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Patterns of flammability across the vascular plant phylogeny, with special emphasis on the genus *Dracophyllum*

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Xinglei Cui

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Fire has been part of the environment for the entire history of terrestrial plants and is a common disturbance agent in many ecosystems across the world. Fire has a significant role in influencing the structure, pattern and function of many ecosystems. Plant flammability, which is the ability of a plant to burn and sustain a flame, is an important driver of fire in terrestrial ecosystems and thus has a fundamental role in ecosystem dynamics and species evolution. However, the factors that have influenced the evolution of flammability remain unclear. The aim of this thesis is to explore the evolutionary patterns of plant flammability and examine the potential factors that have influenced its evolution. To do this, I examined evolutionary patterns of shoot-level flammability at a range of taxonomic levels, including across the Tracheophyta (194 vascular plant species), within a single genus (21 *Dracophyllum* species), and within a single species (eight populations of *Dracophyllum rosmarinifolium*). I also explored the potential factors that have influenced variation in flammability across different taxonomic groups.

Firstly, I examined evolutionary patterns of flammability across the Tracheophyta (vascular plants). I measured shoot-level flammability of 194 vascular plant species and related these to phylogeny, the fire-proneness of the species' natural habitat and species' growth form. I found phylogeny, fire-proneness of habitat and growth form were important predictors of the shoot flammability of vascular plant species. Shoot flammability was generally correlated with phylogenetic relatedness, although some closely related species in some families, such as *Dracophyllum* species (Ericaceae), varied in their flammability. Species in fire-prone ecosystems tend to have higher flammability than species from non-fire-prone ecosystems, suggesting that fire may play an important role in the evolution of plant

flammability. Growth form also influenced flammability: forbs were less flammable than grasses, trees and shrubs, while grasses had higher biomass consumption by fire than other groups. The results suggested that shoot flammability of plants was largely correlated with phylogenetic relatedness and high flammability may result in parallel evolution driven by environmental factors, such as fire regime.

Secondly, I examined evolutionary patterns of flammability within a single genus. In the first objective, I found flammability varied widely across *Dracophyllum* genus. So in the second objective, I explored the phylogenetic patterns of variation in shoot-level flammability across 21 *Dracophyllum* (Ericaceae) species. I found species in the subgenus *Oreothamnus* had higher flammability and smaller leaves than those in the subgenus *Dracophyllum*. Shoot flammability (ignitability, combustibility and consumability) and leaf length showed phylogenetic conservatism across genus *Dracophyllum*, but exhibited lability among some closely related species, such as *D. menziesii* and *D. fiordense*, perhaps due to occupying different habitats. Shoot flammability of *Dracophyllum* species was negatively correlated with leaf length and shoot moisture content, but had no relationship with the geographic distribution of *Dracophyllum* species. In conclusion, I found that shoot-level flammability varied widely in the genus *Dracophyllum*, but showed phylogenetic conservatism. The higher flammability of the subgenus *Oreothamnus* may be an incidental or emergent property due to the evolution of flammability-related traits, such as smaller leaves, which were selected for other functions that may have facilitated drought and frost tolerance during the Pleistocene and incidentally changed flammability.

Finally, I examined evolutionary patterns of flammability within a single species *D. rosmarinifolium*. *D. rosmarinifolium* is an extremely polymorphic species. There is considerable variation in the size of the lamina across *D. rosmarinifolium* populations. In this objective, I measured shoot-level flammability of 62 *D. rosmarinifolium* individuals from eight populations across the South Island of New Zealand. To explore the potential factors that influenced the intraspecific variation in flammability, I examined the relationship between flammability and a suite of climatic and geographic variables, including latitude, mean annual air temperature and mean annual precipitation of the sample locations, and elevation. I found all flammability components varied significantly across populations. Populations at higher elevations had higher combustibility. My results suggest that elevation appear to have influenced the intraspecific variability of flammability within *D. rosmarinifolium*, suggesting that shoot flammability may be influenced by habitat environment in the largely fire-free environment of New Zealand.

In this study, I demonstrated that flammability has a strong phylogenetic component, which is consistent with the idea that flammability having evolved and been selected for. However, I also found evidence for high flammability having arisen in the absence of selective pressure by fire. These results suggest that flammability has likely both emerged *and* been selected for; it depends on the context and whether a species or population occurs in a non-fire-prone or fire-prone habitat.

Statement

I declare that this thesis titled "Patterns of flammability across the vascular plant phylogeny, with special emphasis on the genus *Dracophyllum*" is my own work and has not been submitted in any form for another degree at any other university or institution. I also certify that this thesis is an original piece of research and has been written by me. All sources of information and literature used are cited in the thesis.

Xinglei Cui

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Chapter 1

Introduction

1.1 Global Fire History

Fire is a widespread process in the earth system that can influence global ecosystem patterns and processes, including vegetation distribution and structure, the carbon cycle, and climate (Bond and Keeley 2005, Bowman *et al.* 2009). To produce fire, three necessary conditions must be met: oxygen, fuel and an ignition source (Pausas and Keeley 2009). Ignition sources, such as lightning strikes and volcanoes, probably have existed throughout the history of Earth. Oxygen levels increased with the appearance of photosynthetic organisms and by the beginning of the Paleozoic Era (540 million years ago - MYA), the oxygen level in the atmosphere was sufficient to support fire (Pausas and Keeley 2009). The last condition, fuel, was not met until the appearance of terrestrial plants, at least 420 MYA (Wellman *et al.* 2003, Morris *et al.* 2018). With the arrival of terrestrial plants, fire appeared on earth (Glasspool *et al.* 2004).

The evidence for the earliest wildfire comes from rare fossils dated in the Silurian, representing the charred remains of low-growing vegetation burnt during a low-temperature fire (Glasspool *et al.* 2004). The subsequent fire history on Earth is marked by periods of alternating high and low activity, which seemed to be significantly controlled by atmospheric oxygen levels (Scott and Glasspool 2006). In recent decades, fire regimes have been altered quickly as a result of significant shifts in the human population and land management (Pausas and Keeley 2009). In the future, fires are expected to become more intense and frequent because of the rising temperatures, stronger winds, and more frequent droughts in many parts of the world associated with anthropogenic climate change (Williams *et al.* 2013, IPCC Climate Change 2014, Enright *et al.* 2015).

From the onset, fire has had both geological and biological impacts (Judson 2017). Many terrestrial ecosystems on earth are fire-prone, such that their composition and structure are largely determined by their fire regimes (Bond *et al.* 2005, Pausas and Ribeiro 2013, He *et al.* 2019). Fire drives the evolution of plant traits (Bond and Keeley 2005, Keeley *et al.* 2011, He and Lamont 2017), affects soils, air quality and climate (Knicker 2007, Langmann *et al.*

2009), and promotes biodiversity (Simon *et al.* 2009, Rundel *et al.* 2016, Kelly and Brotons 2017, He *et al.* 2019).

1.2   New Zealand Fire History

Most ecosystems in New Zealand experienced low fire frequencies prior to human arrival, primarily due to the limited ignition sources (Perry *et al.* 2014, Kitzberger *et al.* 2016). Most of the pre-Polynesian landscape of New Zealand was covered in temperate rainforest (Ogden *et al.* 1998, Wiser *et al.* 2011, Allen *et al.* 2013). Fire adaptations are generally absent in the flora of New Zealand and most New Zealand woody species neither resprout from lignotubers or epicormic buds, nor benefit from post-fire seedling establishment (Ogden *et al.* 1998). The few indigenous species with distinctive fire adaptations (e.g., serotiny in *Leptospermum scoparium*, resprouting in *Discaria toumatou, Pteridium esculentum* and *Cordyline* spp.), are all closely related to eastern Australian species or are native to Australia, and have a history in New Zealand no earlier than the Pliocene (5-2 MYA) (Mildenhall 1980, Walsh and Coates 1997, McGlone *et al.* 2005, Stephens *et al.* 2005, De Lange *et al.* 2010).

As Keeley *et al.* (2011) emphasise, plants are not adapted to fire, but to fire regimes. Long and unpredictable fire intervals during most of New Zealand's recent ecological history and the general absence of fire adaptations in the flora (Perry *et al.* 2014), coupled with the loss of fire-adapted traits in some taxa (McGlone 2006, Battersby *et al.* 2017b), suggest that the evolution of New Zealand's indigenous species was not influenced by fire (Lawes *et al.* 2014). Therefore, the New Zealand flora provides an opportunity to examine the evolution of plant traits in the absence of selective pressure fire.

1.3   Genus *Dracophyllum*

Dracophyllum, commonly called dragon leaf because of its distinctive spiky growth form (Figure 1-1), is a plant genus of the family Ericaceae. *Dracophyllum* has 51 polymorphic species that are widely distributed in Australia, New Zealand, and nearby oceanic islands. The genus is traditionally divided into three subgenera: *Dracophyllum, Cordophyllum,* and *Oreothamnus* (Oliver 1952). Twenty-nine species have been recognised in subgenus *Oreothamnus*, all of which are endemic to New Zealand, with the exception of *D. minimum*, which is found in Tasmania. Seven of 21 species from subgenus *Dracophyllum* are endemic to New Zealand, while other species in the subgenus occur in New Caledonia (8 spp.), mainland Australia (4 spp.), Lord Howe Island (1 spp.) and Tasmania (1 spp.). The subgenus

Cordophyllum is monospecific, containing *D. involucratum*, which is endemic to New Caledonia (Venter 2009). The subgenus *Cordophyllum* has only one species, *D. involucratum*, which is endemic to New Caledonia (Venter 2009). All *Dracophyllum* species are endemic at the national level (Venter 2009).

The genus *Dracophyllum* reaches its greatest level of species richness and morphological diversity in New Zealand with 35 species, ranging from low-growing cushion plants to trees up to 14 m tall (Figure 1-1) (Wagstaff *et al.* 2010). Of the 35 *Dracophyllum* species found in New Zealand, eight species occur only on the North Island, 21 species are found solely on the South Island, three species occur on both main islands, and three species grow on nearby small islands (Venter 2009). The high level of diversification in this genus makes it a useful tool for evolutionary research.

Except the high level of diversification in this genus, some *Dracophyllum* species exhibit wide morphological differences within species. For example, *Dracophyllum rosmarinifolium* is an extremely polymorphic species and occurs in different habitats across New Zealand: mountain gullies, mountain slopes ranging from 0°–80°, ridges, bluffs, plateaus and valley floors from 152-2100 m altitude (Venter 2009). *Dracophyllum rosmarinifolium* has considerable variation of morphological characters, such as leaf length, branching habit and height, across populations (Venter 2009). These polymorphic characteristics and diverse habitats make *D. rosmarinifolium* a good subject for micro-evolutionary study.

All of these features (such as high level of polymorphism in *Dracophyllum*, extremely polymorphic species) mean that *Dracophyllum* is a useful model taxon in which to explore the evolutionary patterns of plant traits.
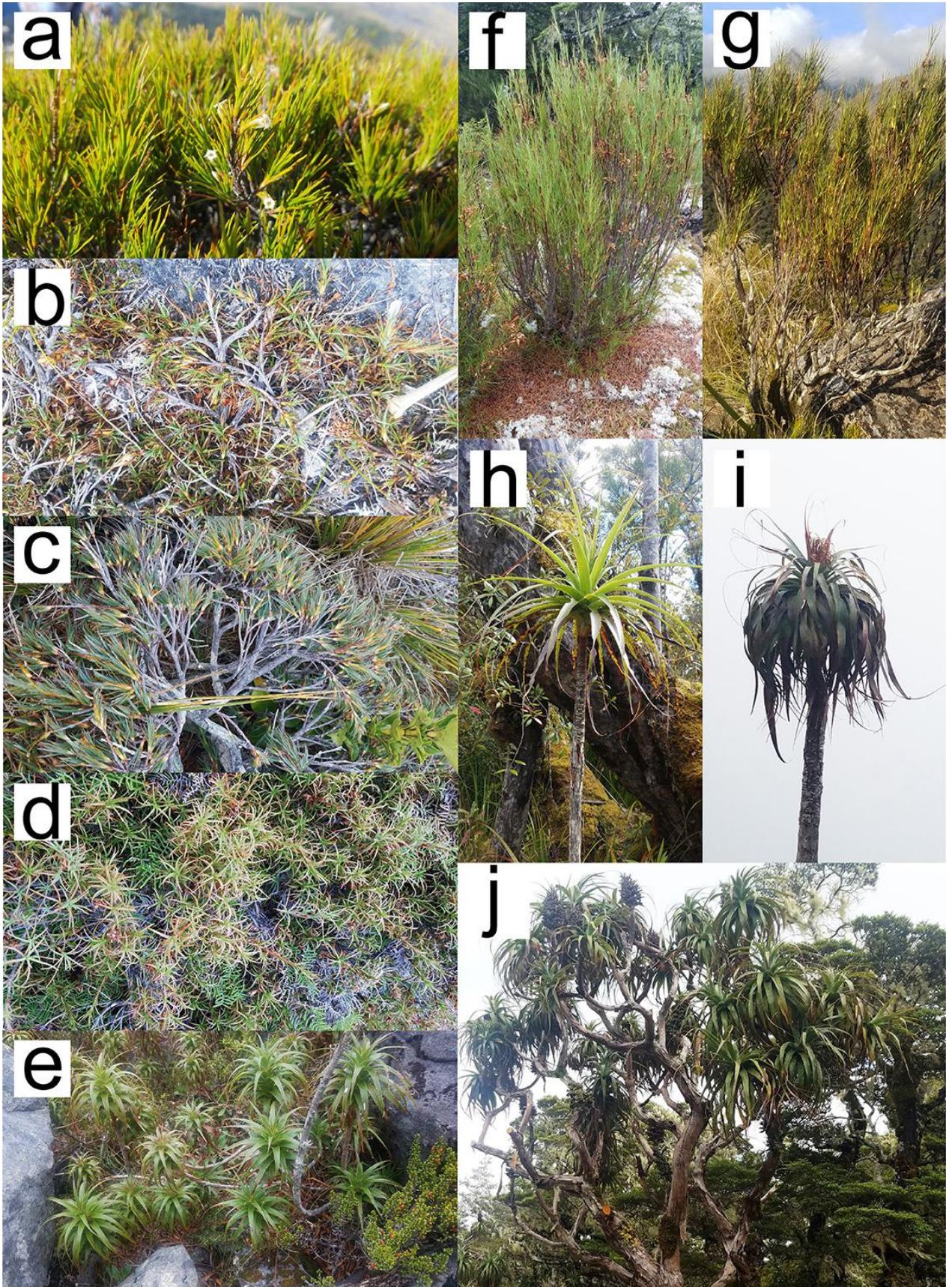
Figure 1-1 Morphological variation among *Dracophyllum* species. a, *D. rosmarinifolium*; b, *D. marmoricola*; c, *D. kirkii*; d, *D. recurvum*; e, *D. menziesii*; f, *D. filifolium*; g, *D. longifolium*; h, *D. latifolium*; i, *D. fiordense*; j, *D. traversii*. Photos: Xinglei Cui.

1.4   The evolution of flammability

We live in a flammable world, and all plants can burn under the right conditions (Pausas and Keeley 2009, Pausas and Ribeiro 2013). Fire has influenced the evolution of plants, and plants have influenced fire characteristics since around 420 MYA (Bond *et al.* 2005, Keeley *et al.* 2011, Schwilk and Caprio 2011). Flammability is one of the main plant traits potentially influenced by the interaction between plants and fire. Flammability varies among and even within species (Pausas *et al.* 2012, Pausas *et al.* 2016, Wyse *et al.* 2016, Battersby 2017, Padullés Cubino *et al.* 2018), but whether flammability has evolved as a specific trait or not continues to be debated (Mutch 1970, Snyder 1984, Bond and Midgley 1995, Schwilk and Kerr 2002, Gagnon *et al.* 2010, Midgley 2013, Bowman *et al.* 2014, Archibald *et al.* 2018). While a growing number of researchers support the idea that fire has selected some plant species to become more flammable (Mutch 1970, Bond and Midgley 1995, Pausas *et al.* 2012, Pausas *et al.* 2017, Archibald *et al.* 2018), or in some cases less flammable (Simon *et al.* 2009, Pausas *et al.* 2017); others have argued that flammability has not evolved in response to fire, but occurs as an exaptation, where increased flammability was an incidental or secondary result of selection for other traits, such as water-use efficiency or nutrient retention, that increased individual fitness (Gould and Vrba 1982, Snyder 1984, Midgley 2013).

The idea that flammability (or non-flammability) might be acted on by natural selection has been hotly contested in the literature and there is a suite of theoretical, modelling, and empirical studies exploring this idea (Archibald *et al.* 2018). The first hypothesis about plant flammability evolution was proposed by (Mutch 1970), who suggested that fire-dependent plant communities burnt more readily than non-fire-dependent communities because natural selection had favoured the development of characteristics that make fire-dependent communities more flammable. The Mutch hypothesis was subsequently criticised for being group-selectionist. Snyder (1984) considered it unlikely that increased flammability can increase the fitness of plants and suggested that many characteristics of species that increased their flammability were merely incidental or secondary results of selection for other traits that increased individual fitness. Later, the "kill thy neighbour" hypothesis was proposed by (Bond and Midgley 1995), which suggested that flammability may enhance inclusive fitness if the resulting fires kill neighbouring less-flammable individuals and create space for the offspring of the flammable individual to recruit. This hypothesis applies quite narrowly to species for which recruitment is fire-stimulated, with soil or canopy-stored seed

banks. Another hypothesis supporting the idea that flammability is selected by fire is the "pyrogenicity as protection" hypothesis, which proposed that pyrogenic tissues that burn rapidly could reduce risk to a plant's below-ground organs and nearby propagules during fires and, therefore be favored by natural selection (Gagnon *et al.* 2010). Midgley (2013) criticised these two explanations as being contradictory, and proposed that flammability has emerged and has no selective advantage. Pausas *et al.* (2017) proposed three plant flammability strategies as 'hot-flammable', 'fast-flammable' and 'non-flammable' that confer fitness benefits to plants living under recurrent fires.

To assess the evolution of plant flammability, macro- and micro-evolutionary approaches can be used. Macro-evolutionary approaches use a dated phylogeny to trace the evolution of flammability-related traits over long time scales (millions of years), and can be used to explore the factors that have influenced the evolution of plant traits (Pausas and Schwilk 2012).

Several macro-evolutionary studies have suggested that fire can be an important selective force on plant traits (He *et al.* 2011, He *et al.* 2012, Pausas 2015). For example, (He *et al.* 2012) provided compelling evidence that fire has influenced the evolution of five fire-adaptive traits (bark thickness, serotiny, branch shedding, grass stage and resprouting capacity) in *Pinus*. Likewise, fire may have been a selective force in the origin of *Banksia* by favouring traits, such as dead floret retention, consistent with adaptation to an increasingly fire-prone environment (He *et al.* 2011).

Fire may not be the only factor that has influenced the flammability of plants (Midgley 2013). Flammability of plants may be an emergent property determined by the local environment, rather than a trait selected for by fire (Midgley 2013). One potential method to test this would be to compare flammability across a clade of species that evolved in the relative absence of fire, and use a macro-evolutionary approach to examine the influence on flammability of factors other than fire. It would also be useful to use quantitative measures of flammability rather than the qualitative measures (e.g. presence/absence of branch shedding in *Pinus*, or retention of dead florets in *Banksia*) used in previous macro-evolutionary studies (He *et al.* 2011, He *et al.* 2012). Qualitative approaches limit the scope of available comparative phylogenetic analyses, and preclude estimation of phylogenetic signal. Furthermore, quantitative measures of flammability properly reflect that flammability is a continuous rather than binary compound trait.

A micro-evolutionary approach, involving investigation of variation in traits within species or populations, is also useful for examining potential factors for the evolution of plant traits. Few micro-evolutionary studies that examined potential factors for the evolution of flammability or fire-related traits have been reported. For example, Pausas *et al.* (2012) used a micro-evolutionary approach to show that individuals of the Mediterranean shrub species *Ulex parviflorus* (Mediterranean gorse, Fabaceae), from localities with a history of high fire frequency, were more flammable than those growing in sites with no recent fires. These findings suggest that the flammability of *U. parviflorus* has increased due to recurrent fires (Pausas *et al.* 2012, Moreira *et al.* 2014). A study on bark thickness of pines suggested that frequent anthropogenic fires could be a powerful selection force for thick bark (Stephens and Libby 2006), although thick bark has also been found among species not exposed to frequent fires (Lawes *et al.* 2014, Richardson *et al.* 2015). Micro-evolutionary studies of plant flammability are still rare, and most of them have attempted to relate flammability or flammability-related traits to fire regimes in fire-prone regions.

1.5 Phylogenetic signal

Closely related species tend to exhibit similarities in traits, including morphological, behavioural, life-history and ecological characteristics (Harvey and Pagel 1991, Kamilar and Cooper 2013). The strength of the correlation between species trait variation and phylogenetic relatedness can be quantified by estimating their phylogenetic signal (Felsenstein 1985, Münkemüller *et al.* 2012). A strong phylogenetic signal indicates that closely related species have similar values of a given trait, while trait similarity decreases with phylogenetic distance (Losos 2008). Conversely, a trait that exhibits a weak phylogenetic signal suggests that it varies randomly across the phylogeny, implying the trait is not passed down from ancestors (Kamilar and Muldoon 2010). Phylogenetic signal has been used in a range of ecological and evolutionary research areas (Pagel 1999, Blomberg *et al.* 2003, Münkemüller *et al.* 2012), however estimating the phylogenetic signal of plant flammability has never been reported.

Various methods have been developed for quantifying phylogenetic signal (Pagel 1999, Blomberg *et al.* 2003, Münkemüller *et al.* 2012). The two most commonly used metrics for continuous characters are Blomberg's K (Blomberg *et al.* 2003) and Pagel's λ (Pagel 1999). Blomberg's K varies continuously from zero, indicating that there is no phylogenetic signal in the trait (i.e. that the trait has evolved independently of phylogeny and thus close relatives are not more similar on average than distant relatives), to infinity. $K = 1$ indicates

that there is strong phylogenetic signal and the trait has evolved according to the Brownian motion model of evolution, while $K > 1$ indicates that close relatives are more similar than expected under a Brownian motion model of trait evolution (Blomberg *et al.* 2003, Kamilar and Cooper 2013). Pagel's λ varies continuously from zero to unity. $\lambda = 0$ indicates that there is no phylogenetic signal in the trait (i.e. that the trait has evolved independently of phylogeny and thus close relatives are not more similar on average than distant relatives). Where $\lambda = 1$ indicates that there is a strong phylogenetic signal, and the trait has evolved according to the Brownian motion model of evolution. Intermediate values of λ indicate that although there is phylogenetic signal in the trait, it has evolved according to a process other than pure Brownian motion (Pagel 1999, Kamilar and Cooper 2013). Molina-Venegas and Rodríguez (2017) found that Pagel's λ was strongly robust to either polytomies and pseudo-branch lengths, and hence may be a more appropriate alternative over Blomberg's K to measure and test phylogenetic signal in most ecologically relevant traits when phylogenetic information is incomplete. Thus, in my study, Pagel's λ was used for assessing the phylogenetic signal in shoot-level flammability.

1.6   Shoot-level flammability measurement

Plant flammability is a compound plant functional trait controlled by chemical and structural traits (Pérez-Harguindeguy *et al.* 2013). It is usually quantified by considering four main components: ignitability, combustibility, sustainability and consumability (Anderson 1970, Martin *et al.* 1993). In previous research, most flammability measurements focused on small plant fragments, such as leaves, small twigs, or litter, which do not reflect whole-plant flammability (Behm *et al.* 2004, Scarff and Westoby 2006, Cornwell *et al.* 2015, Pausas *et al.* 2016). The flammability of small fragments characterises the flammability of the chosen plant tissues, but does not necessarily scale up well to that of whole shoots or entire plants (Schwilk 2003, Jaureguiberry *et al.* 2011, Schwilk 2015). With the increasing occurrence of crown fires worldwide, there is an urgent need to better characterise the flammability of canopy fuels (Mitsopoulos and Dimitrakopoulos 2007). However, few flammability experiments have been performed on whole plants, especially for tree, and large-scale facilities that allow whole plants to be tested are expensive to operate and impractical in many situations. In their handbook of plant trait measurements, Pérez-Harguindeguy *et al.* (2013) advocated a shoot-level approach as a standardised method of assessing plant flammability. This method preserves much of the architecture of the plant, particularly the fine fuels, and has recently been suggested as a suitable way to measure the flammability of samples from the plant

canopy for a wide range of species (Jaureguiberry *et al.* 2011, Pérez-Harguindeguy *et al.* 2013, Schwilk 2015). Additionally, the shoot-level approach has been found to be strongly correlated with expert opinions based on observation of plant flammability in the field (Wyse *et al.* 2016).

In this study, I used shoot-level flammability to assess the flammability of plant species. The measurement of shoot-level flammability largely followed the methods (Figure 1-2) described by Jaureguiberry *et al.* (2011) and Wyse *et al.* (2016).

Figure 1-2 The device used to measure the shoot flammability of plants.

1.7 Research objectives and thesis outline

The aim of this thesis is to better understand the evolutionary patterns of plant flammability and explore the potential factors that have influenced the occurrence of high or low flammability in different taxa and at different taxonomic scales. To do this, I examined evolutionary patterns of shoot-level flammability at a range of taxonomic levels, including across the Tracheophyta (194 vascular plant species), within a single genus (21 *Dracophyllum* species), and within a single species (eight populations in *Dracophyllum rosmarinifolium*). I

also explored the potential factors that have influenced the flammability variation across different taxonomic groups.

This thesis consists of a general introduction, three data chapters, a general discussion and a conclusion. The data chapters are presented as stand-alone manuscripts for publication in different international journals. Their contents are summarised below. Because of this format, there are some duplications among the different data chapters and the format of the data chapters also differs as they were written for different international journals. Each of these chapters has a very distinct aim and study approach.

Hypothesis 1: Shoot flammability of vascular plants is phylogenetically-conserved and related to habitat fire-proneness and growth form

I examined evolutionary patterns of flammability across the Tracheophyta (vascular plants). I measured shoot-level flammability of 194 vascular plant species and related these flammability data to phylogeny, the fire-proneness of the species' habitat and species' growth form. First, I calculated the phylogenetic signal of flammability across the phylogeny to explore the evolutionary patterns of flammability. Second, I compared the flammability of species between fire-prone and non-fire-prone habitats, to examine how fire-proneness of habitat would affect plant flammability. Third, I classified all 194 species into four possible growth forms: trees, shrubs, grass or forbs, and examined the variation of flammability across the growth forms.

Hypothesis 2: Shoot-level flammability across the *Dracophyllum* (Ericaceae) phylogeny: evidence for flammability being an emergent property in a land with little fire

I examined evolutionary patterns of flammability within a single genus. I measured shoot-level flammability of 21 species of *Dracophyllum* (Ericaceae). Using a macro-evolutionary approach, I explored the phylogenetic patterns of variation in shoot-level flammability. I also examined whether leaf size, a trait that varies considerably across *Dracophyllum*, and leaf moisture content, an important trait that drives flammability, were correlated with shoot flammability. To evaluate whether shoot flammability of *Dracophyllum* species was affected by their geographic and climatic conditions, I related the latitudinal range, mean latitude, mean elevation and climate conditions to shoot flammability for each species.

Hypothesis 3: Habitat influences intraspecific variation in shoot flammability

      I examined evolutionary patterns of flammability within a single species. I assessed the intraspecific variation in flammability across eight *D. rosmarinifolium* populations growing in a range of environments to explore which factors have affected the intraspecific variation in flammability of this species. The potential factors that were investigated included elevation, latitude, mean annual air temperature and mean annual precipitation at the sample locations.

Chapter 2

Shoot flammability of vascular plants is phylogenetically-conserved and related to habitat fire-proneness and growth form

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2.1 Abstract:

Terrestrial plants and fire have interacted for at least 420 million years. Whether recurrent fire drives plants to evolve higher or lower flammability and what the evolutionary pattern of plant flammability is remain unclear. Here, we showed that phylogeny, fire-proneness of habitat and growth form were important predictors of the shoot flammability of 194 indigenous and introduced vascular plant species (Tracheophyta) from New Zealand. The phylogenetic signal of the flammability components and the variation in flammability among phylogenetic groups (families and higher taxonomic level clades) demonstrated that shoot flammability is phylogenetically conserved. Some closely related species, such as in *Dracophyllum* (Ericaceae), vary in their flammability, indicating that flammability exhibits evolutionary flexibility. Species in fire-prone ecosystems tend to be more flammable than species from non-fire-prone ecosystems, suggesting that fire may play an important role in the evolution of plant flammability. Growth form also influenced flammability: forbs were less flammable than grasses, trees and shrubs, while grasses had higher biomass consumption by fire than other groups. The results showed that shoot flammability of plants was largely correlated with phylogenetic relatedness and high flammability may result in parallel evolution driven by environmental factors, such as fire regime.

Keywords: evolution; fire; growth form; phylogeny; phylogenetic signal; shoot flammability; vascular plants

2.2   Results and discussion

Fire has affected the distribution and evolution of terrestrial plants globally for at least 420 million years (Bond and Keeley 2005, Bond *et al.* 2005, Bowman *et al.* 2009, He and Lamont 2017, Scott 2018, He *et al.* 2019) and many species have developed adaptations to persist in the face of this disturbance (Keeley *et al.* 2011, He and Lamont 2017). While a growing number of researchers support the idea that fire has selected some plant species to become more flammable (Mutch 1970, Bond and Midgley 1995, Pausas *et al.* 2012, Pausas *et al.* 2017, Archibald *et al.* 2018), or in some cases less flammable (Simon *et al.* 2009, Pausas *et al.* 2017), others have argued that flammability has not evolved in response to fire, but is a result of exaptations, where traits fulfilling other functions also influence flammability (Midgley 2013). Although there is evidence in some taxa that plant flammability has evolved in response to changes in fire regimes (He *et al.* 2011, Pausas *et al.* 2012, Moreira *et al.* 2014), broad-scale phylogenetic patterns in plant flammability remain unclear. Better understanding of the evolution of flammability would facilitate our understanding of the long-term interactions between fire and plants, and may help prepare us for a warmer world, where fire risk may be higher in many regions (Doerr and Santín 2016). One method to decipher the evolutionary patterns of plant flammability is to evaluate variation in flammability with phylogenetic approaches, but few such studies have been reported. These previous studies have mostly focused on specific genera (Engber and Varner 2012) and used qualitative rather than quantitative measures of flammability (He *et al.* 2011, He *et al.* 2012).

We burned 70 cm-long shoots of 194 species (120 indigenous to New Zealand and 74 exotic species introduced from other parts of the world) from across the Tracheophyta (vascular plants) (Appendix A). We measured four flammability components: ignition frequency (ignitability), burning time (sustainability), maximum temperature (combustibility) and percentage of burnt biomass (consumability) and related these to phylogeny, the fire-proneness of the species' habitat and species' growth form. The selected species showed a wide range of shoot flammability attributes: 23 species did not ignite on our device (ignition frequency of zero), while 82 species ignited in 100% of samples. Mean consumed biomass per species ranged from 0% to 94%, the mean maximum temperature for each species was up to 771.5 ± 23.0 °C (mean ± one SE), and mean burning times ranged from 0 to 240 s (Appendix A). Combustibility, consumability and ignitability were strongly positively correlated, while sustainability had a weaker correlation with ignitability and consumability (Figure 2-1).
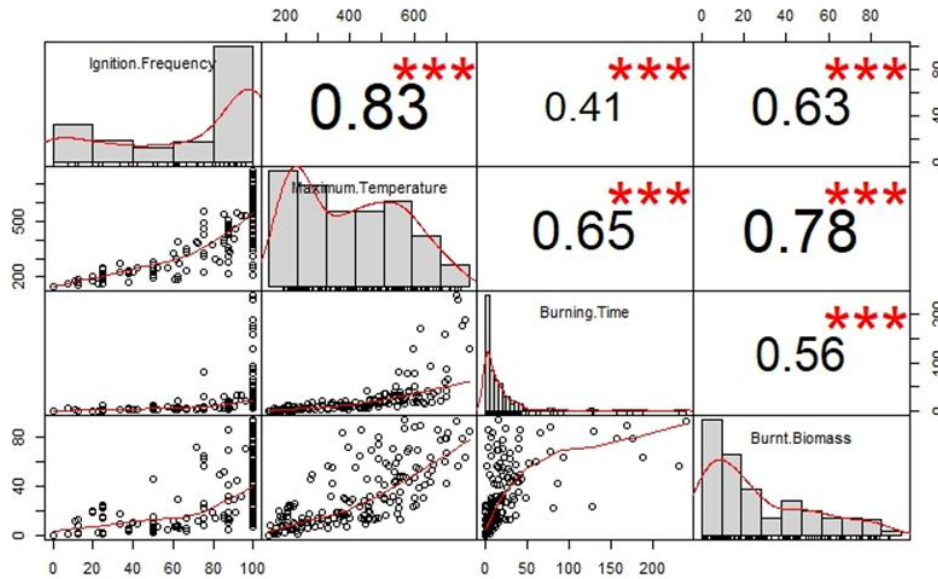
Figure 2-1 Correlations among flammability components (ignition frequency, burning time, maximum temperature and burnt biomass). ***: $P \leq 0.001$

The integration of flammability data with the phylogeny showed that closely related species tend to have similar flammability (Figure 2-2), although flammability varied considerably among some closely related species, e.g., *Dracophyllum* (Ericaceae) species. To evaluate to what extent the related species tend to have similar flammability components, we calculated the phylogenetic signal (Pagel 1999) of each flammability component. We used Pagel's lambda (Pagel 1999) (the value usually varies between 0 [phylogenetic independence] and 1, where species' traits co-vary in direct proportion to their shared evolutionary history (Freckleton *et al.* 2002)) because it is more appropriate than alternatives, such as Blomberg's *K* (Blomberg *et al.* 2003), for testing ecologically relevant traits (Molina-Venegas and Rodríguez 2017) and situations where phylogenetic data are incomplete. Pagel's λ was statistically significant for all flammability components (Table 2-1), confirming that flammability is a phylogenetic trait across the broad range of vascular plant taxa we considered, and demonstrating the usefulness of phylogeny in predicting the flammability characteristics of vascular plant species. The phylogenetic pattern of flammability was consistent even considering possible biases due to unbalanced data regarding habitat and growth form (Supplementary Information section I), although adding more species from different regions of the world may potentially change the phylogenetic signal of flammability. Although it seems likely that species inherited the flammability of their ancestors, the value of the phylogenetic signals (Table 2-1) indicated that flammability exhibits evolutionary

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flexibility. For example, the wide variation in flammability among Poaceae (Poales) and *Raoulia* (Asteraceae) species (Figure 2-2, Appendix A). The variation among closely related species suggested that factors other than phylogeny may influence flammability. In addition, highly flammable species occur in almost any phylogenetic clade across the selected species (Figure 2-2, Appendix A), indicating that high flammability may be a result of parallel evolution driven by environmental factors.
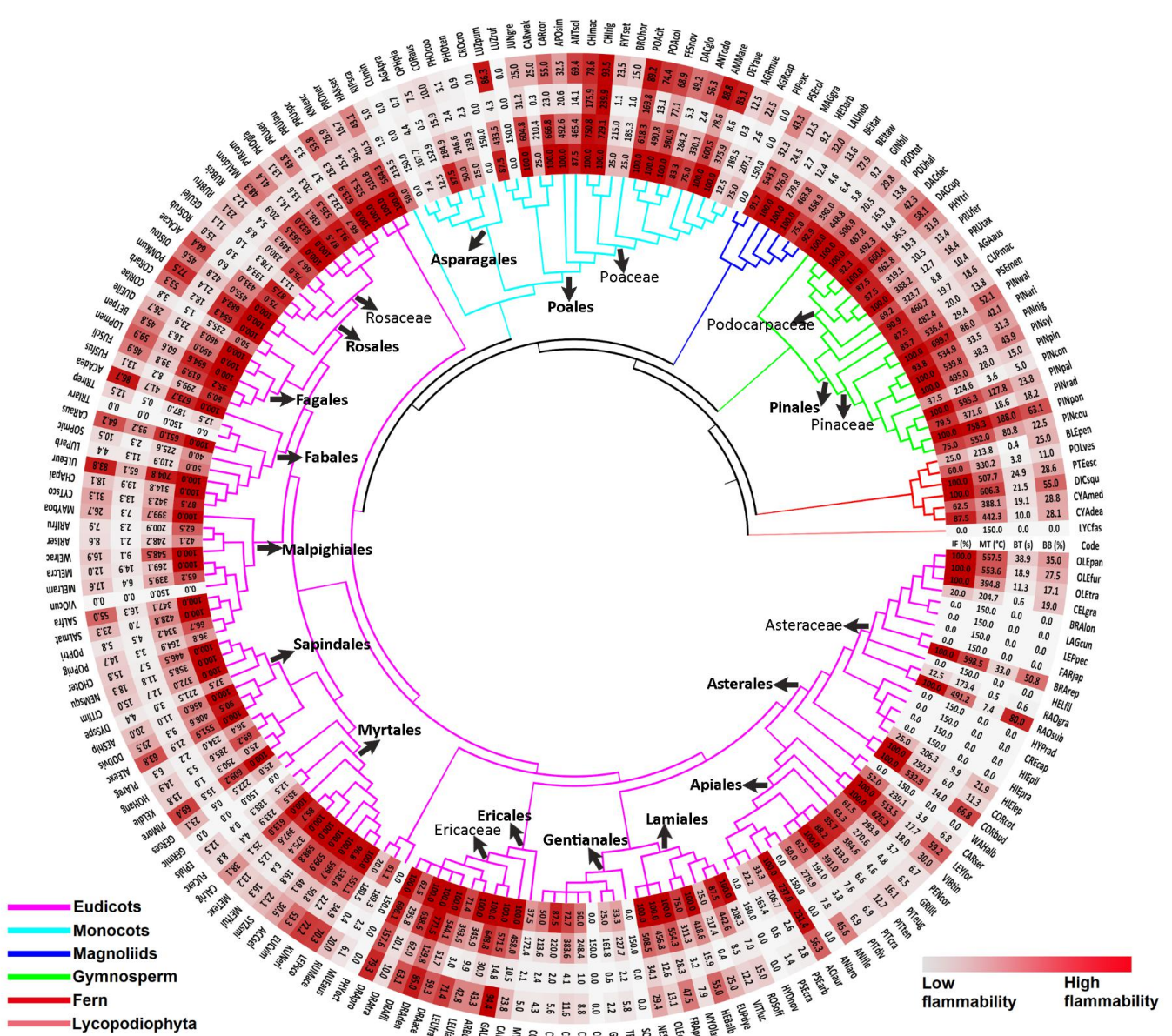
Figure 2-2 Evolution of shoot flammability across the vascular plant phylogeny. The phylogenetic tree (*n* = 194 species) was derived from Open Tree of Life (Hinchliff *et al.* 2015). Cells from the inside to the outside of the phylogeny are the first axis value of PCA (PC1), ignition frequency (IF), maximum temperature (MT), burning time (BT) and burnt biomass (BB). The values of the flammability components increase with the intensity of the color from white to red. Color of branches indicates different clades. Regular typeface denotes names of families; bold typeface denotes names of higher taxonomic level clades (order). See Appendix A for species codes.

Table 2-1 Results of the phylogenetic tests for flammability components across selected indigenous and introduced New Zealand vascular plants species by using Pagel's λ values ($n = 190$ species). P values give the significance of Pagel's λ.

Flammability components	Pagel's λ	
	λ value	p
Ignition frequency	0.74	<0.001
Burning time	0.27	0.005
Maximum temperature	0.51	<0.001
Burnt biomass	0.48	<0.001

To further explore the variation in flammability among phylogenetic clades, we partitioned the species into different phylogenetic groups at different taxonomic levels (families, and higher taxonomic levels clades), each with at least five species. Typically, the families Ericaceae, Myrtaceae, Pinaceae, and Poaceae had high flammability, while Asteraceae had low flammability (Figure 2-3a). At higher taxonomic levels, Ericales, Pinales, Poales and Myrtales had high flammability, largely reflecting the family-level patterns, while Asparagales had low flammability (Figure 2-3b). Among even broader clades, Pinophyta (conifers) had high flammability, while the Lilioid monocots clade generally included low flammablility species (Figure 2-3c). Although only a few phylogenetic clades, with limited replication ($5 \leq n \leq 40$), were analyzed, the flammability variation among phylogenetic clades found here showed it is not randomly distributed across the Tracheophyta, but is influenced by phylogeny.
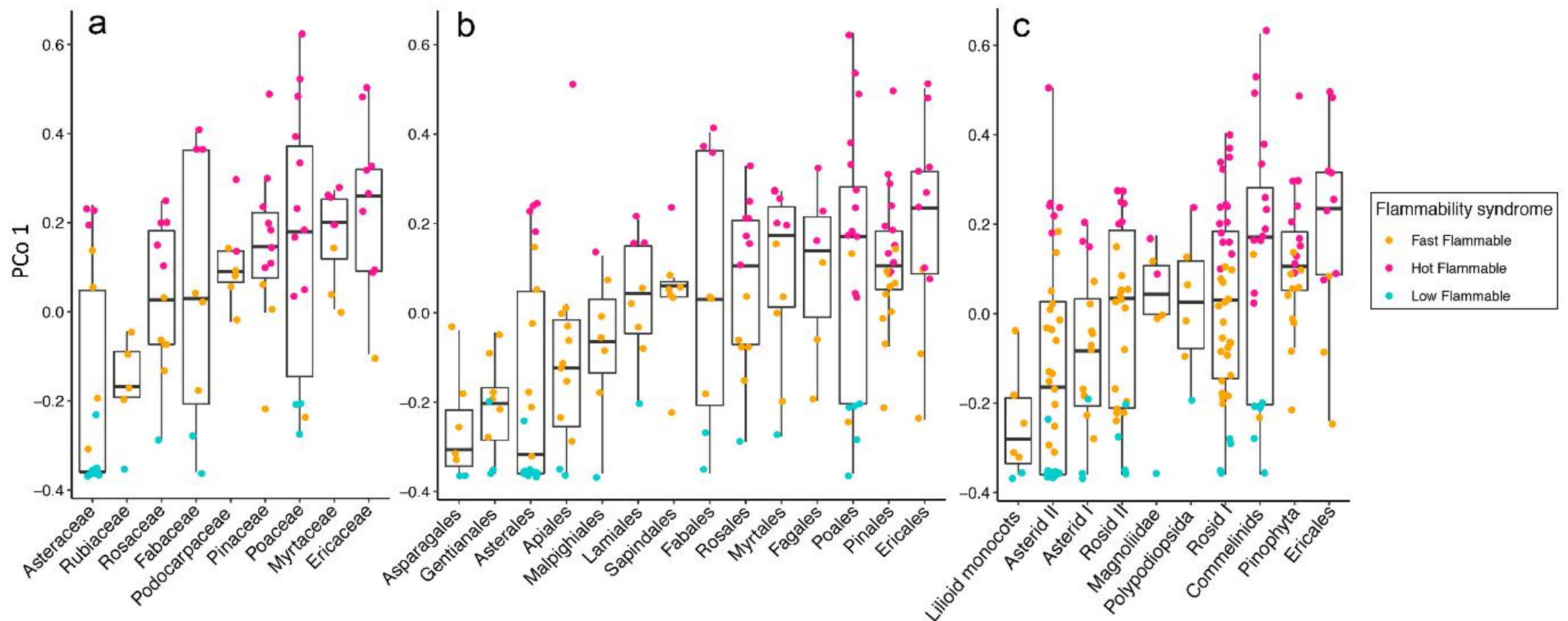
Figure 2-3 Variation in PCo 1 among phylogenetic groups. a, family level ($n = 90$); b and c, higher taxonomic levels ($n = 159$ and $n = 189$). Colour indicates different flammability syndrome. Centre lines show the medians. Box limits indicate the 25th and 75th percentiles. Whiskers indicate the 5th and 95th percentiles. The phylogenetic groups were classified with inference of Angiosperm Phylogeny Group classification (The Angiosperm Phylogeny Group *et al.* 2016).

Hypotheses regarding the evolution of flammability were first proposed by Mutch in 1970 (Mutch 1970), who suggested that fire-dependent plant communities burn more readily than non-fire-dependent communities because natural selection has favoured the development of characteristics that make fire-dependent communities more flammable (Mutch 1970). Nearly 50 years later, the hypothesis that evolution favours increased flammability in some ecosystems remains controversial (Snyder 1984, Bond and Midgley 1995, Midgley 2013, Bowman *et al.* 2014, Archibald *et al.* 2018). Pausas *et al.* (Pausas *et al.* 2017) suggested that one limitation of research considering the evolution of flammability is the concept of flammability itself. They proposed that species in fire-prone ecosystems can be classified into three flammability strategies: hot-flammable (high heat release), fast-flammable (high flame spread rate) and low-flammability (low ignitability) strategies, and suggested that species in such environments would benefit from acquiring one of these strategies (Pausas *et al.* 2017). Several empirical studies have shown that in fire-prone ecosystems, species can exhibit either low(Simon *et al.* 2009) or high flammability(Pausas *et al.* 2012) (in the latter case, either hot or fast flammability), which could be associated with post-fire regeneration strategies of some species, such as post-fire seeders (Pausas *et al.* 2017). We classified the 194 species into three groups using model-based clustering based on the four components of flammability that we measured (Supplementary Information section II, Figure 2-4). Because the flammability strategies pre-supposed an evolutionary approach to fire, we termed the groups as flammability syndromes. The group with the lowest value of flammability attributes was identified as 'low-flammability'. The group with the highest maximum temperature was considered to be 'hot-flammability'. The group with a much shorter burning time than the 'hot-flammability' group was named as 'fast-flammability'. We also categorized the species as originating from fire-prone or non-fire-prone habitats (see methods for details). We found that species provenance from fire-prone habitats tend to have higher flammability than species from non-fire-prone habitats (Figure 2-5). Fifty-one of 59 species in fire-prone ecosystems were classified into fast-flammability and hot-flammability syndromes (Appendix A), indicating that the prevalent flammability syndrome of species in these ecosystems involves being either fast or hot flammable. Few species (30 of 127) from non-fire-prone habitats were classified into hot-flammability (Appendix A), suggesting that high heat release has few evolutionary advantages in such environments. These results reaffirm the value of the low-fast-hot-flammable framework in the consideration of plant flammability from an evolutionary perspective. However, it should be noted that in our study there were some species in each flammability syndrome that had flammability traits more similar to

species in a different flammability syndrome than their own. Hence, flammability should be treated as a continuous trait, and the flammability syndrome as a spectrum rather than a collection of discrete groups.
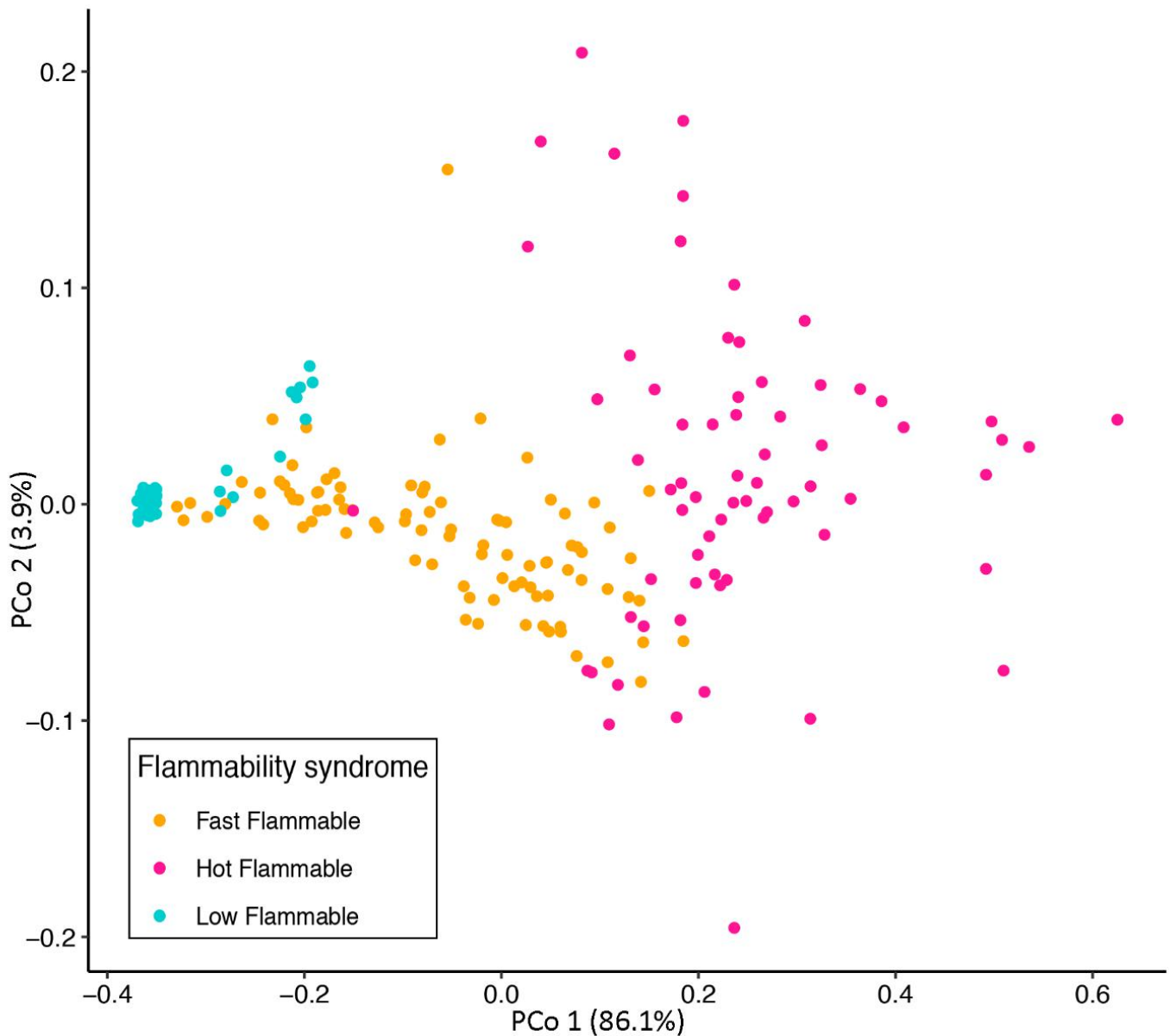
Figure 2-4 PCoA of the mean values per species for the four recorded flammability components (ignition frequency, burning time, maximum temperature and burnt biomass). Points indicate the species (*n* = 194). Color of points indicates the flammability syndromes, which were classified by using model-based clustering. Overlapping points were 'jittered' to better represent them on the figure.

Another potential influence on flammability is growth form (physiognomy). It is widely acknowledged that flammability varies among species (Wyse *et al.* 2016), but variation in flammability across growth forms is less widely reported (Santacruz-García *et al.* 2019). Here we classified all 194 species into four possible growth forms: trees, shrubs, grass or

forbs based on the descriptions from New Zealand Plant Conservation Network (http://www.nzpcn.org.nz). Although flammability varied within growth forms, it also varied significantly among growth forms (Figure 2-5). Forbs were consistently the least flammable growth form, having significantly lower values for all flammability components. Grasses had significantly higher consumability (burnt biomass) than other growth forms, but otherwise generally showed similar levels of flammability to trees and shrubs. The evolution of growth forms since the early diversification of terrestrial plants is a complex history of innovation, complexification, simplification, conservatism, radiation and extinction (Rowe and Speck 2005). Plant growth form is largely determined genetically, but it can be modified by environmental and biotic factors (Rowe and Speck 2005), thus influencing flammability.
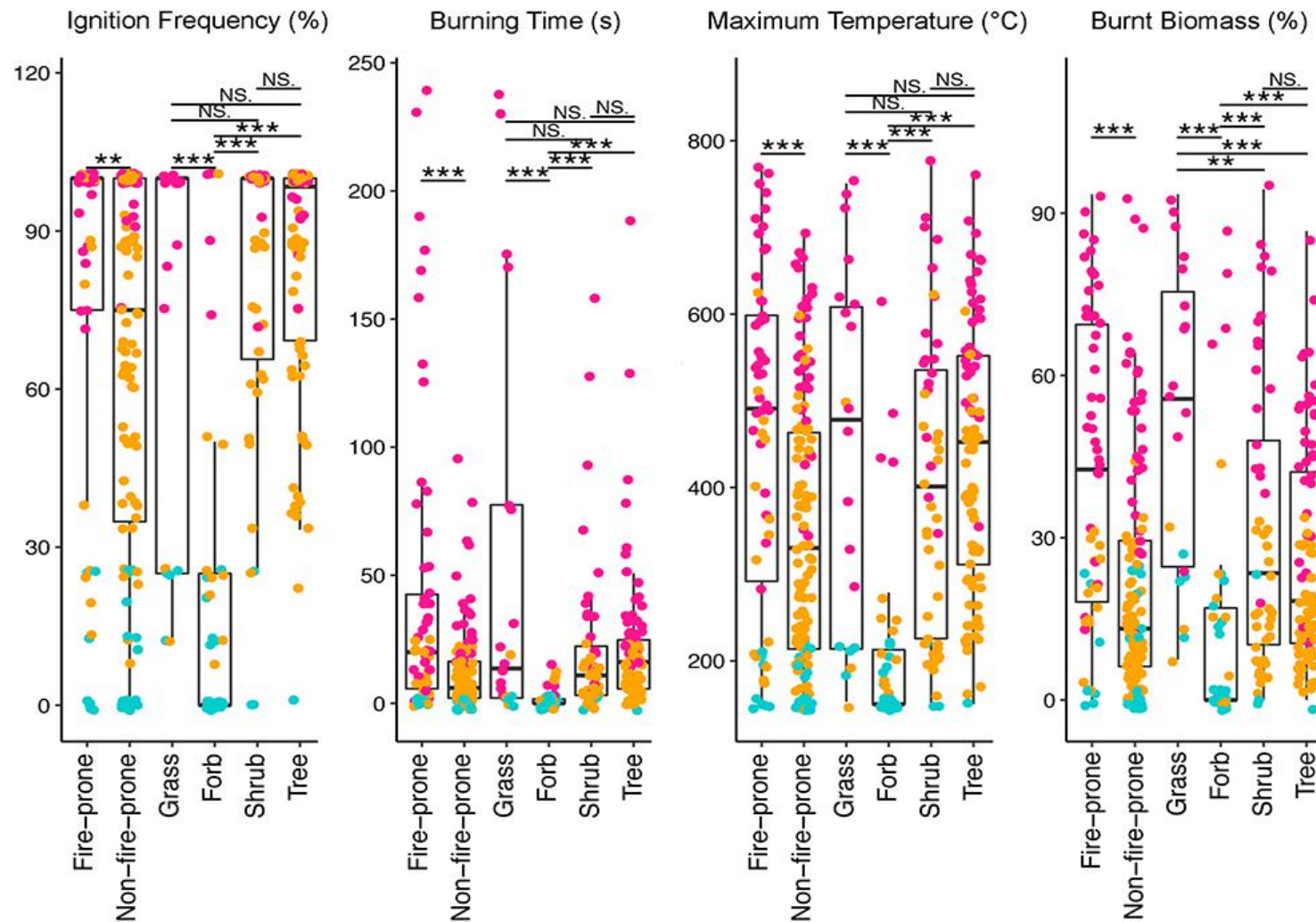
Figure 2-5 Variation in flammability components among plant growth forms (n = 194 species) and habitats (n = 186 species). Colour of points indicates the flammability syndrome. Light blue: low flammability; yellow: fast flammability; red: hot flammability. Centre lines show the medians. Box limits indicate the 25th and 75th percentiles. Whiskers indicate the 5th and 95th percentiles. Statistical differences were analysed using one-way analysis of variance. NS: $P > 0.05$, **: $P \leq 0.01$, ***: $P \leq 0.001$

We assessed the shoot flammability of 194 vascular plants and explored evolutionary patterns of flammability via a phylogenetic approach. Our analyses showed that there is a significant phylogenetic signal of shoot flammability across selected vascular plants (Table 2-1), indicating that closely related taxa tend to have similar flammability and that the shoot flammability of indigenous and introduced New Zealand vascular plants was phylogenetically conserved. That flammability has a phylogenetic component is consistent with the idea that flammability is an emergent trait that can be selected for. However, we cannot rule out flammability being comprised of some exaptations, since the physical and biological conditions in which species live were not considered in this work. The significant variation in flammability among habitats with differing prevalence of fire proneness suggests that fire regimes played an important role in the evolution of flammability traits and indicated that fire-prone plant communities are likely to burn more readily than non-fire-prone communities. Finally, growth form also influenced flammability. That phylogeny, fire proneness of habitat and growth form all influence on the flammability of a wide range of indigenous and introduced New Zealand vascular plant species, suggest that shoot flammability can be relatively predicted from taxonomic relatedness, habitat fire regime and growth form. The results may allow fire managers and ecologists to estimate flammability for a wide range of vascular plant species based on these characteristics, thus expanding our knowledge of how well plants burn at the species level. However, given the wide variability in flammability within each of these predictors, fire managers still need to observe the behaviour and outcomes of fires in specific contexts.

2.3 Methods

2.3.1 Samples collection and measurement of shoot-level flammability

Samples of 194 plant species (120 indigenous to New Zealand and 64 exotic species introduced from other parts of the world) were collected across a broad range of habitats in New Zealand. Nomenclature of species was standardized across the dataset and updated where necessary by querying species names against the New Zealand Plant Conservation Network (http://www.nzpcn.org.nz).

For most species, samples were 70 cm-long, sun-exposed terminal branches from healthy, reproductively mature plants. For small plants (like low grasses and forbs), whole plants were collected in order to preserve the plant's architecture (the roots were removed

prior to burning). In cases where grasses and forbs were taller than 70 cm, the lower 70 cm was sampled and material above that length trimmed and removed. For lianas, a 70 cm shoot was cut from a mature, leafy, terminal branch. For ferns, a section of or a whole single frond up to 70 cm was collected. Shoot samples were collected from each of at least six separate healthy individual plants and kept in separate sealed plastic bags in order to preserve the plant's architecture. The samples were kept in cool places when collecting and then stored at 4-8 °C as soon as possible. Further details on collection protocols are provided by (Wyse *et al.* 2016) and (Padullés Cubino *et al.* 2018).

Measurement of shoot flammability followed the methods of (Wyse *et al.* 2016) and (Jaureguiberry *et al.* 2011). Our device (Figure 1-2) was built following the specifications of (Jaureguiberry *et al.* 2011) and adjusted to meet NZ safety standards. Before burning, all the shoot samples were air-dried at room temperature for 24 h to enable a wider range of species to be ignited by the blowtorch. Then plant samples were preheated for 2 minutes by the burners (150 °C) in the device. After the preheating, the blowtorch was turned on for 10 s to ignite the samples. In this study, ignition frequency (i.e., the percentage of samples that sustained fire after the blowtorched was turned off) was recorded as a parameter to represent ignitibility. The maximum temperature was recorded to represent combustibility. An infrared laser thermometer (Fluke 572; Fluke Corp., Everett, WA, USA) was used to record the maximum temperature of the burning sample after the blowtorch was turned off. Samples that failed to be ignited were given a value of 150 °C as the temperature of the grill of the device. Sustainability was measured as how long the sample burns after turning off the blowtorch. Finally, the consumability was recorded as a percentage of burnt biomass after the flame goes out, calculated by visual observation by at least two observers. Samples that did not burn without the blowtorch were assigned zeros for sustainability and consumability.

2.3.2 Data collection

The fire-proneness of species' habitats were assigned depending on the description of habitat type of each species' biogeographic origin from numerous sources. Species were designated as coming from a fire-prone habitat if they are found in ecosystems that are likely to have recurrent fires, such as grasslands, savanna, or shrublands, or certain forest types, such as eucalypt forests in Australia and pine forests in the northern hemisphere. Species found predominantly in rainforest or closed forest, where fire is unlikely to be a recurrent disturbance and/or a selective pressure, were considered as originating from non-fire-prone

habitats. Cultivated varieties (cultivars) of plants that now occur primarily in gardens were allocated a fire-prone status based on the habitat of the parent species, as we assumed that the fire-prone status of the habitat of cultivated species is the same as that of their parental species. Species in the Pinaceae were all classified from fire-prone habitat (He *et al.* 2012). While this is a simplification of global fire regimes, there are no clear alternative means of categorizing fire regimes of native habitats for such a large number of species.

All species were also classified into four growth forms: trees, shrubs, grass or forbs based on the descriptions from New Zealand Plant Conservation Network (http://www.nzpcn.org.nz). Ferns were classified into shrubs or trees depending on the description. All vines were classified into shrubs.

2.3.3 Testing for phylogenetic signal

In order to evaluate the phylogenetic signal of flammability components, a dated phylogeny for 190 species was obtained from a previously published phylogeny (Slik *et al.* 2018) using Phylomatic software (Webb and Donoghue 2005, Slik *et al.* 2018). Branch lengths were estimated using the BLADJ algorithm based on fossil calibrations of vascular plants (Webb *et al.* 2008, Gastauer and Meira-Neto 2016). The *multi2di* function was used to resolve the polytomies within the phylogeny (Paradis *et al.* 2004). Another phylogeny for all the 196 species was constructed with the Open Tree of Life using the R package *rotl* (Hinchliff *et al.* 2015, Michonneau *et al.* 2016). The second phylogeny was used for the visualization of the flammability changes across the phylogeny (Figure 2-2).

We evaluated the phylogenetic signal by using the R package Picante (Kembel *et al.* 2010) and Phytools (Revell 2012) to calculate Pagel's λ (Pagel 1999). This index uses Brownian models and includes branch-length distances to test for phylogenetic signals against random patterns.

2.3.4 Statistical analysis

All statistical analyses were performed using R 3.5.0 (R Core Team 2018). Principal coordinates analysis (PCoA) was performed using the R packages Vegan 2.5-6 and Labdsv 2.0-1. The relationship among the flammability components was analyzed using the R package *PerformanceAnalytics* (Peterson *et al.* 2018). Flammability syndromes were classified with the four flammability components by using model-based clustering. Model-based clustering was performed using the R package Mclust 5.4.5. One-way ANOVA and

Tukey's test were used to analyze the variation of flammability among growth forms, habitats and phylogenetic groups.

2.4 Supplementary Information

2.4.1 Supplementary Information section I:

One aim of this study is to test the degree to which flammability, as an "emergent trait" resulting from a variety of functional traits, is phylogenetically conserved. Phylogeny may be related to habitat as well as growth form. To further clarify the phylogenetic patterns of flammability and avoid the potential bias in assessing the phylogenetic patterns due to the habitat-phylogeny and growth form-phylogeny relationships, we extracted and reanalysed a subset of the data that was stratified by phylogeny. This subset contained 151 randomly-selected species stratified by genus, whereby any 'replicate' species within each genus had different combinations of habitat fire-proneness and growth form. Phylogenetic signal, as measured by Pagel's lambda, was significant for three of the four flammability components, while burning time was not significant (Table 2-2; Figure 2-6). This result shows that, as an emergent trait, flammability is phylogenetically conserved over and above any correlation with habitat or growth form.

Table 2-2 Results of the phylogenetic tests for flammability components across balanced subset of data ($n = 151$) by using Pagel's λ values. P values give the significance of Pagel's λ.

Flammability components	Blomberg's K	
	K value	p
Ignition frequency	0.65	<0.001
Burning time	<0.001	1
Maximum temperature	0.51	<0.001
Burnt biomass	0.46	<0.001

We also calculated the phylogenetic signal of flammability traits separately across the indigenous species and introduced species, as well as for all species (Table 2-3). Across New Zealand indigenous species, only burnt biomass was phylogenetically conserved. Across introduced species, three flammability variables were phylogenetically conserved (all except burnt biomass). When a more globally relevant dataset is considered (all species), we find phylogenetic conservation across all components of flammability. We contend that this makes our findings applicable beyond New Zealand ecosystems, as it suggests that the

species introduced to New Zealand are driving phylogenetic patterns in several of the flammability variables.

Table 2-3 The phylogenetic signal of flammability traits across the indigenous species (*n* = 116) and introduced species (*n* = 74) separately as well as for all species (*n* = 190). *P* values give the significance of Pagel's λ.

Species	Flammability components			
	Ignition frequency	Maximum temperature	Burning time	Burnt biomass
Indigenous species	λ = 0.19, *P* = 0.31	λ = 0.21, *P* = 0.10	λ = 0.13, *P* = 0.18	λ = 0.39, *P* < 0.001
Exotic species	λ = 0.99, *P* < 0.001	λ = 0.76, *P* < 0.001	λ = 0.28, *P* = 0.002	λ < 0.001, *P* = 1
All species	λ = 0.74, *P* < 0.001	λ = 0.51, *P* < 0.001	λ = 0.27, *P* = 0.005	λ = 0.48, *P* < 0.001
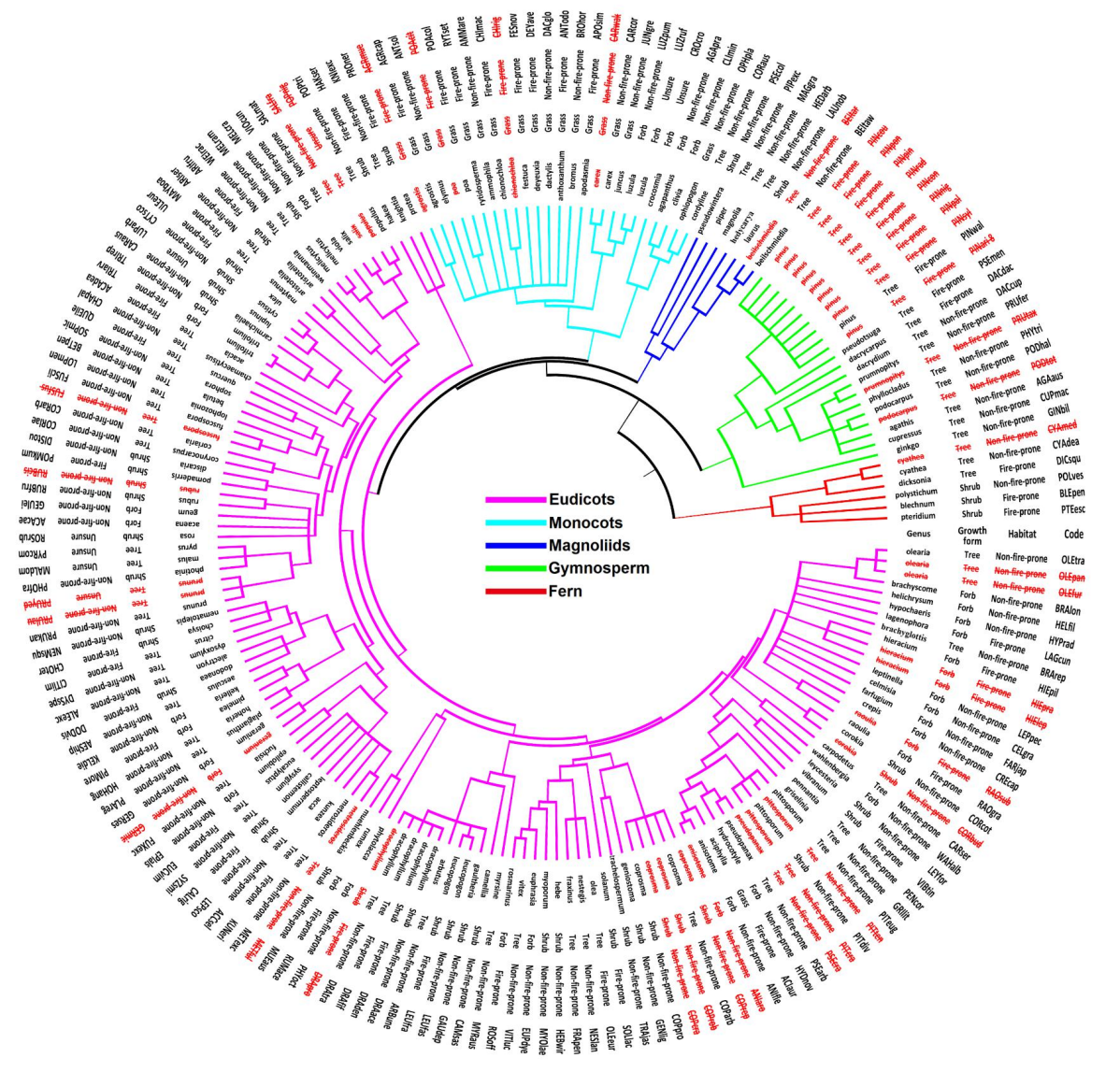
Figure 2-6 The subset of species across phylogeny. Species with red colour and strikethrough were excluded from the subset date (*n* = 43). In the subset (*n* = 151), species that are retained are those from each genus that do not have same designations for habitat fire-proneness and growth form.

2.4.2 Supplementary Information section II:

Pausas *et al.*(2017) described three flammability strategies shown by species growing in fire-prone environments: hot-flammable, fast-flammable and low-flammable. Using quantitative measures of flammability we assigned each of our 194 species to one of these categories (flammability syndromes in our study). In order to show these flammability syndromes present across the 194 species, we performed Principal Coordinates Analysis (PCoA) (Figure 2-4).

It should be noted that the flammability variables that we measured differ from those of Pausas *et al.*, Prior *et al.* and Schwilk *et al.*(Schwilk 2015, Pausas *et al.* 2017, Prior *et al.* 2018). They identified two axes of variation in flammability: 1) heat release and 2) flame spread rate, whereas as our approach was derived from the PCA results with the four flammability variables: ignition frequency, burning time, maximum temperature and burnt biomass.

2.5 Acknowledgment

Chapter 3

Shoot-level flammability across the *Dracophyllum* (Ericaceae) phylogeny: evidence for flammability being an emergent property in a land with little fire

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3.1 Abstract:

Whether flammability is selected for or has incidentally emerged, remain unclear. Phylogenetic analysis of interspecific variation in flammability in a land that has experienced little fire can provide insights into the evolution of plant flammability.

We measured four components of flammability (ignitibility, sustainability, combustibility and consumability) to assess the shoot-level flammability of 21 species of *Dracophyllum* (Ericaceae). Using a macro-evolutionary approach, we explored phylogenetic patterns of variation in shoot-level flammability.

Shoot-level flammability varied widely in *Dracophyllum*. Species in the subgenus *Oreothamnus*, which diverged from subgenus *Dracophyllum* during the Pleistocene, had higher flammability and smaller leaves than those in the subgenus *Dracophyllum*. Shoot flammability (ignitability, combustibility and consumability) and leaf length showed phylogenetic conservatism across genus *Dracophyllum*, but also exhibited lability among some closely related species, such as *D. menziesii* and *D. fiordense*, perhaps due to occupying different habitats. Shoot flammability of *Dracophyllum* species was negatively correlated with leaf length and shoot moisture content, while had no relationship with the distribution of *Dracophyllum* species.

Shoot-level flammability varied widely in the genus *Dracophyllum*, but showed phylogenetical conservatism. The higher flammability in the subgenus *Oreothamnus* may be an incidental or emergent property due to the evolution of flammability-related traits, such as smaller leaves, which were selected for other functions that may have facilitated drought and frost tolerance during the Pleistocene, and incidentally changed flammability.

Key words: *Dracophyllum*, evolution, fire, flammability, phylogenetic signal, phylogeny

3.2 Introduction

Terrestrial plants evolved around 420 million years ago (Wellman *et al.*, 2003). These early plants provided fuel and increased oxygen in the atmosphere to support fire (Glasspool *et al.*, 2004; Pausas & Keeley, 2009). Fire has influenced the evolution of plants, and plants have influenced fire behaviour (Bond *et al.*, 2005; Keeley *et al.*, 2011; Schwilk & Caprio, 2011). Plant flammability is a compound trait emerging from the chemical and physical characteristics of a plant (Schwilk, 2015; Pausas *et al.*, 2017). Different plant species and individuals of the same species growing in different habitats vary in their flammability (Pausas *et al.*, 2012; Murray *et al.*, 2013; Wyse *et al.*, 2016; Krix & Murray, 2018). Investigating the evolution of plant flammability can help us better understand the interaction between fire and plants, and allow us to better prepare for a warmer world, where fire risk may be higher in many regions (Doerr & Santín, 2016). However, the evolutionary mechanisms determining flammability, and whether flammability is selected for or has incidentally emerged, remain unclear (Mutch, 1970; Snyder, 1984; Bond & Midgley, 1995; Midgley, 2013; Bowman *et al.*, 2014).

Macro- and micro-evolutionary approaches have been used to assess the evolution of plant flammability. The macro-evolutionary approach uses a dated phylogeny to trace the evolution of flammability-related traits over extended temporal scales (millions of years) (Pausas & Schwilk, 2012). The micro-evolutionary approach involves investigating variation in traits, such as branch shedding, within species or populations (Pausas, 2015). Several macro-evolutionary studies have suggested that fire can be an important selective force on plant fire-related traits (Crisp *et al.*, 2011; He *et al.*, 2011; He *et al.*, 2012; Pausas, 2015). For example, (He *et al.*, 2012) provided compelling evidence that fire has influenced the evolution of five fire-adaptive traits (bark thickness, serotiny, branch shedding, grass stage and resprouting capacity) in Pinus. Likewise, fire may have played a role in the origin of *Banksia* and the evolution of some traits, such as dead floret retention (He *et al.*, 2011). However, previous macro-evolutionary studies (He *et al.*, 2011; He *et al.*, 2012) have used qualitative traits (e.g., branch shedding/branch retention) rather than quantitative measures of flammability, which reduces the scope of available comparative phylogenetic analyses, such as estimation of phylogenetic signal. Phylogenetic signal is used to evaluate the correlation between species trait variation and phylogenetic relatedness, and has been used in a range of ecological and evolutionary research areas (Felsenstein, 1985; Pagel, 1999; Blomberg *et al.*, 2003; Münkemüller *et al.*, 2012). A strong phylogenetic signal indicates that closely related

species have similar trait values, while trait similarity decreases with phylogenetic distance (Losos, 2008). Conversely, a weak phylogenetic signal suggests that a trait varies randomly across the phylogeny, implying that the trait is not passed down from ancestors (Kamilar & Muldoon, 2010). However, phylogenetic signal has rarely been used in studies of the evolution of plant flammability (but see Cui *et al.*, 2020). Flammability can be quantified by four flammability variables: ignitability (how easily a plant ignites), sustainability (the length of time a plant sustains flames), combustibility (the intensity at which a plant burns), and consumability (the percentage of biomass consumed by fire) (Anderson, 1970; Martin *et al.*, 1993). Estimating phylogenetic signal in these flammability variables will provide insights into the evolution of flammability. Furthermore, quantitative measures of flammability appropriately represent flammability as a continuous rather than binary trait.

New Zealand is an archetypal isolated oceanic ecosystem (McGlone *et al.*, 2016). Most ecosystems in New Zealand experienced low fire frequencies prior to human arrival, primarily due to limited ignition sources (Perry *et al.*, 2014; Kitzberger *et al.*, 2016). Few of New Zealand's indigenous woody species show adaptation to fire (Perry *et al.*, 2014). The indigenous species with distinctive fire adaptations (e.g., serotiny in Leptospermum scoparium, resprouting in Discaria toumatou, Pteridium esculentum and Cordyline spp.), are closely related to eastern Australian species and have a history in New Zealand no earlier than the Pliocene (Mildenhall, 1980; Walsh & Coates, 1997; McGlone *et al.*, 2005; Stephens *et al.*, 2005; De Lange *et al.*, 2010). As Keeley *et al.* (2011) emphasise, species are not adapted to fire but to fire regimes. Long and variable fire intervals during most of New Zealand's ecological history (Perry *et al.*, 2014), coupled with the loss of fire-adapted traits in some taxa (McGlone, 2006; Battersby *et al.*, 2017), suggest that the evolution of New Zealand's indigenous species was not influenced by fire (Lawes *et al.*, 2014). Whether flammability is selected by fire or emerges incidentally has been widely debated (Mutch, 1970; Snyder, 1984; Bond & Midgley, 1995; Midgley, 2013; Bowman *et al.*, 2014). However, most previous studies of the evolution of flammability have focused on species in fire-prone ecosystems (Pausas *et al.*, 2012; Archibald *et al.*, 2018). No study has used a macro-evolutionary approach on a clade of species that evolved in the relative absence of fire, to evaluate the influence of factors other than fire on the evolution of flammability. Therefore, the New Zealand flora provides an opportunity to explore whether flammability is an incidental or emergent property (i.e. is not a specific fire adaptation) (Mason *et al.*, 2016).

In this study, we measured the shoot flammability of 21 *Dracophyllum* species (six in the subgenus *Dracophyllum* and 15 in the subgenus *Orethamnus*) from New Zealand. With reference to published *Dracophyllum* phylogenies (Venter, 2009; Wagstaff *et al.*, 2010), we explored evolutionary patterns in shoot flammability across the genus. We also explored whether the flammability variation among the *Dracophyllum* genus is selected for or incidentally emerged.

3.3   Materials and methods

3.3.1   Sample collection

The genus *Dracophyllum* Labili. (Ericaceae) contains 51 polymorphic species, divided into three subgenera *Dracophyllum*, *Oreothamnus*, and *Cordophyllum* (Table 2-1) (Oliver, 1952; Venter, 2009). *Dracophyllum* reaches its greatest level of species richness and morphological diversity in New Zealand with 35 species, ranging from low-growing cushion plants to small trees up to 14 m tall (Figure 1-1) (Wagstaff *et al.*, 2010). Of the 35 *Dracophyllum* species native to New Zealand, eight are restricted to the North Island, 21 occur only on the South Island, three can be found on both main islands, and three grow on nearby offshore islands (Venter, 2009). The high level of polymorphism in this genus makes it a useful model for evolutionary research.

Table 3-1 The geographic distribution of *Dracophyllum* species.

Genus	Subgenera	Distribution
Dracophyllum (51 species)	*Dracophyllum* (21 spp.)	New Zealand (7 spp.), New Caledonia (8 spp.), mainland Australia (4 spp.), Lord Howe Island (1 sp.), Tasmania (1 sp.)
	Oreothamnus (29 spp.)	New Zealand (28 spp.), Tasmania (1 sp.)
	Cordophyllum (1 sp.)	New Caledonia (1 sp.)

All shoot samples from the 21 *Dracophyllum* species were collected during one summer/autumn season (November 2018 to April 2019) from public conservation lands in New Zealand under permit from the Department of Conservation. The collection sites were selected using information from Venter (2009), iNaturalist (https://inaturalist.nz/) and the Allan Herbarium. Healthy terminal shoots of 70 cm length were collected from healthy individuals, preserving branch architecture, and kept in separate sealed plastic bags to prevent

moisture loss. For *Dracophyllum* species with branches shorter than 70 cm, such as *D. densum*, whole plants above the roots were collected. We sampled at least seven individuals of each species. Shoot samples were kept cool when collecting and then stored at 4-8 °C as soon as possible. All shoot samples were burned within one week of collection.

3.3.2 Flammability measurement

Shoot flammability was measured for each sample following the methods described by Jaureguiberry *et al.* (2011) and Wyse *et al.* (2016), using the same device as Wyse *et al.* (2016). The samples for flammability measurement were 70 cm-long shoot samples. For each species, at least seven samples were collected, each from a different individual plant. Prior to burning, all shoot samples were air-dried at room temperature for 24 h to match the sample moisture content to the ignition source (following Wyse *et al.* 2016, 2018). For the flammability measurements, samples were first placed on our device for preheating for two minutes at 150 °C. Then, a blowtorch was turned on for 10 s to ignite the samples. Ignitability was represented by an ignition score (Padullés Cubino *et al.*, 2018; Wyse *et al.*, 2018). Ignitability was recorded first as time to ignition (between 0 and 10 s), which was then converted to an ignition score by subtracting the time to ignition from 10, e.g. a sample that took 1 s (i.e. rapid ignition) to ignite had an ignition score of 9. Samples that did not ignite after 10 s were given a zero value. The maximum temperature of flames during burning was measured using an infrared laser thermometer (Fluke 572; Fluke Corp., Everett, WA, USA) to represent combustibility. Samples that failed to ignite were given a value of 150 °C, representing the grill temperature (Padullés Cubino *et al.*, 2018; Wyse *et al.*, 2018). Sustainability was measured as the period of time that a sample burned (i.e., had flaming combustion) after the blowtorch was turned off. Consumability was measured as the mean value of the percentage of burnt biomass after flaming combustion ceased, assessed by visual observation by at least two observers. Samples that did not sustain flaming combustion after the blowtorch was turned off were assigned scores of zero for sustainability and consumability.

3.3.3 Other Data collection

We obtained the GPS coordinates of observations (until May 2019) for each *Dracophyllum* species from iNaturalist (https://inaturalist.nz/) (the observation locations that are obscured were excluded). For four species without accurate observation information on iNaturalist (the location of observations are obscured), observation records by Venter (2009)

were used. The elevation of all observation records was estimated from the New Zealand national digital elevation model (25 m resolution, downloaded from https://lris.scinfo.org.nz/). Individual geographical references of each species were used to obtain climatic information (annual mean air temperature and annual mean precipitation) from the WorldClim database (30 seconds (~1 km^2), https://www.worldclim.org/). The climate data were obtained by using the R package DISMO (version 1.1-4) (Hijmans *et al.*, 2017). To characterise the climatic and geographic conditions across each species distribution, the mean values for mean annual air temperature, mean annual precipitation, elevation, and latitude from across the recorded distribution for each species were calculated. The latitudinal range of observations was used as an indicator of the overall latitudinal range size for each species.

The midpoint of the range of values of adult leaf length was taken from Venter (2009) and used as the species measure of leaf length. To calculate the moisture content, a sub-sample of twigs and leaves was taken from each sample and weighed to determine their fresh mass (FM). These sub-samples were oven-dried at 65 °C for 48 h and weighed for dry mass (DM). Moisture content (MC; %) of the sub-samples was calculated as:

$$MC = (FM - DM)/DM \times 100\%$$

3.3.4 Testing for phylogenetic signal

A phylogeny for the 21 *Dracophyllum* species was obtained from a maximum parsimony tree for visualizing the flammability variation across the 21 *Dracophyllum* species () (Venter, 2009). However, this phylogeny does not have branch length and cannot be used to calculate phylogenetic signal. A branch-length phylogeny was constructed with the chloroplast-encoded genes *rbcL* and *matK* using MEGA 7 software () (Kumar *et al.*, 2016). The chloroplast-encoded genes *rbcL* and *matK* were obtained for 14 *Dracophyllum* species from (Wagstaff *et al.*, 2010). We used the R packages Picante (version 1.8) (Kembel *et al.*, 2010) and Phytools (version 0.6-99) (Revell, 2012) to calculate the phylogenetic signal, Pagel's λ (Pagel, 1999), which is is more appropriate than alternatives, such as Blomberg's *K* (Blomberg *et al.*, 2003), for testing ecologically relevant traits (Molina-Venegas & Rodríguez, 2017). Pagel's λ varies continuously from zero to unity. A value of $\lambda = 0$ indicates no phylogenetic signal in the trait, i.e. 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 Brownian motion model of evolution. Intermediate values of λ indicate that although there is a phylogenetic

signal in the trait, it has evolved according to a process other than pure Brownian motion (Kamilar & Cooper, 2013).

3.3.5 Statistical analysis

All statistical analyses were conducted with R 3.5.0 (R Core Team, 2018). Principal component analysis (PCA) of the four flammability components was performed to evaluate the shoot flammability for every species using the *princomp* function in R. The value of the first PCA component was positively correlated with all flammability components, and was used as an aggregate index of shoot flammability (Wyse *et al.*, 2016). All flammability components were compared across species using one-way ANOVA. The proportion of variation across/within populations were calculated by dividing the sum of squares across/within populations by the sum of squares total using ANOVA. Leaf length, shoot moisture and environmental conditions were compared with shoot flammability for each species by using generalised linear regression. Associations among the index of shoot flammability (PC1), leaf length and shoot moisture content were evaluated with partial correlation analyses (using the Pearson method), controlling for leaf length or shoot moisture content, using the R package *ppcor* (version 1.1) (Kim, 2015).

3.4 Results

3.4.1 Shoot flammability varies among *Dracophyllum* species

We collected 251 samples from 21 *Dracophyllum* species across the two main islands of New Zealand, at elevations ranging from 80 m to 1260 m above sea level (Table 3-2, Figure 3-1). These species range from low-growing sprawling shrubs (e.g., *D. densum*, *D. kirkii*) to small trees up to 14 m in height (*D. elegantissimum*). The proportion of variance in all shoot flammability traits other than burning time (sustainability) was higher between species (ignition score: 92.9%; maximum temperature: 51.4%; burning time: 44.0%; burnt biomass: 66.6%) than within species (ignition score: 7.1%; maximum temperature: 48.6%; burning time: 56.0%; burnt biomass: 33.4%). The four shoot flammability components were positively correlated (Table 3-3) and varied significantly across the *Dracophyllum* species (ANOVA, ignition score: $F_{20,230} = 150.50$, $P < 0.001$; maximum temperature: $F_{20,230} = 12.15$, $P < 0.001$; burning time: $F_{20,230} = 9.03$, $P < 0.001$; burnt biomass: $F_{20,230} = 22.91$, $P < 0.001$). Some species (e.g. *D. sinclairii* and *D. trimorphus*) on average ignited within 1 s (ignition

score > 9), while some species (e.g. *D. fiordense* and *D. traversii*) took longer than 8 s to ignite (ignition score < 2). Mean burnt biomass per species ranged from 5.0% for *D. fiordense,* to 90.0% in *D. trimorphum*. The mean maximum temperature of *D. densum* reached 771.5 ± 23.0 °C (Mean ± one SE), while the mean maximum temperature of *D. fiordense* was only 277.7 ± 61.7 °C. Mean burning time varied from 6.7 ± 4.2 s (*D. fiordense*), to 157.6 ± 18.2 s (*D. pronum*). *Dracophyllum fiordense* was the least flammable of the 21 *Dracophyllum* species, with the lowest values for all four flammability components. *Dracophyllum traversii* and *D. elegantissimum* also showed low flammability, requiring more than 6 s to ignite and with burnt biomass less than 15%. The two most flammable species were *D. densum* and *D. pronum*, with both sustaining a flame for more than two minutes (Table 3-4).

A PCA was performed using the mean values of the four flammability components of each species to assess overall shoot flammability across the 21 *Dracophyllum* species. The values of the first two axes of the PCA explained 78.6% and 12.3% of the variation, respectively (Figure 3-2). The loadings of the four flammability components on the first axis were 0.491 (ignition score), 0.514 (maximum temperature), 0.448 (burning time) and 0.541 (burnt biomass). This index of shoot flammability (i.e. PC1) ranged from -4.50 to 2.45 and was positively correlated with all flammability components. According to this index of shoot flammability, *D. densum*, *D. pronum*, and *D. marmoricola* were the most flammable *Dracophyllum* species, while *D. fiordense*, *D. traversii* and *D. elegantissimum* were the least. The index of shoot flammability differed between the two subgenera, with species in subgenus *Dracophyllum* significantly less flammable than those in *Oreothamnus* (Figure 3-2). Another PCA was performed using the flammability components of all individual samples and the results were similar (Figure 3-3).
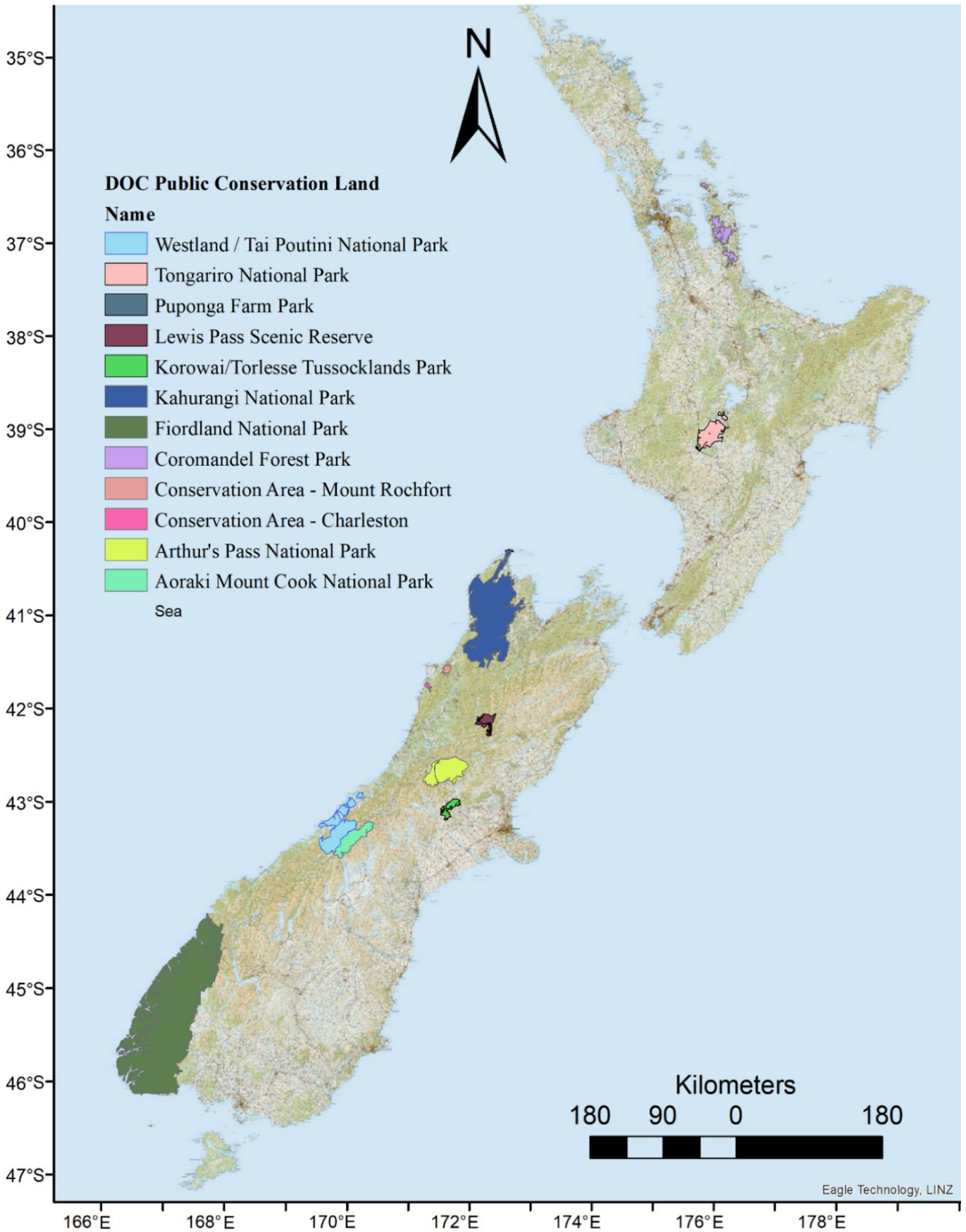
Figure 3-1 Public conservation lands where we collected *Dracophyllum* species.

Table 3-2 DOC public conservation lands where we collected *Dracophyllum* species

DOC public conservation land	*Dracophyllum* species
Korowai/Torlesse Tussocklands Park	*D. pronum; D. acerosum; D. rosmarinifolium*
Arthur's Pass National Park	*D. longifolium; D. traversii*
Conservation Area - Charleston	*D. townsonii; D. elegantissima; D. longifolium*
Conservation Area - Mount Rochfort	*D. densum; D. plaustris; D. oliveri; D. rosmarinifolium*
Lewis Pass Scenic Reserve	*D. rosmarinifolium*
Kahurangi National Park	*D. filifolium; D. Rosmarinifolium; D. Marmoricola; D. Ophioliticus*
Puponga Farm Park	*D. trimorphum*
Mount Cook National Park	*D. rosmarinifolium; D. longifolium; D. kirkii*
Westland/Tai Poutini National Park	*D. fiordense; D. rosmarinifolium; D. longifolium*
Fiordland national park	*D. menziesii; D. rosmarinifolium; D. longifolium*
Tongariro National Park	*D. subulatum; D. recurvum*
Coromandel Forest Park	*D. sinclairii; D. latifolium*

Table 3-3 Pearson's correlation coefficient among four flammability variables, $n = 251$, ***: $P < 0.001$, **: $P < 0.01$, *: $P < 0.05$, ns: $P > 0.05$. *p* values were adjusted with Bonferroni correction.

Flammability variables	Maximum temperature (°C)	Burning time (s)	Burnt biomass (%)
Ignition score	0.50***	0.35***	0.68***
Maximum temperature (°C)		0.53***	0.76***
Burning time (s)			0.58***

Table 3-4 The data we collected for *Dracophyllum* species.

The flammability traits (mean value±SE), leaf length, shoot moisture content (mean value±SE), geographic (mean value±SE), climatic conditions, distribution information and subgenus information.

Species	N	Mean ignition score	Mean maximum temperature (°C)	Mean burning time (s)	Mean burnt biomass (%)	PCA component 1	Leaf length (mm)	Mean shoot moisture content (%)	Altitude (m)	Latitude (°)	Latitude range (°)	Mean annual air temperature (°C)	Mean annual rainfall (mm)	Subgenera	Distribution
D. menzisii	8	6.1±0.3	694.0±23.5	41.1±6.1	69.4±2.7	0.052	155	46±0.5	949.05	-45.00	3.84	5.68	2541.05	*Dracophyllum*	South island
D. fiordense	7	0.7±0.4	277.7±61.6	6.7±4.2	5.0±3.5	-4.4987	550	52±1.3	1033.80	-44.46	1.50	6.00	3203.80	*Dracophyllum*	South island
D. elegantissimum	8	3.6±0.5	557.0±45.7	29.3±4.6	12.8±2.0	-2.3513	665	50±0.9	488.57	-41.47	1.45	10.42	2686.35	*Dracophyllum*	South island
D. latifolium	8	5.1±0.4	657.0±25.4	56.0±11.4	51.9±4.6	-0.4591	422.5	42±1.3	317.98	-36.75	4.30	13.85	1786.36	*Dracophyllum*	North island
D. townsonii	8	7.5±0.2	599.3±45.3	38.8±11.8	46.9±5.7	-0.5641	215	46±1.9	617.77	-41.92	1.72	9.82	3267.08	*Dracophyllum*	South island
D. traversii	7	1.1±0.5	295.8±63.4	20.1±10.7	10.0±3.8	-4.0606	195	47±1.0	900.61	-41.19	8.58	8.65	2894.30	*Dracophyllum*	Both
D. rosmarinifolium	6	8.2±0.1	619.8±15.4	70.9±4.8	70.2±2.8	0.5811	24.25	44±0.5	1103.77	-43.21	5.47	7.13	2129.99	*Oreothamnus*	Both
D. oliveri	7	8.9±0.1	658.1±40.3	39.9±7.2	64.3±6.7	0.3402	62.5	39±1.3	542.20	-43.25	4.36	9.40	2810.20	*Oreothamnus*	South island
D. sinclairii	8	9.3±0.1	607.9±27.3	51.0±4.4	74.4±2.0	0.5685	66	42±2.4	97.67	-36.65	2.54	14.97	1367.71	*Oreothamnus*	North island
D. longifolium	4	8.4±0.1	559.8±15.4	59.8±5.2	56.0±2.3	-0.0797	90	45±0.8	599.57	-44.47	11.77	8.09	2067.24	*Oreothamnus*	Both
D. trimorphus	1	9.2±20.5	702.5±7.6	65.4±1.3	90.0±0.1	1.4653	32	30±1.4	70.00	-40.53	0.06	12.90	2286.50	*Oreothamnus*	South island
D. filifolium	8	8.3±0.1	638.6±39.2	62.0±10.3	63.1±3.7	0.3992	95	40±1.2	711.93	-39.92	4.85	10.02	2298.34	*Oreothamnus*	Both
D. marmoricola	8	8.9±0.1	698.1±32.5	87.0±10.8	89.4±1.5	1.6578	18.8	36±1.3	1504.20	-41.14	0.04	6.86	2660.20	*Oreothamnus*	South island
D. pronum	7	8.1±0.1	696.1±31.3	157.6±18.2	79.3±4.3	2.2263	6.75	44±0.8	1275.37	-43.37	4.17	6.10	2160.32	*Oreothamnus*	South island
D. densum	8	9.0±0.1	771.5±23.0	129.8±22.6	85.0±6.8	2.4479	14	27±0.9	984.00	-41.86	0.59	8.70	3411.00	*Oreothamnus*	South island
D. kirkii	8	8.9±0.1	638.0±38.1	89.9±9.5	65.6±4.9	0.9548	30	43±1.3	1043.12	-43.26	3.79	6.04	3234.06	*Oreothamnus*	South island
D. subulatum	8	8.9±0.1	695.5±27.3	75.9±4.1	88.1±2.3	1.4848	31.5	38±1.5	796.37	-38.89	1.17	9.71	2152.42	*Oreothamnus*	North island
D. palustris	7	8.8±0.1	761.7±33.6	53.7±4.9	85.7±2.3	1.3728	20.5	38±1.2	606.14	-42.73	1.94	9.56	3128.00	*Oreothamnus*	South island
D. acerosum	7	8.0±0.2	544.1±35.1	51.7±5.7	59.3±4.4	-0.2459	110	44±0.5	791.81	-43.47	1.40	8.66	1380.85	*Oreothamnus*	South island
D. ophioliticus	8	8.9±0.1	438.8±20.4	36.0±8.7	38.1±3.9	-1.1621	35.5	44±1.2	854.25	-41.12	0.04	8.30	2359.25	*Oreothamnus*	South island
D. recurvum	8	9.1±0.1	513.5±26.4	48.9±6.6	62.5±4.8	-0.1294	22.5	41±1.5	1261.70	-39.40	0.93	7.77	2646.96	*Oreothamnus*	North island
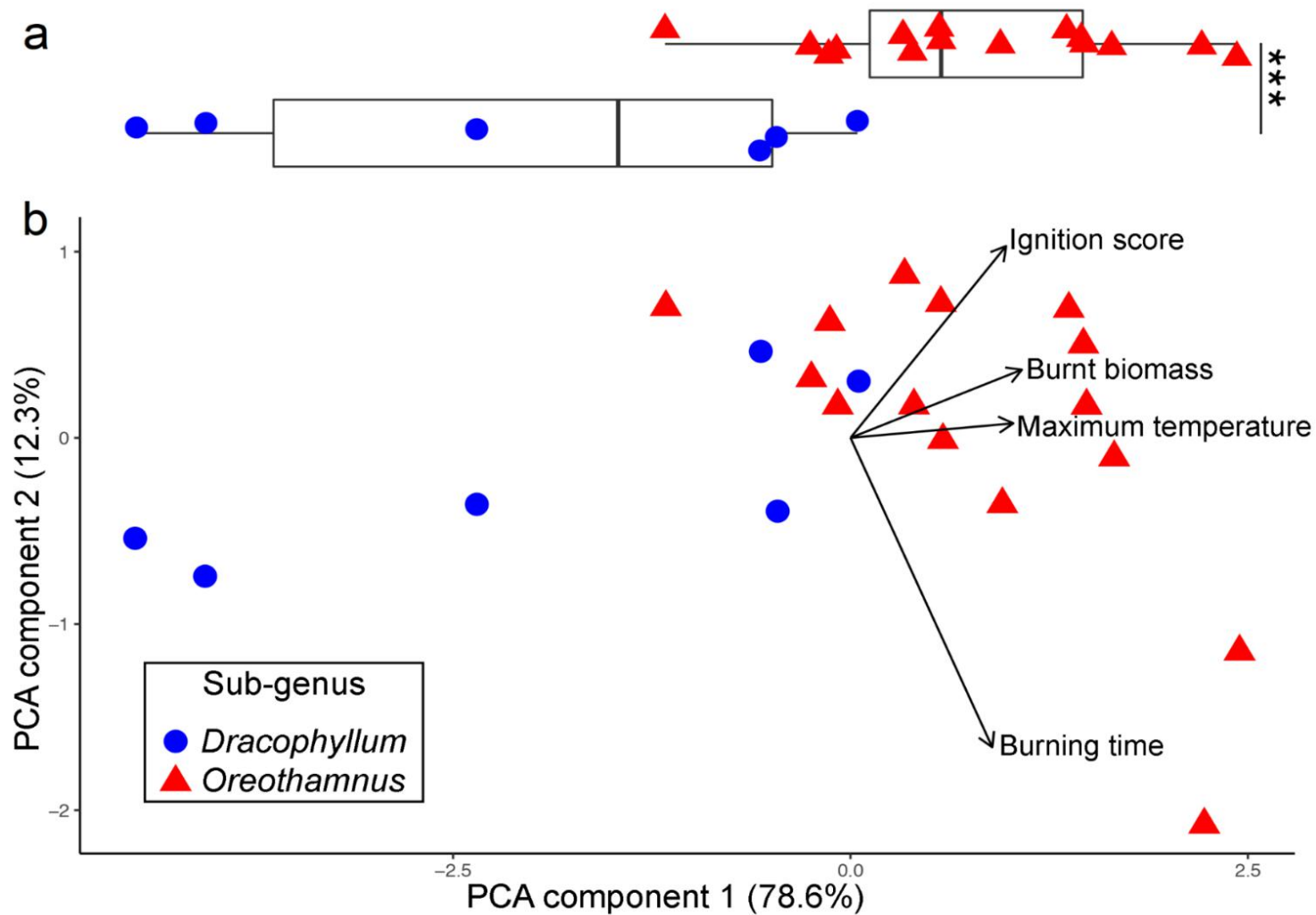
Figure 3-2 Difference in PCA component 1 between subgenera *Dracophyllum* and *Oreothamnus* (a); PCA of flammability variables (b). Blue points indicate species in the subgenus *Dracophyllum*, red triangles indicate species in the subgenus *Oreothamnus*. In the box plots, the boundary of the box closest to zero indicates the 25th percentile, a black line within the box marks the median, and the boundary of the box farthest from zero indicates the 75th percentile. Whiskers left and right of the box indicate the 5th and 95th percentiles. ***: P<0.001 (ANOVA).
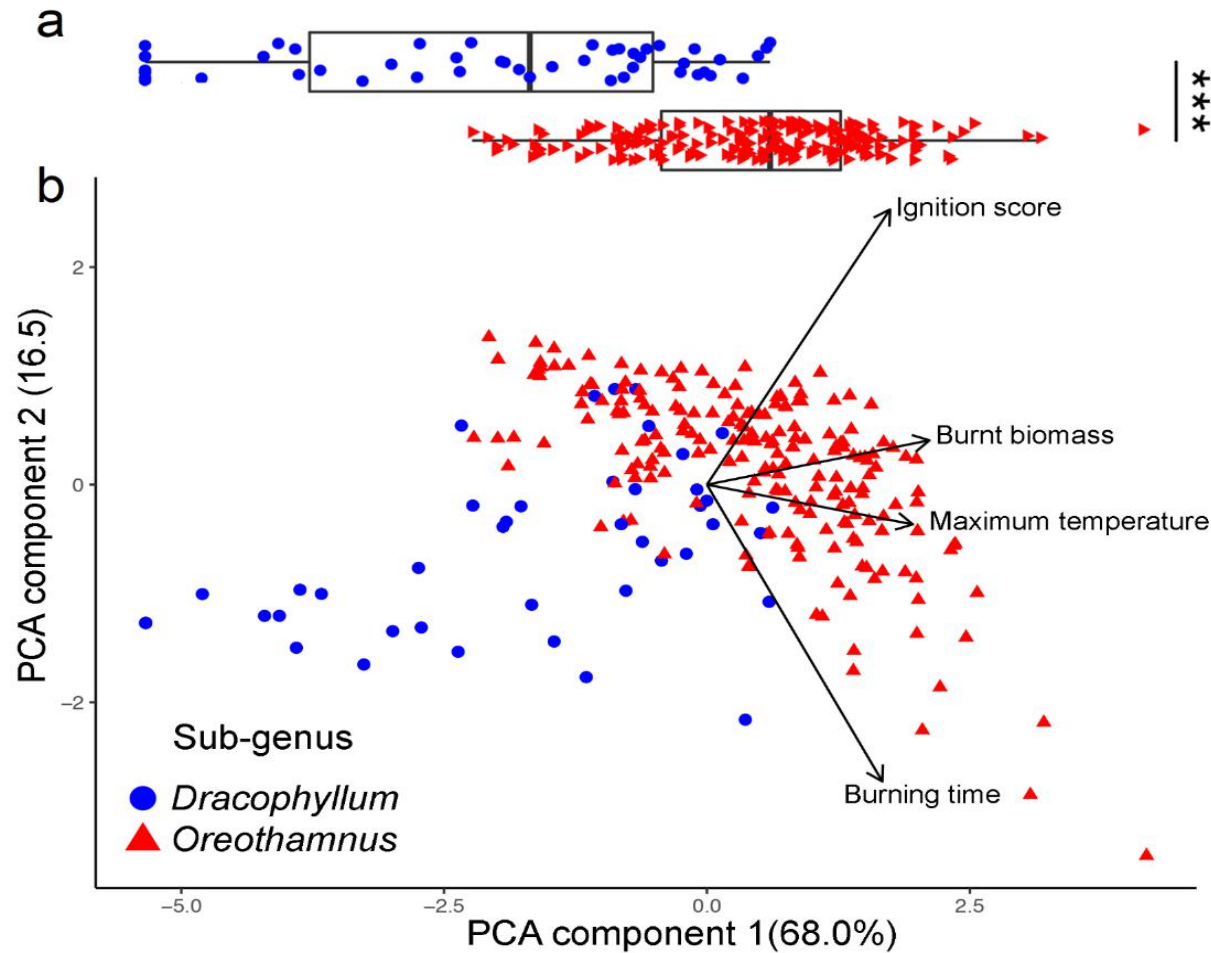
Figure 3‑3 The variation of PCA component 1 between subgenera *Dracophyllum* and *Oreothamnus* (a); PCA of flammability components of all individual samples (b). Blue points indicate species in the subgenus *Dracophyllum*, red triangles indicate species in the subgenus *Oreothamnus*. In the box plots, the boundary of the box closest to zero indicates the 25th percentile, a black line within the box marks the median, and the boundary of the box farthest from zero indicates the 75th percentile. Whiskers left and right of the box indicate the 5th and 95th percentiles. ***: P<0.001 (ANOVA).

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3.4.2 Shoot flammability across *Dracophyllum* shows phylogenetic conservatism

Although shoot-level flammability varied significantly across *Dracophyllum* species (ANOVA, PC1: $F_{20,230} = 29.3$, $P < 0.001$), integrating the flammability data and phylogenetic data showed that closely-related species tended to have similar flammability (Figure 3-5). We divided the 21 species into six identified clades (Figure 3-5) based on their phylogenetic relatedness. Variation in flammability variables, except maximum temperature, was higher among clades (index of flammability: 65.9%, ignition score: 70.9%, burning time: 76.0%, maximum temperature: 44.5%, burnt biomass: 62.3%) than among species (index of flammability: 34.1%, ignition score: 29.1%, burning time: 24.0%, maximum temperature: 55.5%, burnt biomass: 37.7%). The phylogenetic signal across a subset of 14 of the 21 *Dracophyllum* species (Figure 3-4) showed that flammability components, except burning time, were highly phylogenetically conserved, and the index of shoot flammability showed significant phylogenetic signal (Table 3-5). Although shoot flammability showed phylogenetic conservatism, it exhibits obvious lability between some closely related species; for example, *D. menzisii* and *D. fiordense* are closely related, but their shoot flammability differs significantly (ANOVA, $P < 0.001$ for all flammability components, Figure 3-5).
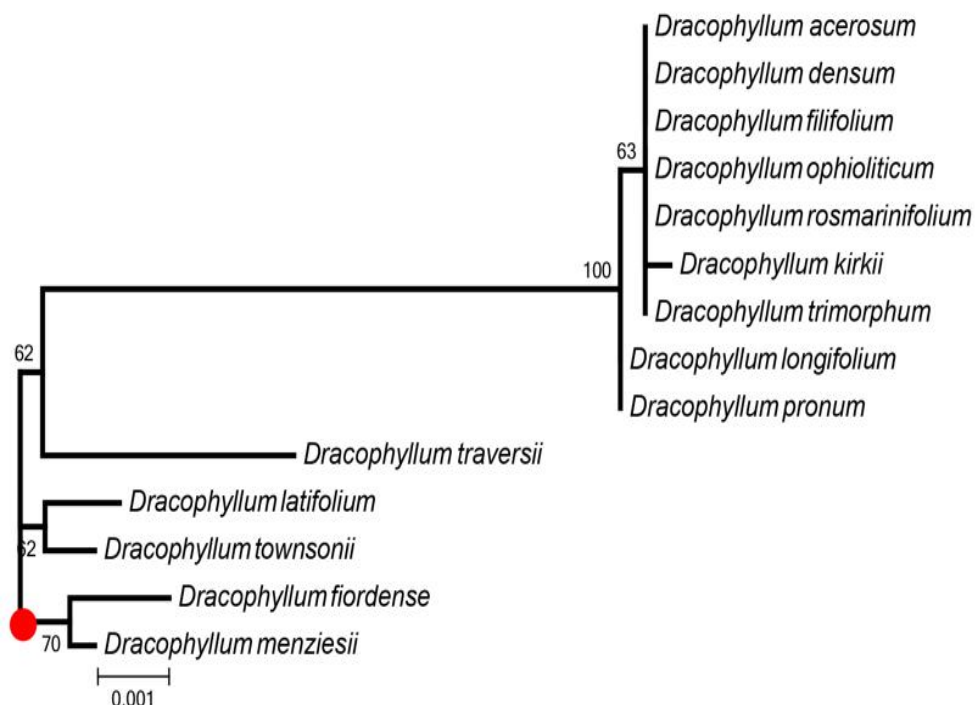
Figure 3-4 Molecular phylogeny of 14 *Dracophyllum* species. The molecular phylogeny was constructed by the maximum likelihood method with *matK* and *rbcL* sequences (Wagstaff *et al.* 2010).

Table 3-5 Phylogenetic signal of shoot flammability variables, leaf length and shoot moisture content across 14 *Dracophyllum* species (Figure 3-5). Bold denotes significant ($P < 0.05$).

Flammability components	Pagel's λ	
	λ value	*p*
Ignition score	0.994	**<0.001**
Maximum temperature	0.923	**0.031**
Burning time	0.344	0.092
Burnt biomass	0.910	**0.027**
PC1	0.914	**0.010**
Shoot moisture content	0.260	0.241
Leaf length	0.987	**<0.001**

	Mean ignition score	Mean maximum temperature (°C)	Mean burning time (s)	Mean burnt biomass (%)	Mean shoot moisture content (%)	Leaf length (mm)
D.rosmarinifolium	8.19	619.76	70.85	70.16	44.27	24.25
D.palustre	8.79	761.71	53.71	85.71	38.42	20.50
D.subulatum	8.94	695.50	75.88	88.13	37.82	31.50
D.acerosum	8.00	544.14	51.71	59.29	44.06	110.00
D.recurvum	9.06	513.50	48.88	62.50	40.66	22.50
D.ophioliticum	8.88	438.75	36.00	38.13	44.24	35.50
D.kirkii	8.94	638.00	89.88	65.63	43.19	30.00
D.pronum	8.14	696.14	157.57	79.29	44.33	6.75
D.marmoricola	8.88	698.13	87.00	89.38	36.03	18.80
D.densum	9.00	771.50	129.75	85.00	26.94	14.00
D.sinclairii	9.25	607.88	51.00	74.38	42.44	66.00
D.oliveri	8.93	658.14	39.86	64.29	38.90	62.50
D.longifolium	8.35	559.78	59.75	56.00	44.90	90.00
D.trimorphum	9.20	702.50	65.40	90.00	29.86	32.00
D.filifolium	8.25	638.63	62.00	63.13	40.39	95.00
D.traversii	1.13	295.75	20.13	10.00	46.60	195.00
D.townsonii	7.50	599.25	38.75	46.88	45.94	215.00
D.latifolium	5.13	657.00	56.00	51.88	42.11	422.50
D.elegantissimum	3.63	557.00	29.25	12.75	49.77	665.00
D.menziesii	6.06	694.00	41.13	69.38	45.72	155.00
D.fiordense	0.71	277.71	6.71	5.00	52.03	550.00

Index of shoot flammability

Oreothamnus

Dracophyllum

-5   0   3

Figure 3-5 The integration of phylogeny of the genus *Dracophyllum*, shoot flammability data, leaf length and shoot moisture content. The phylogeny and drawings were obtained from (Venter 2009). Color of branches in phylogeny indicates subgenera. Green data bars indicate the mean value of shoot flammability traits, leaf length and shoot moisture content. Color of data bars in the right section of the figure indicates positive (brown - high flammability) or negative (blue - low flammability) values in the index of shoot flammability. The drawings are underlined species *D. rosmarinifolium, D. subulatum, D. ophioliticum, D. densum, D. oliveri* and *D. fiordense* from top to bottom.

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3.4.3 Shoot flammability of *Dracophyllum* species decreases with leaf size and shoot moisture content

Leaf size varied across *Dracophyllum* species and discriminated the sub-genera with *Dracophyllum* having longer leaves than *Oreothamnus*. Shoot flammability of *Dracophyllum* species was negatively associated with leaf length ($R^2 = 0.525$, $P < 0.001$, Figure 3-6); that is, species with longer leaves were less flammable. Ignition score and burnt biomass were negatively related to leaf length, while maximum temperature and burning time were less strongly related (Table 3-6). Shoot moisture content was significantly negatively correlated with shoot flammability ($R^2 = 0.536$ and $P < 0.001$ for PC1, Figure 3-6, Table 3-6). Partial correlation analysis showed that shoot flammability (PC1) is significantly correlated with shoot moisture content ($r = -0.53$, $P = 0.016$) and leaf length ($r = -0.55$, $P = 0.013$), after controlling for leaf length and shoot moisture content, respectively. The phylogenetic signal of leaf length and shoot moisture content showed that leaf length was highly phylogenetically conserved, while shoot moisture content was not phylogenetically conserved (Table 3-5).

Table 3-6 Leaf length and shoot moisture content in relation to flammability components across 21 *Dracophyllum* species. Bold denotes significant ($P < 0.05$).

	Leaf length	Shoot moisture content
PC1	R^2=0.525, **P<0.001**	R^2=0.536, **P<0.001**
Ignition score	R^2=0.647, **P<0.001**	R^2=0.393, **P=0.002**
Maximum temperature	R^2=0.209, **P=0.037**	R^2=0.446, **P<0.001**
Burning time	R^2=0.283, **P=0.013**	R^2=0.277, **P=0.014**
Burnt biomass	R^2=0.590, **P<0.001**	R^2=0.575, **P<0.001**
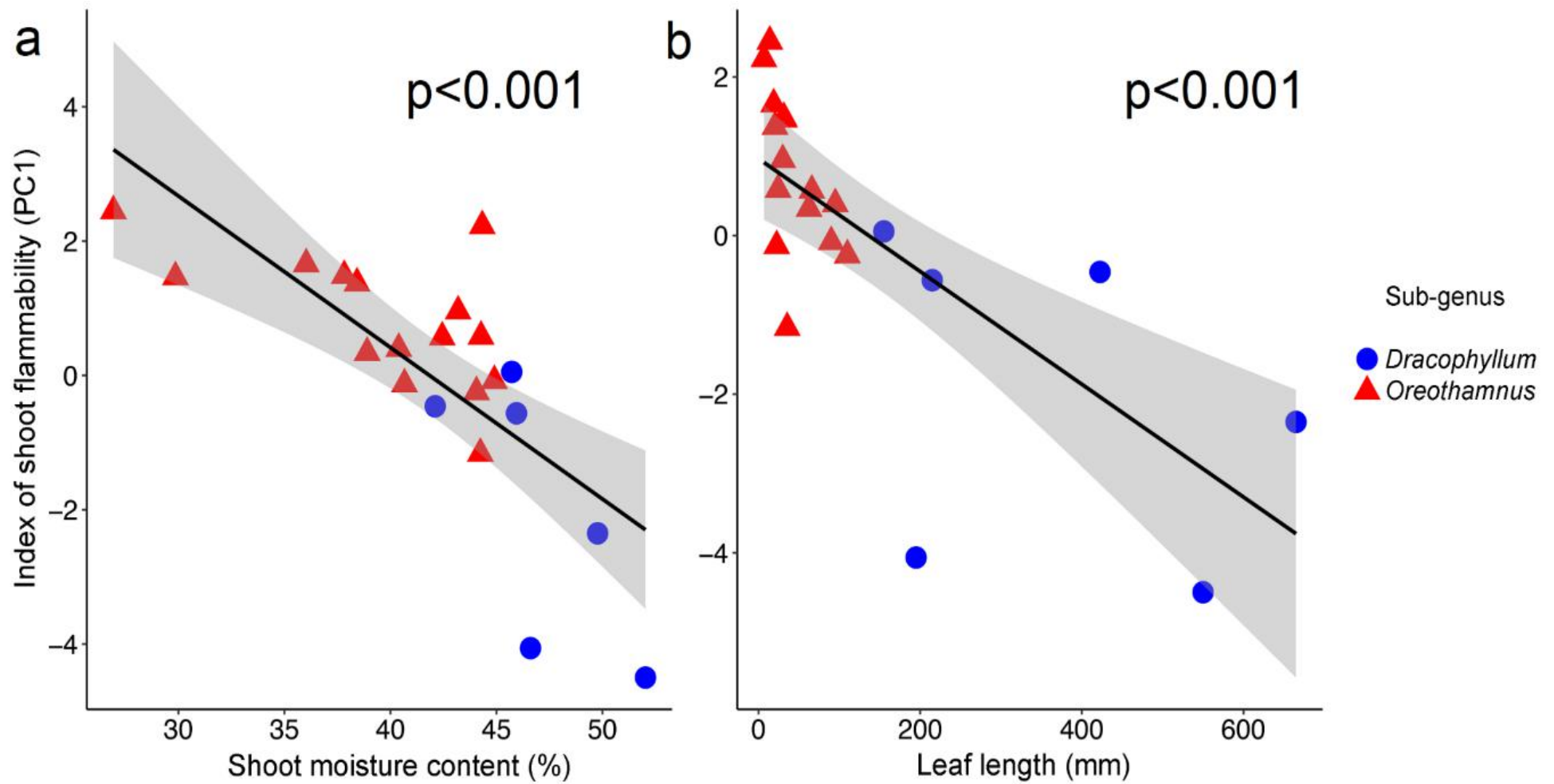
Figure 3-6 The relationship between the index of shoot flammability (PC1) and moisture content (a), and leaf length (b). The shaded area indicates the range of the 95% confidence intervals. Blue points indicate subgenus *Dracophyllum* species, red triangles indicate subgenus *Oreothamnus* species.

3.4.4 Shoot flammability of *Dracophyllum* species has no relationship with their distribution

The latitudinal range of *Dracophyllum* species had no relationship with their shoot flammability (Table 3-7). Of the 21 *Dracophyllum* species, four species occurred only in the North Island and 13 species only in the South Island (Table 3-4). Shoot-level flammability of *Dracophyllum* species did not differ between the two main islands of New Zealand (Figure 3-7). Geographic and climatic conditions (latitude, elevation, mean annual air temperature and mean annual rainfall) were not correlated with shoot-level flammability (Table 3-7, Figure 3-8).

Table 3-7 The relationship between flammability components and environmental conditions.

Flammability components	Altitude (m)	Latitudinal range (°)	Latitude (°)	Mean annual air temperature (°C)	Mean annual rainfall (mm)
Ignition score	$P = 0.860$	$P = 0.320$	$P = 0.524$	$P = 0.600$	$P = 0.326$
Burning time	$P = 0.102$	$P = 0.325$	$P = 0.928$	$P = 0.439$	$P = 0.861$
Maximum	$P = 0.745$	$P = 0.366$	$P = 0.660$	$P = 0.424$	$P = 0.793$
Burnt biomass	$P = 0.787$	$P = 0.790$	$P = 0.547$	$P = 0.664$	$P = 0.391$
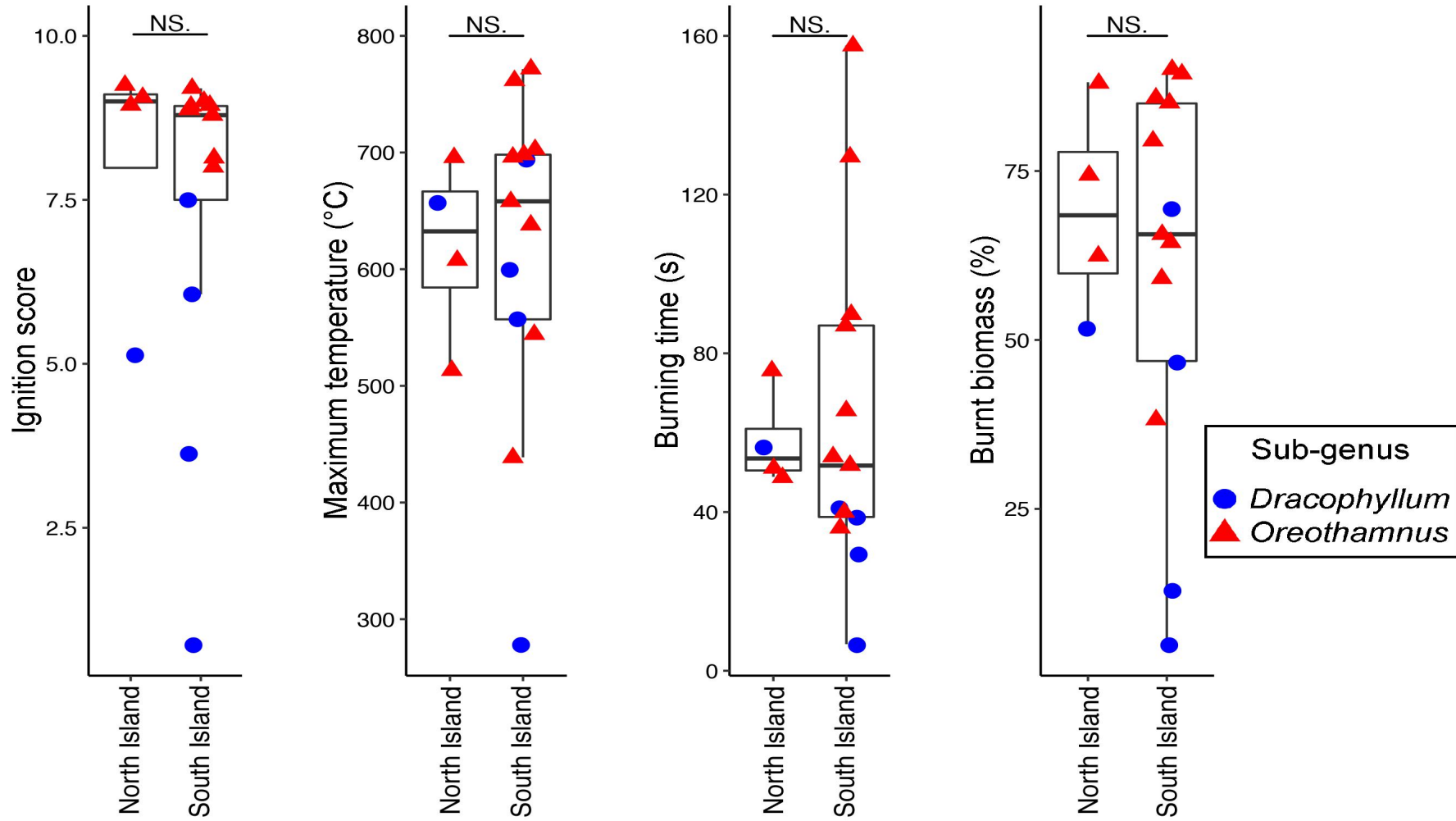
Figure 3-7 Variation in flammability components between North Island and South Island *Dracophyllum* species. In the box plots, the boundary of the box closest to zero indicates the 25th percentile, a black line within the box marks the median, and the boundary of the box farthest from zero indicates the 75th percentile. Whiskers up and down of the box indicate the 5th and 95th percentiles. Species that were distributed on both islands were not included in the analysis. Blue points indicate subgenus *Dracophyllum* species, red triangles indicate subgenus *Oreothamnus* species. NS: P>0.05 (ANOVA).
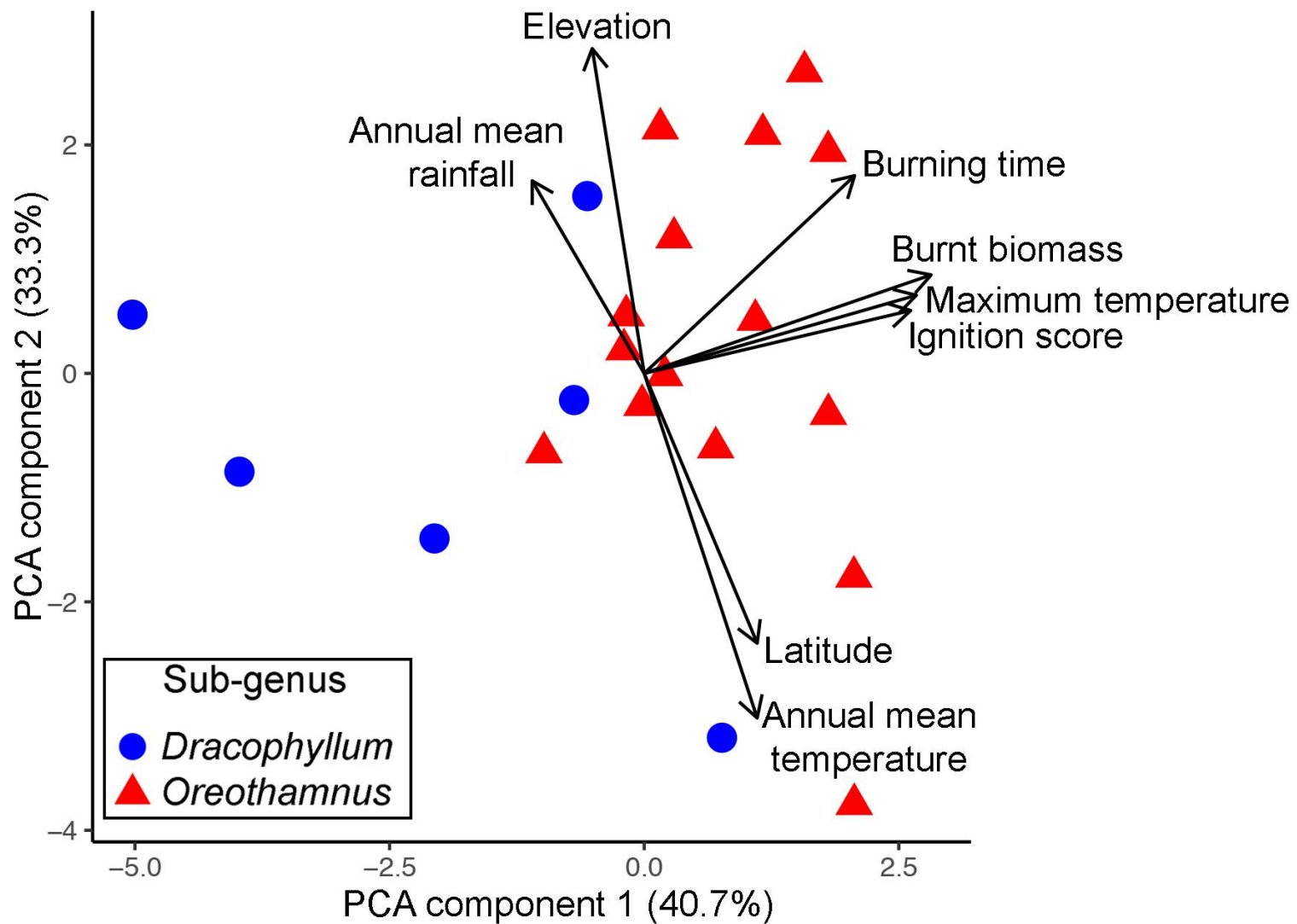
Figure 3-8 Flammability components in relation to environmental conditions. Blue points indicate subgenus *Dracophyllum* species, red triangles indicate subgenus *Oreothammnus* species.

3.5 Discussion

Plant flammability can vary widely across species (Engber & Varner, 2012; Fuentes-Ramirez *et al.*, 2016; Simpson *et al.*, 2016; Wyse *et al.*, 2016; Padullés Cubino *et al.*, 2018). However, how the components of flammability vary between closely related species and whether such species have similar flammability, especially at the shoot-level, has rarely been reported (Engber & Varner, 2012; Cornwell *et al.*, 2015). Based on quantitative measures of shoot flammability from many species of a highly polymorphic genus (*Dracophyllum*), we demonstrated that flammability can vary widely at the genus level. For example, some *Dracophyllum* species, such as *D. trimorphum*, had on average 90% of their biomass consumed by fire in our device, while individuals of some other species (e.g. *D. fiordense*) could not be ignited. The existence of high flammability among *Dracophyllum* species confirms that high flammability species can occur in communities that rarely experience fire (Bowman *et al.*, 2014; Calitz *et al.*, 2015; Wyse *et al.*, 2016; Cui *et al.*, 2020). Despite the wide variation in the genus, shoot flammability was generally more similar in close relatives than distant relatives. Thus, although flammability is a compound trait affected by many functional traits, it retains phylogenetically conserved patterns. Phylogenetic analysis of the shoot flammability of 194 vascular plant species (from 72 families) showed a statistically significant phylogenetic signal in shoot flammability across the Trachaeophyta (Cui *et al.*, 2020), indicating that flammability was phylogenetically conserved at higher taxonomic levels.

The phylogenetic component of shoot flammability is consistent with the notion that flammability, as an emergent trait, may be selected for. However, a more likely explanation for the patterns of flammability seen in New Zealand *Dracophyllum* is that flammability is an incidental or emergent property, and it is environmentally determined (Snyder, 1984, Midgley, 2013). The variation in flammability between the closely related species *D. menzisii* and *D. fiordense* provided evidence for flammability being affected by the environment. *Dracophyllum menzisii*, which mainly grows on mountain slopes, has never been recorded in forest communities and is the only true grassland species in the genus; while *D. fiordense* usually occurs in high rainfall areas and receives additional moisture from mist (Venter, 2009). The difference in flammability between these two closely related species may be a result of adaptation to different environments, indicating that flammability is environmentally determined in this case.

The subgenus *Oreothamnus* diverged from subgenus *Dracophyllum* in the Pleistocene approximately 1-2 MYA and evolved to be more flammable (Gibbard & Van Kolfschoten, 2004; Wagstaff *et al.*, 2010). Fire in most regions of New Zealand is believed to have been infrequent prior to human settlement, although charcoal is found in New Zealand sediments of all ages (Ogden *et al.*, 1998; Perry *et al.*, 2014). This low fire frequency suggests that fire was not a selective force during the divergence of low/high flammability subgenera in *Dracophyllum*. A more likely selective force than fire during this period may have been the shifts in climate associated with glacial-interglacial periods. The repeated climatic changes and glaciation during the Pleistocene are believed to have shaped the New Zealand flora (Wardle, 1988; Winkworth *et al.*, 2005; Heenan & McGlone, 2013; Millar *et al.*, 2017). The cold and dry climate of glacial periods may have influenced the origin and evolution of *Oreothamnus* species, and selected for certain traits, such as smaller leaves, that facilitated frost and drought tolerance (Lusk *et al.*, 2016; Reichgelt *et al.*, 2017), and that incidentally increased flammability. Consequently, we conclude that high shoot-level flammability in *Oreothamnus* is an incidental or emergent property associated with leaf-form as selected through the glacial cycles of the Pleistocene. This result indicates that flammability could be an incidental property, at least in ecosystems with little fire.

Linking functional traits to flammability can facilitate the prediction of flammability across species (Alam *et al.*, 2019). Different plant traits may influence different aspects of flammability, and traits important for crown fire behavior will differ from those important for surface fires (Schwilk & Caprio, 2011). Many studies exploring the influence of traits on flammability have considered the flammability of small plant components, mostly leaves and small twigs (Alessio *et al.*, 2008; De Lillis *et al.*, 2009; Engber & Varner, 2012; Murray *et al.*, 2013; Grootemaat *et al.*, 2015; Pausas *et al.*, 2016; Simpson *et al.*, 2016). The flammability of these small components may not adequately represent the flammability of an entire plant. Shoot level flammability is likely to be a better surrogate for whole plant flammability than flammability of small fragments, although it does not fully capture the influence of plant architecture, especially for tall trees. For example, branch shedding can be important in lessening flammability of conifers, but is not captured by shoot flammability. Moisture content is generally accepted to be a strong determinant of fuel flammability (Dimitrakopoulos & Papaioannou, 2001; Ganteaume *et al.*, 2010; Grootemaat *et al.*, 2015). Leaf size affects litter flammability (Schwilk & Caprio, 2011; Cornwell *et al.*, 2015), but how leaf size influences canopy fires has not been adequately studied. That shoot-level flammability of *Dracophyllum* species was negatively correlated with leaf size and shoot moisture content, suggests that shoot moisture content and leaf size can predict the shoot

flammability of unmeasured *Dracophyllum* species. However, whether leaf size is negatively correlated with shoot flammability at higher taxonomic levels or across species in other genera is unclear. For example, Padullés Cubino *et al.*, (2018) found leaf length to be positively related to shoot flammability in species from tussock grasslands, while Alam *et al.*, (2020) found no correlation between leaf length and shoot flammability in an analysis of 43 tree and shrub species.

We have demonstrated that shoot-level flammability of 21 *Dracophyllum* species varied widely and was negatively correlated with leaf size and shoot moisture content. Shoot-level flammability showed phylogenetic conservatism across the *Dracophyllum* phylogeny, but also occasional lability between some closely related species, perhaps due to differing habitats. Subgenus *Oreothamnus*, which arose (1-2 MA) in the Pleistocene and may have evolved in the absence of fire, exhibited high flammability, suggesting that the climate of the Pleistocene may have favoured and selected for characteristics, such as smaller leaves, that were suited to other functions (e.g. drought and frost tolerance) and incidentally increased shoot-level flammability. Our study has provided evidence that, at least in relatively fire-free environments, high flammability could be an incidental or emergent property that is comprised of traits that arose in response to selective forces independent of fire. However, other studies have suggested that flammability can evolve in fire-prone habitats (Pausas *et al.* 2012, Moreira *et al.* 2014, Cui *et al.* 2020), emphasising the importance of considering fire regimes when examining the evolution of plant flammability.

3.6 Acknowledgments

Chapter 4

Habitat influences intraspecific variation in shoot flammability

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[This project was developed and designed by XC, TC and AP. Plant samples and flammability data were collected by XC, AA & KB. XC did the statistical analyses with advice from AP, TC, SW. XC, TC & AP led the writing of the manuscript, with input from all co-authors.]

4.1 Abstract:

Flammability is a compound trait that varies significantly across natural populations within species. Investigating the causes of intraspecific variation in flammability can provide insights into the evolution of plant flammability.

We measured four flammability variables, representing ignitibility (time to ignition), sustainability (total burning time), combustibility (maximum temperature during burning) and consumability (percentage of biomass consumed by fire) to assess the shoot-level flammability of 62 individuals from eight populations of *Dracophyllum rosmarinifolium* (G. Forst.) (Ericaceae), a polymorphic species distributed throughout New Zealand. To explore the potential factors that influenced the intraspecific variation in flammability, we examined the relationship between flammability and a suite of climatic and geographic variables, namely elevation, latitude, mean annual air temperature and mean annual precipitation of the sample locations.

All flammability components and moisture content varied significantly across the eight populations. Populations at higher elevations had higher combustibility and populations at lower latitude had higher ignitibility. Mean annual air temperature and mean annual precipitation of the sample locations didn't related to flammability components. Shoot moisture content was not related to environmental variables.

Elevation appears to have influenced the intraspecific variability of flammability within *D. rosmarinifolium*, suggesting that shoot flammability may be influenced by habitat environment in the largely fire-free environment of New Zealand.

Key words: flammability; *Dracophyllum*; New Zealand; evolution; elevation; latitude

4.2 Introduction

Plant flammability is an important determinant of fire behavior in terrestrial ecosystems and plays a fundamental role in ecosystem dynamics and species evolution (Belcher *et al.* 2010; Bond and Scott 2010; Pausas *et al.* 2012; Belcher and Hudspith 2017). Exploring the factors that have influenced plant flammability can help us predict changes in wildfire hazard and behaviour in a given ecosystem, and provide insights into the evolution of plant flammability. A micro-evolutionary approach, involving investigation of variation in traits within species or populations, is useful for identifying the factors that may have influenced the evolution of plant traits (Merilä *et al.* 2001; Pausas 2015). Several micro-evolutionary studies have examined potential factors in the evolution of flammability or fire-related traits (Pausas *et al.* 2012; Pausas *et al.* 2016; Battersby *et al.* 2017). Pausas *et al.* (2012) showed that individuals of the Mediterranean shrub species *Ulex parviflorus* (Mediterranean gorse, Fabaceae) from sites with a history of frequent fire were more flammable than those growing in sites without recurrent fire. These findings suggest that the flammability of *U. parviflorus* has increased due to recurrent fires (Pausas *et al.* 2012; Moreira *et al.* 2014). A study on bark thickness of pines suggested that frequent anthropogenic fires could be a powerful selection force for thick bark (Stephens and Libby 2006), although thick bark has been observed in species not exposed to frequent fires (Lawes *et al.* 2014; Richardson *et al.* 2015). In *Leptospermum scoparium* (mānuka, Myrtaceae), serotinous populations were rarely found at sites with no history of fire and serotiny was generally stronger (proportion of closed capsules) in populations where the landscape had experienced some fire; however, no association was found between shoot-level flammability and Holocene site fire history, nor flammability and serotiny (Battersby *et al.* 2017).

Micro-evolutionary studies of plant flammability remain rare, and most of them have attempted to relate flammability or flammability-related traits to fire regimes in fire-prone regions (Stephens and Libby 2006; Pausas *et al.* 2012; Moreira *et al.* 2014). Although the hypothesis that flammability is selected by fire has received support (Archibald *et al.* 2018; Cui *et al.*, 2020), there is still the possibility that flammability is a result of exaptations, whereby increased flammability is an incidental or secondary result of selection for traits, such as water-use efficiency or nutrient retention, that increased individual fitness (Gould and Vrba 1982; Snyder 1984; Midgley 2013), especially in non-fire-prone ecosystems ((Mason *et al.* 2016). New Zealand has a history of low fire frequency prior to human arrival (Perry *et al.* 2014; Kitzberger *et al.* 2016), and most ecosystems in New Zealand are unlikely to have been influenced by fire before human arrival (Ogden *et al.* 1998; Lawes *et al.* 2014; Perry *et al.*

2014). Therefore, the New Zealand flora provides an opportunity to better examine the influence of environmental factors on plant flammability and, investigate whether flammability could have been affected by exaptations in the absence of selective pressure from fire.

Dracophyllum Labili. (Ericaceae) is found in Australia, New Zealand and nearby oceanic islands, and reaches its highest species richness and morphological diversity in New Zealand, ranging from low-growing subshrubs to trees (Venter 2009; Wagstaff *et al.* 2010). *Dracophyllum rosmarinifolium* is an extremely polymorphic species and occurs in different habitats across New Zealand: mountain gullies, mountain slopes ranging from 0°–80° in steepness, ridges, bluffs, plateaus and valley floors from 152–2100 m elevation (Venter 2009). Widespread species are often specialized to particular local environmental conditions (Joshi *et al.* 2001). It is unclear whether *D. rosmarinifolium* has adapted to local habitats, but it shows considerable variation in morphological characters, such as leaf length, branching habit and height, across populations (Venter 2009). These polymorphic characteristics and its occurrence in diverse habitats make *D. rosmarinifolium* a good model for micro-evolutionary study.

In this study we collected and measured the shoot flammability of 62 *D. rosmarinifolium* individuals from eight populations. We examined the variation of flammability among populations and sought to identify the geographic and environmental factors (elevation, latitude, mean annual air temperature and mean annual precipitation of the sample locations) correlated with intraspecific variation in plant flammability.

4.3   Materials and methods

4.3.1   Sample collection

Eight sites were selected for sample collection (Figure 4-1), using the information on species distributions from (Venter 2009), iNaturalist (https://inaturalist.nz/) and the Allan Herbarium. The eight collections sites spanned a large proportion of the latitudinal range of *D. rosmarinifolium* in the South Island, New Zealand and are believed to have an historical low fire frequency, as fire frequencies were low across most of New Zealand prior to human settlement, with the exception of some wetland systems in the North Island (Ogden *et al.* 1998; Rogers *et al.* 2007; Perry *et al.* 2014). Eight samples of *D. rosmarinifolium* were collected from each site (except for two of the sites, where seven samples were collected). Healthy terminal shoots of 70 cm length were cut from healthy individuals, preserving branch architecture, and kept in separate sealed plastic bags to prevent moisture loss. The shoot

samples were kept cool when collecting and then stored at 4-8 °C on the same day. All samples were collected over one summer (2018-2019) to eliminate the influence of seasonal and annual variability, and were burned within one week of collection.

4.3.2 Flammability measurement

Shoot flammability was measured for each sample following the methods described by Jaureguiberry *et al.* (2011) and Wyse *et al.* (2016), using the same device as Wyse *et al.* (2016). Prior to burning, all shoot samples were air-dried at room temperature for 24 h to match the sample moisture content to the ignition source (Wyse *et al.* 2016, 2018). For the flammability measurements, samples were first placed on our device for preheating for two minutes at 150 °C. Then, a blowtorch was turned on for 10 s to ignite the samples. Ignitability was represented by an ignition score (Padullés Cubino *et al.* 2018). Ignitability was recorded first as time to ignition (between 0 and 10 s), which was converted to an ignition score by subtracting the time to ignition from 10, e.g. a sample that took 1 s to ignite (i.e. rapid ignition) had an ignition score of 9. Samples that did not ignite after 10 s were given a zero value. The maximum temperature of flames during burning was recorded using an infrared laser thermometer (Fluke 572; Fluke Corp., Everett, WA, USA) to represent combustibility. Samples that failed to ignite were given a value of 150 °C, representing their grill temperature (Padullés Cubino *et al.* 2018). Sustainability was measured as the period of time that a sample burned for (had flaming combustion) after the blowtorch was turned off. Consumability was recorded as the mean value of the percentage of burnt biomass after flaming combustion ceased, assessed by visual observation by at least two observers. Samples that did not sustain a flame after the blowtorch was turned off were assigned zero for sustainability and consumability.

4.3.3 Data collection

GPS coordinates and the elevation of the collection sites were recorded during collection. Interpolated climate data (annual mean air temperature and mean annual precipitation) for each collection site were obtained using a spline model (Hutchinson 1991, Wratt *et al.* 2006). To calculate the sample's moisture content of, a sub-sample of twigs and leaves was taken from each sample and weighed to determine their fresh mass (FM). These sub-samples were then oven-dried at 65 °C for 48 h and weighed for dry mass (DM). Moisture content (MC; %) of the sub-samples was calculated as:

$$MC = (FM – DM)/DM \times 100\%$$

4.3.4 Statistical analysis

Principal components analysis (PCA) of the four flammability components was performed to evaluate the shoot flammability for every sample using the *princomp* function in R. The flammability components, PC1, and PC2, were compared across the eight populations using one-factor ANOVA and Tukey's test. Environmental conditions (latitude, elevation, mean annual air temperature and mean annual rainfall) were used for regression analysis with flammability variables of each sample using generalised linear regression. All statistical analyses were conducted in R 3.5.0 (R Core Team 2018).

4.4 Results

4.4.1 Shoot flammability varies significantly across *D. rosmarinifolium* populations

We collected 62 shoot samples in total across the eight sites, ranging from 840 m to 1310 m in elevation and from -41.1977 ° to -44.8137 ° in latitude (Figure 4-1, Table 4-1). All the samples ignited successfully on our device during the flammability measurements. The proportion of variance in shoot moisture content and all the shoot flammability traits, except burning time, was higher among populations (shoot moisture content: 64.6%, ignition score: 60.1%; maximum temperature: 70.9%; burning time: 44.7%; burnt biomass: 87.5%) than within populations (shoot moisture content: 35.4%, ignition score: 39.9%; maximum temperature: 29.1%; burning time: 55.3%; burnt biomass: 22.5%). All flammability components and shoot moisture content varied significantly across the populations (Figure 4-2, ANOVA: P<0.001). Individuals from Homer Tunnel had the lowest mean value of ignition score (7.31±0.09), maximum temperature (439.50±29.34 °C), and burnt biomass (33.75±4.51 %). The Lewis Pass population had the shortest burning time (23.14±3.89 s). The maximum temperature and burnt biomass of Homer Tunnel and Lewis Pass were both significantly lower than other populations (Figure 4-2). The Lewis Pass individuals had low values for burning time (23.14±3.89 s), maximum temperature (456.00±31.86 °C) and burnt biomass (36.43±2.37 %), and had a high value in ignition score (8.71±0.10). Samples from Mt Arthur were the most flammable with the highest mean value of ignition score (8.81±0.09), maximum temperature (724.38±30.56 °C), and burnt biomass (88.75±1.57 %). The longest burning time occurred in the Alex Knob population, with a mean value of 93.88 ±18.12 s.

Shoot moisture content is positively correlated with burning time, while not significantly correlated with other flammability components (Table 4-2).
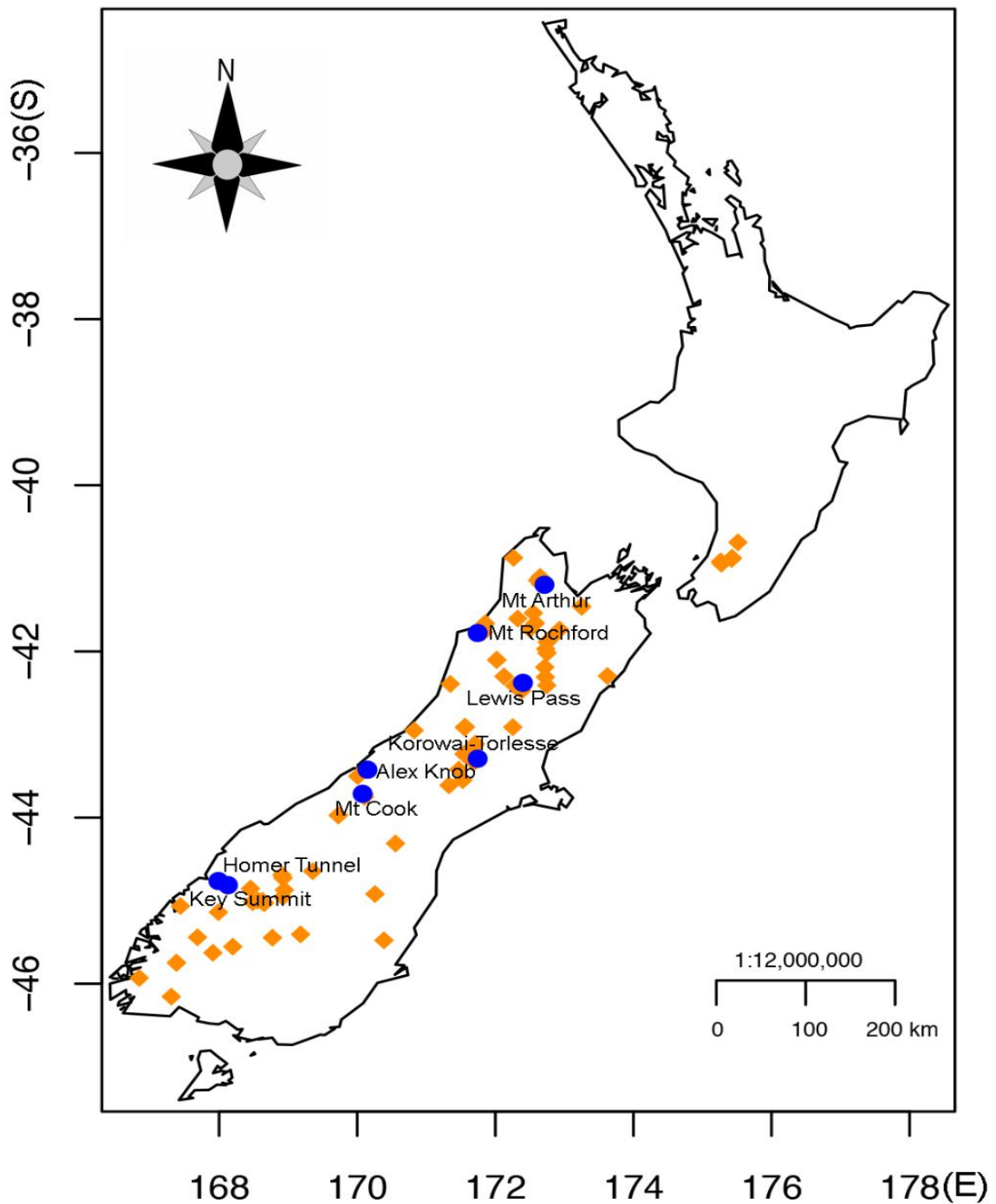
Figure 4‑1 Map of New Zealand displaying collection sites in this study. Blue points indicate the collection sites. Orange points indicate the observations (until May 2019 on iNaturalist) of *D. rosmarinifolium*, showing the range of *D. rosmarinifolium*.

Table 4-1 Mean flammability scores, location details, elevation and interpolated climate data for collection sites of *D. rosmarinifolium*.

Sites	N	Flammability scores						Environmental conditions				
		Mean ignition score	Mean maximum temperature (°C)	Mean burning time (s)	Mean burnt biomass (%)	Mean PC1	Mean PC2	Latitude (°)	Longitude (°)	Elevation (m)	Mean annual air temperature (°C)	Mean annual rainfall (mm)
Alex Knob	8	8.4±0.2	680.1±31.3	93.9±18.1	76.3±4.3	1.1±0.5	0.2±0.3	-43.4242	170.1495	1200	6.77	5675
Homer Tunnel	8	7.3±0.1	439.5±29.3	44.5±6.4	33.8±4.5	-2.9±0.3	-1.5±0.2	-44.7638	167.9890	920	4.55	6521
Key Summit	8	7.9±0.3	674.8±16.6	105.0±7.8	86.3±1.3	1.4±0.1	-1.1±0.5	-44.8137	168.1286	910	7.10	4805
Korowai-Torlesse	7	7.9±0.1	677.3±16.8	77.0±10.3	86.4±1.4	0.8±0.2	-0.8±0.2	-43.2915	171.7441	1100	7.32	1236
Lewis Pass	7	8.7±0.1	456.0±31.9	23.1±3.9	36.4±2.4	-2.7±0.3	1.6±0.2	-42.3779	172.4007	840	7.81	2747
Mt Arthur	8	8.8±0.1	724.4±30.6	81.3±7.4	88.8±1.6	1.6±0.2	1.2±0.1	-41.1977	172.7119	1310	6.21	2279
Mt Cook	8	8.3±0.1	618.3±19.0	81.1±16.1	75.6±3.5	0.4±0.4	-0.0±0.2	-43.7142	170.0780	1140	6.97	4927
MT Rochford	8	8.3±0.1	674.5±15.3	55.8±4.8	75.6±2.4	0.2±0.2	0.3±0.2	-41.7786	171.7428	1020	8.58	3539
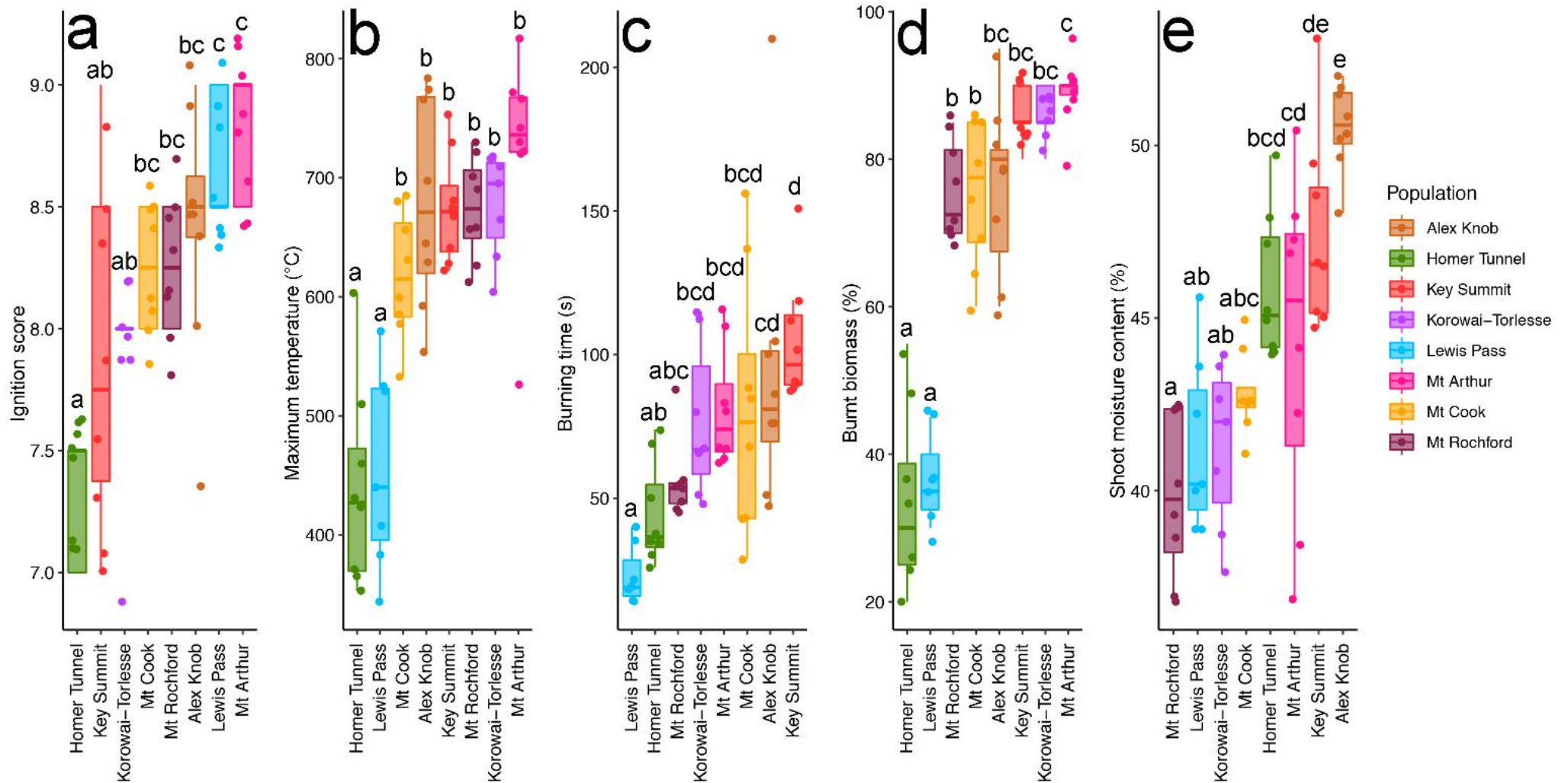
Figure 4-2 Variation in flammability components and shoot moisture content across populations. a: ignition score, b: burning time, c: maximum temperature, d: burnt biomass, e: shoot moisture content. Points indicate the individual samples. Colour of the points indicates the populations. Whiskers indicate the 95% percentile. Populations with the same letter code are not significantly different, based on Tukey's multiple comparisons of means (P<0.05).

A PCA was conducted with the four flammability components of all samples (Figure 4‑3a). The values of the first two axes of PCA explained 61.6% and 24.5% of the variation, respectively. Burning time, maximum temperature and burnt biomass were positively correlated with each other. The ignition score was independent of other flammability components (Table 4-2). The scores on the first axis represent an integrated measure of combustibility, sustainability and consumability, and the second axis describes ignitability. Multiple comparisons of PC1 and PC2 across populations showed that they varied significantly (ANOVA: $P < 0.001$, Figure 4‑3). The PC1 scores for the Homer Tunnel and Lewis Pass populations were significantly lower than for the other six populations, which had a similar value of PC1. Homer Tunnel population has the lowest value of both PC1 and PC2, indicating individuals from Homer Tunnel were least flammable. Lewis Pass samples have a very low value in PC1, however, these individuals also have the highest values in PC2, showing that these individuals ignited most readily.

Table 4-2 Pearson's correlation coefficient among four flammability variables. $n = 62$, NS: P>0.05; ***: P < 0.001. p-values were adjusted with Bonferroni correction.

Flammability variables	Maximum temperature (°C)	Burning time (s)	Burnt biomass (%)
Ignition score	0.24[NS]	0.029[NS]	0.24[NS]
Maximum temperature (°C)		0.58***	0.87***
Burning time (s)			0.65***
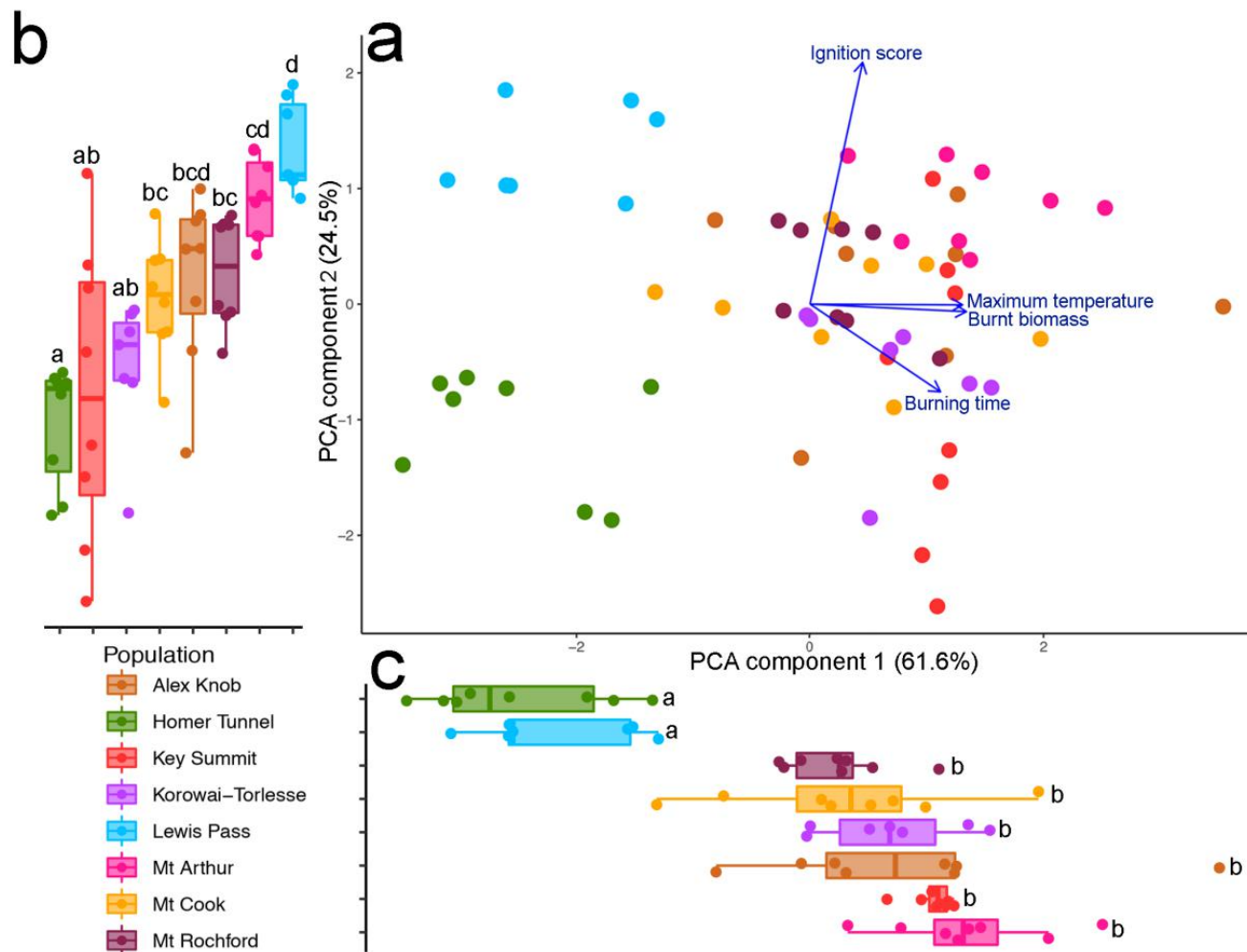
Figure 4-3 a: Principal components analysis (PCA) of flammability components (ignition score, burning time, maximum temperature and burnt biomass), b: The variation of PC1 across the populations, c: the variation of PC2 across the populations. Points indicate the individual samples. Colour of the points indicates the populations. Whiskers indicate the 95% percentile. Populations with the same letter code are not significantly different, based on Tukey's multiple comparisons of means (P<0.05).

4.4.2 The environment of habitat influences shoot flammability

To explore which factors may influence intraspecific variability in flammability of *D. rosmarinifolium*, interpolated environmental data (mean annual air temperature and mean annual rainfall) and geographic conditions (elevation and latitude) of collection sites were analyzed against the flammability variables.

Elevation was positively correlated with combustibility of *D. rosmarinifolium*. Higher elevation populations had higher values in maximum temperature (Figure 4-4). Latitude was positively correlated with ignitibility; populations at lower latitude had higher ignition score. Mean annual temperature and mean annual rainfall were not related to shoot flammability. Shoot moisture content was not related to flammability components and environmental conditions (Table 4-3).

Table 4-3 The relationship between flammability components and environmental conditions. NS: $P>0.05$; *: $P<0.05$. Bold typeface indicates P values that <0.05.

Flammability components	Elevation (m)	Latitude (°)	Mean annual air temperature (°C)	Mean annual rainfall (mm)	Shoot moisture content (%)
Ignition score	$P=0.299^{NS}$	**$R^2=0.621$, $P=0.020$***	$P=0.225^{NS}$	$P=0.261^{NS}$	$P=0.743^{NS}$
Burning time (s)	$P=0.167^{NS}$	$P=0.198^{NS}$	$P=0.943^{NS}$	$P=0.799^{NS}$	$P=0.150^{NS}$
Maximum temperature (°C)	**$R^2=0.424$, $P=0.048$***	$P=0.429^{NS}$	$P=0.389^{NS}$	$P=0.411^{NS}$	$P=0.777^{NS}$
Burnt biomass (%)	$P=0.076^{NS}$	$P=0.618^{NS}$	$P=0.424^{NS}$	$P=0.383^{NS}$	$P=0.839^{NS}$
Shoot moisture content (%)	$P=0.655^{NS}$	$P=0.205^{NS}$	$P=0.192^{NS}$	$P=0.082^{NS}$	
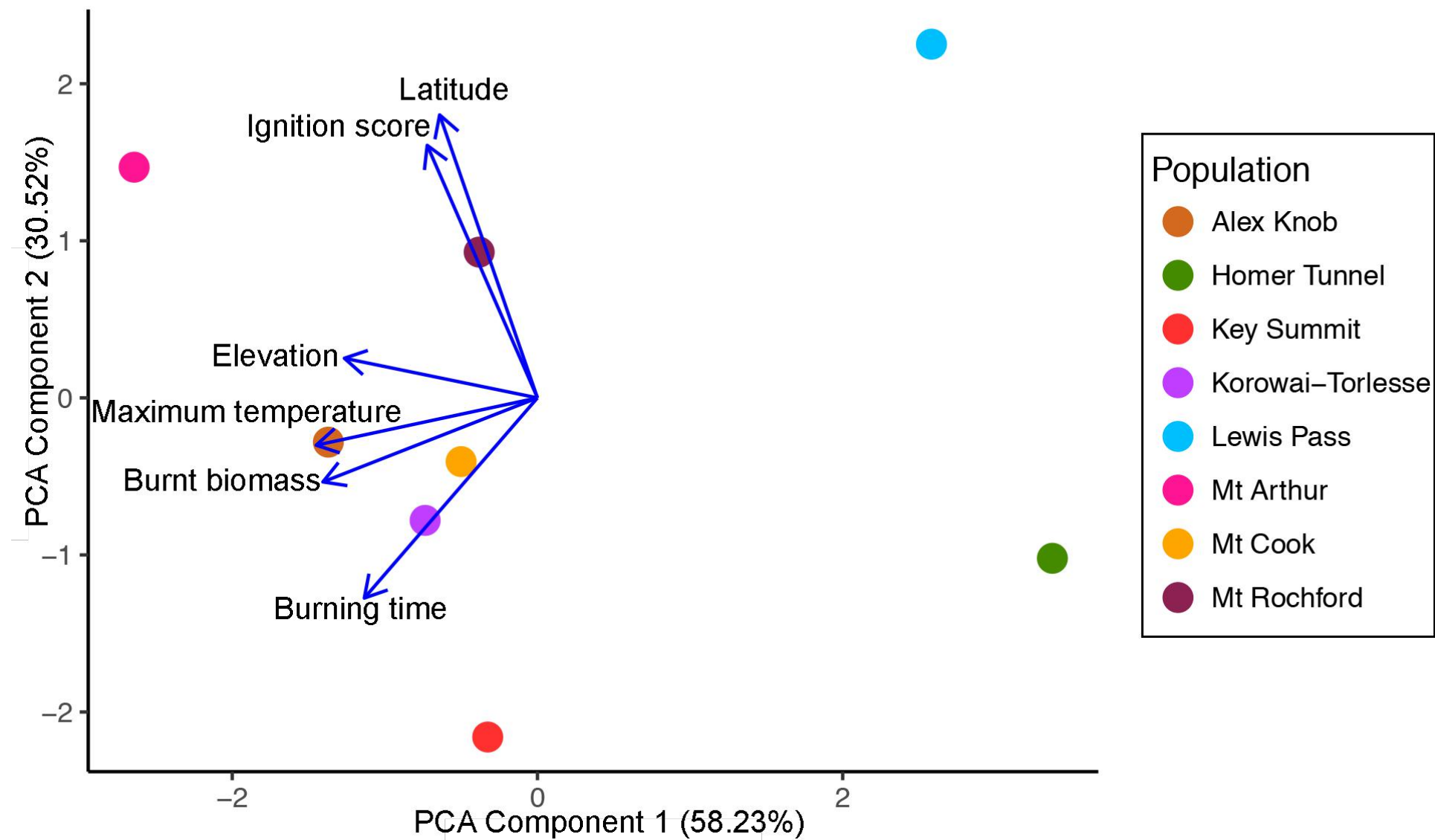
Figure 4-4 Relationship among flammability components, latitude and elevation of habitat. Points indicate populations. Colour indicates the population.

4.5 Discussion

Micro-evolution can be observed in nature and in the laboratory, while macro-evolution cannot usually be directly witnessed as it occurs over intervals that far exceed the human lifespan (Reznick and Ricklefs 2009). Plant populations can change rapidly in response to altered environmental conditions within dozens of generations (Bone and Farres 2001; Gómez-González *et al.* 2011; Moreira *et al.* 2014). Such rapid evolutionary changes allow us to observe evolution over a short period of time and identify its potential drivers. Previous micro-evolutionary studies of plant flammability have focused on the influence of fire regimes (Pausas *et al.* 2012; Battersby *et al.* 2017) or fire-related traits (Stephens and Libby 2006; Hernández-Serrano *et al.* 2013). However, flammability may be an emergent property determined by local environments, rather than a trait directly selected for by fire (Snyder 1984; Midgley 2013). The influence of environmental conditions, rather than fire, on plant flammability has been rarely reported. Here we conducted our experiments in New Zealand, where fire was unlikely to have strongly influenced the evolution of plants (Ogden *et al.* 1998; Lawes *et al.* 2014; Perry *et al.* 2014), to better examine how environmental factors could influence plant flammability. We found that shoot flammability of *D. rosmarinifolium* increased with elevation and decreased with latitude. Our findings indicate that the environment of habitat has influenced the flammability of *D. rosmarinifolium*, suggesting that, at least in non-fire prone environments, flammability can be an emerged property that could be a result of exaptations (Gould and Vrba 1982; Snyder 1984).

Elevational and latitudinal gradients are commonly examined in ecological and evolutionary studies (Körner 2007; Swenson and Enquist 2007). A change in elevation is usually accompanied by changes in a range of environmental variables, including atmospheric pressure, air temperature and solar radiation (Blumthaler *et al.* 1997; Körner 2007). The changes in environmental conditions with elevation can cause genetic and phenotypic changes within species (Ronghua *et al.* 1984; von Arx *et al.* 2006; Giordano *et al.* 2007; Swenson and Enquist 2007; Gonzalo-Turpin and Hazard 2009; Scheepens *et al.* 2010; Montesinos-Navarro *et al.* 2011). For example, *Festuca eskia* Ramond (Poaceae), a perennial alpine grass common in the Pyrenean Mountains, was found to be adapted to local climate and has a reduced plant stature with increasing elevation (Gonzalo-Turpin and Hazard 2009). In *D. rosmarinifolium*, combustibility increased with elevation; shoot moisture content, however, did not change with elevation (Table 4-3). Increased elevation may affect flammability-enhancing plant traits

other than moisture content, such as leaf characteristics or plant architecture (DeLucia and Berlyn 1984; Schwilk 2003; Ma *et al.* 2010; Alam *et al.* 2019). Temperature decreases with increasing elevation, which would act to cause the decrease in plant flammability. However, we observed flammability to increase with elevation, suggesting that other environmental factors, such as solar radiation, which also change with elevation (Körner 2007), play more important roles than air temperature in influencing plant flammability-related traits.

Latitude also predicts intraspecific variability of flammability in *D. rosmarinifolium*. Latitude is an important determinant of local environmental conditions that can lead to the evolution of different local varieties within a given species (Winn & Gross 1993; Li *et al.* 1998; Hultgren *et al.* 2018). Latitude captures a complex environmental gradient, along which temperature, solar radiation and soil conditions can all vary (Li *et al.* 1998). Trait variation among plant populations along latitudinal gradients has been extensively investigated (Li *et al.* 1998; Oleksyn *et al.* 2003; Santamaría *et al.* 2003; Kollmann & Bañuelos 2004; Molina-Montenegro & Naya 2012). Our results demonstrated that ignitability increased with a decrease in latitude, that is, more northern individuals in our southern hemisphere study were more easily ignited.

Temperature and precipitation have been suggested to be major climatic determinants of plant traits (Woodward and Williams 1987; Choat *et al.* 2007; Franks *et al.* 2007; Sandel *et al.* 2010; Moles *et al.* 2014). Many functional traits of plant are correlated with temperature, including leaf nutrient content (Reich and Oleksyn 2004), specific leaf area (Rosbakh *et al.* 2015) and wood density (Swenson and Enquist 2007), while mean annual precipitation is correlated with traits, such as plant hydraulics (Choat *et al.* 2007) and leaf venation (Sack and Scoffoni 2013). However, our study showed that mean annual temperature and mean anuual precipitation of habitat were not related with flammability components of *D. rosmarinifolium* individuals.

Intraspecific variation of shoot-level flammability among *D. rosmarinifolium* populations suggested that flammability is influenced by local environmental conditions. Our results are consistent with plant flammability being an emergent property that may be determined by environment (Snyder 1984; Midgley 2013). However, these conclusions should be interpreted as a hypothesis, as we are uncertain whether the variation in flammability is heritable or a result of phenotypic plasticity (e.g. whether there is a genetic difference across the populations) (Schlichting 1986; Sultan 1987, 1995). Further studies, such as reciprocal transplant experiments and genetic studies, are needed to explore whether

the flammability variability is inheritable. In addition, more flammability-related traits should be measured to help ascertain why flammability differs among populations.

4.6 Conclusion

Dracophyllum rosmarinifolium individuals from populations at higher elevations and lower latitudes tend to be more flammable. Our findings suggest that the environment of habitat has influenced the intraspecific variability of flammability within *D. rosmarinifolium*, and that shoot flammability may be an emergent property that is comprised of exaptations in the largely fire-free environment of New Zealand.

4.7 Acknowledgments

Chapter 5

General discussion

Fire has influenced the evolution of land plants, and land plants have influenced fire characteristics since their appearance on earth around 420 MYA (Bond and Keeley 2005, Keeley *et al.* 2011, Schwilk and Caprio 2011). To improve our knowledge of the long-term interactions between fire and plants, I explored the phylogenetic patterns and evolution of plant flammability, as well as examined the potential factors that influence the occurrence of high or low flammability in different taxa and at different taxonomic scales. I have found that differences in flammability can arise even in the virtual absence of fire; however, highly flammable plants were much more likely to occur in fire-prone environments. Flammability of plants may have been the result of selection by fire regimes as well as emerging incidentally in the absence of fire as a selective force.

5.1 The phylogenetic patterns of shoot-level flammability of plants

Plant flammability varies widely across species (Engber and Varner 2012, Fuentes-Ramirez *et al.* 2016, Simpson *et al.* 2016, Wyse *et al.* 2016, Padullés Cubino *et al.* 2018). However, variation in flammability across closely related species, and whether such species have similar flammability, especially at the shoot-level, has rarely been reported (Engber and Varner 2012, Cornwell *et al.* 2015). An understanding of broad-scale phylogenetic patterns in plant flammability would enhance our knowledge of the evolution of flammability and why certain species are more flammable than others, thus helping us prepare for a warmer world (Moritz *et al.* 2014, Doerr and Santín 2016). Previous studies (He *et al.* 2011, He *et al.* 2012) have mostly used qualitative rather than quantitative measures of flammability, which reduces the scope of available comparative phylogenetic analyses, such as estimating phylogenetic signal. Furthermore, quantitative measures of flammability appropriately represent flammability as a continuous rather than binary trait. Cornwell *et al.* (2015) and Engber & Varner (2012) quantitatively compared litter flammability across 39 gymnosperm and 18 oaks species, respectively, but litter flammability is unlikely to reflect the flammability of canopy fuels (Schwilk 2015; Alam *et al.* 2019).

In this study, I demonstrated that shoot-level flammability of plant species is phylogenetically conserved. All flammability components had statistically significant phylogenetic signals, indicating that closely related taxa tend to have similar flammability.

Shoot flammability was generally conserved at family and higher taxonomic levels across 194 vascular plant species. In addition, I investigated phylogenetic patterns in flammability across the genus *Dracophyllum*, a group of New Zealand shrubs and trees in the family Ericaceae. Shoot flammability was also phylogenetically conserved in *Dracophyllum*. Together, these results indicated that although shoot-level flammability of plants is a compound trait that is affected by many characteristics (Schwilk 2003, Alam *et al.* 2019), it still retains phylogenetic patterns at the genus and higher taxonomic levels, indicating species likely inherit the flammability of their direct ancestors. The strong phylogenetic component of shoot flammability across vascular plants is consistent with that flammability of plants may be a trait that can be selected for.

While flammability is phylogenetically conserved, I found flammability exhibited evolutionary flexibility among some closely related species. For example, species in the Poaceae (Poales) vary considerably in their flammability. At the genus level, evolutionary flexibility also existed among some closely related species, such as *D. menziesii* and *D. fiordense* in the *Dracophyllum* genus, which grow in different habitats. The evolutionary flexibility of shoot flammability indicated that factors other than phylogeny, such as abiotic environment, may influence evolutionary patterns in flammability.

5.2   The evolution of plant flammability

Better understanding the evolution of flammability would facilitate our understanding of the long-term interactions between fire and plants, and may help prepare us for a warmer world (Moritz *et al.* 2014, Doerr and Santín 2016). However, whether flammability of plants is selected for by fire or emerges incidentally continues to be debated (Mutch 1970, Snyder 1984, Bond and Midgley 1995, Midgley 2013, Bowman *et al.* 2014).

As I explained above, I showed that flammability is phylogenetically conserved, which is consistent with flammability being a trait that can be selected for. In Chapter 2, I categorised the 194 species as coming from fire-prone or non-fire-prone habitats depending on the description of each species from numerous sources and, showed that species from fire-prone habitats tend to have higher flammability than non-fire-prone habitats. Most species with a hot-flammability syndrome are from fire-prone habitats, indicating that the preferred flammability syndrome of species in fire-prone ecosystems involves being high flammable. In low-fire-prone ecosystems, species have significantly lower flammability than those from fire-prone habitats, suggesting that high heat release has few evolutionary advantages in such

environments. Together these findings suggest that fire regimes of the source habitat played an important role in the evolution of flammability and that fire-prone plant communities are likely to burn more readily than non-fire-prone communities. In addition, these results provide macro-evolutionary support for the micro-evolutionary studies, which suggested that fire enhances the plant flammability (Pausas *et al.* 2012, Moreira *et al.* 2014).

Flammability of plants could also emerge as an incidental property and have no selective advantage (Midgley 2013). Many characteristics of species that increase their flammability may be merely incidental or secondary results of selection for these traits, such as water-use efficiency and nutrient retention, that increased individual fitness (Snyder 1984). The hypothesis that flammability is a result of exaptation has received little support, with most of the studies conducted in fire-prone ecosystems (Archibald *et al.* 2018). Most ecosystems in New Zealand experienced low fire frequencies prior to human arrival; therefore, its flora provides an opportunity to explore whether flammability is a result of exaptations (i.e. is not a specific fire adaptation) (Ogden *et al.* 1998, Lawes *et al.* 2014, Perry *et al.* 2014, Mason *et al.* 2016). In Chapters 3 and 4, I provided evidence that flammability has emerged incidentally in New Zealand. Given that *Dracophyllum* species in the subgenus *Oreothamnus* evolved during the Pleistocene (Wagstaff *et al.* 2010) and I found that they had significantly higher flammability than those in the subgenus *Dracophyllum*, the high flammability in the subgenus *Oreothamnus* is an incidental property to the climatic conditions associated with repeated climate changes and glaciations during the Pleistocene. The cold and dry climate of glacial periods may have selected for traits, such as smaller leaves, that facilitated frost and drought tolerance (Lusk *et al.* 2016, Reichgelt *et al.* 2017), and incidentally increased shoot-level flammability.

The micro-evolutionary evidence for flammability being an emergent property is the intraspecific variability within *D. rosmarinifolium*. Environmental factors were correlated with shoot-level flammability of *D. rosmarinifolium* species, suggesting that shoot flammability may be an emergent or incidental in the largely fire-free environment of New Zealand, although it is unclear whether the variation in flammability is heritable or due to phenotypic plasticity.

In conclusion, my findings suggest that flammability has likely both emerged *and* been selected for, depending on the context and the fire regime of the source habitat (non-fire-prone or fire-prone habitat).

5.3   Recommendations for further research

The use of shoot flammability measurements to examine evolutionary patterns in flammability is still in its infancy, but the research forming this thesis shows the promise it holds. Recommendations for further research are provided below.

For the first project (Chapter 2), we compared shoot flammability across 194 vascular plant species and explored the evolutionary pattern of shoot flammability across the phylogeny. Such a large set of quantitative data relating to species flammability has not, to our knowledge, been reported before. Through this project, we found shoot flammability can be predicted from taxonomic relatedness, habitat fire regime and growth form. However, most of the species we used (120 of 194) are indigenous to New Zealand, a largely fire-free island, until recent human settlement. The sampling of more species from fire-prone ecosystems is needed to better understand the evolutionary patterns of plant flammability. In addition, species from many phylogenetic groups are absent from our data. For example, the 194 species were from 72 families, only 17% of all families in the APG IV system (The Angiosperm Phylogeny Group *et al.* 2016). More species from a wider range of clades are needed in further to improve taxonomic diversity, in order to better understand the evolutionary patterns of flammability.

For the second project (Chapter 3), we measured the shoot flammability of 21 *Dracophyllum* species. With reference to existing phylogenies, the flammability data provided some information on the evolutionary patterns of shoot flammability within the genus. But the species we measured only account for around 40% of *Dracophyllum* species; many species, especially those that grow outside of New Zealand, were not measured for flammability. In addition, molecular studies are needed to construct a better phylogeny for this group. We could only obtain sequence data for genes *matK* and *rbcL* from 14 *Dracophyllum* species. More species and a better phylogeny are needed to better understand the evolutionary patterns of flammability in the genus, although it is unlikely to change the main findings from my study, as I concentrated on the broad sub-generic difference in flammability.

For the third project (Chapter 4), the significant variation in shoot flammability among *D. rosmarinifolium* suggested that climatic and geographic factors have influenced the intraspecific variability of flammability in *D. rosmarinifolium*, and that shoot flammability may be a result of exaptation. However, it is not clear whether the variation in flammability is heritable or due to phenotypic plasticity (i.e. whether there is a genetic difference across the

populations). Further studies, such as reciprocal transplant experiments and genetic analyses, are required to explore whether the flammability variability is heritable. In addition to the environmental conditions included in this study (elevation, latitude, mean annual temperature and mean rainfall), more environmental factors (e.g. soil type and fertility, solar radiation) should be examined to better understand how climate and geography influence the evolution of plant flammability. The collection locations were only on the South Island of New Zealand, more collection locations, especially on the North Island, should be included to span a wider range of habitats. In addition, some flammability-related traits should be measured to help ascertain why flammability differs among populations.

My thesis suggests that flammability of plants is likely the result of the interaction of selection and exaptation. In future studies, understanding the evolution of plant flammability should be considered in the light of identifying the roles of both adaptation and exaptation, potentially based on the fire regimes of species' habitats.

Chapter 6

Conclusion

The main conclusions of this thesis are as follows.

1. Shoot-level flammability of vascular plants was influenced by taxonomic relatedness, habitat fire regime and growth form. Closely related taxa tend to have similar flammability and the components of flammability were phylogenetically conserved across vascular plant species. Fire regimes in the source habitat played an important role in the evolution of flammability and fire-prone plant communities are likely to burn more readily than non-fire-prone communities, suggesting that high flammability may result in parallel evolution driven by environmental factors, such as fire regime. Growth form also influenced shoot-level flammability: forbs were less flammable than grasses, trees and shrubs, while grasses had higher biomass consumption by fire than other groups. The strong phylogenetic component of flammability is consistent with flammability being a trait that can be selected for, but I cannot rule out flammability being an incidental property.

2. Shoot flammability varied widely across *Dracophyllum* species, but was highly phylogenetically conserved across the genus. Subgenus *Oreothamnus,* which arose (1-2 MA) in the Pleistocene and may have evolved in the absence of fire, exhibited high flammability, suggesting that the climate of the Pleistocene may have favoured and selected for characteristics, such as smaller leaves, that were suited to other functions (e.g. drought and frost tolerance) and incidentally increased shoot-level flammability. My study has provided evidence that, at least in relatively fire-free environments, high flammability could be an incidental or emergent property that is comprised of traits that arose in response to selective forces independent of fire.

3. Shoot flammability varies at the intraspecific level and is affected by environmental factors. I found that shoot flammability of *D. rosmarinifolium* varied significantly across populations. Individuals from populations at higher elevations and lower latitudes tend to be more flammable. These results suggest that environmental factors have influenced the intraspecific variability of flammability within *D. rosmarinifolium*, and that in the largely fire-free environment of New Zealand shoot flammability is likely to be an emerged property and influenced by the environment of habitat.

In conclusion, I have demonstrated that flammability has a strong phylogenetic component, which is consistent with flammability being a trait that has evolved and been selected for. However, I also found evidence for flammability being an emergent property in New Zealand, where the evolution of plants was not likely influenced by fire. My results suggest that flammability is likely phylogenetically conserved but with flexibility of selection responses in local habitats. Plant flammability has likely both been selected for *and* emerged, depending on the context and whether a species or population occurs in a fire-prone habitat or non-fire-prone habitat. My study facilitates the understanding of the evolution of flammability and can help prepare us for a more warmer world.

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Appendix A
The 194 species we collected and measured for shoot flammability

Species	Code	Mean ignition frequency (%)	Mean maximum temperature (±SE) (°C)	Mean burning time (±SE) (s)	Mean burnt biomass (±SE) (%)	N	Family	Order	Class	Growth form	Flammability syndrome	Habitat
Acacia dealbata	ACAdea	100.0	673.7±32.7	41.7±6.0	86.7±2.5	6	Fabaceae	Fabales	Rosid I	Tree	Hot Flammable	Fire-prone
Acaena caesiiglauca	ACAcae	75.0	433.0±79.6	6.0±2.0	64.4±14.4	8	Rosaceae	Rosales	Rosid I	Forb	Hot Flammable	Non-fire-prone
Acca sellowaiana	ACCsel	100.0	599.9±57.3	49.1±12.9	30.6±6.6	8	Myrtaceae	Myrtales	Rosid II	Tree	Hot Flammable	Non-fire-prone
Aciphylla aurea	ACIaur	100.0	737.0±36.7	231.4±35.6	56.3±11.5	8	Apiaceae	Apiales	Asterid II	Grass	Hot Flammable	Fire-prone
Aesculus hippocastanum	AEShip	100.0	456.0±49.2	11.0±1.9	20.0±3.4	6	Sapindaceae	Sapindales	Rosid II	Tree	Fast Flammable	Non-fire-prone
Agapanthus spp.	AGApra	7.4	167.7±17.7	4.4±3.8	0.7±0.4	27	Amaryllidaceae	Asparagales	Lilioid monocots	Forb	Fast Flammable	Non-fire-prone
Agathis australis	AGAaus	69.2	323.7±45.7	8.8±4.3	10.4±3.5	13	Araucariaceae	Pinales	Pinophyta	Tree	Fast Flammable	Non-fire-prone
Agrostis capillaris	AGRcap	25.0	207.1±37.7	2.6±2.2	22.5±14.9	8	Poaceae	Poales	Commelinids	Grass	Low Flammable	Fire-prone
Agrostis muelleriana	AGRmue	12.5	189.5±39.5	0.25±0.25	12.5±12.5	8	Poaceae	Poales	Commelinids	Grass	Low Flammable	Fire-prone
Alectryon excelsus	ALEexc	100.0	551.9±67.3	21.9±4.7	63.8±7.0	8	Sapindaceae	Sapindales	Rosid II	Tree	Hot Flammable	Non-fire-prone
Ammophila arenaria	AMMare	100.0	600.5±35.7	78.6±6.0	88.8±1.8	8	Poaceae	Poales	Commelinids	Grass	Hot Flammable	Non-fire-prone
Anisotome aromatica	ANIaro	0.0	150±0	0±0	0±0	9	Apiaceae	Apiales	Asterid II	Forb	Low Flammable	Non-fire-prone
Anisotome flexuosa	ANIfle	50.0	278.9±51.3	7.8±4.0	45.6±17.4	8	Apiaceae	Apiales	Asterid II	Forb	Fast Flammable	Non-fire-prone
Anthosachne solandri	ANTsol	87.5	465.4±56.1	14.1±6.2	69.4±10.6	8	Poaceae	Poales	Commelinids	Grass	Hot Flammable	Fire-prone
Anthoxanthum odoratum	ANTodo	75.0	330.1±49.6	2.4±0.9	56.3±14.0	8	Poaceae	Poales	Commelinids	Grass	Hot Flammable	Fire-prone
Apodasmia similis	APOsim	100.0	492.6±32.6	20.6±3.4	32.5±4.5	8	Restionaceae	Poales	Commelinids	Grass	Fast Flammable	Non-fire-prone
Arbutus unedo	ARBune	100.0	648.8±32.5	30.0±5.4	43.3±9.1	6	Ericaceae	Ericales	Ericales	Tree	Hot Flammable	Fire-prone
Aristotelia fruticosa	ARIfru	62.5	200.9±21.0	2.3±0.9	7.9±2.5	8	Elaeocarpaceae	Oxalidales	Rosid I	Shrub	Fast Flammable	Non-fire-prone
Aristotelia serrata	ARIser	42.1	248.2±34.3	2.1±0.8	8.6±3.9	19	Elaeocarpaceae	Oxalidales	Rosid I	Tree	Fast Flammable	Non-fire-prone
Beilschmiedia tarairi	BEItar	75.0	458.9±76.4	4.6±1.4	13.6±4.7	8	Lauraceae	Laurales	Magnoliidae	Tree	Fast Flammable	Non-fire-prone
Beilschmiedia tawa	BEItaw	92.9	398.0±39.0	6.4±1.2	27.9±5.6	14	Lauraceae	Laurales	Magnoliidae	Tree	Fast Flammable	Non-fire-prone
Betula pendula	BETpen	100.0	490.0±37.7	16.3±2.7	45.8±5.8	6	Betulaceae	Fagales	Rosid I	Tree	Hot Flammable	Fire-prone

Blechnum penna-marina	BLEpen	25.0	213.8±42.6	0.4±0.3	25.0±16.4	8	Blechnaceae	Athyriales	Polypodiopsida	Shrub	Low Flammable	Non-fire-prone
Brachyglottis repanda	BRArep	100	598.5±13.8	33.0±5.0	50.8±3.8	6	Asteraceae	Asterales	Asterid II	Tree	Hot Flammable	Non-fire-prone
Brachyscome longiscapa	BRAlon	0.0	150±0	0±0	0±0	8	Asteraceae	Asterales	Asterid II	Forb	Low Flammable	Non-fire-prone
Bromus hordeaceus	BROhor	25.0	185.3±23.4	1.0±0.9	15.0±10.0	8	Poaceae	Poales	Commelinids	Grass	Fast Flammable	Fire-prone
Callistemon rigidus	CALrig	100.0	613.0±32.4	25.1±5.3	38.1±7.7	8	Myrtaceae	Myrtales	Rosid II	Shrub	Hot Flammable	Non-fire-prone
Camellia sasanqua Setsugekka	CAMsas	100.0	458.0±70.9	10.5±2.9	23.8±6.9	4	Theaceae	Ericales	Ericales	Shrub	Fast Flammable	Non-fire-prone
Carex coriacea	CARcor	100.0	666.8±21.3	23.0±3.0	55.0±2.2	6	Cyperaceae	Poales	Commelinids	Grass	Hot Flammable	Non-fire-prone
Carex wakatipu	CARwak	25.0	210.4±39.7	0.3±0.2	25.0±16.4	8	Cyperaceae	Poales	Commelinids	Grass	Low Flammable	Non-fire-prone
Carmichaelia australis	CARaus	100.0	651±93.2	93.2±24.2	64.2±11.9	6	Fabaceae	Fabales	Rosid I	Shrub	Hot Flammable	Non-fire-prone
Carpodetus serratus	CARser	52.0	239.1±26.2	3.9±1.5	6.8±1.7	25	Rousseaceae	Asterales	Asterid II	Tree	Fast Flammable	Non-fire-prone
Celmisia gracilenta	CELgra	20.0	204.7±36.8	0.6±0.4	19.0±12.7	10	Asteraceae	Asterales	Asterid II	Forb	Low Flammable	Non-fire-prone
Chamaecytisus palmensis	CHApal	100.0	314.8±46.1	19.9±5.9	18.1±1.9	8	Fabaceae	Fabales	Rosid I	Tree	Fast Flammable	Fire-prone
Chionochloa macra	CHImac	100.0	750.8±17.9	175.9±26.2	78.6±4.6	16	Poaceae	Poales	Commelinids	Grass	Hot Flammable	Fire-prone
Chionochloa rigida	CHIrig	100.0	729.1±27.8	239.9±36.8	93.5±2.6	8	Poaceae	Poales	Commelinids	Grass	Hot Flammable	Fire-prone
Choisya ternata	CHOter	100.0	446.5±30.7	5.7±1.0	15.8±1.5	6	Rutaceae	Sapindales	Rosid II	Shrub	Fast Flammable	Fire-prone
Citrus limon	CITlim	100.0	372.0±47.5	12.7±5.0	15.0±3.7	6	Rutaceae	Sapindales	Rosid II	Tree	Fast Flammable	Non-fire-prone
Clivia miniata	CLImin	0.0	150±0	0±0	0±0	8	Amaryllidaceae	Asparagales	Lilioid monocots	Forb	Low Flammable	Non-fire-prone
Coprosma arborea	COParb	50.0	248.4±45.0	1.0±0.5	8.8±3.4	8	Rubiaceae	Gentianales	Asterid I	Tree	Fast Flammable	Non-fire-prone
Coprosma crassifolia	COPcra	87.5	220.0±19.0	2.0±0.5	5.6±1.5	8	Rubiaceae	Gentianales	Asterid I	Shrub	Fast Flammable	Non-fire-prone
Coprosma propinqua	COPpro	50.0	213.6±26.4	2.43±1.0	4.3±1.6	14	Rubiaceae	Gentianales	Asterid I	Shrub	Fast Flammable	Non-fire-prone
Coprosma repens	COPrep	0.0	150±0	0±0	0±0	8	Rubiaceae	Gentianales	Asterid I	Shrub	Low Flammable	Non-fire-prone
Coprosma robusta	COProb	72.7	383.6±41.0	4.1±1.5	11.6±3.3	22	Rubiaceae	Gentianales	Asterid I	Shrub	Fast Flammable	Non-fire-prone
Cordyline australis	CORaus	87.5	284.9±38.0	15.88±5.0	10.0±2.7	8	Asparagaceae	Asparagales	Lilioid monocots	Tree	Fast Flammable	Non-fire-prone
Coriaria arborea	CORarb	100.0	654.3±24.8	18.2±4.0	53.3±8.0	6	Coriariaceae	Cucurbitales	Rosid I	Tree	Hot Flammable	Non-fire-prone
Corokia buddleioides	CORbud	100.0	532.9±18.1	14.0±2.1	66.8±9.1	8	Argophyllaceae	Asterales	Asterid II	Shrub	Hot Flammable	Non-fire-prone
Corokia cotoneaster	CORcot	100.0	250.3±17.3	6.0±11.3	11.3±2.3	8	Argophyllaceae	Asterales	Asterid II	Shrub	Fast Flammable	Non-fire-prone
Corynocarpus laevigatus	CORlae	50.0	235.5±40.5	1.5±0.7	3.8±1.6	8	Corynocarpaceae	Cucurbitales	Rosid I	Tree	Fast Flammable	Non-fire-prone
Crepis capillaris	CREcap	0.0	150±0	0±0	0±0	8	Asteraceae	Asterales	Asterid II	Forb	Low Flammable	Unsure

Species	Code						Family	Order	Clade	Growth form	Flammability	Fire status
Crocosmia x crocosmiiflora	CROcro	0.0	150±0	0±0	0±0	8	Iridaceae	Asparagales	Lilioid monocots	Forb	Low Flammable	Non-fire-prone
Cupressus macrocarpa	CUPmac	90.9	460.2±45.7	19.7±7.6	18.6±4.3	11	Cupressaceae	Pinales	Pinophyta	Tree	Fast Flammable	Non-fire-prone
Cyathea dealbata	CYAdea	87.5	442.3±56.4	10.0±2.3	28.1±5.0	8	Cyatheaceae	Cyatheales	Polypodiopsida	Tree	Fast Flammable	Non-fire-prone
Cyathea medullaris	CYAmed	62.5	388.1±78.9	19.1±8.5	28.8±10.2	8	Cyatheaceae	Cyatheales	Polypodiopsida	Tree	Fast Flammable	Non-fire-prone
Cytisus scoparius	CYTsco	87.5	342.3±45.0	13.3±4.7	31.3±7.9	8	Fabaceae	Fabales	Rosid I	Shrub	Fast Flammable	Fire-prone
Dacrycarpus dacrydioides	DACdac	92.3	492.3±58.1	16.4±4.4	42.3±6.7	13	Podocarpaceae	Pinales	Pinophyta	Tree	Hot Flammable	Non-fire-prone
Dacrydium cupressinum	DACcup	100.0	660.4±36.0	36.5±7.5	58.1±9.8	8	Podocarpaceae	Pinales	Pinophyta	Tree	Hot Flammable	Non-fire-prone
Dactylis glomerata	DACglo	83.3	284.2±44.4	5.3±1.7	49.2±10.8	6	Poaceae	Poales	Commelinids	Grass	Hot Flammable	Fire-prone
Deyeuxia avenoides	DEYave	100.0	375.9±25.4	8.6±1.7	83.1±3.4	8	Poaceae	Poales	Commelinids	Grass	Hot Flammable	Fire-prone
Dicksonia squarrosa	DICsqu	100.0	606.3±24.2	21.5±3.1	55.0±7.7	8	Dicksoniaceae	Cyatheales	Polypodiopsida	Tree	Hot Flammable	Non-fire-prone
Discaria toumatou	DIStou	100.0	455.0±35.9	42.8±11.2	45.6±4.2	23	Rhamnaceae	Rosales	Rosid I	Shrub	Hot Flammable	Fire-prone
Dodonaea viscosa	DODvis	90.5	408.6±33.1	9.3±1.7	29.5±4.7	21	Sapindaceae	Sapindales	Rosid II	Shrub	Fast Flammable	Non-fire-prone
Dracophyllum acerosum	DRAace	100.0	544.14±35.12	51.71±5.71	59.29±4.42	7	Ericaceae	Ericales	Ericales	Shrub	Hot Flammable	Fire-prone
Dracophyllum densum	DRAden	100.0	771.5±23.0	129.8±22.6	85.0±6.8	8	Ericaceae	Ericales	Ericales	Shrub	Hot Flammable	Fire-prone
Dracophyllum pronum	DRApro	100.0	696.1±31.3	157.6±18.1	79.3±4.3	7	Ericaceae	Ericales	Ericales	Shrub	Hot Flammable	Fire-prone
Dracophyllum filifolium	DRAfli	100.0	638.63±39.18	62±10.33	63.13±3.65	8	Ericaceae	Ericales	Ericales	Tree	Hot Flammable	Non-fire-prone
Dracophyllum traversii	DRAtra	62.5	295.8±63.4	20.1±10.7	10.0±3.8	8	Ericaceae	Ericales	Ericales	Tree	Fast Flammable	Non-fire-prone
Dysoxylum spectabile	DYSspe	37.5	221.5±51.3	3.0±2.5	4.4±3.1	8	Meliaceae	Sapindales	Rosid II	Tree	Fast Flammable	Non-fire-prone
Epilobium alsinoides	EPIals	12.5	188.3±38.3	0.4±0.4	12.5±12.5	8	Onagraceae	Myrtales	Rosid II	Forb	Low Flammable	Non-fire-prone
Eucalyptus viminalis	EUCvim	100.0	599.7±33.3	50.8±7.5	53.3±5.8	30	Myrtaceae	Myrtales	Rosid II	Tree	Hot Flammable	Fire-prone
Euphrasia dyeri	EUPdye	25.0	217.4±44.1	0.4±0.3	25.0±16.4	8	Orobanchaceae	Lamiales	Asterid I	Forb	Low Flammable	Non-fire-prone
Farfugium japonicum	FARjap	0.0	150±0	0±0	0±0	8	Asteraceae	Asterales	Asterid II	Forb	Low Flammable	Non-fire-prone
Festuca novae-zelandiae	FESnov	100.0	580.9±27.0	77.1±4.7	68.9±3.1	8	Poaceae	Poales	Commelinids	Grass	Hot Flammable	Fire-prone
Fraxinus pennsylvanica	FRApen	100.0	554.3±38.9	28.3±8.2	47.5±11.4	6	Oleaceae	Lamiales	Asterid I	Tree	Hot Flammable	Non-fire-prone
Fuchsia excorticata	FUXexc	38.5	233.9±41.8	4.4±2.2	8.8±5.2	13	Onagraceae	Myrtales	Rosid II	Tree	Fast Flammable	Non-fire-prone
Fuscospora cliffortioides	FUScli	95.2	619.9±29.1	39.8±6.7	46.9±5.5	21	Nothofagaceae	Fagales	Rosid I	Tree	Hot Flammable	Non-fire-prone
Fuscospora fusca	FUSfus	80.9	299.9±21.8	8.2±1.5	13.1±1.9	47	Nothofagaceae	Fagales	Rosid I	Tree	Fast Flammable	Non-fire-prone
Gaultheria depressa	GAUdep	100.0	571.5±49.9	14.8±3.1	94.4±2.0	8	Ericaceae	Ericales	Ericales	Shrub	Hot Flammable	Non-fire-prone

Species	Code						Family	Order	Clade	Form	Flammability	Fire status
Geniostoma ligustrifolium	GENlig	25.0	161.8±11.8	0.6±0.4	2.2±1.5	8	Loganiaceae	Gentianales	Asterid I	Shrub	Fast Flammable	Non-fire-prone
Geranium microphyllum	GERmic	0.0	150±0	0±0	0±0	8	Geraniaceae	Gentianales	Rosid II	Forb	Low Flammable	Non-fire-prone
Geranium sessiliflorum	GERses	25.0	222.5±47.6	0.6±0.5	23.1±15.2	8	Geraniaceae	Gentianales	Rosid II	Forb	Low Flammable	Non-fire-prone
Geum leiospermum	GEUlei	11.1	178.3±28.3	1.0±1.0	11.1±11.1	9	Rosaceae	Rosales	Rosid I	Forb	Low Flammable	Non-fire-prone
Ginkgo biloba	GINbil	100.0	448.8±25.6	5.8±1.4	9.2±2.0	6	Ginkgoaceae	Ginkgoales	Ginkgoales	Tree	Fast Flammable	Non-fire-prone
Griselinia littoralis	GRIlit	63.3	270.6±22.7	4.8±1.0	6.5±2.0	30	Griseliniaceae	Apiales	Asterid II	Tree	Fast Flammable	Non-fire-prone
Hakea sericea	HAKser	100.0	584.3±39.0	40.5±9.3	43.1±7.2	8	Proteaceae	Proteales	Proteales	Shrub	Hot Flammable	Fire-prone
Hebe Wiri Mist	HEBalb	100.0	418.6±52.4	15.9±6.1	55.0±9.6	8	Plantaginaceae	Lamiales	Asterid I	Shrub	Hot Flammable	Non-fire-prone
Hedycarya arborea	HEDarb	100.0	279.8±34.0	2.7±0.3	9.2±0.8	6	Monimiaceae	Laurales	Asterid II	Tree	Fast Flammable	Non-fire-prone
Helichrysum filicaule	HELfil	0.0	150±0	0±0	0±0	8	Asteraceae	Asterales	Asterid II	Forb	Low Flammable	Non-fire-prone
Hieracium lepidulum	HIElep	25.0	206.3±42.5	9.9±8.4	21.9±14.4	8	Asteraceae	Asterales	Asterid II	Forb	Fast Flammable	Fire-prone
Hieracium pilosella	HIEpil	0.0	150±0	0±0	0±0	8	Asteraceae	Asterales	Asterid II	Forb	Low Flammable	Fire-prone
Hieracium praealtum	HIEpra	0.0	150±0	0±0	0±0	8	Asteraceae	Asterales	Asterid II	Forb	Low Flammable	Fire-prone
Hoheria angustifolia	HOHang	69.2	285.6±25.5	5.3±1.4	14.9±2.7	26	Malvaceae	Malvales	Rosid II	Tree	Fast Flammable	Non-fire-prone
Hydrocotyle novae-zelandiae	HYDnov	0.0	150±0	0±0	0±0	8	Araliaceae	Apiales	Asterid II	Forb	Low Flammable	Non-fire-prone
Hypochaeris radicata	HYPrad	0.0	150±0	0±0	0±0	8	Asteraceae	Asterales	Asterid II	Forb	Low Flammable	Non-fire-prone
Juncus gregiflorus	JUNgre	100.0	604.8±31.4	31.2±9.1	25.0±3.2	6	Juncaceae	Poales	Commelinids	Grass	Hot Flammable	Non-fire-prone
Kelleria dieffenbachii	KELdie	25.0	250.3±65.8	1.0±0.7	13.8±9.2	8	Thymelaeaceae	Malvales	Rosid II	Forb	Fast Flammable	Non-fire-prone
Knightia excelsa	KNIexc	100.0	525.1±35.2	25.4±8.8	26.9±8.3	8	Proteaceae	Proteales	Proteales	Tree	Hot Flammable	Non-fire-prone
Kunzea ericoides	KUNeri	96.8	538.6±21.6	22.2±1.8	72.2±4.0	62	Myrtaceae	Myrtales	Rosid II	Tree	Hot Flammable	Fire-prone
Lagenophora cuneata	LAGcun	0.0	150±0	0±0	0±0	8	Asteraceae	Asterales	Asterid II	Forb	Low Flammable	Fire-prone
Laurus nobilis	LAUnob	100.0	463.8±61.1	12.4±3.8	32.0±3.0	5	Lauraceae	Laurales	Magnoliidae	Shrub	Fast Flammable	Non-fire-prone
Leptinella pectinata	LEPpec	0.0	150±0	0±0	0±0	8	Asteraceae	Asterales	Asterid II	Forb	Low Flammable	Non-fire-prone
Leptospermum scoparium	LEPsco	100.0	551.1±22.7	34.9±3.9	70.3±5.0	14	Myrtaceae	Myrtales	Rosid II	Shrub	Hot Flammable	Fire-prone
Leucopogon fasciculatus	LEUfas	100.0	345.9±51.8	9.9±2.7	42.8±7.5	9	Ericaceae	Ericales	Ericales	Shrub	Hot Flammable	Non-fire-prone
Leucopogon fraseri	LEUfra	71.4	393.6±66.9	3.0±1.0	71.4±18.4	7	Ericaceae	Ericales	Ericales	Shrub	Hot Flammable	Fire-prone
Leycesteria formosa	LEYfor	100.0	513.5±68.9	17.7±6.0	59.2±8.6	6	Caprifoliaceae	Dipsacales	Asterid II	Shrub	Hot Flammable	Non-fire-prone
Lophozonia menziesii	LOPmen	100.0	694.6±23.8	60.6±9.9	59.9±7.7	14	Nothofagaceae	Fagales	Rosid I	Tree	Hot Flammable	Non-fire-prone

Species	Code						Family	Order	Clade	Form	Flammability	Fire
Lupinus arboreus	LUParb	50.0	210.9±55.1	11.3±8.8	4.4±1.8	8	Fabaceae	Fabales	Rosid I	Shrub	Fast Flammable	Unsure
Luzula pumila	LUZpum	87.5	433.5±41.8	4.3±1.1	86.3±12.4	8	Juncaceae	Poales	Commelinids	Forb	Hot Flammable	Non-fire-prone
Luzula rufa	LUZruf	0.0	150±0	0±0	0±0	8	Juncaceae	Poales	Commelinids	Forb	Low Flammable	Unsure
Lycopodium fastigiatum	LYCfas	0.0	150±0	0±0	0±0	8	Lycopodiaceae	Lycopodiales	Lycopodiophyta	Forb	Low Flammable	Non-fire-prone
Magnolia grandiflora	MAGgra	100.0	476.0±45.2	24.5±5.0	12.5±1.1	6	Magnoliaceae	Magnoliales	Magnoliidae	Tree	Hot Flammable	Non-fire-prone
Malus spp.	MALdom	100.0	563.5±38.2	20.9±5.9	48.3±7.7	12	Rosaceae	Rosales	Rosid I	Tree	Hot Flammable	Unsure
Maytenus boaria	MAYboa	100.0	399.7±26.4	7.3±0.6	26.7±2.8	6	Celastraceae	Celastrales	Rosid I	Tree	Fast Flammable	Fire-prone
Melicytus crassifolius	MELcra	100.0	269.1±16.2	14.9±3.9	12.0±1.8	8	Violaceae	Malpighiales	Rosid I	Shrub	Fast Flammable	Non-fire-prone
Melicytus ramiflorus	MELram	65.2	339.5±42.9	6.4±2.1	17.6±5.0	23	Violaceae	Malpighiales	Rosid I	Tree	Fast Flammable	Non-fire-prone
Metrosideros excelsa	METexc	85.7	397.6±43.9	12.5±3.9	13.2±3.0	14	Myrtaceae	Myrtales	Rosid II	Tree	Fast Flammable	Non-fire-prone
Metrosideros fulgens	METful	100.0	375.4±61.0	6.4±1.7	16.3±4.6	8	Myrtaceae	Myrtales	Rosid II	Tree	Fast Flammable	Non-fire-prone
Muehlenbeckia australis	MUEaus	61.1	189.3±13.3	2.3±0.6	6.1±1.3	18	Polygonaceae	Caryophyllales	Rosid II	Shrub	Fast Flammable	Non-fire-prone
Myoporum laetum	MYOlae	75.0	311.3±37.7	3.2±0.8	7.9±2.0	12	Scrophulariaceae	Lamiales	Asterid I	Shrub	Fast Flammable	Non-fire-prone
Myrsine australis	MYRaus	37.5	172.4±22.4	2.1±1.6	5.0±2.7	8	Primulaceae	Ericales	Ericales	Tree	Fast Flammable	Non-fire-prone
Nematolepis squamea	NEMsqu	100.0	358.5±28.2	11.8±2.7	18.3±2.1	6	Rutaceae	Sapindales	Rosid II	Shrub	Fast Flammable	Non-fire-prone
Nestegis lanceolata	NESlan	100.0	508.5±48.6	34.1±9.4	29.4±8.0	8	Oleaceae	Lamiales	Asterid I	Tree	Hot Flammable	Non-fire-prone
Olea europaeus	OLEeur	100.0	456.8±54.0	12.6±1.7	13.1±5.2	8	Oleaceae	Lamiales	Asterid I	Tree	Fast Flamuable	Fire-prone
Olearia furfuracea	OLEfur	100.0	553.6±24.6	18.9±2.6	27.5±6.5	8	Asteraceae	Asterales	Asterid II	Tree	Fast Flammable	Non-fire-prone
Olearia paniculata	OLEpan	100.0	557.5±25.6	38.9±8.5	35.0±5.7	12	Asteraceae	Asterales	Asterid II	Tree	Hot Flammable	Non-fire-prone
Olearia traversiorum	OLEtra	100.0	394.8±28.1	11.3±2.1	17.1±2.8	12	Asteraceae	Asterales	Asterid II	Tree	Fast Flammable	Non-fire-prone
Ophiopogon Black Dragon	OPHpla	12.5	152.9±2.9	0.5±0.5	7.5±7.5	8	Asparagaceae	Asparagales	Lilioid monocots	Grass	Fast Flammable	Non-fire-prone
Pennantia corymbosa	PENcor	61.5	293.9±40.4	3.7±1.5	6.7±2.0	13	Pennantiaceae	Apiales	Asterid II	Tree	Fast Flammable	Non-fire-prone
Phormium cookianum	PHOcoo	50.0	246.6±44.7	2.4±1.0	3.1±1.3	8	Asphodelaceae	Asparagales	Lilioid monocots	Forb	Fast Flammable	Non-fire-prone
Phormium tenax	PHOten	25.0	239.5±59.1	2.3±1.7	0.9±0.6	8	Asphodelaceae	Asparagales	Lilioid monocots	Forb	Fast Flommable	Non-fire-prone
Photinia Red Robin	PHOgla	87.5	436.1±55.2	13.6±4.1	13.1±2.3	8	Rosaceae	Rosales	Rosid I	Shrub	Fast Flomable	Non-fire-prone
Phyllocladus trichomanioides	PHYtri	87.5	462.8±64.6	19.3±6.6	31.9±6.3	8	Podocarpaceae	Pinales	Pinophyta	Tree	Fast Flammable	Non-fire-prone
Phytolacca octandra	PHYoct	0.0	150±0	0±0	0±0	6	Phytolaccaceae	Caryophyllales	Rosid II	Forb	Low Flammable	Non-fire-prone
Pimelea oreophila	PIMore	100.0	609.2±39.7	15.8±3.2	69.4±7.6	9	Thymelaeaceae	Malvales	Rosid II	Forb	Hot Flammable	Fire-prone

Pinus arizonica	PINari	100.0	699.7±20.4	86.0±12.8	42.1±6.5	7	Pinaceae	Pinales	Pinophyta	Tree	Hot Flammable	Fire-prone
Pinus contorta	PINcon	37.5	224.6±45.0	3.6±2.0	5.0±2.7	8	Pinaceae	Pinales	Pinophyta	Tree	Fast Flammable	Fire-prone
Pinus coulteri	PINcou	75.0	552.0±91.8	80.8±30.8	22.5±7.4	8	Pinaceae	Pinales	Pinophyta	Tree	Hot Flammable	Fire-prone
Pinus nigra	PINnig	93.3	534.9±49.1	33.5±6.5	31.3±5.5	15	Pinaceae	Pinales	Pinophyta	Tree	Hot Flammable	Fire-prone
Pinus palustris	PINpal	100.0	595.3±124.1	127.8±75.9	23.8±6.9	4	Pinaceae	Pinales	Pinophyta	Tree	Hot Flammable	Fire-prone
Pinus Pinea	PINpin	100	495.0±72.9	28.0±7.6	15.0±4.3	6	Pinaceae	Pinales	Pinophyta	Tree	Hot Flammable	Fire-prone
Pinus ponderosa	PINpon	100.0	758.3±28.7	188.0±22.5	63.1±5.9	8	Pinaceae	Pinales	Pinophyta	Tree	Hot Flammable	Fire-prone
Pinus radiata	PINrad	79.5	371.6±27.0	18.6±3.2	18.2±2.6	39	Pinaceae	Pinales	Pinophyta	Tree	Fast Flammable	Fire-prone
Pinus sylvestris	PINsyl	100.0	539.8±26.2	38.3±8.1	43.9±8.2	9	Pinaceae	Pinales	Pinophyta	Tree	Hot Flammable	Fire-prone
Pinus wallachiana	PINwal	85.7	536.4±75.7	29.4±8.8	52.1±11.1	7	Pinaceae	Pinales	Pinophyta	Tree	Hot Flammable	Fire-prone
Piper excelsum	PIPexc	0.0	150±0	0±0	0±0	6	Piperaceae	Piperales	Magnoliidae	Tree	Low Flammable	Non-fire-prone
Pittosporum crassifolium	PITcra	100.0	391.0±26.7	7.6±2.2	6.9±0.9	14	Pittosporaceae	Apiales	Asterid II	Tree	Fast Flammable	Non-fire-prone
Pittosporum divaricatum	PITdiv	62.5	191.0±17.8	3.8±1.4	6.9±2.2	8	Pittosporaceae	Apiales	Asterid II	Shrub	Fast Flammable	Non-fire-prone
Pittosporum eugenioides	PITeug	85.7	384.6±41.8	4.6±0.8	16.1±2.9	14	Pittosporaceae	Apiales	Asterid II	Tree	Fast Flammable	Non-fire-prone
Pittosporum tenuifolium	PITten	88.2	333.0±20.9	6.6±1.7	12.7±1.9	34	Pittosporaceae	Apiales	Asterid II	Tree	Fast Flammable	Non-fire-prone
Plagianthus regius	PLAreg	36.4	234.0±26.9	2.2±0.8	6.3±2.1	22	Malvaceae	Malvales	Rosid II	Tree	Fast Flammable	Non-fire-prone
Poa cita	POAcit	100.0	618.3±22.5	169.8±33.2	89.2±3.3	6	Poaceae	Poales	Commelinids	Grass	Hot Flammable	Fire-prone
Poa colensoi	POAcol	100.0	490.8±22.9	13.1±4.2	74.4±1.5	8	Poaceae	Poales	Commelinids	Grass	Hot Flammable	Fire-prone
Podocarpus hallii	PODhal	100.0	487.8±58.6	16.9±2.5	13.8±1.6	8	Podocarpaceae	Pinales	Pinophyta	Tree	Fast Flammable	Non-fire-prone
Podocarpus totara	PODtot	100.0	506.9±36.8	20.5±3.7	29.8±4.0	14	Podocarpaceae	Pinales	Pinophyta	Tree	Fast Flammable	Non-fire-prone
Polystichum vestitum	POLves	60.0	330.2±75.6	3.8±2.2	11.0±4.6	5	Dryopteridaceae	Polypodiales	Polypodiopsida	Shrub	Fast Flammable	Non-fire-prone
Pomaderris kumaraho	POMkum	100.0	683.4±21.3	21.4±2.0	77.5±8.5	8	Rhamnaceae	Rosales	Rosid I	Shrub	Hot Flammable	Fire-prone
Populus nigra	POPnig	36.8	264.9±28.9	3.3±1.0	14.7±4.1	39	Salicaceae	Malpighiales	Rosid I	Tree	Fast Flammable	Unsure
Populus trichocarpa	POPtri	66.7	334.2±70.0	4.5±1.9	5.8±2.4	6	Salicaceae	Malpighiales	Rosid I	Tree	Fast Flammable	Non-fire-prone
Protea neriifolia	PROner	100.0	510.8±22.7	36.3±5.2	16.7±2.1	6	Proteaceae	Proteales	Proteales	Shrub	Hot Flammable	Fire-prone
Prumnopitys ferruginea	PRUfer	87.5	319.1±60.0	10.5±6.4	13.4±4.7	8	Podocarpaceae	Pinales	Pinophyta	Tree	Fast Flammable	Non-fire-prone
Prumnopitys taxifolia	PRUtax	100.0	388.2±50.0	12.7±2.7	18.4±4.5	10	Podocarpaceae	Pinales	Pinophyta	Tree	Fast Flammable	Non-fire-prone
Prunus Kanzan	PRUser	91.7	525.5±63.6	20.3±3.5	43.8±7.8	12	Rosaceae	Rosales	Rosid I	Tree	Fast Flammable	Non-fire-prone

Prunus laurocerasus	PRUlau	66.7	232.3±41.6	3.7±1.8	3.3±1.1	6	Rosaceae	Rosales	Rosid I	Tree	Hot Flammable	Non-fire-prone
Prunus × yedoensis	PRUspc	100.0	613.9±30.0	28.3±7.6	53.8±8.4	8	Rosaceae	Rosales	Rosid I	Tree	Hot Flammable	Unsure
Pseudopanax arboreus	PSEarb	33.3	206.7±20.3	2.6±0.9	2.8±0.9	27	Araliaceae	Apiales	Asterid II	Tree	Fast Flammable	Non-fire-prone
Pseudopanax crassifolius	PSEcra	22.2	163.4±11.4	0.6±0.4	1.4±0.7	18	Araliaceae	Apiales	Asterid II	Tree	Fast Flammable	Non-fire-prone
Pseudotsuga menziesii	PSEmen	87.5	482.4±58.7	20.0±7.9	13.8±3.1	8	Pinaceae	Pinales	Pinophyta	Tree	Fast Flammable	Fire-prone
Pseudowintera colorata	PSEcol	91.7	543.3±42.2	32.3±5.8	43.3±6.3	12	Winteraceae	Canellales	Magnoliidae	Shrub	Hot Flammable	Non-fire-prone
Pteridium esculentum	PTEesc	100.0	507.7±22.4	24.9±3.1	28.6±2.3	14	Dennstaedtiaceae	Polypodiales	Polypodiopsida	Shrub	Fast Flammable	Fire-prone
Pyrus 'Louise Bonne of Jersey'	PYRcom	100.0	632.0±51.9	14.1±4.3	41.4±9.6	7	Rosaceae	Rosales	Rosid I	Tree	Hot Flammable	Unsure
Quercus ilex	QUEile	100.0	460.3±58.9	23.9±6.1	26.7±7.9	6	Fagaceae	Fagales	Rosid I	Tree	Fast Flammable	Fire-prone
Raoulia grandiflora	RAOgra	12.5	173.4±23.4	0.5±0.5	0.6±0.6	8	Asteraceae	Asterales	Asterid II	Forb	Fast Flammable	Fire-prone
Raoulia subsericea	RAOsub	100.0	491.2±23.8	7.4±2.0	80.0±6.3	8	Asteraceae	Asterales	Asterid II	Forb	Hot Flammable	Fire-prone
Ripogonum scandens	RIPsca	50.0	213.5±31.7	1.9±0.8	5.0±2.5	8	Ripogonaceae	Liliales	Lilioid monocots	Shrub	Fast Flammable	Non-fire-prone
Rosa rubiginosa	ROSrub	87.5	193.4±18.1	3.0±1.6	15.0±4.6	8	Rosaceae	Rosales	Rosid I	Shrub	Fast Flammable	Unsure
Rosmarinus officinalis	ROSoff	100.0	208.3±21.7	7.0±3.3	15.0±3.8	7	Lamiaceae	Lamiales	Asterid I	Forb	Fast Flammable	Fire-prone
Rubus cissoides	RUBcis	66.7	349.3±56.3	5.4±2.0	12.2±3.6	9	Rosaceae	Rosales	Rosid I	Shrub	Fast Flammable	Non-fire-prone
Rubus fruticosus	RUBfru	75.0	230.0±32.5	8.6±3.2	23.1±7.4	8	Rosaceae	Rosales	Rosid I	Shrub	Fast Flammable	Non-fire-prone
Rumex acetosella	RUMace	20.0	180.5±20.4	0.4±0.3	20.0±13.3	10	Polygonaceae	Caryophyllales	Rosid II	Forb	Fast Flammable	Fire-prone
Rytidosperma setifolium	RYTset	25.0	215.0±42.7	1.1±0.9	23.5±15.4	8	Poaceae	Poales	Commelinids	Grass	Low Flammable	Fire-prone
Salix fragilis	SALfra	100.0	347.1±48.1	16.3±2.7	55.0±8.5	7	Salicaceae	Malpighiales	Rosid I	Tree	Hot Flammrable	Non-fire-prone
Salix matsudana	SALmat	100.0	428.8±37.1	7.0±1.8	23.3±4.2	6	Salicaceae	Malpighiales	Rosid I	Tree	Fast Flammable	Non-fire-prone
Solanum laciniatum	SOLlac	0.0	150±0	0±0	0±0	8	Solanaceae	Solanales	Asterid I	Shrub	Low Flammable	Fire-prone
Sophora microphylla	SOPmic	40.0	225.6±47.5	2.3±1.3	10.5±4.9	10	Fagaceae	Fagales	Rosid I	Tree	Fast Flammable	Non-fire-prone
Syzygium smithii	SYZsmi	100.0	598.8±30.6	16.8±1.1	23.1±2.1	8	Myrtaceae	Myrtales	Rosid II	Tree	Fast Flammable	Non-fire-prone
Trachelospermum jasminoides	TRAjas	33.3	227.7±59.9	2.2±1.5	5.8±3.8	6	Apocynaceae	Gentianales	Asterid I	Shrub	Fast Flammable	Non-fire-prone
Trifolium arvense	TRIarv	0.0	150±0	0±0	0±0	8	Fabaceae	Fabales	Rosid I	Forb	Low Flammable	Fire-prone
Trifolium repens	TRIrep	12.5	187.0±37.0	0.5±0.5	12.5±12.5	8	Fabaceae	Fabales	Rosid I	Forb	Low Flammable	Non-fire-prone
Ulex europaeus	ULEeur	100.0	704.8±30.3	65.1±7.3	83.8±4.8	8	Fabaceae	Fabales	Rosid I	Shrub	Hot Flammable	Fire-prone
Vibranum tinus	VIBtin	100.0	626.2±10.1	18.0±4.8	30.0±3.7	6	Adoxaceae	Dipsacales	Asterid II	Shrub	Fast Flammable	Fire-prone

Viola cunninghamii	VIOcun	0.0	150±0	0±0	0±0	8	Violaceae	Malpighiales	Rosid I	Forb	Low Flammable Non-fire-prone
Vitex lucens	VITluc	87.5	442.6±49.7	8.5±4.4	12.2±3.0	8	Lamiaceae	Lamiales	Asterid I	Tree	Fast Flammable Non-fire-prone
Wahlenbergia albomarginata	WAHalb	0.0	150±0	0±0	0±0	8	Campanulaceae	Asterales	Asterid II	Forb	Low Flammable Non-fire-prone
Weinmania racemosa	WEIrac	100.0	548.5±33.1	9.1±2.6	16.9±4.0	8	Cunoniaceae	Oxalidales	Rosid I	Tree	Fast Flammable Non-fire-prone