were oven dried for 48 hours at 65˚C. Similarly, at the leaf level, the leaves were soaked in water for 7 hours and then oven dried for 48 hours at 65˚C. We weighed fresh mass of leaf and oven dried biomass of both leaf and shoot.

We estimated the relative flammability of taxa by burning shoot and above-ground plant samples using a specially designed device by Jaureguiberry et al.(2011) and modified by Wyse et al. (2016). The device consists of a vertically half cut barrel of size 85 × 60 cm placed horizontally on four metal legs of 100 cm in length with a gas grill and connected to gas cylinder. We collected ca.70 cm long samples for burning from terminal branches of trees and shrubs. For taxa < 70 cm height whole plants were collected for burning. Few taxa were flowering at the time of sampling so material that was tested was mostly vegetative parts.

Prior to burning, we air dried samples at room temperature for 24 hours. We then measured the length, width, and height of samples. We visually estimated percent of dead material (includes leaves, branches, and bark) present on each sample. We laid each sample horizontally on the grill for two minutes, then ignited for 10 s using a blowtorch. Ignition time (if it occurred) and burning time measured were recorded in second (s). The maximum temperature attained during burning was recorded using an infrared thermometer (Fluke 572, Fluke Corp., Everett, WA, USA) in °C. Finally, burnt biomass was visually estimated as the percent of biomass consumed in the fire. Taxa that did not ignite were assigned zero percent consumed and the maximum temperature was recorded as the initial temperature of the grill (Cui, Paterson, Wyse, et al., 2020; Padullés Cubino et al., 2018).

To investigate relationships among taxon flammability, leaf nutrient concentration and leaf morphology and shoot traits, we calculated leaf area, leaf dry matter content, leaf specific leaf area, shoot dry matter content, and shoot moisture content at the individual level, following previous studies (Padullés Cubino et al., 2018). We estimated taxa-level values for each flammability, leaf nutrient concentration, leaf morphology, and shoot trait by taking the mean of values for individual samples within 23 taxa. For taxa that were not sampled, we collated data from existing sources (Cui et al., 2020; Padullés Cubino et al., 2018; Wyse et al., 2016, Richardson et al. unpublished), resulting leaf nutrient concentration data and at least partial trait data for 29 taxa.

To determine the phylogenetic signal of plant flammability (PC1) among species, phylogeny of 29 taxa was assessed using function ‘phylo.maker’ that quantifies the phylogenetic properties (e.g. phylogenetic diversity and phylogenetic relatedness) of vascular plants (Qian & Jin, 2016). To visualize species flammability (PC1) pattern across the phylogeny, a phylogenetic tree was made. The phylogenetic signal was evaluated using Pagel’s labda (λ) correlation structure using function ‘corPagel’ (Freckleton et al., 2002). Pagel’s λ varies from zero to unity. A value of λ = 0 indicates that there is no phylogenetic signal in the trait, that is, that the trait has evolved independently of phylogeny and thus close relatives are not more similar on average than distant relatives; λ = 1 indicates a strong phylogenetic signal, and that the trait has evolved according to the evolutionary model of Brownian motion model structure. But values in between 0 and 1 indicate that there is phylogenetic signal in the traits, and also evolved according to other stochastic ecological pressures rather than linear increase in divergence among the species with time (Freckleton et al., 2002). Candidate models were set up where species flammability (PC1) as a response variable and leaf nutrient and morphological traits (PC1_nutrients, PC1_morph and PC2_morph) as predictor in phylogenetic generalised least squared (PGLS) to evaluate phylogenetic pattern of taxon flammability and morphological traits association.