Patterns in Plant Leaf Flammability of Woodlands and Forests of Eastern Australia

Daniel William Krix

Thesis submitted for the degree of Doctor of Philosophy

February 2020

Supervisors: Dr Brad R. Murray and Dr Megan L. Phillips

Certificate of Original Authorship

I, Daniel Krix declare that this thesis, is submitted in fulfilment of the requirements for the award of Doctor of Philosophy, in the School of Life Sciences at the University of Technology Sydney.

This thesis is wholly my own work unless otherwise reference or acknowledged. In addition, I certify that all information sources and literature used are indicated in the thesis.

This document has not been submitted for qualifications at any other academic institution.

This research is supported by an Australian Government Research Training Program.

Signature: Production Note:
Signature removed prior to publication.

Date: 10/08/19

Acknowledgments

Firstly, I'd like to thank my supervisor Brad Murray, who took me on for my Honours project, and worked hard to secure a scholarship without which I'd not have been able to continue on to work on this thesis. He's given me the space to develop my own ideas and managed to pull me out of my 'rabbit holes', many, many times, and sometimes with much resistance on my part! His enthusiasm and kind support have been absolutely invaluable through all phases of this project. Also, it was he who first suggested I try R; my getting to grips with programming since then has been unbelievably rewarding. Thanks also to my co-supervisor Megan Phillips, and to Leigh Martin, who have both provided helpful comments on various aspects of this work.

The lab staff at UTS were also incredibly helpful, particularly Gemma Armstrong, who modified the lab for the leaf burning experiments, and let me continue using the muffle furnace in spite of my causing several heat-induced breakdowns due to its use in an application it was patently not designed for. My parents, Sharyn and Michael provided countless cups of tea and space to sort through samples in the Blue Mountains, along with storage for bags of soil and various bits of equipment from my many failed ideas. Also, thanks to the Sunday Coffee Boys, Luke Blattman, Guy Dernee, Hayden Fryer and Bob Lloyd, who listened to me bang on about my project so many times.

I'll be forever grateful to my wife Caroline, who first suggested I find a new career path, and who has supported me in this crazy endeavour for nearly a decade now. She has given me the time to follow this road out as far as it goes, and it's proven to be more satisfying than I'd ever imagined. Finally, my daughter Charlotte, and the little man who's

almost here, who let me see the world with new eyes, and desire to make it better for them, in whatever small way I might.

Table of Contents

List of Figures

List of Tables

List of Abbreviations in this Thesis

Context	Abbreviation	Definition
Flammability attributes	TTS	Time to smoke
	SD	Smoking duration
	TTI	Time to incandescence (equivalent to time to ignition used in Chapter 2)
	ID (BD)	Incandescence duration (equivalent to burn duration used in Chapter 2)
	TTF	Time to flaming
	FD	Flaming duration
	MLR	Mass loss rate
Leaf traits	LA	Leaf area
	LMA	Leaf mass per area
	LWC	Leaf water content
	FMC	Fuel moisture content
	FLM	Fresh leaf mass
	DLM	Dry leaf mass
Miscellaneous	PGLS	Phylogenetic generalised least squares
	OU	Ornstein-Uhlenbeck
	WUI	Wildland-urban interface
	OLFI	Overall leaf flammability index
	MPD	Mean pairwise distance
	FM	Full model

REM	Radiant energy model
LFM	Leaf flaming model

Abstract

Exacerbated by global change, wildfires are causing unprecedented impacts on ecosystems, human lives and infrastructure. Thus, there is a pressing need to better understand the drivers of wildfire in this changing world. I investigated interspecific patterns in plant leaf flammability in fire-prone vegetation of eastern Australia to determine the flammability dynamics of leaves given their essential role as fuels for wildfires.

At a landscape scale, I found that leaves of forest gully species had faster ignitibility and higher combustibility relative to woodland ridgetop species. These differences were driven by strong relationships between high flammability and both large leaf area and low leaf mass per area. For these plant communities, I explored relationships among leaf ignitibility, sustainability and combustibility and showed that faster ignitibility (higher flammability) was associated with short sustainability (lower flammability), and long sustainability (higher flammability) with higher combustibility (high flammability). Given the opposing relationship between ignitibility and sustainability, I established an overall leaf flammability index to assist in identifying low-leaf-flammability species at the wildland-urban interface. Close inspection of the flammability of ten species showed that increasing radiant energy, representing increases from low to moderate intensity wildfires, led to faster ignitability and a higher proportion of leaves flaming, such that species identity became much less important for understanding flammability dynamics. However, species identity remained particularly important for leaf sustainability and time to flaming, signalling that species differences in these flammability attributes may be helpful in understanding the dynamics of moderate intensity wildfires. Finally, I built predictive models of leaf ignitibility, sustainability and combustibility using a combination of radiant energy and leaf area, mass per area, and water content, and tested the accuracy of the models using a validation dataset. Including leaf traits in these models dramatically increased the ability to predict leaf flammability. One application of these models will be to estimate leaf flammability for large numbers of plant species using just their leaf traits, without the need for flammability experiments if they are not feasible.

This thesis provides novel insight into interspecific variation in plant leaf flammability. The findings of my research advance our ecological understanding of leaf flammability, with potential applications to wildfire modelling, the selection of low-leaf-flammability species at the wildland-urban interface, and prediction of leaf flammability for large numbers of species using leaf traits.

Chapter 1

General introduction

1.1 Wildfire and the flammability of plant species

Recent human-induced changes to climate and rainfall patterns (Petit *et al.* 1999, Trenberth 2011, Dai 2013, Dufresne *et al.* 2013) have led to a lengthening of fire seasons across the globe (Flannigan *et al.* 2009, Jolly *et al.* 2015). Longer fire seasons increase the amount of time each year when weather conditions are favourable for wildfires. In the future, wildfires may become more frequent and widespread, with the potential for loss of human lives and destruction of vital infrastructure (Krawchuk *et al.* 2009, Pechony & Shindell 2010, Westerling *et al.* 2011, Nolan *et al.* 2019). In addition, there will likely be ecological impacts on fire-sensitive species which may not recover sufficiently between wildfire events of increased frequency (Enright *et al*. 2015, Fairman *et al*. 2019), or indeed survive higher intensity fires. It is thus crucial that we establish a more complete understanding of wildfires, so as to mitigate the damaging effects of changing fire regimes on both humans and the natural world. Furthering the knowledge of drivers of wildfire behaviour, particularly the relationship between fire and fuels, is an important area of research to attempt to ameliorate these risks.

Many studies have focussed on surface fuels for wildfires such as leaf litter (de Magalhaes & Schwilk 2012, Zhao *et al.* 2016, Prior *et al.* 2017, Kreye *et al.* 2018), and factors which may or may not affect their relative flammability. For example, the degree of litter packing and thus fuel aeration has been found to influence flammability of litter beds, with larger leaf size (Scarff & Westoby 2006, Parsons *et al.* 2015, Zhao *et al.* 2016) and increased leaf 'curliness' (Grootemaat *et al.* 2017) being found to increase flammability of leaf litters, by increasing air spaces through looser packing of litter. In contrast, the flammability of standing live fuel, including plant leaves, has received comparatively less attention. Existing studies from different plant assemblages around the world have found that large variation among species exists in leaf flammability (Table 1.1). Differences in extremes of key flammability measures can be large (e.g., a 2 s minimum for plant species to begin flaming, compared to a 60 s maximum; Table 1.1).

Table 1.1 Results from eight studies investigating the flammability of fresh leaves. The responses measured are time to incandescence (TTI), time to flaming (TTF), incandescence duration (ID) and flaming duration (FD). The number of species included in the study, the range of values in seconds, the focal study region, and study references are provided. An 'X' in the column 'Sig.' denotes a statistical test of differences in the response value among species was made (all tests were significant at α = 0.05).

Response	n species	Range (s)	Sig.	region	Study
TTI	79	7 – 70		Australia	Murray *et al.* (2013)
TTF	50	2 – 53		Australia	Gill & Moore (1996)
	32	2 – 60	X	Australia	Grootemaat *et al.* (2015)
	25	1 – 4	X	S Africa	Simpson *et al.* (2017)
	10	16 – 38	X	S America	Ghermandi *et al.* (2016)

	8	3 – 36	X	France	Ganteaume *et al.* (2013)
	6	2 – 4		S America	Blackhall *et al.* (2012)
	6	11 – 23		S America	Bianchi & Defossé (2015)
ID	32	3 – 80	X	Australia	Grootemaat *et al.* (2015)
FD	32	1 – 15	X	Australia	Grootemaat *et al.* (2015)
	25	4 – 6	X	S Africa	Simpson *et al.* (2017)
	18	34 – 160		N America	Engber & Varner (2012)
	10	1 – 4	X	S America	Ghermandi *et al.* (2016)
	8	5 – 16	X	France	Ganteaume *et al.* (2013)
	6	7 – 12		S America	Blackhall *et al.* (2012)
	6	3 – 19		S America	Bianchi & Defossé (2015)

The differential flammability of plant species has long been a source of global scientific interest, both theoretical and for practical use in identifying species which might promote or slow wildfires. In a foundation study for research in the area of the ecology of plant flammability, Mutch (1970) proposed that plants from plant communities that experience frequent fire might evolve higher flammability, and so reinforce a regime of more frequent fire, or evolve high flammability to kill neighbouring plants competing for resources (Bond & Midgley 1995). Recent research, however, has found little evidence for this (Bradshaw *et al.* 2011, Midgley 2013, Bowman *et al.* 2014). For example, Clarke *et al.*

(2014) analysed leaf and litter bed flammability in 11 congeners from rainforest and eucalypt forest, finding no difference between the habitat types, where the Mutch hypothesis would predict eucalypt forest, experiencing frequent fire would be of higher flammability. In a study comparing the energy content and the ignitibility of *Pinus* spp. needles from two habitats with contrasting fire risk, Dimitrakopoulos *et al.* (2011), found no evidence of higher flammability in species from the more fire prone habitat.

Quantification of the flammability of individual species has been shown to be of practical value in fire behaviour modelling by Zylstra *et al.* (2015). They incorporated species-specific fuel parameters into fire behaviour models, which resulted in increased accuracy in modelling fire severity compared to current fire behaviour models, which account only for surface fuel classes and moisture content (Rothermal 1972, Scott & Burgan 2005), and are not necessarily well fit to the modelled environment (Boer *et al.* 2017). In a 2017 study, Prince *et al.* (2017) used manzanita shrubs to test a flame spread model, incorporating flammability data derived from burning single leaves to make predictions of the three-dimensional movement of flames. Results from this modelling gave estimations of flame height and the duration of burning, which agreed closely with the observed patterns. Others have highlighted the need for further research on the properties of live fuels (Mell *et al.* 2010, Weise & Wotton 2010, Gallacher *et al.* 2015) for these types of applications. Fire modelling using this approach of including plant species flammability is a recent development, with most fire models in common use being developed from the McArthur fire model (Luke & McArthur 1978). These models consider fuels to be homogenous within a vegetation type, and only include dead fuels (e.g. leaf litters, coarse woody debris) in their calculation, with no consideration of live standing fuels.

Homes and infrastructure that sit at the boundary of built-up and natural areas (the wildland-urban interface [WUI]) are often at greatest risk during fire, with clearing land up to 30–40 m around structures the most effective way to reduce the risk of damage or loss during wildfire (Gibbons *et al.* 2012, Syphard *et al.* 2014). Knowledge of plant flammability, in particular that of the naturally occurring species in an area, could guide selective plantings of low-flammability plant species at the junction of cleared and natural land, to further lower risk of wildfire spread to built-up areas. The same logic may also be applied to selection of species for home gardens, where plants are often in close proximity to structures and may present a risk during wildfire. Indeed, this concept has been extended to the planting of 'green firebreaks' where strategically positioned banks of low flammability plant species could slow fire spread or provide protection to structures (Curran *et al.* 2018, Murray *et al.* 2018, Cui *et al.* 2019).

1.2 Leaf flammability attributes and leaf traits

Most methods used to determine live plant flammability measure one or more of the components first proposed by Anderson (1970). Anderson defined the terms ignitibility, sustainability and combustibility to reflect the properties of a burning fuel during forest fire. Ignitibility was described as the time taken for a fuel to begin combustion after exposure to a heat source, sustainability as how well a fire will burn without further heat being supplied after ignition, and combustibility as the heat output from a combusting fuel. Where litter beds, larger amounts of plant material, or the methodology used lead to incomplete combustion of samples, consumability is often measured as the proportion of the material that combusts (Behm *et al.* 2004, Curt *et al.* 2011). Measurement of ignitibility and sustainability are usually simply time-based measures. Combustibility can be more difficult to quantify, with calorimetry often used (measuring the heat content of the sample). Several calorimetry methods exist, such as bomb calorimetry, this however usually requires samples to be entirely dried and ground, giving an energy content which does not necessarily reflect rates at which natural materials burn. More complicated calorimetry methods such as mass loss calorimetry measure heat output and change in sample weight in real time, however, such testing is often prohibitively expensive and requires specialised equipment.

When more than a single dimension of plant flammability is measured, the possibility arises that plants may consistently be of either high or low flammability in all of these dimensions. Alternatively, it is possible that plants may demonstrate contrasting patterns of flammability, which leads to difficulties in the absolute classification of particular species as either being of low or high flammability. A recent conceptual model of plant flammability developed by Pausas *et al.* (2017), together considers plant ignitibility, heat release (combustibility), and fire spread rate (i.e., a measure of how quickly fire can move across a plant's tissues). Using this framework, the authors go on to describe a conceptual model, using a trinary continuum of species as either non-flammable (low heat release and low fire spread rate), hot flammable (high heat release and intermediate spread rate), or fast flammable (low heat release and high spread rate), with non-flammable species having low ignitibility and the other two having high ignitibility. Findings of Fuentes-Ramirez *et al.* (2016) led them to classify plant species as 'spreaders' and 'igniters', in an ecosystem consisting of a low-flammability native shrub species invaded by exotic grass species. Under this classification, spreaders (the invasive grass species) burnt quickly with low heat output, spreading fire to igniters (small native species which grow under the non-flammable shrub species), which in turn burned at higher heat output for longer, igniting dead branches in the low flammability shrub species promulgating fire to the upper branches of the shrub.

Due to the inherent difficulties in burning whole plants in the laboratory, researchers have used representative plants parts to test flammability, with live leaves often chosen (as distinct from senesced leaves or leaf litter which has undergone decay; Gill & Moore 1996, Engstrom *et al.* 2004, Fletcher *et al.* 2007, Pickett *et al.* 2009, Murray *et al.* 2013, Grootemaat *et al.* 2015). For determination of single leaf flammability, ignitibility is usually measured as the time delay for combustion to start after a fuel begins heating (Gill & Moore 1996, White & Zipperer 2010, Murray *et al.* 2013, Grootemaat *et al.* 2015) and sustainability as how long leaves burn after ignition (Murray *et al.* 2013, Grootemaat *et al.* 2015). Sample incandescence (i.e., a sample combusting and giving off visible light), or beginning to flame is the response most often measured, with some researchers measuring both (e.g., Grootemaat *et al.* 2015). The method of flammability testing can vary widely with samples being held in the interior of a furnace (Gill & Moore 1996, Murray *et al.* 2013, Grootemaat *et al.* 2015), placed on or held above the surface of an epiradiator (a silica-quartz element with high wattage, Engstrom *et al.* 2004, Kauf *et al.* 2014), or burned over a large quartz element in combination with an epiradiator (Fletcher *et al.* 2007, Pickett *et al.* 2009). In some cases, a small flame or spark-producing instrument is used to aid ignition. Consumability is less often measured than with leaf litter studies, and may be more related to the heat output of the method chosen not being great enough to support total combustion of samples.

Leaf flammability has been found to be strongly correlated with the traits of the leaves themselves, as these traits determine many of the physical properties of leaves important to combustion (Gill & Moore 1996, Ganteaume *et al.* 2013, Murray *et al.* 2013, Grootemaat *et al.* 2015). Traits such as larger leaf width and larger leaf area (Murray *et al.* 2013), lower leaf mass per area (LMA) and lower leaf water content (LWC) in Grootemaat *et al.* (2015), and leaf thickness (Ganteaume *et al.* 2013) have been found to be associated with faster ignitibility (i.e., a shorter period between heat exposure and combustion beginning). Higher LMA and greater dry mass of leaves has been shown to be related to longer sustainability (Grootemaat *et al.* 2015).

For ignitibility, leaf flammability relationships with LMA, LWC and leaf thickness likely reflect the thermal mass of the sample. Having higher tissue density, thicker tissue, or a greater concentration of water in leaf tissues inhibits heating, and thus lengthens the time to reach the critical temperature where the leaf ignites. Leaf width or area possibly influence ignitibility through providing a greater surface area to intercept heat, raising leaf temperature more quickly than for a smaller leaf. For sustainability, mass likely also plays a role, here simply providing more material to burn, increasing the time taken for denser and/or heavier leaves to combust. Leaf chemical composition has also been found to influence leaf flammability, with leaf volatiles shown to increase ignitibility (Alessio *et al.* 2008, Pausas *et al.* 2016, Della Rocca *et al.* 2017).

1.3 Research novelty and significance

The main focus of this thesis is to provide an understanding of patterns and processes in interspecific variation in plant leaf flammability. Broadly, the findings of this work will further our knowledge of the links between leaf flammability and leaf traits, how differences in leaf flammability may be related to plant habitat, and the ability to predict leaf flammability across a range of fire intensities on the basis on leaf traits. This thesis establishes a temporal pathway of leaf combustion and examines the interrelationships among leaf flammability attributes in detail. This is an important consideration when attempting to identify low-leaf-flammability species, as leaf flammability attributes may not be coordinated in a manner that allows easy classification of overall flammability. I also test the importance of interspecific differences in flammability attributes across a fire intensity gradient, which provides understanding of how flammability attributes respond to increases in heat output. Finally, I present predictive models of flammability attributes using leaf traits as predictors, that have potential to estimate leaf flammability attributes accurately.

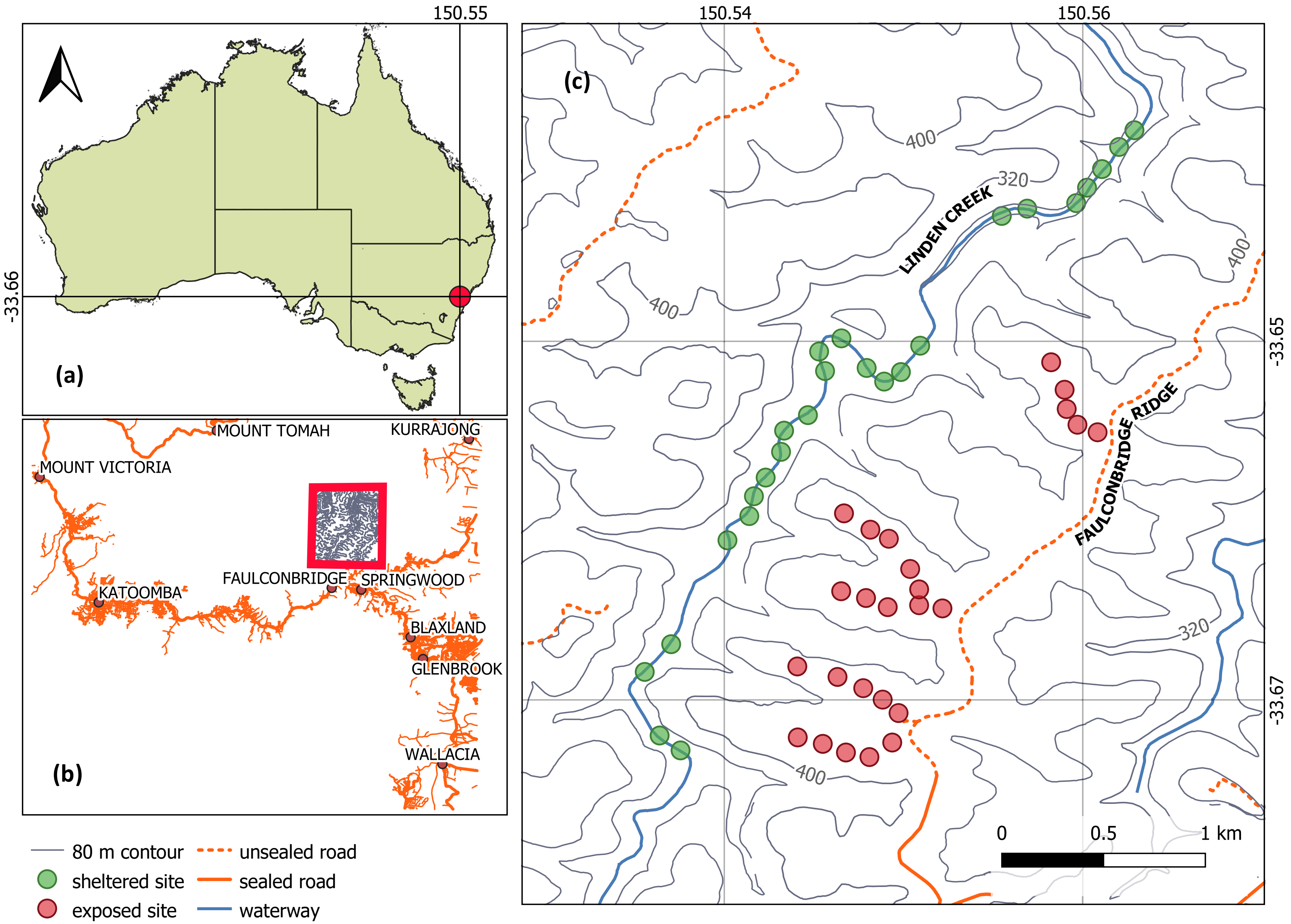
1.4 Study region

The Great Diving Range, which runs nearly the entire length of the east coast of Australia, supports a diverse array of ecosystems including alpine meadows, temperate and tropical rainforest, and various types of forest and woodland. Most parts of the range experience extreme wildfire events relatively frequently (e.g., a 20 to 30 year interval, Hammill & Tasker 2010). In response, plant species have evolved adaptations to persist through fire events, such as establishment of soil seedbanks that allow post-fire recruitment, resprouting from a protected below-ground lignotuber after destruction of above-ground tissues, or through a combination of protective bark and resprouting of leaves post-fire. Built-up areas have developed in close proximity to or are set within areas of natural vegetation, along with various roads passing over the range from eastern cities onto the plains to the west. This conjunction of fire-prone vegetation and human development has resulted in destructive events, such as the Ash Wednesday and Black

Saturday fires, which were collectively responsible for over 200 deaths in Victoria, and fires in New South Wales in 2013 that destroyed more than 200 homes.

The specific study region chosen for this study was the Blue Mountains of New South Wales, west of Sydney (Fig. 1.1). This area was an ideal location for the study, given the large area of undisturbed bushland available, the diversity of vegetation types (e.g., closed forest, open woodland), its fire-prone nature (Hammill & Tasker 2010), and proximity to built-up areas, which are often impacted by wildfire. It is also a listed World Heritage Area, supporting many endemic species, along with pockets of temperate rainforest and closed forest which are relatively sensitive to fire. Vegetation surveys were undertaken in two disparate vegetation types with differing degrees of openness (see Chapter 2 for further details; Fig. 1.1), and data collected from the area of these sites for analysis in Chapters 2-5.

Fig. 1.1 (following page) Map of the location of the study sites, with the sites broad location shown in (a), their situation within the Blue Mountains (b), and the topography and waterways of the sites in (c). The red square delineates the area shown in (c). Exposed sites (woodland vegetation) and sheltered sites (closed forest vegetation) are indicated by green and red circles respectively. The altitude of the sites varied from 200 m to 470 m above sea level.


150.55
-33.66
(a)
MOUNT TOMAH
KURRAJONG
MOUNT VICTORIA
FAULCONBRIDGE
SPRINGWOOD
KATOOMBA
BLAXLAND
GLENBROOK
WALLACIA
(b)
150.54
150.56
(c)
400
320
LINDEN CREEK
400
400
FAULCONBRIDGE RIDGE
-33.65
320
-33.67
400
0
0.5
1 km
80 m contour
sheltered site
exposed site
unsealed road
sealed road
waterway

1.5 Thesis aims

I address six overarching research aims in this thesis:

1. To quantify interspecific patterns in leaf flammability attributes in woodland and forest plant species.
2. To compare leaf flammability attributes between two contrasting habitats.
3. To explore the relationships among leaf flammability attributes, and identify plant species with low-leaf-flammability.
4. To provide further insight into the relationship between leaf flammability attributes and leaf traits.
5. To examine the effect fire intensity may have on flammability attributes.
6. To build predictive models of flammability attributes.

1.6 Chapter structure and descriptions

I address the research aims of the thesis in the following chapters:

Using traditional statistical analyses and a complementary phylogenetic approach, Chapter 2 (published in *Ecosphere*, Krix & Murray 2018) provides the first major quantification and comparison of leaf flammability attributes for woodland and forest species of eastern Australia. Leaf traits of the species were contrasted between the habitats, before being used as predictors of flammability attributes. The relationship of habitat to leaf flammability attributes over and above those between flammability attributes and leaf traits was also examined.

Drawing on data from sixty plant species, Chapter 3 (Published in *International Journal of Wildland Fire*, Krix *et al*. 2019) defines a novel temporal pathway of leaf combustion including seven flammability attributes representing ignitibility, sustainability and combustibility of leaves. These attributes were then related to each other to understand the relationships amongst them. An overall leaf flammability index was developed to score species on their flammability before being related to leaf traits.

To understand the possible interaction between the importance of species characteristic leaf flammability and fire intensity, in Chapter 4 I burned the leaves of ten plant species representative of a wide range of leaf traits at increasing levels of radiant energy representing a gradient of fire intensity. I then assessed the magnitude of the change in flammability attributes in relation to radiant energy and follow this with analyses which test if species leaf flammability attributes converge to more similar values with increasing radiant energy.

In Chapter 5, non-linear regression and binary logistic regression were used to build predictive models of ignitibility, sustainability and the presence of leaf flaming, using leaf traits and radiant energy as predictors. As a test of the predictive utility and accuracy of the models, the models were applied to a validation dataset and the error in predictions quantified.

Chapter 6 provides a discussion of the implications of the findings of Chapters 2-5, and suggests directions for future research.

Chapter 2

Landscape variation in plant leaf flammability is driven by leaf traits responding to environmental gradients

Published in Ecosphere: Krix DW, Murray BR (2018) Landscape variation in plant leaf flammability is driven by leaf traits responding to environmental gradients. *Ecosphere* **9**, e02093. CC BY 3.0 (https://creativecommons.org/licenses/by/3.0/legalcode).

2.1 Introduction

Research in trait-based ecology has identified fundamental patterns of variation in plant traits along environmental gradients (Reich *et al.* 1992, Reich *et al.* 2003, Wright *et al.* 2004, McGill *et al.* 2006, Poorter *et al.* 2009, Wright *et al.* 2010). Plant leaves, given their critical role in plant metabolism, have been a key focus of much of this research. Landscape differences in abiotic conditions such as available light, ambient temperature, vapour pressure deficit, and rainfall have selected for physical adaptations in leaves to intercept sufficient light and maintain transpiration at acceptable levels, while maintaining a low carbon 'cost' in construction (Wright *et al.* 2004). Low light conditions favour larger leaves that are better at intercepting scarcer available light, often at a lower carbon investment per unit area (i.e. leaf mass per area, LMA; Bragg & Westoby 2002, Cornwell & Ackerly 2009). In brighter environments, which are also often drier and hotter, smaller leaves with higher LMA provide a better fit to abiotic conditions, given that light availability is not a strong limiting factor and that higher leaf mass per area allows lower transpirational water loss and greater resistance to wilting (Castro-Díez *et al.* 1997, Wright *et al.* 2001).

While landscape variation among species in traits such as leaf mass per area is driven largely by environmental gradients, laboratory studies have also found to varying degrees that interspecific variation in leaf traits can often be a predictor of variation in leaf flammability (Gill & Moore 1996, Ganteaume *et al.* 2013, Murray *et al.* 2013, Grootemaat *et al.* 2015). For example, lower leaf water content and lower LMA are associated with faster leaf ignition (Bianchi & Defossé 2015, Grootemaat *et al.* 2015), while higher LMA and larger leaf area are related to longer duration of leaf burn (Grootemaat *et al.* 2015). What has yet to be considered, however, is the possibility that if leaf traits are found to vary among species as a function of environmental conditions across a landscape, with these traits in turn driving differences among species in leaf flammability, then landscape variation in leaf level flammability might be largely predictable on the basis of variation in a few key leaf traits responding to environmental gradients. Uncovering such a predictive relationship, underpinned by fundamental environmental filtering of key leaf traits, is critical as it has the potential to provide an important initial link between flammability research at the leaf scale and research examining flammability at the scale of vegetation communities (Gill & Zylstra 2005). Identifying such links between leaf and community scales is crucial considering that leaves are considered to be one of the most important flammable plant structures (Gill & Moore 1996, Etlinger & Beall 2004). Leaves are frequently the first structures to ignite during bushfire (Pickett *et al.* 2009), promulgating fire to other plant structures and fuel sources. Furthermore, leaves contribute a large proportion of the living biomass available to a fire and recent modelling has shown that the properties of living fuel, in particular plant leaves, are an important factor in landscape fire (Zylstra *et al.* 2016).

Leaf flammability is a multidimensional plant trait (Pérez-Harguindeguy *et al.* 2013) with implications for fire behaviour based on ignitibility, sustainability and combustibility

(Anderson 1970). Ignitibility is a measure of how quickly combustion begins when a leaf is exposed to a heat source and how soon it can contribute heat from its own combustion to a larger fire. Sustainability represents how long combustion continues once a leaf has ignited and the length of the period it is generating heat from combustion. Combustibility is how much heat is given off whilst the leaf is burning. Taken together, a highly flammable leaf could be considered as having high ignitibility (easily ignited), high sustainability (burning for a long period), and high combustibility (giving off a large amount of heat in a given amount of time). Several studies across the world have found that these three leaf flammability attributes vary substantially among species. For instance, leaves of some plant species ignite within a few seconds while others take much longer to ignite, if at all (Murray *et al.* 2013, Grootemaat *et al.* 2015).

In the present study, we first compare three key leaf traits including LMA, leaf area (LA) and fuel moisture content (FMC) between plant species of sheltered forest vegetation along gullies (low light, moist habitat; Fig. 2.1a) and plant species of exposed woodland vegetation on ridge tops (high light, dry habitat; Fig. 2.1b), in a rugged area prone to intense wildfires in the Blue Mountains of south-eastern Australia. We test predictions that, relative to species from exposed woodland habitat, leaves of species from sheltered forest habitat have larger area to maximise light interception, lower LMA as transpiration is relatively less costly and water stress less likely, and higher FMC as water availability is greater in sheltered gullies with water courses. We then test the hypothesis that leaf flammability attributes differ across the landscape in a way that is tightly coordinated with the primary strategic response of leaf traits to the environmental gradient between the habitats. To do this, we first compare three major leaf flammability attributes representing ignitibility (time to ignition), sustainability (burn duration) and combustibility (mean mass loss rate, a proxy for the mean rate heat is generated by combustion; Grootemaat *et al.* 2017, Prior *et al.* 2017) between sheltered forest and exposed woodland species to determine habitat differences in leaf flammability. We then examine interspecific relationships between the three leaf traits and the three flammability attributes to test the predictions that high ignitibility is related to large LA and low LMA found in gully species, and that overall these two leaf traits counteract the buffering effect of high FMC in gully species; and that high sustainability and high combustibility are related to large LA and high LMA in gully species. These predictions are based on high ignitibility being driven by large LA which increases the surface area available to intercept thermal energy and by low LMA which decreases thermal mass; on high sustainability being driven by large LA and high LMA which represent an increase in both the area and amount of material over which combustion can spread; and on high combustibility being driven by long burn durations generating higher temperatures at the leaf surface through preheating.

2.2 Methods

2.2.1 Study region

The study was undertaken in the Blue Mountains of south-eastern Australia, 75 km west of Sydney (-33°39’31”N, 150°32’45”E). The area experiences a mild climate (mean temperature 17.2 °C), with warm summers (mean temperature 21.9 °C) and cool winters (mean temperature 11.9 °C), and a mean annual rainfall of 1086 mm with the majority of

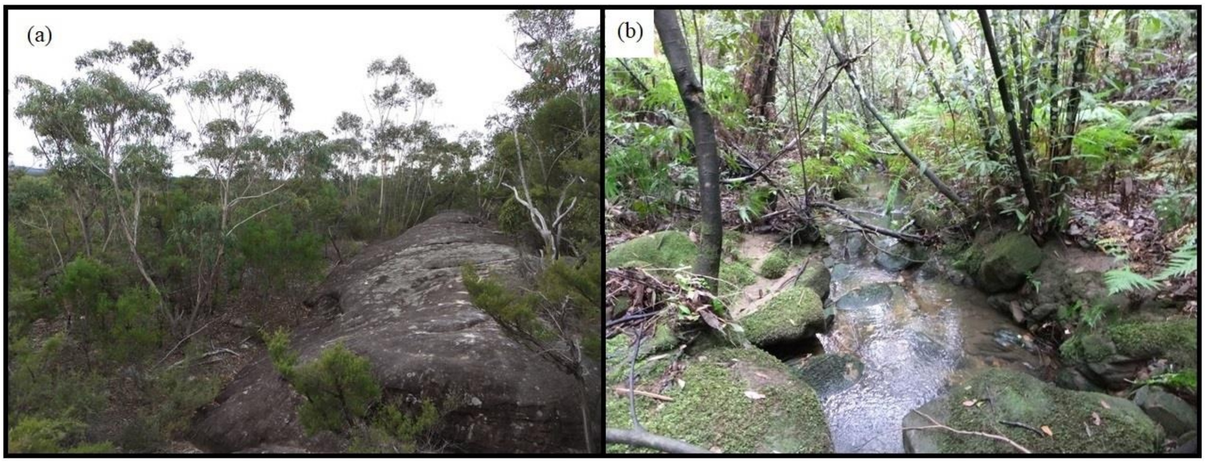


Fig. 2.1 Typical exposed woodland habitat on ridge tops (a) and sheltered forest habitat (b), in the study region. Despite large differences in abiotic conditions, these habitats can often be found within short distances of each other (< 500 m).

this falling in the summer (Australian Bureau of Meteorology 2017). The region is a deeply dissected sandstone plateau, with a system of ridges exposed to high solar insolation and deep, steep-sided gullies with lower light availability and permanent or ephemeral waterways at their base. The vegetation of the region varies from dry sclerophyll woodland on exposed ridgetop areas to temperate closed forest in sheltered gullies.

Exposed woodland vegetation is characterized by an open canopy consisting mostly of species in the family Myrtaceae such as *Corymbia gummifera*, *Eucalyptus piperita*, and *E. sparsifolia*, and a high diversity of shrub species e.g. *Acacia suaveolens, Banksia spinulosa*, *Petrophile pulchella*. Sheltered forest vegetation is dominated by canopy species such as *Backhousia myrtifolia*, *Ceratopetalum apetalum*, and *Tristaniopsis collina*, and understorey species including *Acrotriche divaricata*, *Austromyrtus tenuifolia*, and *Hibbertia saligna*, along with fern (e.g. *Calochlaena dubia*, *Blechnum cartilagineum*) and climber species (e.g. *Cissus hypoglauca*, *Smilax australis*). These two vegetation associations are representative of large areas of the Blue Mountains and the Great Dividing Range, a World Heritage listed area that is prone to wildfire. Wildfire frequency can be variable, however most areas in the region experience high intensity fire every ten years (Hammill & Tasker 2010). Fire events may last a single day in localised cases or continue for weeks and burn hundreds of hectares as fire moves over the landscape. Sheltered forests in gullies tend to burn less frequently than exposed woodlands on ridgetops (Penman *et al.* 2007, Leonard *et al.* 2014), due largely to gully forests being sheltered from high winds by topography. Sheltered areas also tend to experience relatively lower intensity fires which leaves the tree canopy intact in contrast to exposed areas where canopy (or 'crown') fires more often occur (Bradstock *et al.* 2010). Plant species in both sheltered and exposed habitats have adaptations to persist through fire, either as an individual by re-sprouting after fire events, or through offspring via canopy held seed or soil seed banks.

2.2.2 Study sites and species

We performed plant species surveys in contiguous unmodified vegetation in the study region to generate a list of common species of exposed woodland habitat on ridgetops and common species of sheltered forest habitat in gullies adjacent to creeks (Appendix 2.1). We recorded all plant species present in a total of 50 sites across a 6 km^2 area to ensure a representative sample of commonly occurring species in the habitats was obtained, with 25 sites located in each of the two habitats. Each site measured 25 m^2 (5 m x 5 m) and all sites were located at least 100 m from each other. Species identified in our surveys were assigned to either the understory stratum (< 3 m mature height) or the overstory stratum (> 3 m mature height). A total of 92 plant species were included in the study, comprising 57 species from exposed woodland habitat (10 overstory species, 47 understorey species) and 35 species from sheltered gully habitat (12 overstory species, 23 understorey species). Six species were found to occur in both habitats (*Lepidosperma laterale*, *Lomatia silaifolia*, *Phyllanthus hirtellus*, *Pteridium esculentum*, *Stylidium graminifolium*, *Xanthorrhoea media*). We excluded this small number of species from the study as our focus was on the distinctive flora of each habitat and we wanted to avoid the potentially confounding issue of the same species being represented in both habitat groups in our statistical analyses. One further unidentified species was excluded as only one individual was recorded. Taxonomic nomenclature for the study taxa followed Fairley & Moore (2010).

2.2.3 Leaf collection

Fully-expanded, non-senescent leaves were collected from the outer exposed plant canopy from five mature individual plants representative of each species within the study region (Pérez-Harguindeguy *et al.* 2013). Each of the five sampled plants of each species occurred at five different sites from among the 50 study sites, with collection sites for each species dependent on the presence of the species in abundance. For woody species, short sections of a branch with several adult leaves attached were cut from the plant. For fern species, a section of rachis with several pinnae attached were cut from the frond. For climbers, sections of stem with several leaves attached were cut and removed. No more than two plant sections with leaves or pinnae of a given species were collected on a single day, with collections spread across June to August, 2016. After removal from the plant, plant sections were wrapped in wet cloth, placed inside airtight plastic bags, and refrigerated overnight, consistent with the procedure outlined in Pérez-Harguindeguy *et al.* (2013), before measurement of leaf traits and leaf flammability the following day. The potential for this method of leaf storage to allow rehydration of leaf samples (Breshears *et al.* 2008) was minimized by ensuring quick turnaround between leaf collection and leaf measurements.

2.2.4 Leaf trait and flammability measurements

To sample leaves for measurements of the three leaf traits and three flammability attributes, leaves or phyllodes were detached at natural abscission points from the five collected plant sections of each species. In the case of ferns, pinnae were cut at the junction of the pinna and rachis. Only one compound-leafed species was included in the study, the bipinnate species *Acacia terminalis*, which was processed by detaching full lengths of a secondary rachis where it joined a primary rachis. Phyllodes, pinnae and rachises are all hereafter referred to as leaves. Measurements of LMA and FMC require total dehydration of samples. As our focus was on the flammability of fresh leaves and not dried leaves, it was not feasible to use the same leaves for trait and flammability measurements. Thus, measurements of LMA and FMC involved the use of leaves directly adjacent to the leaf that was used to measure flammability on each of the five replicate plant sections. First, five 'trait' leaves adjacent to a 'flammability' leaf were detached from each of the five plant sections and scanned to calculate LA using ImageJ (Schneider *et al.* 2012). Following this, the five leaves were weighed on a Sartorius R200D balance to give their fresh mass, and then dried in an oven for three days at 80 °C (Pérez-Harguindeguy *et al.* 2013), before reweighing to determine dry leaf mass. FMC was then calculated as ([fresh leaf mass - dry leaf mass] / dry leaf mass) * 100, with low values representing leaves with low water content. Values of FMC ranged from 70 (*Leucopogon setiger*, exposed habitat) to 330 (*Hibbertia saligna*, sheltered habitat). We calculated LMA as (leaf dry mass in g per leaf area in m^2) to give LMA in units of g m^{-2}. Values of LMA ranged from 15 g m^{-2} (*Adiantum aethiopicum*, sheltered habitat) to 640 g m^{-2} (*Lomandra multiflora*, exposed habitat). For each flammability leaf, LA was measured directly, by scanning the leaf immediately prior to the leaf being burnt and later analysing the scan in ImageJ (LA of the five adjacent leaves was used only to calculate LMA). Values of LA ranged from 13 mm^2 (*Leptospermum trinervium*, exposed habitat) to 5900 mm^2 (*Calochlaena dubia*, sheltered habitat).

Experimental burns of leaves were performed in a fan-forced muffle furnace set to 700 °C following established procedures (Gill & Moore 1996, Murray *et al.* 2013, Grootemaat *et al.* 2015). This temperature permitted clear differentiation among species in leaf flammability and represents fire front temperatures during fire in eucalypt forest (300 °C to 1100 °C, Wotton *et al.* 2012). Our study focused on leaf flammability, and while this is only one of several important components contributing to fire behaviour in fire-prone systems, it is a critical component given that leaves are frequently the first structures to ignite during bushfire (Gill & Moore 1996, Pickett *et al.* 2009) and will likely dictate much of the behaviour of fire spread through vegetation (Zylstra *et al.* 2016). Once the furnace temperature was stable at 700 °C, the furnace door was opened and the leaf sample placed in the centre of the furnace, so that there was no contact between the sample and the furnace walls. Samples were clamped by their petiole to the arm of a wheeled stand, horizontally orientated with their adaxial surface parallel to the uppermost surface of the furnace. This allowed us to place samples of all species in the furnace interior at a consistent height and orientation. Species with long leaves too large to fit in the interior of the furnace (e.g. *Lomandra* and *Lepidosperma* spp.) were cut into 15 cm long samples. Tri-foliate species (e.g. *Gompholobium grandiflorum*) were burned as three complete leaflets. Experimental burns of leaves were recorded and analysed using a digital video recorder. Ignitibility was measured as the time taken to the first appearance of glowing combustion (TTI, time to ignition in s), sustainability was measured as the time duration between the start and finish of combustion (BD, burn duration in s), and combustibility was calculated as (leaf dry mass in mg per BD in s) for each leaf to give the mean rate of combustion (mean MLR, mass loss rate in mg s^{-1}). Our measure of MLR should not be interpreted as a measure of intrinsic MLR (see Appendix 2.2). Initial leaf dry mass corresponded approximately with the total mass of leaf that burnt in the muffle furnace (Grootemaat *et al.* 2017). Values of leaf dry mass were calculated using LA values of flammability leaves and LMA values of the five adjacent trait leaves: (LA[flammability leaf] * LMA[adjacent trait leaves]).

2.2.5 Statistical analyses

Mean values for traits (LA, LMA and FMC), and flammability attributes (TTI, BD and MLR) were calculated for each species (five replicate values for each trait/attribute per species) for use in statistical analysis. We employed traditional general linear models (GLMs) matched with complementary phylogenetic generalised least squares (PGLS) models to examine interspecific patterns in leaf traits (LA, LMA, FMC) and leaf flammability attributes (TTI, BD, MLR). We used a two-way ANOVA design in GLMs and PGLS models to determine whether our response variables (the three leaf traits and the three flammability attributes in separate models) varied significantly as a function of habitat (fixed explanatory variable with two levels, exposed vs sheltered), vegetation stratum (fixed explanatory variable with two levels, understory vs overstory) or the habitat x stratum interaction.

We used a multiple regression design in GLMs and PGLS models to determine relationships between each of the three flammability attributes (response variables) and the three leaf traits (continuous explanatory variables). These models included the three categorical variables habitat (sheltered or exposed), stratum (understory or overstory) and the habitat x stratum interaction term as control variables. Thus, if any of these categorical variables were statistically significant in a model for one of the flammability attributes, then other unmeasured variables differentiating the habitats or strata would explain significant variation in that flammability attribute, in addition to any variation significantly explained by our measured leaf traits. However, if habitat, stratum or the habitat x stratum interaction did not have a significant effect on a flammability attribute, then any significant differences in leaf flammability attributes between the habitats could be principally explained by the differences in leaf traits between habitats. This final test was important to provide support for our overarching hypothesis that contrasting environmental conditions between the two habitats first and foremost drive habitat differences in leaf traits of species which are then responsible for differences in leaf flammability between habitats.

In multiple regression models, we employed a partial regression technique to determine whether each leaf trait could uniquely (i.e., independently of the other two leaf traits) explain variation in each flammability attribute. First, we calculated residuals from a series of separate multiple regression models of each flammability attribute (response variable) regressed against two of the leaf traits (the non-target predictor variables) and excluding the leaf trait (the target predictor variable) of interest. These 'non-target residuals' represented the unexplained variation in a flammability attribute after accounting for the non-target predictors. We then removed collinearity effects among target and non-target predictors by calculating model residuals of the target predictor regressed against the non-target predictors. These ‘target residuals’ represented variation in the target predictor not correlated with variation in the two non-target variables. Finally, the target residuals were regressed against the non-target residuals to give the variation in a flammability attribute uniquely explained by a target leaf trait predictor and independent of the two non-target leaf trait predictors.

A phylogenetic tree with branch lengths for the PGLS models was created for our species using the phylogeny of Zanne *et al.* (2014) generated in Phylomatic (Web & Donoghue 2005). We built separate PGLS models assuming either Brownian motion (BM) or Ornstein-Uhlenbeck (OU) processes (Appendix 2.3). The models were compared to each other using Akaike’s information criterion (AIC). The best fitting PGLS model (BM or OU) was then selected on the basis of the lowest AIC value. To account for unequal species numbers in models containing categorical terms, marginal sums of squares (type II sums of squares) were used for significance testing. In the end, across all analyses in the study, the role of phylogeny was minimal, with results from phylogenetically informed analyses differing little, if at all, from traditional modelling.

All responses and continuous predictors were log transformed prior to analysis. Analyses and plotting were performed in R 3.3.1 (R Core Team 2016), using the packages ape (Paradis *et al.* 2004), beanplot (Kampstra 2008), car (Fox & Weisberg 2011), nlme (Pinheiro *et al.* 2016), and phytools (Revell 2012).

2.3 Results

2.3.1 Leaf traits in relation to habitat and stratum

We found that LA was significantly larger in sheltered forest species compared with exposed woodland species (GLM: $F_{1,88} = 11.6$, $P = 0.0009$; PGLS (BM): $F_{1,88} = 46.7$, $P < 0.0001$) and in the overstory compared with the understory stratum in both habitats (GLM: $F_{1,88} = 15.2$, $P = 0.0002$; PGLS (BM): $F_{1,88} = 65.7$, $P < 0.0001$) (Fig. 2.2a), with no significant habitat x stratum interaction (GLM: $F_{1,88} = 2.8$, $P = 0.1$; PGLS (BM): $F_{1,88} = 3.1$, $P = 0.08$). Values of LMA in sheltered forest species were significantly lower than for exposed woodland species (GLM: $F_{1,88} = 73.0$, $P < 0.0001$; PGLS (OU): $F_{1,88} = 73.0$, $P < 0.0001$; Fig. 2.2b) and significantly lower in the understory compared with the overstory stratum in both habitats (GLM: F1,88 = 14.0, $P = 0.0003$; PGLS (OU): $F_{1,88} = 14.0$, $P = 0.0003$; Fig. 2.2b), with no significant habitat x stratum interaction (GLM: $F_{1,88} = 0.8$, $P = 0.4$; PGLS (OU): $F_{1,88} = 0.8$, $P = 0.4$). Significantly higher FMC was found in sheltered forest species compared with exposed woodland species (GLM: $F_{1,88} = 38.3$, $P < 0.0001$; PGLS (OU): $F_{1,88} = 38.3$, $P < 0.0001$; Fig. 2.2c) and in the understorey of both habitats (GLM: F1,88 = 17.5, $P < 0.0001$; PGLS (OU): F1,88 = 17.5, $P < 0.0001$; Fig. 2.2c), with no significant habitat x stratum interaction emerging for FMC (GLM: $F_{1,88} = 0.2$, $P = 0.7$; PGLS (OU): $F_{1,88} = 0.2$, $P = 0.7$).

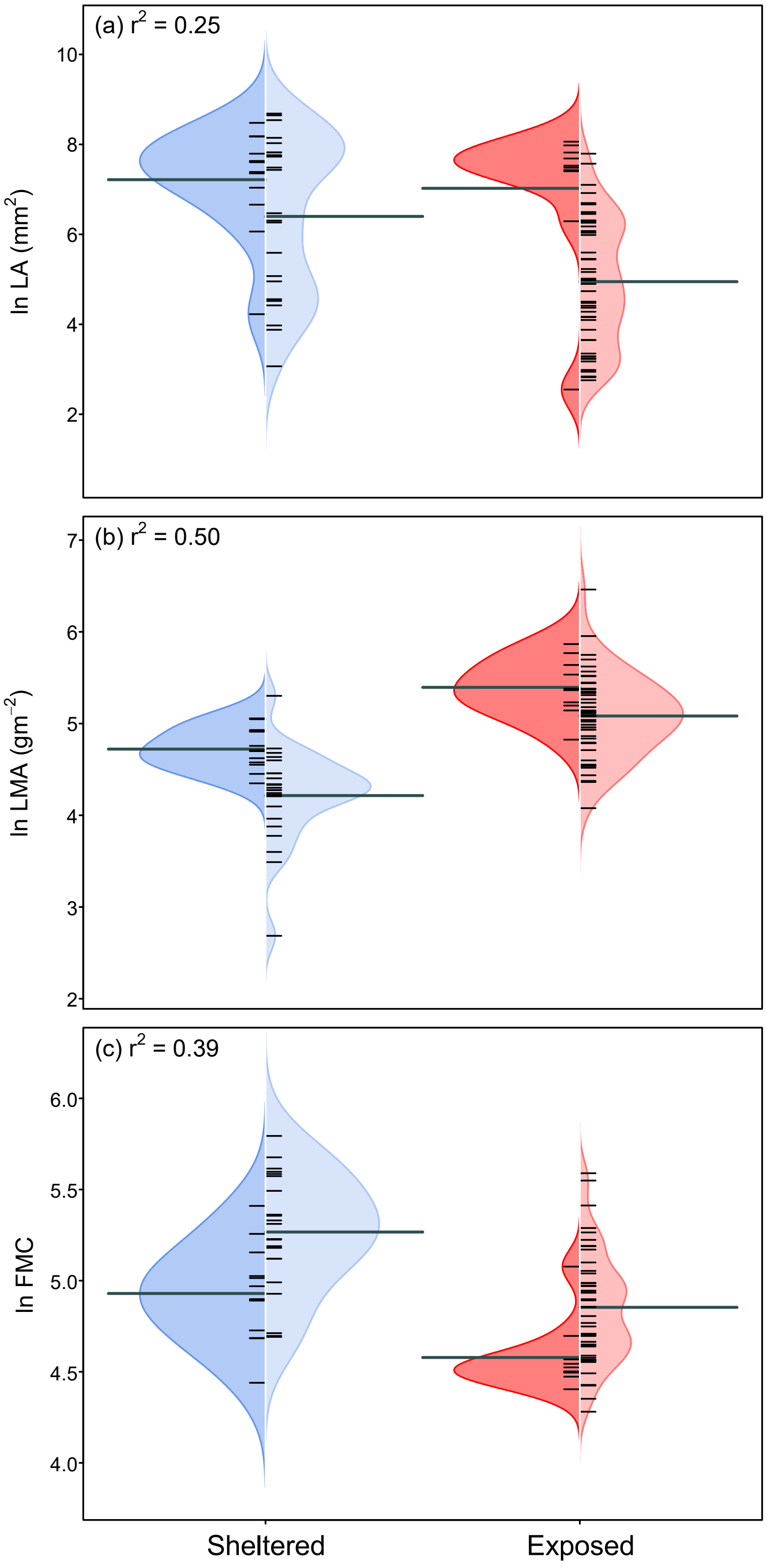
2.3.2 Leaf flammability attributes in relation to habitat and stratum

We found that TTI (ignitibility) was significantly faster in sheltered forest species compared with exposed woodland species (GLM: $F_{1,88} = 34.1$, $P < 0.0001$; PGLS (OU): $F_{1,88} = 34.2$, $P < 0.0001$; Fig. 2.3a). There was no significant difference in TTI between the overstory and understory strata in either of the habitats (GLM: $F_{1,88} = 0.2$, $P = 0.7$; PGLS (OU): $F_{1,88} = 0.1$, P =

0.7; Fig. 2.3a), and no significant habitat x stratum interaction (GLM: $F_{1,88} = 3.1$, $P = 0.08$; PGLS (OU): $F_{1,88} = 3.0$, $P = 0.09$). It emerged that BD (sustainability) did not differ significantly between sheltered and exposed habitats (GLM: $F_{1,88} = 3.2$, $P = 0.08$; PGLS (OU): $F_{1,88} = 2.9$, $P = 0.09$; Fig. 2.3b), and there was no significant habitat x stratum interaction (GLM: $F_{1,88} = 0.3$, $P = 0.6$; PGLS (OU): $F_{1,88} = 0.3$, $P = 0.6$). We found that BD was, however, significantly longer in the overstory compared with the understory in both habitats (GLM: $F_{1,88} = 19.4$, $P < 0.0001$; PGLS (OU): $F_{1,88} = 19.4$, $P < 0.0001$; Fig. 2.3b).

Values of MLR were significantly higher in sheltered forest species than in exposed woodland species (GLM: $F_{1,88} = 4.6$, $P = 0.04$; PGLS (BM): $F_{1,88} = 33.5$, $P < 0.0001$) and in the overstory compared with the understory in both habitats (GLM: $F_{1,88} = 14.8$, $P = 0.0002$; PGLS (BM): $F_{1,88} = 38.7$, $P < 0.0001$) (Fig. 2.3c), with no significant habitat x stratum interaction (GLM: $F_{1,88} = 2.1$, $P = 0.1$; PGLS (BM): $F_{1,88} = 3.0$, $P = 0.08$).

Fig. 2.2 (following page) Bean plots of leaf traits (a) LA, (b) LMA and (c) FMC by habitat and stratum. Blue beans are sheltered habitat, and red beans are exposed habitat. Darker beans represent overstorey species and lighter beans represent understorey species. The shaded areas of the beans represent the estimated density of the distribution with short black lines in the shaded areas of the beans showing the observations. Long black lines are means of observations for a given group.


(a) r^2 = 0.25
ln LA (mm^2)
10
8
6
4
2
(b) r^2 = 0.50
ln LMA (gm^{-2})
7
6
5
4
3
2
(c) r^2 = 0.39
ln FMC
6.0
5.5
5.0
4.5
4.0
Sheltered
Exposed

2.3.3 Relationships between leaf flammability attributes and leaf traits

In all models, habitat, stratum and the habitat x stratum interaction were non-significant terms (Table 2.1), which meant that the three leaf traits LA, LMA and FMC on their own were the most important features of habitats and strata driving observed differences in leaf flammability between the two habitats and the two strata. Faster TTI was significantly and uniquely related to larger LA ($t_{1,90} = -4.7$, $P < 0.0001$, partial $r^2 = 0.20$; Fig. 2.4a), lower LMA ($t_{1,90} = 18$, $P < 0.0001$, partial $r^2 = 0.78$; Fig. 4b), and lower FMC ($t_{1,90} = 9.2$, $P < 0.0001$, partial $r^2 = 0.49$; Fig. 2.4c).

Longer BD was significantly and uniquely related to larger LA ($t_{1,90} = 17.1$, $P < 0.0001$, partial $r^2 = 0.76$; Fig. 2.4d) and higher LMA ($t_{1,90} = 9.7$, $P < 0.0001$, partial $r^2 = 0.51$; Fig. 2.4e), but not to FMC ($t_{1,90} = -1.0$, $P = 0.3$, partial $r^2 = 0.01$; Fig. 2.4f). Higher MLR was significantly related to larger LA ($t_{1,90} = 43.5$, $P < 0.0001$, partial $r^2 = 0.95$; Fig. 2.4g) and higher LMA ($t_{1,90} = 7.2$, $P < 0.0001$, partial $r^2 = 0.36$; Fig. 2.4h), but not to FMC ($t_{1,90} = 0.8$, $P = 0.4$, partial $r^2 = 0.007$; Fig. 2.4i).

Fig 2.3 (following page) Bean plots of flammability attributes (a) ignitibility, (b) sustainability and (c) combustibility by habitat and stratum. Blue beans are sheltered habitat, and red beans are exposed habitat. Darker beans represent overstorey species and lighter beans represent understorey species. The shaded areas of the beans represent the estimated density of the distribution with short black lines in the shaded areas of the beans showing the observations. Long black lines are means of observations for a given group.

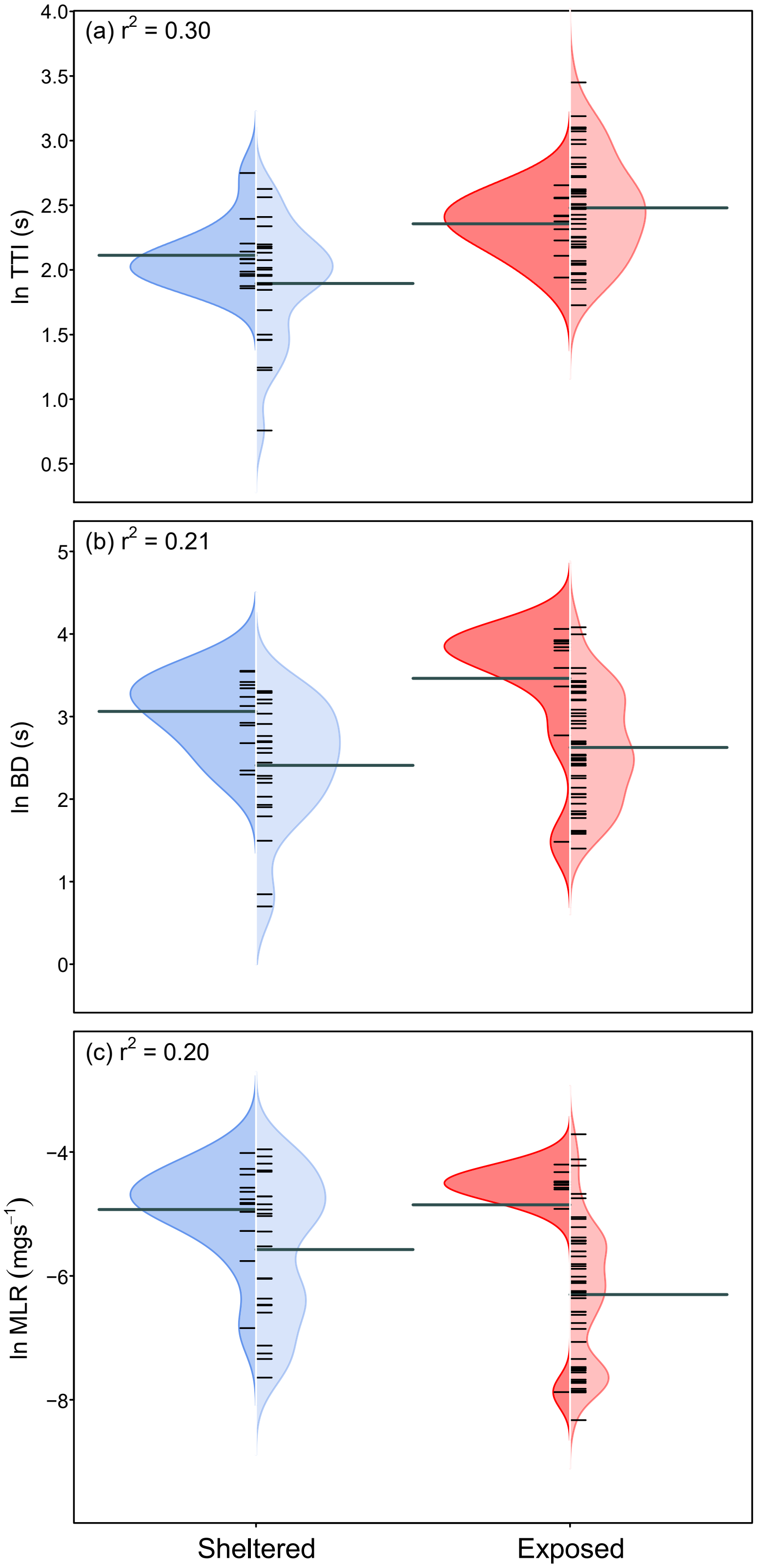

(a) r^2 = 0.30
4.0
3.5
3.0
2.5
2.0
1.5
1.0
0.5
ln TTI (s)
(b) r^2 = 0.21
5
4
3
2
1
0
ln BD (s)
(c) r^2 = 0.20
−4
−6
−8
ln MLR (mgs^{-1})
Sheltered
Exposed

Table 2.1 Results from GLMs and PGLS models (with PGLS OU models in parentheses) of flammability attributes as a function of habitat, stratum, habitat and stratum interaction, and leaf traits (leaf area, LMA, FMC).

Response	**Term**	**$F_{6,85}$**	**P**
Ignitibility	Habitat	1.3 (1.3)	0.3 (0.3)
	Stratum	0.2 (0.2)	0.6 (0.6)
	Habitat x Stratum	2.4 (2.4)	0.1 (0.1)
	LA	10.3 (12.9)	< 0.0001 (0.0006)
	LMA	188.4 (198.3)	< 0.0001 (< 0.0001)
	FMC	73.6 (75.1)	< 0.0001 (< 0.0001)
Sustainability	Habitat	1.5 (1.5)	0.2 (0.2)
	Stratum	0.01 (0.01)	0.9 (0.9)
	Habitat x Stratum	0.6 (0.6)	0.4 (0.4)
	LA	204.7 (208.8)	< 0.0001 (< 0.0001)
	LMA	48.2 (50.7)	< 0.0001 (< 0.0001)
	FMC	0.8 (0.02)	0.4 (0.4)
Combustibility	Habitat	1.8 (1.8)	0.2 (0.2)
	Stratum	1.9, (1.9)	0.2 (0.2)
	Habitat x Stratum	0.08 (0.08)	0.8 (0.8)
	LA	1211.3 (1267.3)	< 0.0001 (< 0.0001)
	LMA	42.5 (42.8)	< 0.0001 (< 0.0001)
	FMC	0.02 (0.02)	0.9 (0.9)

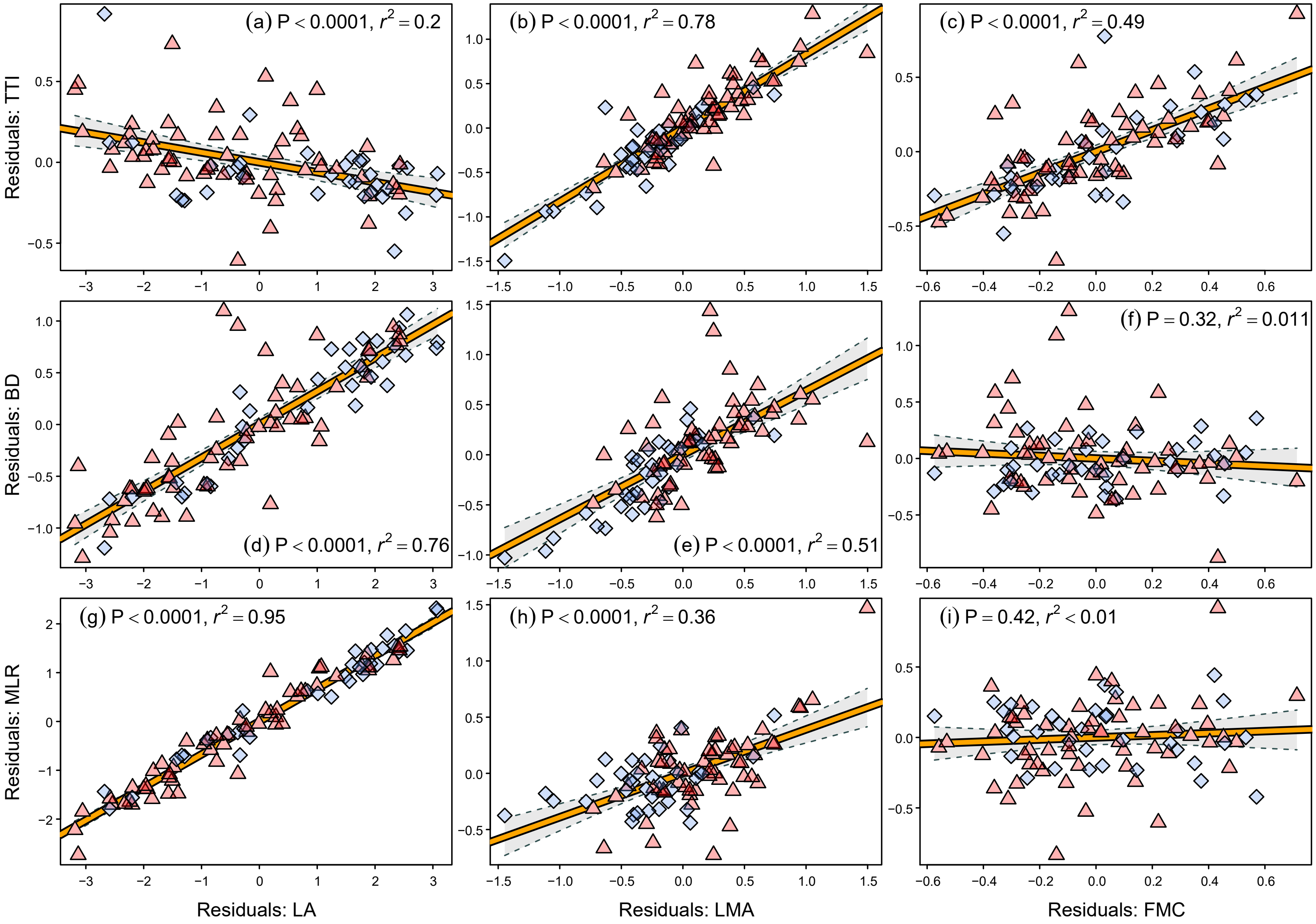

(a) P < 0.0001, $r^2 = 0.2$
(b) P < 0.0001, $r^2 = 0.78$
(c) P < 0.0001, $r^2 = 0.49$
(d) P < 0.0001, $r^2 = 0.76$
(e) P < 0.0001, $r^2 = 0.51$
(f) P = 0.32, $r^2 = 0.011$
(g) P < 0.0001, $r^2 = 0.95$
(h) P < 0.0001, $r^2 = 0.36$
(i) P = 0.42, $r^2 < 0.01$
Residuals: TTI
Residuals: BD
Residuals: MLR
Residuals: LA
Residuals: LMA
Residuals: FMC
−3
−2
−1
0
1
2
3
−1.5
−1.0
−0.5
0.0
0.5
1.0
1.5
−0.6
−0.4
−0.2
0.0
0.2
0.4
0.6

Fig. 2.4 (previous page) Scatter plots of partial regressions of flammability attributes (y-axes) against leaf traits (x-axes). Blue rhombuses represent sheltered species, red triangles represent exposed species. Line of best fit from GLM model shown as an orange line (identical to best fitting PGLS model). The grey shaded area represents the 95% confidence interval of the mean.

2.4 Discussion

Our study has provided evidence supporting the hypothesis that leaf flammability attributes vary across the landscape in a way that is tightly coordinated with the primary strategic response of leaf traits to an environmental gradient. The hypothesis is centred on the notion that variation in the leaf traits LA, LMA and FMC first and foremost represents adaptations to the environmental gradient between the two habitats. These trait responses then secondarily drive variation in leaf flammability, rather than the leaf traits themselves having evolved to increase (or decrease) flammability at the leaf level. Thus, the differences we observed in leaf flammability between the two habitats are driven principally by leaf trait responses to the environmental conditions in each of the habitats. While our analyses are correlative, we believe that this description of the nature of trait and flammability patterns is the most parsimonious explanation. We first showed that all three leaf traits LA, LMA and FMC differed significantly and as predicted between sheltered forest species and exposed woodland species. Sheltered forest species had leaves with larger LA, higher LMA and higher FMC than exposed woodland species. We then showed that leaf ignitibility (time to ignition) and combustibility (mean mass loss rate) were significantly higher in sheltered forest species than in exposed woodland species, which matches two of our predictions that high ignitibility is related to large LA and low LMA found in gully species, and that overall these two leaf traits counteract the buffering effect of high FMC in gully species; and that high combustibility is related to large LA and high LMA in gully species. Our analyses of interspecific relationships between the leaf traits and the flammability attributes quantitatively confirmed the predictions. Importantly, in all of these models relating the leaf traits to the leaf flammability attributes, the habitat and stratum terms did not explain significant variation in leaf flammability. Thus, significant differences in leaf flammability attributes between the habitats were principally explained by the differences in leaf traits between habitats. Furthermore, all three leaf traits explained unique variation in the three leaf flammability attributes to varying degrees. Notably, LMA emerged as a consistently important trait driving variation in leaf flammability, even playing a more important unique role than FMC in lengthening TTI.

Ignitibility was best predicted (i.e. largest partial r^2) by LMA, followed by FMC, with higher values of both being associated with lower ignitibility, and then by LA, with higher LA being related to higher ignitibility. Interestingly, the effect of FMC on lengthening TTI was weaker than that of LMA, so that while sheltered habitat species generally exhibit higher FMC, their much lower LMA and larger LA resulted in their overall higher ignitibility than exposed woodland species. These findings are consistent with those of some previous studies (Gill & Moore 1996, Grootemaat *et al.* 2015, Mason *et al.* 2016). The differences in all leaf traits between overstorey and understorey did not result in significant canopy stratum differences in TTI. Relative to overstorey species, understorey species have smaller leaves and lower LMA, both related to quicker TTI, however FMC was also higher which contributed to slowing leaf ignition. Sustainability, which did not differ between habitats, was best predicted by LA and then LMA, with larger leaved and higher LMA species burning for a longer period, with no significant effect of FMC on sustainability. The lack of a significant difference in sustainability between habitats can be explained by the combination of larger LA and lower LMA in sheltered forest species and the combination of smaller LA and higher LMA leaves in exposed woodland species both providing within combination trade-offs precluding either faster or longer burning times for leaves. While large area leaves will burn for longer than small area leaves, the lower LMA of large area leaves shortens BD times in sheltered forest species. And while leaves with higher LMA will burn for longer than leaves with lower LMA, the smaller area of high LMA leaves shortens BD times in exposed woodland species. This also explains the significantly longer BD of overstorey species in both habitats, as overstorey species tend to have larger, higher LMA leaves, relative to understorey species. Combustibility was best predicted by LA and then LMA, with FMC having no significant effect. Higher LA and LMA were both associated with greater combustibility, but unlike sustainability, these two traits worked with each other in this case to increase flammability (i.e. mass loss rate) in sheltered habitat species. Overstorey species showed significantly higher combustibility compared to understorey species, similarly to the effect on BD, this is likely due to their larger, higher LMA leaves. Again, FMC had no significant effect on combustibility. With respect to FMC, we suggest that the lack of significant effect of FMC on both sustainability and combustibility is likely due to leaf water being largely evaporated by the time the leaf has ignited.

Mutch (1970) hypothesised that fire-prone plant communities have evolved to promote fire, with subsequent research and argument focused on the possibility that plant flammability is an evolved trait (Bond & Midgley 1995, Gagnon *et al.* 2010). Given that fire-prone plant communities are often found in hot, dry regions, maximising flammability would require evolution towards traits unlike those that are actually observed, and increasing flammability in one dimension may mean another dimension is decreased (e.g. increased ignitibility with large area, low LMA leaves, and decreased combustibility). This does leave open the possibility that evolutionary ‘fire strategies’ exist, with only one or few dimensions of flammability being selected for, although how such strategies would be defined given the large number of possible measures of flammability is unclear. With our findings, evolution towards increased flammability at leaf level would seem unlikely, as it would require modification of important, interrelated leaf traits that allow plant species to persist in their environment. It is more parsimonious to interpret leaf flammability as arising from what is ultimately physical and physiological adaptation to the abiotic environment.

With predicted increases in the number of ‘fire weather’ (hot, dry and windy) days each year likely to be experienced in the region as a result of climate change (Pitman *et al.* 2007, Clarke *et al.* 2011), sheltered forest habitat in south-eastern Australia in particular will experience more frequent and intense wildfires (Clarke 2015). Currently, sheltered forest tends to burn less frequently and less intensely than exposed woodland (Penman *et al.* 2007, Bradstock *et al.* 2010, Leonard *et al.* 2014), due largely to such forests being sheltered from high winds by topography and being overall ‘wetter’ environments with less direct insolation. However, the projected changes to climate will allow wildfires to overcome the once protective nature provided by topography to sheltered forest vegetation. Worryingly, our results indicate that a critical fuel component essential to wildfires – plant leaves – are significantly more flammable in sheltered forest species than in exposed woodland species. This would have the potential to exacerbate the effects of changing weather conditions and would place sheltered forest habitat, their plants and their animals, at even higher risk of catastrophic wildfire. This has serious implications for native biodiversity, as during intense wildfires, sheltered forests can be the only remaining vegetation in an otherwise completely burnt landscape, providing critical refuge habitat and food resources for animal species during fire after it has passed (Collins *et al.* 2012; Robinson *et al.* 2014; Chia *et al.* 2015; Swan *et al.* 2016). In burnt areas, abundances of small mammal species (Banks *et al.* 2011, Roberts *et al.* 2015) and bird species are reduced (Robinson *et al.* 2014), with sheltered forests providing refugia until surrounding burnt areas have recovered.

Our study has focussed on intrinsic leaf flammability, which is just one important part of a larger story that must be considered in order to reach a comprehensive understanding of how plants contribute to wildfire behaviour (Gill & Moore 1996, Grootemaat *et al.* 2015, Zylstra *et al.* 2016). Future work in this area needs to explore how plant leaf flammability scales up to larger plant sections (e.g. branches, Wyse *et al.* 2016) and to whole plants, which will be facilitated through understanding how leaves are arranged spatially and how leafing intensity varies among species. Such work will help us to gain a better understanding of what traits might influence plant flammability at these larger scales.

Chapter 3

Relationships among leaf flammability attributes and identifying low-leaf-flammability species at the wildland-urban interface

Published in the International Journal of Wildland Fire: Krix DW, Phillips ML, Murray BR. (2019) Relationships among leaf flammability attributes and identifying low-leaf-flammability species at the wildland–urban interface. *International Journal of Wildland Fire* **28**, 295-307.

3.1 Introduction

Recent years have seen extreme wildfires burn across landscapes with substantial impacts on ecosystems, human lives and infrastructure (Moritz *et al*. 2014; Abatzoglou & Williams 2016; Kramer *et al*. 2018). The spread of wildfires is dictated not only by the availability of plants as fuel for fire, but by variation in the flammable properties of plant fuels (Schwilk 2015; Fares *et al*. 2017). Although differences among species in the flammable properties of plant leaves in the litter bed have been widely examined (de Magalhaes & Schwilk 2012; Ganteaume *et al*. 2013a; Zhao *et al*. 2016; Ganteaume 2018; Kreye *et al*. 2018), fewer studies have explored interspecific variation in the flammable properties of live leaves suspended aboveground in foliage (Engber & Varner 2012; Murray *et al*. 2013; Grootemaat *et al*. 2015). Yet, understanding variation in the flammability of live foliage leaves is critical given that they contribute large amounts of fuel for wildfires (McCaw *et al*. 1996), are often the first live plant structures to ignite (Pickett *et al*. 2009), and play a central role in fire behaviour at the landscape scale (Engstrom *et al*. 2004; Zylstra *et al*. 2016; Krix & Murray 2018). Furthermore, variation among species in leaf flammability provides contrasting opportunities for wildfires not only to spread vertically (‘laddering’ upwards) to the upper canopy, but to expand horizontally within a plant stratum.

Leaf flammability is a multidimensional plant functional trait (Pérez-Harguindeguy *et al*., 2013) that can be characterized along three main dimensions including ignitibility (the time taken for a leaf to start burning), sustainability (the duration of leaf burning), and combustibility (how well a leaf burns, linked to flame spread rate) (Anderson 1970; Gill & Zylstra 2005; Pausas *et al*. 2017). Determining how these flammability dimensions are related to each other across species not only provides information about the properties of leaves as fuels in the wildland-urban interface (WUI), it can also offer a particularly effective way to identify low-leaf-flammability species, whose leaves, comparatively, will take a long time to ignite (slow ignitibility), burn for a short duration (short sustainability), and will not enter flaming combustion (low combustibility). For leaves in particular, however, apart from a small number of studies (Engber & Varner 2012; Grootemaat *et al.* 2015), little is known about relationships and patterns of covariation among these flammability dimensions. Notably, it is still unclear as to whether these dimensions covary in a way that yields low-leaf-flammability species with leaves with the combination of slow ignitibility, short sustainability, and low combustibility. Furthermore, it is not known whether attributes used to quantify ignitibility including time to smoking (TTS), incandescence (TTI) and flaming (TTF) covary positively with each other, or whether attributes used to quantify sustainability including smoking duration (SD), incandescence duration (ID) and flaming duration (FD) also covary positively with each other. Clarification of these interspecific patterns in leaf flammability will help to guide the best way to identify low-leaf-flammability species from among a large group of co-occurring plant species.

Identifying low-leaf-flammability species has important implications for the selection of plant species for use in green firebreaks at the WUI. Green firebreaks, when considered in conjunction with other issues pertinent to establishing low-flammability landscapes in the WUI in fire-prone areas (Penman *et al*. 2014; Syphard *et al*. 2014; Smith *et al*. 2016), offer protection for people, properties and infrastructure under low intensity wildfire conditions (White and Zipperer 2010; Ganteaume *et al*. 2013b; Curran *et al*. 2018; Murray *et al*. 2018). There are inherent difficulties, however, in determining the flammability attributes of very large plants, such as trees and shrubs for instance, given that their size often precludes replicated whole-of-plant burning experiments. One way to overcome such difficulties is first to quantify interspecific patterns in leaf flammability and identify the species which possess leaves of lower overall flammability. Such information provides a crucial reference point that may then be combined with other plant architectural features which include, for example, dead branch retention (which can increase plant flammability; Schwilk 2003) and canopy branching patterns (which may in some cases counteract leaf flammability properties; Bowman *et al*. 2014), to further elucidate the largely unknown nature of scaling relationships from leaf to whole-of-plant flammability (Schwilk 2015).

In the present study, we examine relationships among leaf flammability attributes across 60 native plant species found in the WUI in south-eastern Australia to identify species which possess leaves of lower overall flammability. We ask (1) are the ignitibility attributes TTS, TTI and TTF correlated positively with each other; (2) are the sustainability attributes SD, ID and FD correlated positively with each other; and (3) do ignitibility, sustainability and combustibility covary such that there are low-leaf-flammability species with leaves that take a long time to ignite, burn for a short duration, and that do not enter flaming combustion? In answering these questions, we quantitatively identify species with the lowest, as well as those with the highest, overall leaf flammability and employ multiple regression analyses to demonstrate how much variation in leaf flammability can be explained by three functionally important leaf traits including leaf mass per area (LMA), leaf area (LA) and leaf water content (LWC), traits identified in previous studies as important drivers of flammability (Gill & Moore 1996; Murray *et al*. 2013, Grootemaat *et al*. 2015, Krix & Murray 2018).

3.2 Methods

3.2.1 Study species and leaf collection

The 60 study species (Appendix 3.1) are widespread and abundant in woodlands and forests of the Blue Mountains National Park (–33°39031″ N, 150°32045″ E), a World Heritage Listed Area in south-eastern Australia that is prone to wildfires (Hammill & Tasker 2010). The region experiences a mild climate (mean temperature 17.2°C), with warm summers (mean temperature 21.9°C) and cool winters (mean temperature 11.9°C), and a mean annual rainfall of 1086 mm (Australian Bureau of Meteorology 2014). The study species vary widely with respect to growth form (trees, shrubs, herbs, climbers) and taxonomic breadth (18 plant families and 44 plant genera) and are commonly found in native bushland on, and backing onto, many residential properties in the region in the WUI.

We collected stem sections from climbers, and branch sections from trees, shrubs and herbs. Each plant section held more than six fully expanded, non-senescent leaves. Plant sections were collected from five individuals of each species. Each individual of a species was sampled at a different location from the other individuals of the species. Locations were selected from among 50 previously identified locations in the region (described in Krix & Murray 2018), with collection sites for each species dependent on the presence of the species in abundance. No more than two leaf samples of a given species were collected on a single day, with collections spread across June to August 2016. To minimise leaf dehydration, plant sections were wrapped in moistened cloth and sealed in airtight plastic bags after collection for transport to the laboratory. These samples were refrigerated overnight, consistent with the procedure outlined in Pérez-Harguindeguy *et al*. (2013), before measurement of leaf flammability and leaf traits the following day.

3.2.2 Leaf flammability attributes

We measured three attributes to quantify leaf ignitibility (TTS, TTI and TTF) and three attributes to quantify leaf sustainability (SD, ID and FD). These six leaf flammability attributes fully characterize the temporal pathway of plant leaf combustion (Fig. 3.1). The combustion pathway begins with the first emission of smoke (TTS) indicating the time taken for pyrolysis (the thermal decomposition of plant leaves at elevated temperatures) to begin (Friedman 1998). The length of time over which smoke is emitted is the duration of this lower-temperature form of combustion (SD). How rapidly leaves reach incandescent combustion (TTI) measures the time taken for the emission of visible light from the thermal decomposition of plant leaves at elevated temperatures to begin (Friedman 1998). The length of time over which incandescent combustion continues (ID) is important for wildfire propagation as heat is given off which can contribute to a larger fire. The first sign of flame (TTF) measures how quickly leaves reach flaming combustion (luminous oxidation of gases evolved from rapid thermal decomposition of plant leaves at elevated temperatures), with flame duration (FD) measuring how long a leaf continues to flame. Measurements of flaming combustion are important to fire spread, with flaming combustion comparatively more likely to spread fire to surrounding leaves and neighbouring plants. Our focus on time-based measures of leaf flammability is because of their comparative ease of measurement which can be replicated by others who may want to identify low-leaf-flammability species based on the approach presented in our study.

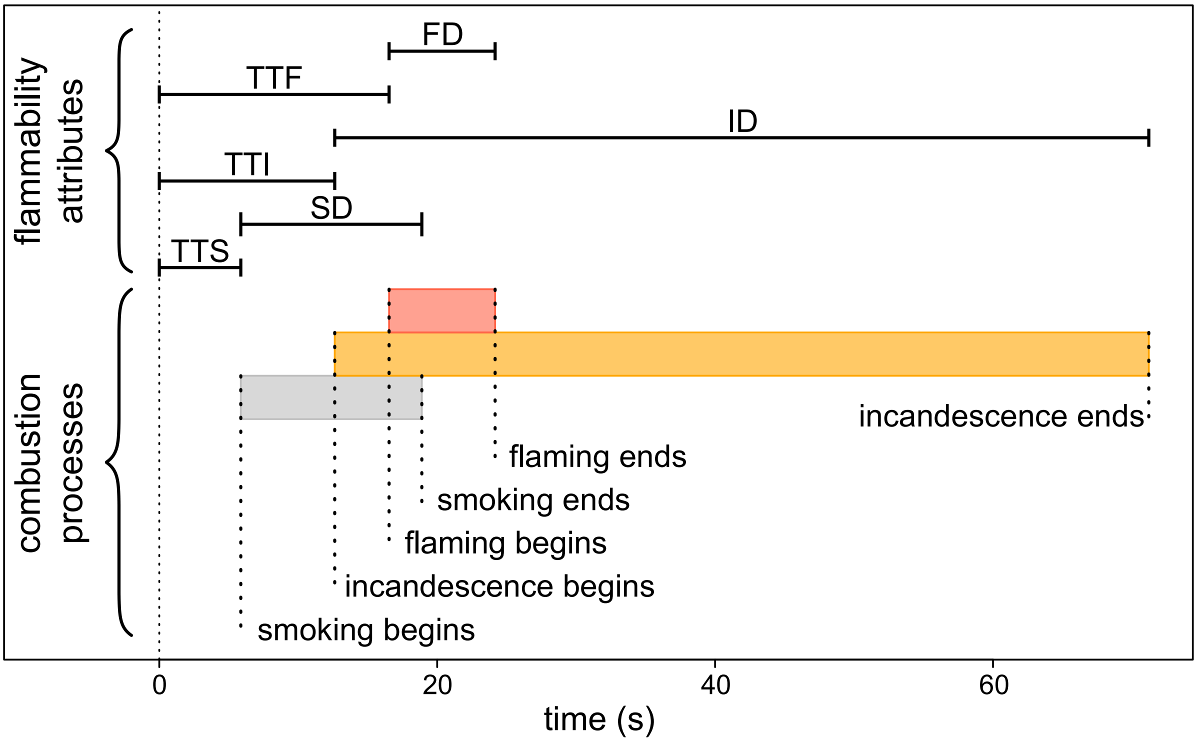


Fig. 3.1 Temporal pathway of typical plant leaf combustion, here showing values from a single sample of *Corymbia gummifera*. Length of time for each flammability attribute is represented in the top of the figure (TTS, time to smoking; TTI, time to incandescence; TTF, time to flaming; SD, smoking duration; ID, incandescence duration; FD, flaming duration). The grey bar represents smoking, the orange bar represents incandescence, and the red bar represents flaming. Vertical dotted lines delineate physical combustion processes.

3.2.3 Measurements of leaf ignitibility, sustainability and combustibility

We used a Nabertherm LT 15/11HA muffle furnace to measure leaf flammability attributes following procedures established in several previous studies (Gill & Moore 1996; Murray *et al*. 2013; Grootemaat *et al*. 2015; Krix & Murray 2018). The furnace was situated in a wellventilated laboratory room without strong drafts, with its door open during measurements to ensure an abundant oxygen supply and to allow filming of the flammability processes within (Grootemaat *et al*. 2015). Individual leaves were exposed to a temperature of 700°C radiating from two sides by ceramic heating plates. Single leaves were detached from field-collected plant sections and clamped by their petiole to a clip on a wheeled stand, before being positioned in the centre (by depth, height and width) of the furnace interior (furnace chamber size: 230 x 330 x 170 mm). Leaves were placed consistently in the centre of the furnace, without contacting the furnace walls, to ensure that convective heat flow from the heated air and radiant heat from the furnace heating plates would ignite them. Leaves were oriented so their adaxial surface was parallel to the top surface of the furnace. Five replicate leaves, each from a separate stem or branch section, were experimentally burned for each species.

Leaves were filmed while burning with a digital video recorder, and this footage later analysed to provide timings of ignitibility and sustainability events to 0.1 s resolution (Krix & Murray 2018). The times elapsed from the leaf sample entering the furnace to the first appearance of smoke, incandescence, and flaming, were recorded, as well as the elapsed times when smoke ceased to be seen, and incandescence and flaming ended. Mean values of each flammability attribute were calculated for each species using the five replicate leaf burns. We recorded whether leaves produced flames or not as a binary measure of leaf combustibility for each species. The leaves of all species burned completely and consistently to minute amounts of a fine white ash, without leaving remnant portions of whole, unburnt plant material.

3.2.4 Measurement of leaf traits

Five leaves were detached at their natural abscission point from each stem or branch section and weighed as a group on a Sartorius R200D balance to give fresh leaf mass (FLM). The leaves were then scanned on a flatbed scanner and ImageJ was used to measure their combined LA (Schneider *et al*. 2012). The leaves were dried for 48 h at 80°C and weighed again to give dry leaf mass (DLM). To calculate LWC, the difference between FLM and DLM was divided by FLM and multiplied by 100 to give LWC as a percentage. To calculate LMA, DLM was divided by LA to give LMA in units of g m^{-2}.

Mean LMA and LWC values of individual leaves were calculated within each group of five leaves by dividing group total values by five. These individual leaf mean values were then used to calculate species' mean values of LMA and LWC across the five replicate branches or stems for each species. Prior to burning, the LA of the leaf to be burned was measured using the flatbed scanner and ImageJ. Species' mean values of LA were calculated using the five replicate burn leaves.

3.2.5 Relationships among flammability attributes

We used standard Pearson correlations to quantify interspecific relationships between all pairs of ignitibility attributes (TTS, TTI, TTF) and between all pairs of sustainability attributes (SD, ID, FD), as well as to quantify all pairwise relationships between ignitibility and sustainability attributes and indices. Ignitibility and sustainability attributes and indices were related to combustibility (whether a species' leaves flamed or not) using point-biserial correlations. We created two separate indices to represent on the one hand the three ignitibility attributes (TTS, TTI, TTF) and the three sustainability attributes (SD, ID, FD) on the other (procedure adapted from Perez-Harguindeguy *et al*. 2013). Each species value of TTS, TTI, TTF, SD, ID and FD was centred (by subtracting the mean value of the attribute across all species) and scaled (by dividing the centred value by the standard deviation of the attribute) to place the attributes on a comparable range of values (Appendix 3.2). This gave each attribute a mean of zero and a range between approximately -3 and 3. Each species' value of the ignitibility index was calculated by taking the mean across of the three centred and scaled ignitibility attributes (TTS, TTI, TTF), while each species' value of the sustainability index was calculated by taking the mean across the three centred and scaled sustainability attributes (SD, ID, FD).

3.2.6 Calculation of an Overall Leaf Flammability Index (OLFI)

To determine the five species with leaves of the lowest flammability and the five species with leaves of the highest flammability, we ranked all species by an Overall Leaf Flammability Index (OLFI). Each species' value of the ignitibility and sustainability indices was centred (by subtracting the mean value of the ignitibility index across all species) and scaled (by dividing the centred value by the standard deviation of the ignitibility index) to ensure the indices were on comparable scales. To arrive at the final OLFI values, the centred and scaled values were then summed for each species, and the summed values centred and scaled to give values on a scale with a mean equal to zero and a standard deviation of one (Appendix 3.2). For this calculation and for ease of interpretation, the sign of ignitibility values was reversed so that higher values of both ignitibility and sustainability represented higher flammability. Thus, lower values of the OLFI indicated that a species was at the low flammability end of the spectrum of values of the index. The five species with the lowest values of the OLFI that had leaves which did not flame (i.e., low-combustibility leaves), and the five species with the highest values of the OLFI that had leaves which did flame (i.e., high-combustibility leaves), were respectively identified as the species with the lowest and highest leaf flammability. In addition to the OLFI rankings (Appendix 3.2), the numerical rankings for each species for the six leaf flammability attributes (TTS, TTI, TTF, SD, ID, FD), as well as the ignitibility and sustainability indices, are provided in Appendix 3.3.

3.2.7 Relationships between leaf flammability and leaf traits

Multiple linear regression analyses were used to relate the three leaf traits (continuous explanatory variables) to the ignitibility index, sustainability index and OLFI (each a continuous response variable) in separate models. Leaf traits (continuous explanatory variables) were related to combustibility (binomial response variable, flaming vs no flaming) using a generalised linear model with a binomial error structure.

Prior to correlation and regression analyses, attributes were transformed as follows to meet the assumptions of parametric statistical analyses: SD, ID, FD, LMA, LA and LDM were log transformed; TTS and TTI were square root transformed; LWC was logit transformed; and no transformation was required for TTF. All indices were calculated using untransformed flammability attributes with none of the indices requiring transformation. All analyses and plotting were conducted in R (R Core Team 2017), using the packages Hmisc (Harrell 2014), MASS (Venables & Ripley 2002), pBrackets (Schulz 2014) and rsq (Zhang 2018)

3.3 Results

3.3.1 Relationships between ignitibility attributes

There were significant positive correlations between all pairs of ignitibility attributes (Fig. 3.2a; the distribution of species’ values are presented as boxplots, Fig. 3.2b). Species with leaves that were slower to smoke (relatively slower TTS across the range of observed species' values) were also those that were slower to incandesce (slower TTI; $r = 0.93$, $P < 0.0001$) and slower to flame (slower TTF; $r = 0.81$, $P < 0.0001$); and species with leaves that were slower to incandesce (slower TTI) were those that were slower to flame (slower TTF; $r = 0.86$, $P < 0.0001$).

3.3.2 Relationships between sustainability attributes

There were significant positive correlations between two of the three pairs of sustainability attributes (Fig. 3.2a; the distribution of species' values are presented as boxplots, Fig. 3.2b). Species with leaves that spent shorter periods of time smoking (relatively shorter SD across the range of observed species' values) were those that spent shorter periods of time in incandescence (shorter ID; $r = 0.77$, $P < 0.0001$) and flaming (shorter FD; $r = 0.78$, $P < 0.0001$). There was no significant relationship between SD and FD ($r = 0.27$, $P = 0.20$).

3.3.3 Relationships between ignitibility, sustainability and combustibility attributes

Significant positive correlations emerged in five of the nine relationships between ignitibility and sustainability attributes (Fig. 3.2a). Across species, slow-ignitibility leaves with slower TTS and slower TTI were long-sustainability leaves with longer SD (TTS vs SD: $r = 0.58$, $P < 0.0001$; TTI vs SD: $r = 0.58$, $P < 0.0001$) and longer ID (TTS vs ID: $r = 0.37$, $P < 0.01$; TTI vs ID: $r = 0.28$, $P < 0.03$). Slow-ignitibility leaves with slower TTF were long-sustainability leaves with longer SD ($r = 0.61$, $P < 0.001$). Species with low-combustibility leaves were those with shorter SD ($r = 0.54$, $P < 0.001$) and shorter ID ($r = 0.89$, $P < 0.0001$) (Fig. 3.3). There was no significant correlation between ID and TTF ($r = 0.22$, $P = 0.30$), and FD was not significantly correlated with any of the three ignitibility attributes (TTS $r = -0.06$, $P < 0.80$; TTI $r = -0.15$, P

< 0.50; TTF *r* = -0.11, *P* < 0.60). Leaf combustibility was not significantly related to either TTS (*r* = 0.17, *P* = 0.30) or TTI (*r* = 0.05, *P* = 0.70).

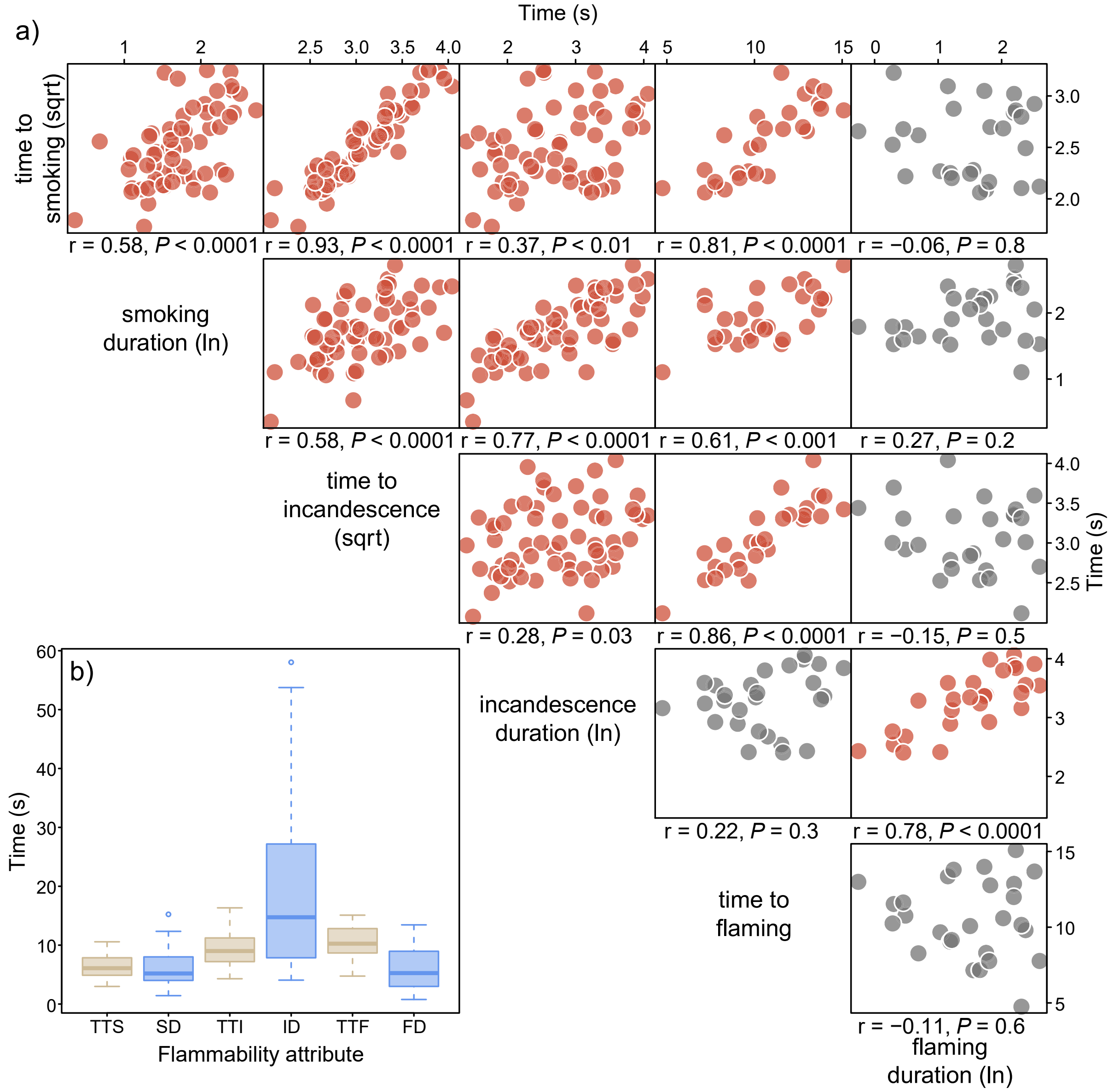


Fig. 3.2 (a) Correlations between pairs of flammability attributes. Both x and y axes are time measurements (s). Red circles indicate significant relationships. (b) Boxplots of the distribution of species' values for each of the flammability attributes (TTS, time to smoking; TTI, time to incandescence; TTF, time to flaming; SD, smoking duration; ID, incandescence duration; FD, flaming duration).

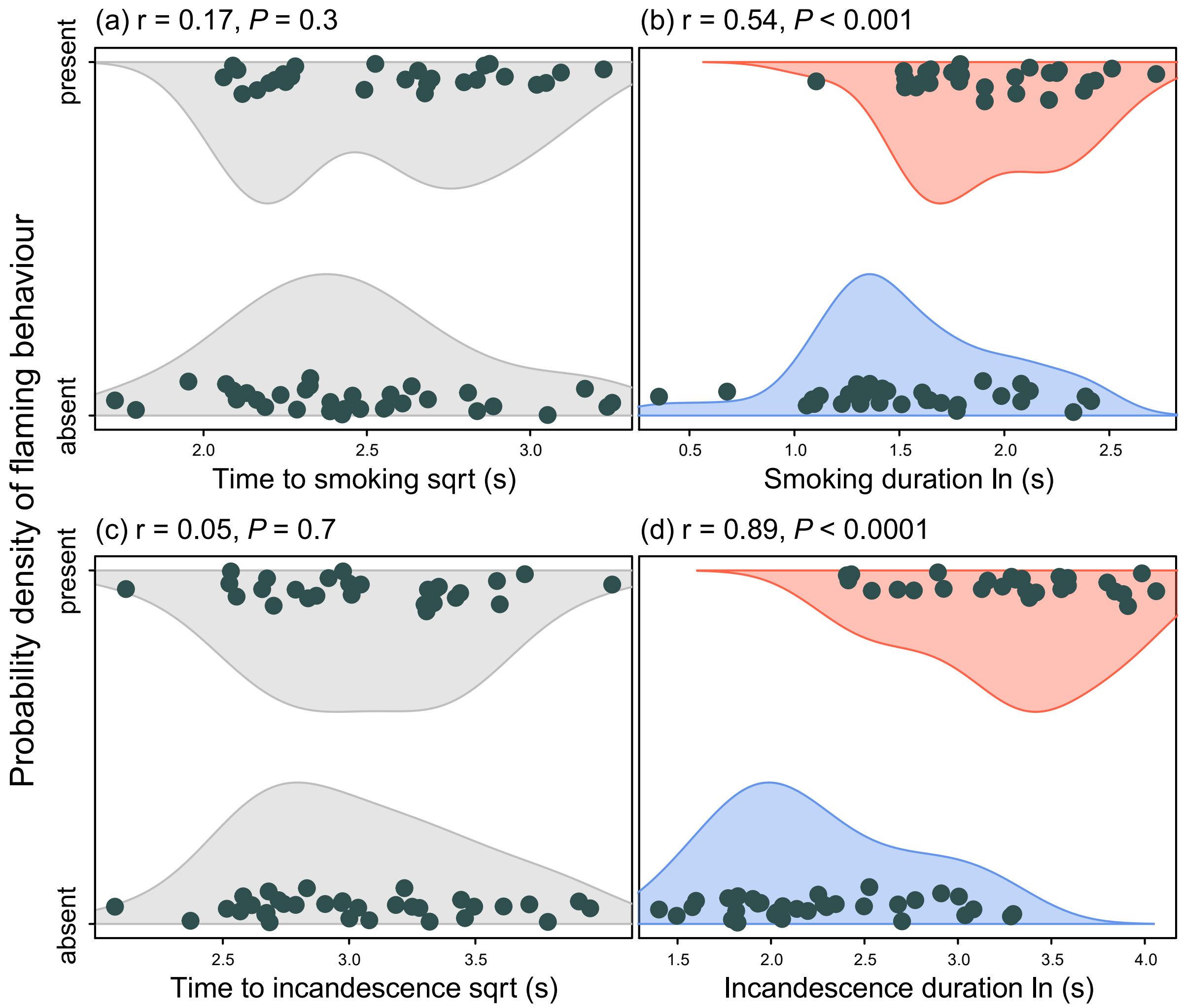


Fig. 3.3 Relationships between combustibility (flaming or not) and (a) time to smoking, (b) smoking duration, (c) time to incandescence and (d) incandescence duration. Species' values are within shaded probability densities, and have been jittered on the y-axis to increase visibility. Where there is a significant relationship, density shapes are coloured blue for the absence of flaming, and red for the presence of flaming.

3.3.4 Identification of low-leaf-flammability species

There was a significant positive correlation between the ignitibility and sustainability indices ($r = 0.44$, $P < 0.0005$) such that species with slow-ignitibility leaves were those with long-sustainability leaves (Fig. 3.4). Species with long-sustainability leaves were significantly more likely to flame ($r = 0.66$, $P < 0.0001$), while there was no significant relationship between the ignitibility index and flaming ($r = -0.09$, $P = 0.6$). Overall, the five low-leaf-flammability species (low OLFI values, no flaming combustion) that we identified were *Dampiera stricta*, *Persoonia linearis*, *Philotheca hispidula*, *Pimelea linifolia* and *Tetratheca rupicola.* With the exception of *P. linearis* (a shrub species), all of these species were herbs with relatively small leaves. The five high-leaf-flammability species (high OLFI values, flaming combustion) that we identified were *Astrotricha latifolia*, *Callicoma serratifolia*, *Eucalyptus punctata*, *Notelaea venosa* and *Pomaderris elliptica*, all tree or shrub species with relatively large leaves (Appendix 3.2).

3.3.5 Relationships between leaf functional traits and low leaf flammability

Multiple regression analyses (Table 3.1) showed that all three leaf traits explained significant interspecific variation in the ignitibility index (full model $r^2 = 0.89$), the sustainability index (full model $r^2 = 0.82$), and the OLFI (full model $r^2 = 0.74$). Small LA (partial $r^2 = 0.48$) was the only leaf trait that significantly explained the likelihood of a leaf not entering flaming combustion in the full model for combustibility ($r^2 = 0.51$). High LMA (partial $r^2 = 0.89$) and high LWC (partial $r^2 = 0.82$) played stronger roles than small LA (partial $r^2 = 0.30$) in explaining slow ignitibility. Small LA (partial $r^2 = 0.70$) was the most significant contributor to short sustainability; here, low LWC was only marginally related significantly to short sustainability (partial $r^2 = 0.07$; $P = 0.047$), reinforcing the importance of small LA, followed by low LMA (partial $r^2 = 0.54$), as drivers of short sustainability. Small LA (partial $r^2 = 0.72$), high LWC (partial $r^2 = 0.55$), and high LMA (partial $r^2 = 0.46$) were all significant contributors to low OLFI values. Here, high LMA was related to low values of the OLFI because of the stronger relationship between LMA and the ignitibility index, compared to the relationship between LMA and the sustainability index (Table 1).

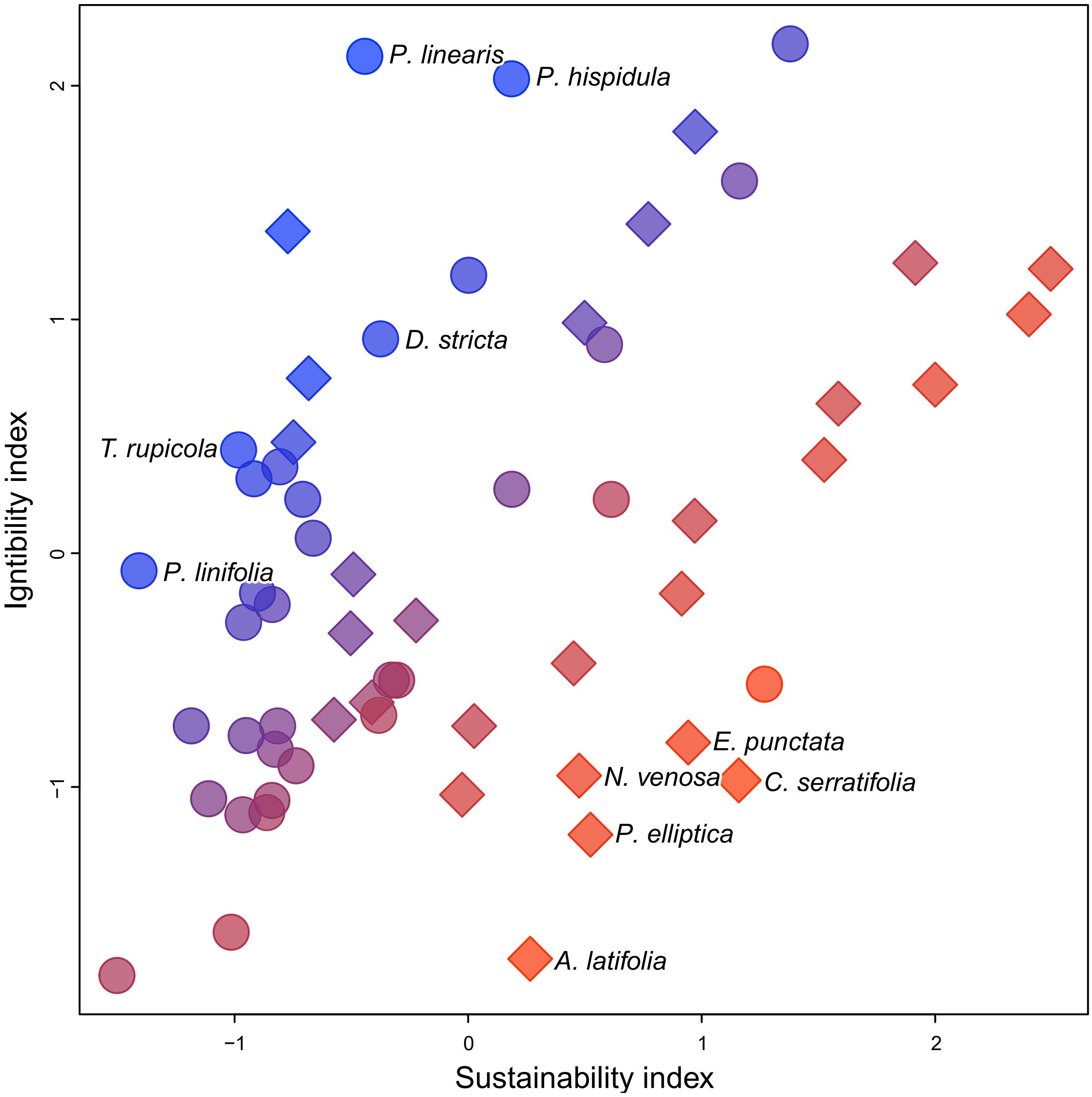


Fig. 3.4 Relationship between the ignitibility index and sustainability index for the 60 study species. High y-axis values are represented by slow-ignitibility species and high x-axis values are represented by long-sustainability species. Low-combustibility species are represented by circles and high-combustibility species are represented by rhombuses. Labelled are the

five low-leaf-flammability species (blue points indicating low OLFI scores) and the five high-leaf-flammability species (red points indicating high OLFI scores).

Table 3.1. Multiple regression analyses relating leaf flammability indices, the Overall Leaf Flammability Index (OLFI) and leaf combustibility to the leaf traits as predictors. Abbreviations: LMA, leaf mass per area; LA, leaf area; LWC, leaf water content

Response	**Model r^2**	**Predictor**	**Partial r^2**	**Coefficient (SE)**	***t***	***P***
Ignitibility	0.89	LMA	0.89	2.75 (0.13)	21.72	< 0.0001
		LA	0.30	-0.12 (0.02)	-4.92	< 0.0001
		LWC	0.82	2.42 (0.15)	15.91	< 0.0001
Sustainability	0.82	LMA	0.54	1.15 (0.14)	8.19	< 0.0001
		LA	0.70	0.31 (0.03)	11.50	< 0.0001
		LWC	0.07	0.34 (0.17)	2.03	0.047
OLFI	0.74	LMA	0.46	-1.37 (0.20)	-6.93	< 0.0001
		LA	0.72	0.46 (0.04)	12.21	< 0.0001
		LWC	0.55	-1.96 (0.24)	-8.24	< 0.0001
Combustibility	0.51	LMA	< 0.01	0.54 (1.05)	0.52	0.60
		LA	0.48	1.25 (0.26)	4.81	< 0.0001
		LWC	0.05	-1.71 (1.33)	-1.28	0.20

3.4 Discussion

Our findings demonstrate that the three dimensions of leaf flammability do not covary to yield low-leaf-flammability species with an overall combination of the slowest ignitibility, shortest sustainability, and lowest combustibility. In fact, we found that leaf ignitibility and leaf sustainability worked in opposition to each other as dimensions of leaf flammability. Species with leaves that were the slowest to ignite were those with leaves that burned for the longest, and vice versa. Furthermore, although species with the lowest leaf combustibility were those that burned for the shortest period of time, they were not those with the slowest (or fastest) ignitibility. Our analyses did reveal positive relationships between pairs of ignitibility attributes, and between pairs of sustainability attributes. The tight correlations that emerged show that leaf flammability attributes are generally reliable proxies for the other attributes within the ignitibility and sustainability dimensions of leaf flammability.

A small number of studies have previously examined relationships between leaf flammability attributes. Some of the results of our study are consistent with this earlier work. For example, Engber & Varner (2012) and Grootemaat *et al.* (2015) reported positive relationships between the two sustainability attributes ID and FD. Our results are also consistent with Grootemaat *et al.* (2015) in the lack of a positive or negative relationship between the ignitibility attribute TTI and the sustainability attribute FD. In contrast to the findings of Grootemaat *et al.* (2015), however, we found a significant positive relationship between the ignitibility attribute TTI and the sustainability attribute ID. If this difference is due to our inclusion of relatively smaller-leaved species (< 1 cm), then this would suggest that small-leaved species are particularly influential in the observed relationship between

TTI and ID. This idea is supported by our finding that smaller LA was significantly related to both slower TTI and to shorter ID.

We found that a coordinated suite of leaf traits was characteristic of low-leaf-flammability species. Small LA, high LMA and high LWC were distinguishing features of species with comparatively lower OLFI values. Functionally, leaves with smaller LA have smaller boundary layers of surrounding air than leaves with larger LA (Yates *et al.* 2010; Leigh *et al.* 2017). The overall effect of this difference is that leaves with larger LA have higher average temperatures than smaller leaves (Leigh *et al*. 2012). We suggest that this contributes to larger leaves reaching ignition temperatures more quickly than smaller leaves. Larger LA also means that there is more leaf material available to burn, which leads to longer burning times. The association between high LMA and low OLFI values arose because of the much stronger influence of high LMA on slow ignitibility, which overpowered the relationship between high LMA and long sustainability. Mechanistically, higher LMA represents a greater thermal mass per leaf area that requires heating to the critical temperature for leaf ignition, with higher LWC acting as a further buffer against temperature increases. The thermal buffering effect of leaf water content has been noted in a previous study of variation in times to ignition among native and exotic plants of dry sclerophyll woodland (Murray *et al*. 2013).

Among the leaf traits that we assessed, only large LA was significantly related to high combustibility. This may suggest an important contribution of interspecific variation in leaf oils and other volatiles to variation among species in leaf combustibility. Flaming combustion occurs when the gases evolved from thermal decomposition of plant leaves are ignited. On a volume basis, it is likely that species with small LA have a comparatively smaller supply of oils and other volatiles, which would lead to a lower probability of flaming combustion from the ignition of evolved gases. This resource-supply argument for the occurrence of leaf combustibility is supported by the observed relationship between species with large LA having significantly longer sustainability (Table 1). Interestingly, among our study species, two species that probably have high concentrations of leaf oils (both species have large oil glands on their leaves and are aromatic when crushed) actually fell at opposite ends of the OLFI continuum. *Philotheca hispidula* (Rutaceae) was a low-OLFI species with low leaf combustibility, whereas *Eucalyptus punctata* (Myrtaceae) was a high-OLFI species with high leaf combustibility. Thus, we suggest that future research on leaf combustibility might usefully focus not just on the supply of leaf oils and other volatiles, but also on characterising both the types of oils (e.g., classes of terpenes) present in plant leaves and their concentrations (Pausas *et al.* 2016; Della Rocca *et al.* 2017).

Under our experimental temperature conditions (700°C), which reflected temperatures during moderate-intensity wildfires (~ 500–800°C; Wotton *et al.* 2011), differences among species in the occurrence of flaming combustion will be important because leaves that produce flame have the most potential to promulgate fire to surrounding leaves and plant structures (Wyse *et al.* 2018). Under high-intensity fires (temperatures > 800°C), however, the leaves of most species will likely enter flaming combustion (although experimental tests of this assumption are difficult to find) and thus differences among species in the occurrence of leaf flaming will probably not be found. However, differences in the duration of leaf flaming among species may still be important, as species which flame for relatively longer periods may retain this characteristic across a higher range of fire temperatures.

The results of our study have implications for species selection for green firebreaks. Firstly, leaves are a major fuel source for wildfires and contribute to fire behaviour (McCaw *et al*. 1996; Engstrom *et al*. 2004; Zylstra *et al*. 2016; Krix & Murray 2018). In this context, quantification of leaf flammability attributes and their relationships can provide a finer level of understanding about the flammability dimensions of fuels present in firebreaks. Secondly, identifying low-leaf-flammability species provides crucial reference point information for determining how plant traits influence crown fire, which is still a major challenge for fire ecology (Schwilk 2015). While it is not yet well understood how leaf flammability scales up to whole plant flammability (cf. leaf-to-litterbed flammability scaling, e.g., Ganteaume *et al*. 2013a; Grootemaat et al. 2017), it will no doubt require consideration of a range of factors that may modulate leaf flammability patterns, including the retention of dead branches in the canopy (Schwilk 2003) and branching patterns in association with leaf size (Bowman *et al*. 2014). Future studies will need to explore how plant architectural attributes such as numbers of leaves and branches in a given canopy volume, distances among leaves, the size of leaves, and retention of dead plant material all interact with the leaf flammability dimensions examined in the present study. This work will have enormous potential to overcome the problems posed by large trees and shrubs whose size often precludes replicated whole-of-plant burning experiments, to lead to an improved understanding of whole-plant flammability differences among species and which species are the most appropriate for green firebreaks.

Identifying low-flammability plants is only one of the factors for consideration when creating green firebreaks (Curran *et al.* 2018; Murray *et al.* 2018). Other fire-related factors that are important, for instance, include the physical spacing of plants and the influence of exotic plant species that co-occur with native plants (Brooks *et al.* 2004; Wyse *et al.* 2018). It is also important to take into account high-flammability species which can be selectively thinned (or even removed) from remnant vegetation at the WUI to reduce the flammability of vegetation adjacent to homes and infrastructure. This may be particularly useful where residents at the WUI favour retention of a natural appearance of surrounding vegetation (Nelson *et al.* 2004) or are financially unable (Penman *et al.* 2017) or unwilling to clear land to create defensible spaces around homes (Syphard *et al.* 2014). Green firebreaks (Della Rocca *et al.* 2015, Curran *et al.* 2018) or garden plantings consisting of low-flammability species may also be incorporated into garden design to balance aesthetic values with lowered fire risk to traditional gardens (Murray *et al.* 2018).

Chapter 4

Do plant leaves become more flammable with increasing radiant heat?

4.1 Introduction

The flammability experiments I performed in the previous two chapters all focused on a standardized temperature of 700°C. Pilot tests across a range of temperatures (both lower and higher than 700°C) demonstrated that at this temperature, it was possible to quantify meaningful differences in leaf flammability attributes among the suite of study species. It also allowed identification of the functional roles of leaf traits in driving plant leaf flammability. Previous studies have also mainly used an approach of a standardized experimental temperature in leaf flammability research (Gill & Moore 1996, Ganteaume *et al.* 2013, Murray *et al.* 2013, Grootemaat *et al.* 2015).

The standardized temperature I used in my earlier chapters provided a representation of heat conditions in wildfires of moderate intensity. A key question arises from this work: how might the strong differences observed in leaf flammability attributes among species at 700°C change with increases in temperature representing more intense wildfire conditions? The first possibility is that greater incoming radiant heat could lead to leaves igniting more quickly and burning more fiercely for a shorter period of time. In this situation, I predict that interspecific variation in leaf flammability attributes will be reduced and species will become more similar in their values for ignitibility, sustainability and in the prevalence of leaves reaching flaming combustion. If this is indeed the case, interspecific differences in flammability attributes will matter progressively less with increasing fire intensity and may converge to the point where species are practically indistinguishable. Alternatively, a second possibility is that meaningful and readily observable differences in flammability attributes across species may be retained despite increasing fire intensity, indicating that even during intense fire, variation in leaf flammability attributes across species remain an important consideration in fire behaviour. It is thus imperative to determine which of these two scenarios holds for leaf flammability attributes, as the distinction has the potential to prove useful for the development of landscape flammability models and for informing the selection of low-flammability species for 'green firebreaks' (Curran *et al.* 2018), or garden species for homes at the wildland-urban interface (Murray *et al.* 2018).

In this chapter, I examine the effect that increasing radiant energy has on leaf flammability attributes, focussing on the ignitibility attributes time to incandescence (TTI) and time to flaming (TTF), the sustainability attributes incandescence duration (ID) and flaming duration (FD), and leaf combustibility (the occurrence of flaming combustion). I test the following predictions to determine which of the two scenarios outlined above applies to each of the leaf flammability attributes: (1) TTI and TTF become faster in response to increases in radiant energy; (2) ID and FD become shorter in response to increasing radiant energy; and (3) the propensity of leaves to enter flaming combustion (i.e., combustibility) increases with high radiant energy. A consequence of these predictions being upheld is that variation among species in leaf flammability attributes is reduced as radiant energy increases, and species become more similar in the time it takes to incandesce and flame, and in the durations of incandescence and flaming.

4.2 Methods

4.2.1 Study region and species

I selected ten plant species commonly found in high abundance in fire-prone woodlands of the Blue Mountains in south-eastern Australia (e.g., Murray *et al*. 1999). Topographically rugged, this region experiences wildfire every five to ten years (Hammil and Tasker 2010) and is characterised by sclerophyllous plant species with a variety of fire survival adaptations, a mild climate (mean temperature 17.2°C) and moderate rainfall (1085 mm y^{-1}). The study species comprised eight shrub species (*Acacia myrtifolia*, *Acacia suaveolens, Banksia serrata*, *Banksia spinulosa*, *Callistemon citrinus*, *Grevillea phylicoides*, *Lambertia formosa* and *Persoonia mollis*) and two tree species (*Corymbia gummifera* and *Eucalyptus sparsifolia*). The leaves of these species varied in size from 0.80 cm^2 (*G. phylicoides*) to 27 cm^2 (*B. serrata*) (Fig. 4.1).

4.2.2 Leaf collection and measurement of flammability attributes

Short sections of branch supporting nine or more healthy leaves were collected from ten healthy individuals of each of the ten species in the field (see Chapters 2 and 3 for further details on sample collection across study sites). Branch sections were wrapped in moist cloth and sealed in air-tight plastic bags immediately following collection to preserve the water content of the samples (Pérez-Harguindeguy *et al.* 2013). Samples were refrigerated overnight (to lessen dehydration and leaf wilting) before trait measurement and burning the following day. In the laboratory, a single fresh leaf was detached from each branch section at the natural abscission point immediately prior to placement in a fan-forced muffle

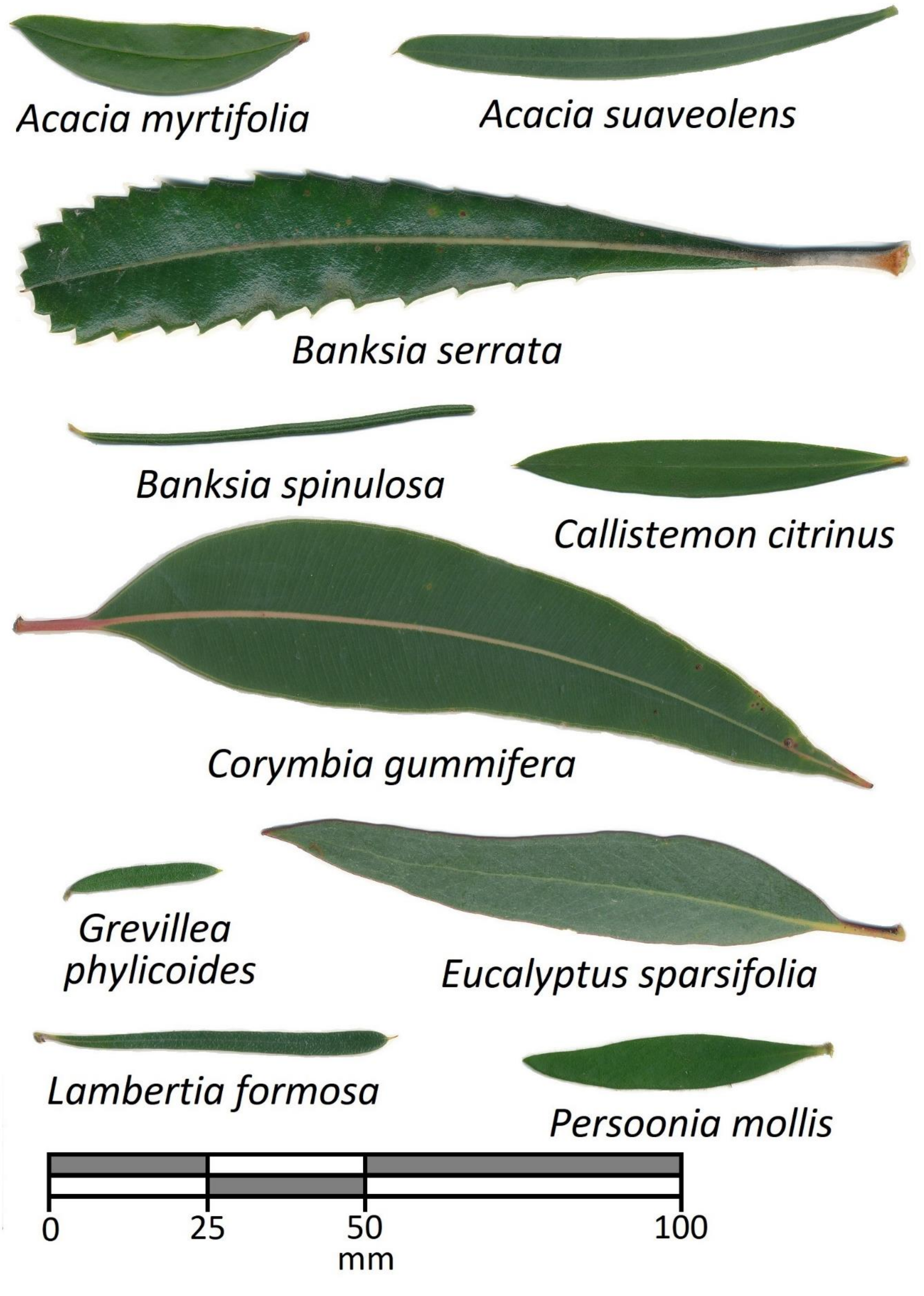


Fig. 4.1 Representative, fully expanded adult leaves of each of the ten study species.

furnace for the experimental burns. Ten leaves of each species were burned at each of the four temperatures, 600°C, 700°C, 800°C and 900°C. Radiant energy emitted from the furnace walls was calculated using the equation:

$$q = \varepsilon \sigma T^4$$

Where q is equal to heat transfer per unit time, ε is emissivity of the hot object (set to 0.9 for white ceramic, Gubareff *et al.* 1960), and T is the temperature of the hot object in degrees kelvin. At this range of temperatures, the radiant energy was estimated to be 29.6 kWm^{-2}, 45.7 kWm^{-2}, 67.6 kWm^{-2}, and 96.6 kWm^{-2}. This range of radiant energy was selected to replicate the temperatures reached in low to higher intensity forest fire (Wotton *et al.* 2011).

A single leaf was clamped by its petiole to a clip attached to a wheeled stand, which was used to move the leaf sample into the centre of the furnace. This system allowed each leaf sample to be placed in the same place in the furnace while avoiding direct contact between the leaf and the furnace interior walls. Leaves were orientated with their adaxial surface parallel to the roof of the muffle furnace and allowed to burn until fine white ash remained. A digital camera was used to film the leaves while burning, and the footage later analysed in Windows Media Player Classic (https://mpc-hc.org/) to quantify the elapsed time taken to begin incandescent combustion (TTI) and flaming combustion (TTF) as well as the duration of incandescent combustion (ID) and the duration of flaming (FD) to one tenth of a second accuracy.

4.2.3 Statistical analysis

First, to determine how flammability attributes varied across species in relation to increasing radiant energy, I built separate general linear models where each flammability attribute was the response variable (with mean values for each species used as replicates) and radiant energy was a fixed ordinal variable (with four levels, 29.6 kWm^{-2}, 45.7 kWm^{-2}, 67.6 kWm^{-2}, and 96.6 kWm^{-2}). To test whether the incidence of flaming across species increased with radiant energy, I calculated the proportion of samples for each species that flamed at each level of radiant energy, before fitting a binomial regression model with a logit link with radiant energy as a categorical predictor.

Following this, to examine whether species became more similar to each other in their flammability attributes in response to increasing radiant energy these analyses were repeated with the inclusion of a term for species (a fixed categorical variable with ten levels, one for each species) and the radiant energy x species interaction. Here, samples were replicates for the continuous responses (TTI, ID, TTF and FD), and the proportion of samples flaming within each level of radiant energy for each species for the binomial model of leaf flaming. For both sets of analyses, species which ignited fewer than four times within a given radiant energy level were excluded from that radiant energy level for the analyses of TTI and ID. Species which flamed fewer than four times within a given radiant energy level were excluded from those levels in the analyses of TTF and FD, including *P. mollis*, which flamed only at 96.6 kWm^{-2}. A significant model interaction combined with convergence among species in mean values for a given flammability attribute would demonstrate increasing similarity among species at higher radiant energy compared with radiant energy. I then fitted models to each species individually where significant interactions were found in the case of any of the flammability attributes, using radiant energy as the predictor, to distinguish whether any species behaved in a vastly different way to most other species (e.g., a flammability attribute may decline in most species but stay consistently high in other species with increasing radiant energy). Prior to analysis, the continuous flammability attributes (TTI, ID, TTF and FD) were log transformed, and the radiant energy predictor was sqrt transformed.

To test if species' flammability attributes became more alike with increasing radiant energy, I calculated mean pairwise distance (MPD) as the absolute distance between mean values for all unique paired combinations of species for each flammability attribute, within each level of radiant energy. I then used a series of general linear models with MPD values for a given flammability attribute as the response variable and radiant energy as a fixed categorical variable to test if differences amongst the levels of radiant energy existed. Tukey's HSD pairwise comparisons were used to identify significant differences between levels of radiant energy. For TTF and FD, two separate models were fitted for each attribute, one that included all species which flamed at least four times at 45.7 $kWm^{-2}$and higher, and the other for species which flamed at least four times at 67.6 $kWm^{-2}$and higher. *P. mollis*, which flamed only at 96.6 kWm^{-2} was excluded as there was no comparison available at the lower radiant energy.

All analyses were performed in R version 3.6.1 (R Core Team, 2017), using the packages car (Fox & Weisberg, 2011), and multcomp (Hothorn *et al.* 2008). The full outputs of all statistical models with two factors and an interaction term are provided in Appendix 4.1. Where appropriate, type II sums of squares (marginal means) were used to account for the unbalanced design due to species being excluded for not igniting/flaming more than three times at certain levels of radiant energy.

4.3 Results

4.3.1 Responses of flammability attributes to increasing radiant energy

Across species, TTI ($F_{3,35} = 50.76$, $P < 0.0001$; Fig. 4.2a) and TTF ($F_{3,15} = 23.70$, $P < 0.0001$; Fig. 4.2c) became significantly faster with each level of increasing radiant energy. I found that ID was marginally significantly shorter with increasing radiant energy ($F_{3,35} = 2.95$, $P = 0.04$; Fig. 4.2b) and that there was no significant effect of radiant energy on FD ($F_{3,15} = 0.26$, $P = 0.90$; Fig. 4.2d). The proportion of leaves that entered flaming combustion rose significantly with increasing radiant energy ($\chi^2 = 23.51$, $P < 0.0001$; Fig. 4.2e).

4.3.2 Evidence for convergence among species in their flammability attributes at higher radiant energy

There were significant radiant energy x species interactions for TTI ($F_{9,364} = 4.56$, $P = < 0.0001$), ID ($F_{9,364} = 6.99$, $P = < 0.0001$) and TTF ($F_{6,148} = 3.33$, $P = 0.004$), with mean species' values of TTI (Fig. 4.3a), ID (Fig. 4.3b) and TTF (Fig. 4.3c) becoming more similar to each other at higher compared with lower radiant energy (full ANOVA results presented in Appendix 4.1). Analysis of each species separately showed that TTI, ID and TTF decreased significantly with increasing radiant energy in all species (all P values < 0.01; Appendix 4.2). No significant radiant energy x species interaction was found for FD ($F_{6,148} = 1.89$, $P = 0.09$; Fig. 4.3d), and there was no significant relationship between radiant energy and FD ($F_{1,148} = 0.19$, $P = 0.7$). However, there were significant differences in FD among species ($F_{6,148} = 197.81$, $P < 0.0001$).

A significant radiant energy x species interaction for the proportion of samples flaming ($\chi^2_{9,20} = 21.26$, $P = 0.012$) emerged, with 8 of the ten species showing a significant

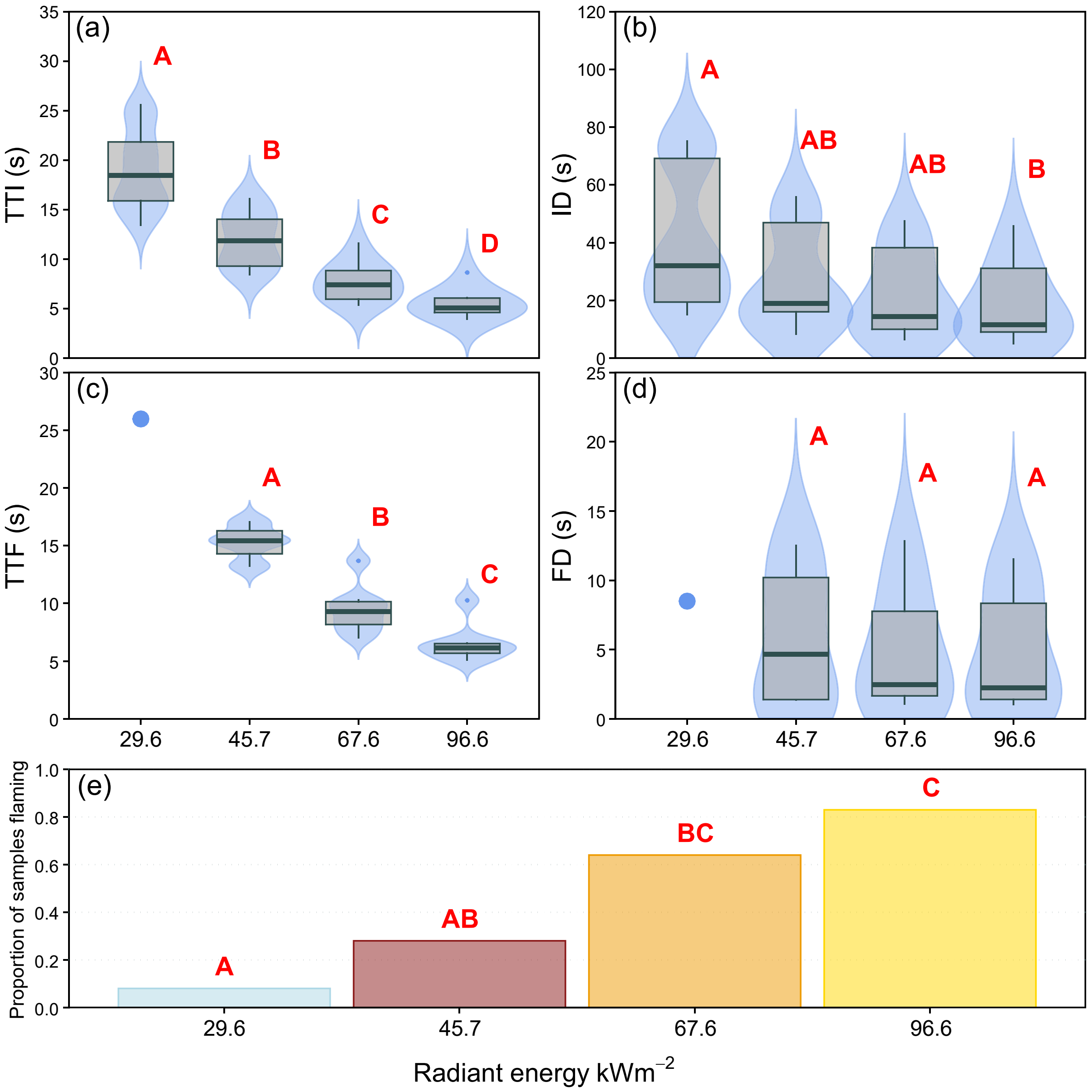


Fig. 4.2 Probability density plots of species mean values for (a) TTI, (b) ID, (c) TTF, (d) FD and (e) the proportion of all samples flaming as a function of radiant energy. In (a) to (d), blue shaded areas show probability density, overlaid with boxplots. Letters indicate where significant differences ($P < 0.05$, after correction for multiple comparisons) exist among levels of radiant energy. Points at 29.6 kWm^{-2} in (c) and (d) indicate the mean value for *B. serrata*, the only species which consistently flamed at this level of radiant energy.

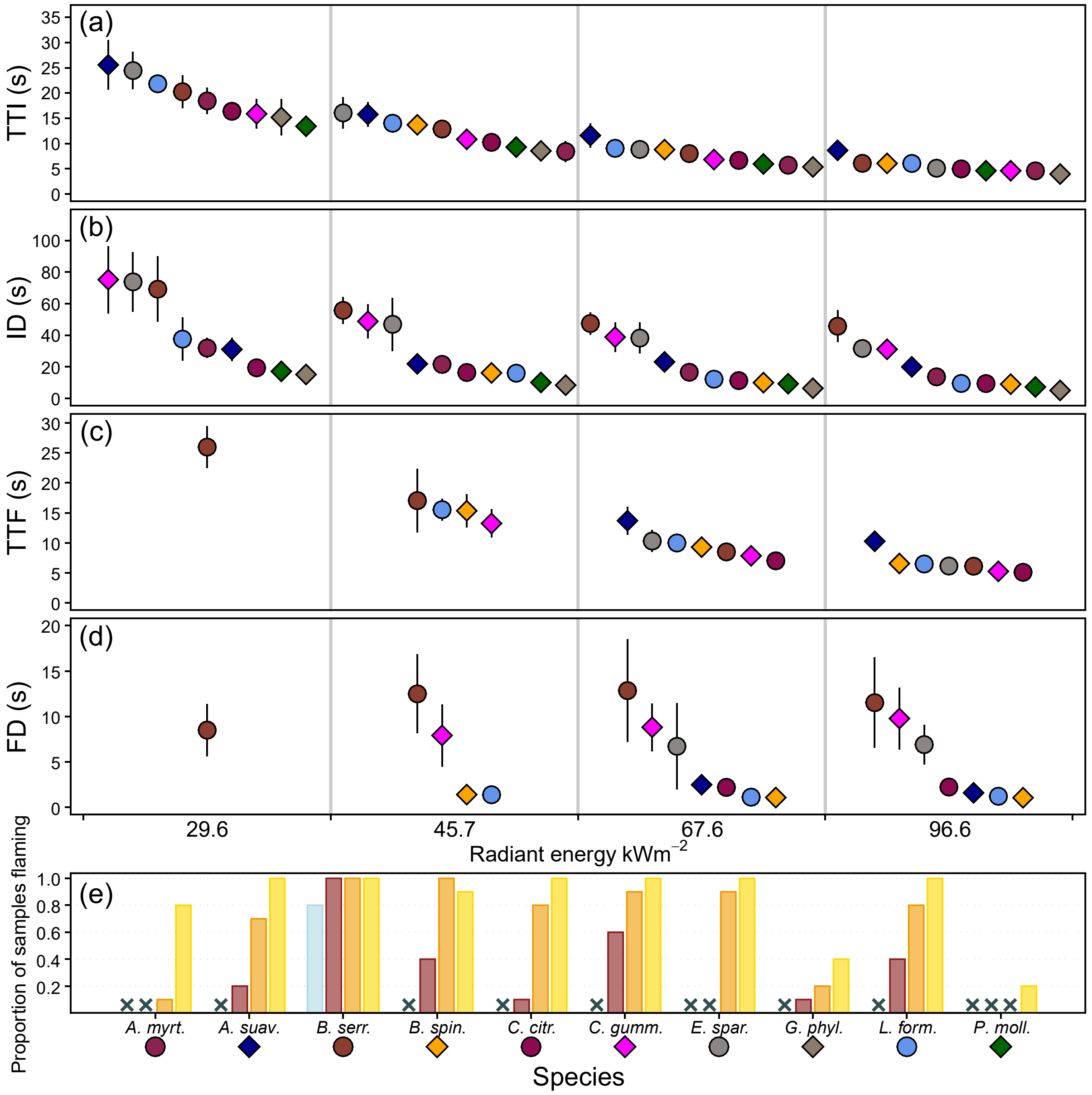


Fig. 4.3 Mean species' values for (a) TTI, (b) ID, (c) TTF and (d) FD by radiant energy level (± SD). Point colours correspond to the colour key shown on the x-axis of (e). In (e), the proportion of samples flaming for each species at each level of radiant energy is shown, with light blue for 29.6 kWm^{-2}, red for 45.7 kWm^{-2}, orange for 67.6 kWm^{-2} and yellow for 96.6 kWm^{-2}. Crosses indicate no samples flaming for a species at a given level of radiant energy.

relationship between flaming and increasing radiant energy (all P values ≤ 0.03; Appendix 4.2). Of the two species which did not show a significant relationship between flaming and radiant energy, *B. serrata* flamed at all levels of radiant energy, and *P. mollis* only at the highest level of radiant energy. While higher proportions of samples flamed with higher radiant energy within species, the patterns of increase differed widely among species (Fig. 4.3e). Some species showed relatively steady increases in the proportion of samples flaming (e.g. *A. suaveolens*, *L. formosa*), with others displaying a large increase in flaming between levels of radiant energy (e.g., *A. myrtifolia* between 67.6 kWm^{-2} and 96.6 kWm^{-2}, *C. citrinus* between 45.7 kWm^{-2} and 67.6 kWm^{-2}), or a pattern of flaming not occurring at a lower radiant energy level before being observed in the majority of samples at the next radiant energy level (*C. gummifera* between 45.7 kWm^{-2} and 67.6 kWm^{-2}, *E. sparsifolia* between 67.6 kWm^{-2} and 96.6 kWm^{-2}). With increasing radiant energy, MPD significantly decreased for both TTI ($F_{3,167} = 22.70$, $P < 0.0001$; Fig. 4.4a) and ID ($F_{3,1676} = 6.09$, $P = 0.0006$; Fig. 4.4b). In both cases, a threshold at 67.6 kWm^{-2} was reached after which declines in MPD for TTI and ID appeared to slow down, which was particularly strong for ID (Fig. 4.4a and 4.4b). Values of MPD for TTF did not decrease significantly with radiant energy, either in the set of species that flamed consistently from 45.7 kWm^{-2} and higher ($F_{2,15} = 3.41$, $P = 0.06$; Fig. 4.4c) or in the set of species that flamed at both 67.6 kWm^{-2} and 96.6 kWm^{-2} ($F_{1,4} = 0.37$, $P = 0.60$). No significant decrease in MPD with increasing radiant energy was found for the set of species flaming at 45.7 kWm^{-2} and higher ($F_{2,15} = 0.03$, $P = 0.97$; Fig. 4.4d) or the set of species flaming at 67.6 kWm^{-2} and 96.6 kWm^{-2} ($F_{1,4} = 0.07$, $P = 0.8$). At 96.6 kWm^{-2}, values of MPD were relatively small for TTI (< 2 s), TTF (< 1 s for the set of species flaming at 45.7 kWm^{-2} and higher, and < 4 s for the set of species flaming at 67.6 kWm^{-2} and 96.6 kWm^{-2}), and FD for the set of species flaming at only at 67.6 kWm^{-2} and 96.6 kWm^{-2} (~ 3 s). For ID, MPD values were much larger, remaining above 15 s at 96.6 kWm^{-2}, and moderately large for FD for the set of species flaming at 45.7 kWm^{-2} and higher (> 6 s).

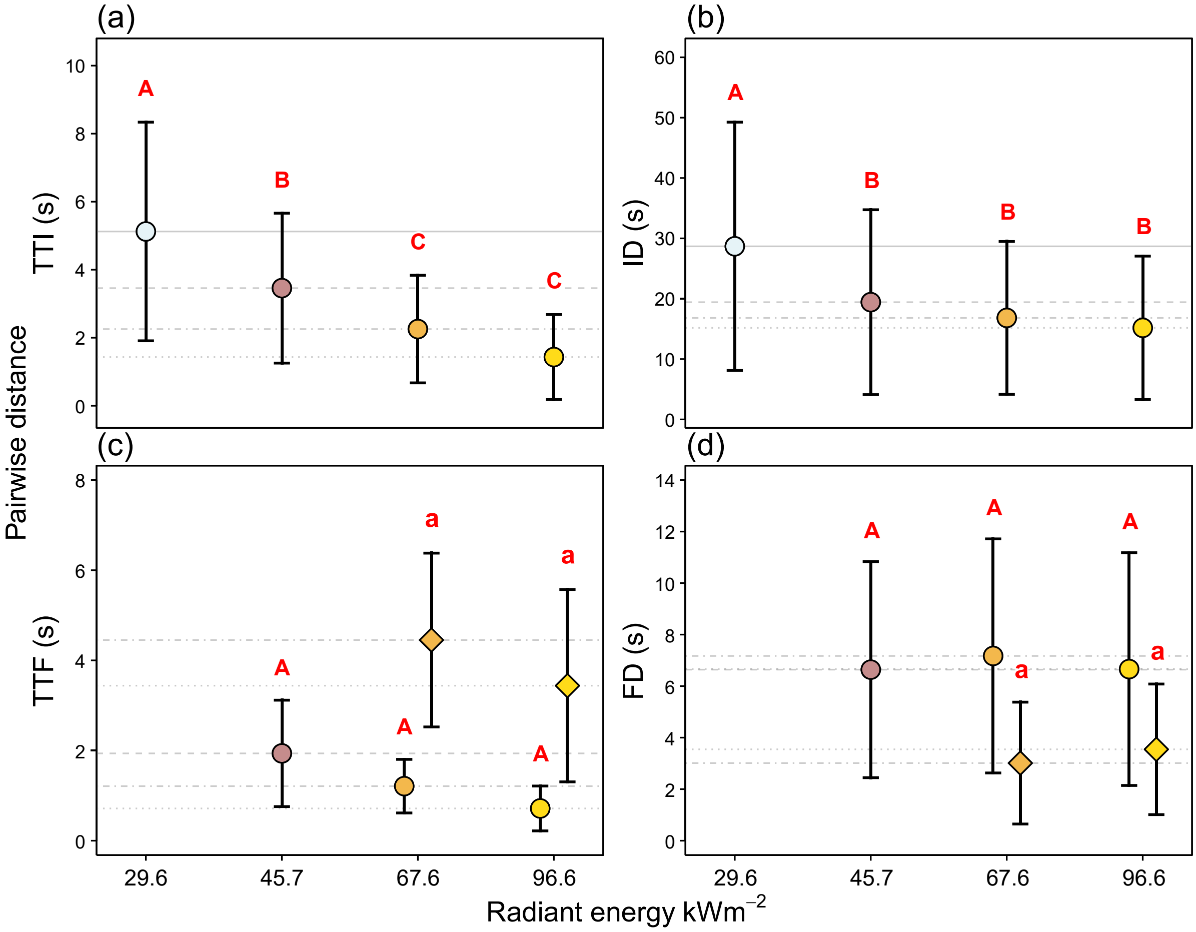


Fig. 4.4 Plots of MPD (± SD) for (a) TTI, (b) ID, (c) TTF and (d) FD as a function of radiant energy. Letters indicate where significant differences ($P < 0.05$, after correction for multiple comparisons) exist among levels of radiant energy. In (c) and (d), letters indicate differences within two groups; species that flamed consistently from 45.7 kWm^{-2} and higher, (indicated by circular points) and species that flamed consistently from 67.6 kWm^{-2} and higher (indicated by rhomboid points). Species that flamed only at 96.6 kWm^{-2} were excluded.

4.4 Discussion

I found TTI, TTF and ID all decreased significantly with increasing radiant energy, and proportions of samples flaming increased at higher radiant energies. For these attributes, there was significant convergence towards lower values across species, with the values of these attributes becoming increasingly alike across species with higher radiant energy, reflecting the predicted relationship between ignitibility and increasing radiant energy. Interestingly, FD did not decrease significantly with increasing radiant energy, with FD values for individual species remaining relatively fixed, showing a lack of significant convergence towards lower values across species. In addition, ID showed weak convergence towards lower values with increasing energy, contrary to the predicted relationships of decreasing differences among species sustainability with increased radiant energy. Patterns in flaming across species did show the expected relationship, with more samples flaming at higher energy, while individual species exhibited dissimilar flaming behaviour.

I found particularly strong convergence in ignitibility (TTI and TTF) in the data. In contrast, sustainability attributes (ID and FD) retained relatively larger differences among species relative to ignitibility, despite significant convergence in ID being detected, with large differences among species observed in the data. At low to moderate radiant energy, flaming behaviour was markedly different, displaying patterns which were peculiar to individual species. These findings show that while species identity may be equally important for ignitibility and sustainability at lower fire intensity, their relative importance shifts with higher fire intensity. At moderate to high intensity, differences in interspecific TTI and TTF become increasingly less important, with flaming occurrence showing species specific effects up to a high fire intensity when the leaves of all species will likely flame. At high fire intensity, only the sustainability attributes retain meaningful differences among species.

Attention has been given to quantifying the relative flammability of plant species (White & Zipperer 2010, Grootemaat *et al.* 2015, Schwilk 2015, Varner *et al.* 2015), however once fire reaches a high intensity, the living component of the available fuel for a fire may differ relatively little in its flammability, regardless of which species might be present or their relative individual flammability at lower radiant energy. However, experimental burns at stand level detailed in Alexander (2010) reported a crown fire in *Pinus banksiana* (Jack Pine) which did not spread to an abutting plot of *Populus tremuloides* (Trembling Aspen), which may indicate that plant species do sufficiently differ in their flammability to affect fire behaviour across all intensities. At local scale and low to moderate fire intensity, plant species might most influence fire behaviour through flaming, with flaming leaves able to propagate fire to adjacent leaves on the same individual or to neighbouring plants. If species whose leaves flame during lower intensity fire are present, they might serve to make the entire plant assemblage more flammable (Wyse *et al.* 2018). The implications of this for fire behaviour are complex given that species abundance, leafing intensity and the spatial arrangement of leaves will influence the wider effect flaming leaves might have. For instance, a cool litter fire spreading under low vegetation layers consisting of species whose leaves flame easily might spread fire vertically much faster than species with leaves which flame only at higher radiant energy. Similarly, plant assemblages which contain species which deploy leaves close to the ground or those whose leaves are crowded (within and/or across species) would be more susceptible to fire spread through individual leaves flaming.

For modelling of fire behaviour, the data for the relative flammability of individual species might be most usefully incorporated early during fire spread, or during cooler fires (typical of fuel reduction burning outside of fire seasons), where differences among species in their flammability attributes are largest. Here, flaming is again likely the most important attribute to account for, with the potential for future flammability research to add to our understanding of the leaf trait relationships of leaf flaming occurrence and scaling up from leaves to branches. As leaf flammability is strongly related to leaf traits (Gill and Moore 1996, Ganteaume *et al.* 2013, Murray *et al.* 2013, Grootemaat *et al.* 2015) another useful direction of research would be testing if abiotic filtering (insolation, humidity, etc.) at local scale might select for certain leaf traits which might then affect fire behaviour.

Chapter 5

Predicting changes in plant leaf flammability in response to increasing radiant energy: the importance of leaf functional traits

5.1 Introduction

In Chapter 4 of this thesis, I explored how leaf flammability attributes varied among species of fire-prone woodlands in relation to increasing radiant energy. I showed that interspecific variations in time to incandescence (TTI) and incandescence duration (ID) were considerably reduced at higher vs lower radiant energy, leading to convergence to similarly fast TTI and short ID across species. In addition, the tendency for leaves to flame was much higher in the majority of species at higher radiant energy. Despite convergence in flammability attributes across species at higher radiant energy, however, there remained unexplained variation in these leaf flammability attributes among species. I posit that this remaining variation in flammability is likely driven by interspecific differences in leaf functional traits. This is based on my findings in Chapter 3, where I showed that at the fixed experimental temperature of 700°C, interspecific variation in leaf flammability was strongly related to variation in three key leaf traits: leaf mass per area (LMA), leaf area (LA), and leaf water content (LWC).

Here, I seek to construct predictive models for three leaf flammability attributes – TTI (ignitibility), ID (sustainability), and the presence or absence of leaf flaming (combustibility) – as a function of radiant energy and the leaf traits LMA, LA, and LWC, which were shown in Chapter 2 to have a strong relationship with leaf flammability. Radiant energy and the three leaf traits are included in the models to provide a method to estimate how fire severity and leaf traits work together to determine interspecific variation in leaf flammability. The experimental work to provide data to build the predictive models uses a range of radiant energy that are equivalent to moderate to extreme wildfire events. The accuracy of the model predictions is then tested with an independent dataset not used in the model building process, in order to give an indication of the predictive value of the models.

Part of the rationale for this study is that predictive modelling of leaf flammability based on radiant energy and leaf traits may be a cost-effective alternative to more intensive laboratory-based flammability tests. Flammability testing can become more and more time-consuming and resource intensive when large numbers of species need to be investigated. In contrast, leaf trait and radiant energy data are more readily obtained. For instance, the three traits used in this study are commonly collected in and available from a wide range of ecological studies (Reich *et al.* 1992, Weiher *et al.* 1999, Vendramini *et al.* 2002, Poorter *et al.* 2009, Ordonez & Olff 2013, Brouillette *et al.* 2014), and there are now large online repositories of data for these leaf traits (e.g., TRY Plant Database; Kattge *et al.* 2011). The potential applications of my models of leaf flammability are varied, with possible use in (a) broad-scale fire modelling (where relative flammability for differing vegetation types might need to be quantified); (b) preferential selection of ornamental plant species at the wildland-urban interface as a fire mitigation strategy; and (c) to provide fire-risk assessments of plant species through relative ranking schemes.

5.2 Methods

5.2.1 Study species

The data collected for the ten plant species analysed in Chapter 4 formed the basis for the analyses in this chapter, representing a range of plant families and growth forms (Table 5.1).

All species are widespread and abundant in fire-prone woodlands of the Blue Mountains study region of this thesis (see Chapter 2). Interspecific variation in the leaf traits of the study species broadly represents leaf trait variation observed among common species of Blue Mountains woodland vegetation and wide variation in flammability attributes (Table 5.1).

5.2.2 Measurement of leaf traits and flammability attributes

Short sections of branch with 15 or more leaves attached were collected from 10 healthy individuals of the 10 study species in the field (see Chapters 2 and 3 for further details on sample collection across study sites). Branch sections were wrapped in moist cloth and sealed in air-tight plastic bags immediately following collection to preserve the water content of the samples. Samples were refrigerated overnight (to lessen dehydration and leaf wilting) before trait measurement and burning the following day. Five leaves were detached from each section of branch, and then collectively weighed to give fresh mass, followed by scanning on a flatbed scanner to give leaf area, of each group of five leaves. The leaf scans were analysed using ImageJ (Schneider *et al.* 2012). After scanning, leaves were dried for at least 48 hours at 80°C before reweighing to give the dry mass of the leaves. Leaf dry mass of the five leaves weighed together was then used to calculate leaf water content as a percentage (leaf dry mass/fresh mass x 100) and leaf mass per area (leaf dry mass/leaf area) in g mm^{-2} for each replicate.

Flammability measurements were made by burning single leaves in a fan-forced muffle furnace as detailed in Chapters 2 and 3 of this thesis. Briefly, a leaf was detached from a branch section and clamped by its petiole to a wheeled stand that was used to place

Table 5.1 Mean values of flammability attributes and leaf traits (SE in parentheses) of the study species used in the predictive modelling. The flammability attributes were all measured at 700°C. For 'Flames', a 'Y' or 'N' indicates that the species either entered or didn't enter flaming combustion respectively.

Family	**Species**	**Growth form**	**TTI (s)**	**ID (s)**	**Flames**	**LMA (gm^{-2})**	**LA (mm^2)**	**LWC (%)**
Fabaceae	*Acacia myrtifolia*	Shrub	9.5 (0.55)	20.9 (1.68)	N	163.1 (6.57)	537.5 (75.33)	59.1 (0.25)
Fabaceae	*Acacia suaveolens*	Shrub	13.8 (0.79)	20.2 (2.73)	N	169.0 (13.65)	521.7 (60.47)	65.8 (1.20)
Myrtaceae	*Corymbia gummifera*	Tree	10.1 (0.92)	50.6 (4.17)	Y	213.5 (20.62)	2481.9 (155.65)	48.9 (1.33)
Myrtaceae	*Eucalyptus sparsifolia*	Tree	14.2 (2.38)	46.5 (4.49)	Y	319.9 (14.34)	1637.5 (124.92)	47.9 (0.71)
Myrtaceae	*Callistemon citrinus*	Shrub	10.2 (0.39)	16.4 (1.15)	N	152.8 (3.20)	400.7 (46.95)	50.3 (0.81)
Proteaceae	*Banksia serrata*	Large shrub	12.9 (0.67)	49.9 (2.51)	Y	253.1 (8.43)	2912.9 (230.68)	48.4 (0.96)
Proteaceae	*Banksia spinulosa*	Shrub	11.8 (0.35)	11.4 (1.62)	Y	217.1 (16.53)	114.1 (14.00)	51.0 (1.15)
Proteaceae	*Grevillea phylicoides*	Shrub	7.8 (0.85)	7.9 (0.60)	N	139.2 (10.34)	79.0 (6.22)	49.4 (1.39)
Proteaceae	*Lambertia formosa*	Shrub	13.0 (0.75)	14.6 (0.80)	N	248.6 (14.28)	134.0 (9.71)	46.9 (1.80)
Proteaceae	*Persoonia mollis*	Large shrub	8.0 (0.15)	10.4 (0.84)	N	77.4 (4.60)	429.8 (47.98)	68.9 (1.21)

each leaf consistently in the centre of the furnace, without coming into contact with the furnace walls. Prior to burning, the leaf was scanned to obtain its area. A single leaf from each replicate branch section was burned at each temperature setting of the muffle furnace (600°C, 700°C, 800°C and 900°C). In total, 400 hundred individual leaves were burned (10 species x 10 branch samples x four temperatures). The radiant energy in the furnace interior at each of the four temperature treatments was calculated as $E = \varepsilon \cdot \sigma \cdot T^4$, where E is radiant energy (W), ε is the emissivity of the hot object (the proportional emission of infrared energy of the material compared to a blackbody), σ is the Stefan-Boltzmann constant (5.670^{-8}) and T is the temperature in degrees Kelvin (Fig. 5.1). The value for emissivity was set to 0.9 for white ceramic (the material of the furnace interior; Gubareff *et al.* 1960) and assumed to be in thermal equilibrium with the air inside the furnace. The radiant energy values for each of the increasing furnace temperatures were 29.6 $\mathrm{kWm^{-2}}$, 45.7 $\mathrm{kWm^{-2}}$, 67.6 $\mathrm{kWm^{-2}}$, and 96.6 $\mathrm{kWm^{-2}}$ (Fig. 5.1). Each experimental burn was filmed with a digital camera, and the video later analysed using digital software (Media Player Classic, https://mpc-hc.org/) to give the time taken for incandescent combustion to begin after entering the furnace (TTI), and the length of incandescent combustion (ID) to a tenth of a second resolution. Where leaves began flaming, this was recorded as a binary response (flaming vs non-flaming).

5.2.3 Predictive modelling of TTI and ID

Exploratory analyses of relationships between radiant energy (explanatory variable) and TTI and ID (response variables) showed that both flammability attributes displayed non-linear relationships with increasing the experimental temperatures of the muffle furnace (Fig. 5.2; see also Chapter 4). I therefore used non-linear least squares regressions to model each of

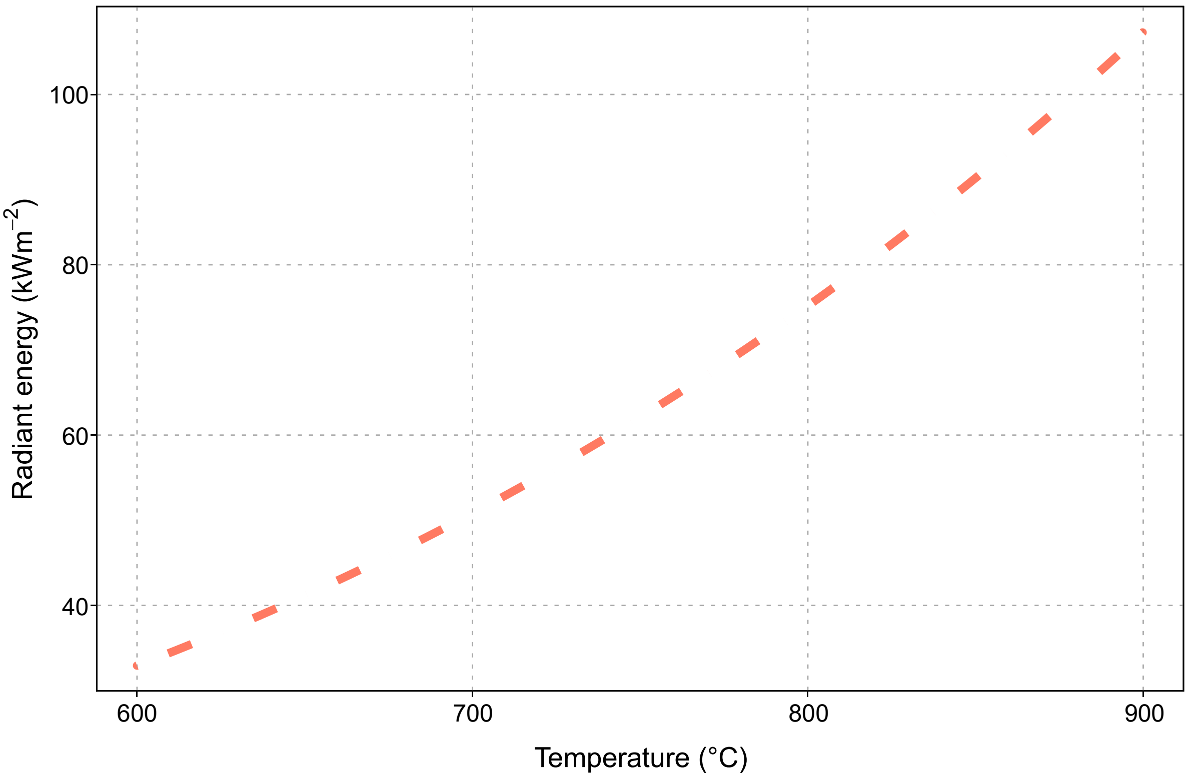


Fig. 5.1 The relationship between air temperature of the muffle furnace and radiant energy derived from the equation $E = \varepsilon \cdot \sigma \cdot T^4$.

the response variables TTI and ID as a function of the set of explanatory variables (radiant energy, LMA, LA and LWC). The following equation was used to fit the models and the Gauss-Newton algorithm applied to estimate the parameters $a, b, c, d,$ and e: $attribute = a \cdot E^b \cdot LMA^c \cdot LA^d \cdot LWC^e$, where attribute is either TTI or ID, E is the radiant energy expressed as kWm^{-2}, LMA as gm^{-2}, LA in mm^2 and LWC as a percentage of fresh leaf mass. The Gauss-Newton algorithm estimates parameters to minimise the sum of squares in non-linear regression, but requires an initial estimate to begin the fitting procedure. To provide these initial parameter estimates the values of b, c, d and e were set to zero, and a (which acts similarly to the intercept in a least squares model) was set to 280 for TTI, and 265 for ID. The initial value of a was determined by building a model including only the parameters

a and E^b and then estimating the value of a at E equal to zero. Fitting these models and allowing all parameters to be estimated through the Gauss-Newton algorithm produced the following equations to predict the flammability attributes TTI and ID in seconds:

$$TTI = 0.055 \cdot E^{-1.106} \cdot LMA^{0.899} \cdot LA^{-0.068} \cdot LWC^{1.343}$$

$$ID = 0.119 \cdot E^{-0.636} \cdot LMA^{0.788} \cdot LA^{0.390} \cdot LWC^{0.313}$$

5.2.4 Predictive modelling of leaf flaming behaviour

The number of leaves that entered flaming combustion increased across the four experimental temperatures. Across the ten study species, 8% of samples flamed at 26.9 kWm^{-2}, 28% at 45.7 kWm^{-2}, 64% at 67.6 kWm^{-2} and 83% at 96.6 kWm^{-2}. To model leaf flaming behaviour with respect to the probability of a leaf flaming with increasing radiant energy, I used a logistic regression model (logit link) with flaming as a binary response (1 for flaming, 0 for non-flaming leaves). The predictors used were sqrt transformed values of E (radiant energy in kWm^{-2}), log transformed values of LMA (gm^{-2}) and LA (mm^{2}), and logit transformed LWC (as a percentage of fresh mass). These transformations were chosen as they resulted in better model fit on the basis of residual model deviance during model building. Fitting the regression model produced the following equation for the linear predictor:

$$-29.795 + \sqrt{E} \cdot 1.416 + ln\ LMA \cdot 3.001 + ln\ LA \cdot 0.537 + logit\ LWC \cdot -1.657$$

From which the probability of flaming was calculated by applying the logit link function to the linear predictor:

$$P = \frac{\exp\ (linear\ predictor)}{1 + \exp\ (linear\ predictor)}$$

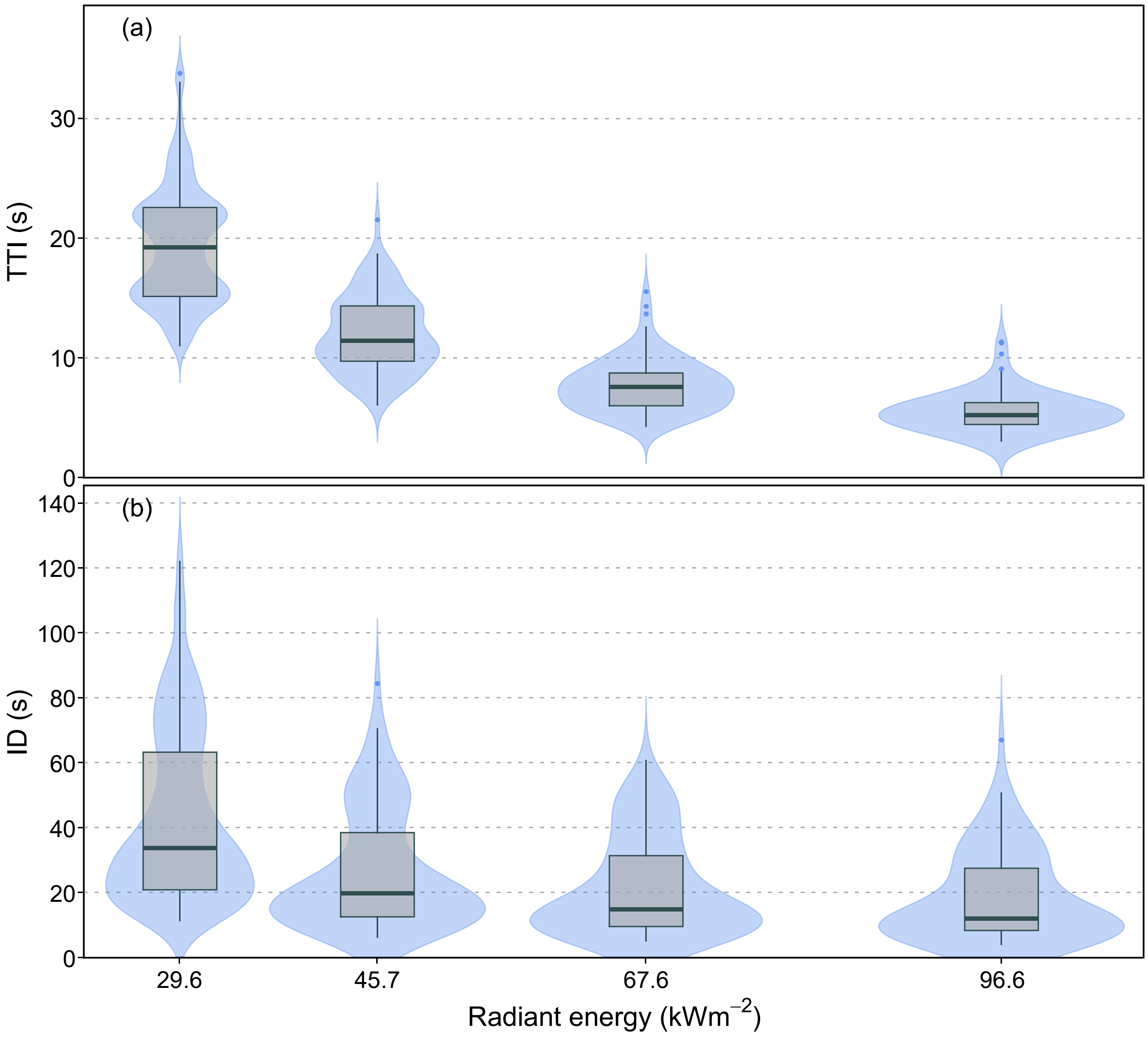


Fig. 5.2 Flammability attributes (a) TTI and (b) ID for the 10 study species used in the predictive modelling across the four experimental levels of radiant energy. The grey boxplots are each linked to blue shaded areas which show probability densities.

The traditional approach of interpreting the binomial probability of flaming as values of $P < 0.5$ indicating the absence of flaming and $P > 0.5$ as indicating the presence of flaming gave a rising false positive rate (i.e., non-flaming samples predicted as flaming) and falling false negative rate (i.e., flaming samples predicted as non-flaming) with increasing radiant energy (Fig. 5.3a). In order to determine more accurate values of P and balance false-positive and false-negative rates across the gradient of radiant energy, it was necessary to identify values of P which best separated the samples which flamed and those that did not at each level of radiant energy. To do this, I calculated the median value of P for samples which flamed, and the median value of P for samples which did not flame for each level of radiant energy. Determining the line of best fit between these median values across the levels of radiant energy allowed me to balance the error rates for each level of radiant energy. A further non-linear regression was then performed on these points to give the equation:

$$P_{flaming} = 0.003772 \cdot \, E^{1.162}$$

Where values of P larger than the $P_{flaming}$ value were then taken as predictions of flaming (Fig. 5.3b). This approach allows appropriate $P_{flaming}$ values to be calculated for any value of radiant energy between 26.9 kWm^{-2} and 96.6 kWm^{-2}. These three equations (the linear predictor, the logit link function, and $P_{flaming}$) were then applied to the leaf trait and radiant energy data, to make predictions of the flaming behaviour of all replicates in the dataset.

5.2.5 Determining the importance of including leaf traits in predictive modelling

To understand how the inclusion of leaf traits improved predictions of leaf TTI and ID beyond using radiant heat on its own, I built a linear model for each of these flammability attributes with radiant energy as a sole explanatory variable (hereafter referred to as the radiant energy model, REM). Radiant energy was entered as a fixed ordinal factor with four levels. Predictions of TTI and ID were made using the REMs, for comparison to the predictions from the non-linear regression models for TTI and ID described in section 5.2.3 (each referred to as the full model, FM). The use of radiant energy as an ordinal factor in the REMs, compared to the use of radiant energy as a continuous predictor in the FMs allowed

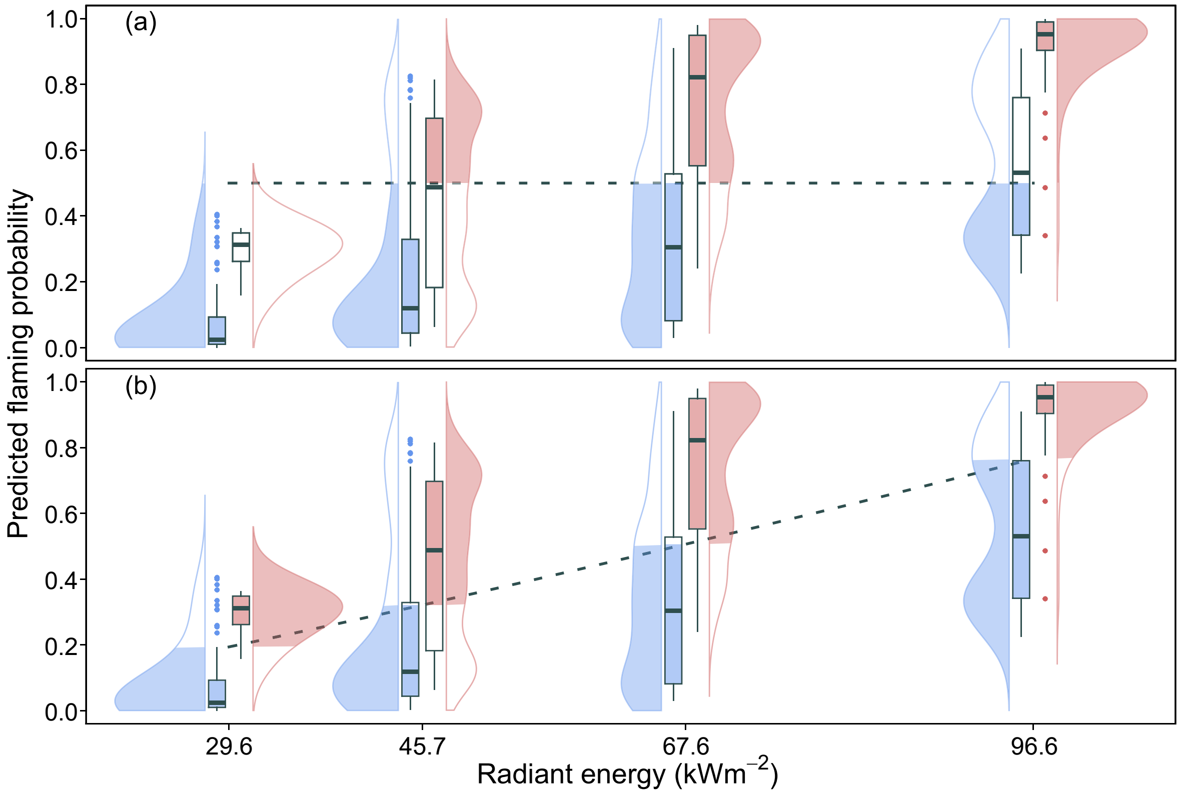


Fig. 5.3 Classification accuracy for non-flaming (blue shaded probability densities and boxplots), and flaming (red shaded probability densities and boxplots). In (a) the 0.5 probability value is shown as a broken line, with shaded blue and red areas indicating correct predictions; (b) shows the non-linear model predicted values for $P_{flaming}$ as a broken line. In both plots, the non-flaming samples below the broken line, and flaming samples above the broken line are correctly predicted. The line in (b) can be seen to pass equidistant between the medians of the flaming and non-flaming samples.

me to model the observations in each level of radiant energy as accurately as possible. This generated two sets of predictions for each of TTI and ID: those from the REMs and those from the FMs. I calculated the absolute distance between predicted and observed values (in seconds) for all samples for both REMs and FMs. Absolute error values indicate the value of the prediction error as a positive number, with higher values indicating greater inaccuracy in prediction. I then statistically compared the absolute error of the predictions from the REMs and the FMs, separately for TTI and ID, to determine whether (i) there was a significant decline in absolute error values in the FM, (ii) there was a relationship between the absolute error and radiant energy, and (iii) any such relationship was consistent between REMs and FMs. To do this I fitted a generalised linear model (Poisson) to a response variable of absolute error values from the REM and FM models. Explanatory variables in the model included a term for which model the absolute errors were generated by (fixed categorical factor with two levels: REM and FM), radiant energy as a fixed continuous factor, and a model error x radiant energy interaction (fixed factor).

To examine the effect of the inclusion of leaf traits in predicting the classification accuracy of leaves as flaming or non-flaming, and to assess the approach of $P_{flaming}$ as a meaningful P adjustment, two logistic regression models were built for comparison to the leaf flaming model (hereafter referred to as the LFM) presented in section 5.2.4. The first model (REM) used radiant energy as the sole ordinal factor (the same approach to build the REM for TTI and ID), and used $P > 0.5$ to indicate flaming. The second model used the same modelling equations as those in section 5.2.4, without the application of the $P_{flaming}$ to classify predictions as flaming/not flaming, i.e., using $P > 0.5$ to indicate flaming (FM model). Comparison of the REM to the FM was used to show the effect of the inclusion of leaf traits on the accuracy of classification of flaming behaviour. Comparison of the FM model to the LFM was performed to quantify the effect of using the $P_{flaming}$ approach on classification accuracy. Classification accuracy of these models was then compared qualitatively overall, and within each of the four levels of radiant energy. The proportion of all non-flaming samples correctly classified as non-flaming (true negative rate, TNR) and the proportion of all flaming samples correctly classified as flaming (true positive rate, TPR) within each level of radiant energy were used to evaluate the performance of the models. The effect of excluding individual leaf traits from the models was also examined, with results for TTI and ID, and leaf flaming included Appendix 5.1 and Appendix 5.2 respectively.

5.2.6 Model validation

I constructed a validation dataset that was not included in building the predictive models to test the accuracy of the predictions made by the models. The validation dataset included 10 species, newly collected, processed, and burned at increments of 50°C between 600°C and 900°C, to give increasing radiant energy levels of 29.6, 37.0, 45.7, 55.9, 67.6 81.2, and 96.6 kWm^{-2}. Three replicate leaf samples per species were burned at each level of radiant energy using the same method of flammability data collection as in the model building dataset. The 10 species used in the new flammability tests included five species that were not in the predictive dataset (*Brachyloma daphnoides*, *Hakea dactyloides*, *Isopogon anemonifolius*, *Philotheca hispidula* and *Woollsia pungens*) and five species that were in the predictive dataset (*A. myrtifolia*, *B. serrata*, *B. spinulosa*, *G. phylicoides* and *L. formosa*). Leaf traits were also collected for the species in the validation dataset using the same method to collect those for the predictive dataset. In the validation dataset, the overall distribution of TTI values was similar to the predictive dataset for species both included and not included in the predictive dataset (Fig. 5.4a and 5.4b), while the predictive dataset had relatively longer ID values compared to the validation dataset (Fig. 5.4c and 5.4d). Similar proportions of samples across all species flamed in the predictive dataset and the species included in the validation data (Fig. 5.4e and 5.4f), while the validation data species not included in the modelling data had a lower propensity to flame (Fig. 5.4f).

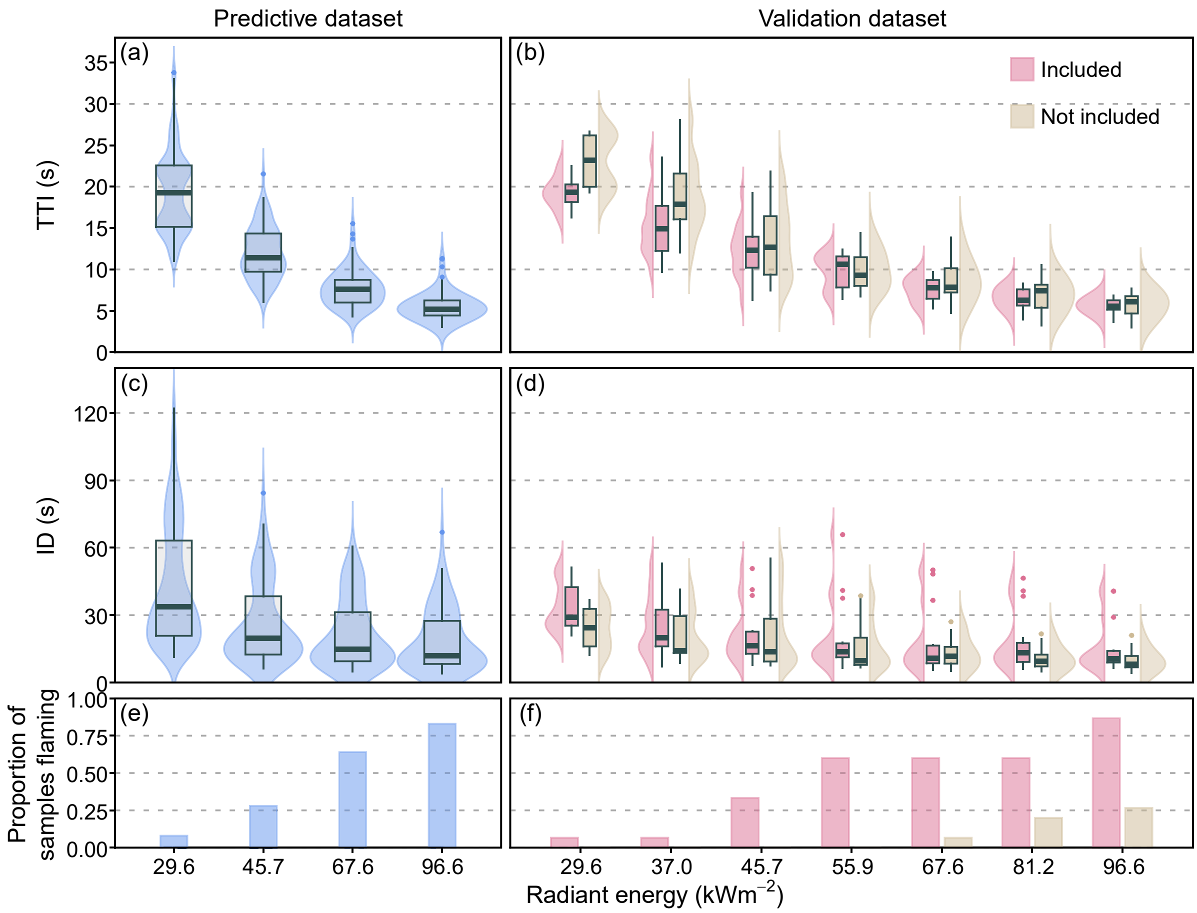


Fig. 5.4 Flammability attributes compared between the predictive and validation datasets. Predictive dataset values for TTI, ID and flaming behaviour are shown in (a), (b) and (c) and validation dataset values in (b), (d) and (f). For both datasets, TTI and ID are shown as boxplots with density distributions as shaded areas. Proportions of samples flaming are indicated by shaded bars in (e, predictive) and (f, validation). In (b), (d) and (f) the species included and those not included in the predictive dataset are presented as adjacent boxplots and density distributions for each level of radiant energy (colour key shown in [b]).

The leaf traits of the validation dataset were then used in the predictive models (built with the predictive dataset) to predict values for TTI and ID, as well as to predict flaming behaviour. These predicted flammability values were divided into values for species included in the predictive dataset, and values for species that were only in the validation dataset. This approach allowed me to compare accuracy of TTI and ID between the predicted flammability values of species to be compared between the same suite of species included in the initial predictive modelling process (to test if new observations of the same species provide similar accuracy to the modelled data) and species which had not been included in the predictive modelling (to give an indication of how accurate the models may be when applied to other species not included in the original modelling). Further, predictions for levels of radiant energy not included in the modelling dataset allowed the accuracy of interpolation from the models to be tested.

To quantify the error in the predicted values of TTI and ID, the absolute error (the absolute distance between the predicted value and the observed value) was calculated for all leaf samples. Accuracy of the predictions of flaming were scored as one for a correct prediction and zero for an incorrect prediction. To statistically test the accuracy of model predictions for TTI and ID, using the absolute error values calculated for TTI and ID, generalized linear models with a Poisson distribution were employed to test if differences in accuracy of the predictions existed among the datasets and if the differences were related to radiant energy. Models were fitted with terms for the dataset (three level fixed factor: predictive dataset, species in the validation dataset included in predictive modelling, species in in the validation dataset not included in predictive modelling), radiant energy as a continuous fixed factor, and a dataset x radiant energy interaction term. Where the dataset term was significant, Tukey pairwise post-hoc tests were used to determine which groups differed in their means, and slopes were compared among groups where a significant dataset x radiant energy term was found.

Accuracy in the predictions of flaming were tested by fitting a logistic regression model using the calculated binary accuracy of predictions as the response. Terms for the dataset (three level fixed factor: modelled data, validation species included in modelling, validation species not included in modelling), the observation (two level fixed factor: flaming present, flaming absent), and the dataset x observation interaction term. This allowed me to test if accuracy differed among datasets, if accuracy in identification of samples which flamed or did not flame differed (true positive and true negative rates), or if there were differences among the datasets in their discriminatory value for flaming and non-flaming samples. These tests were not extended to the levels of radiant energy due to the small sample sizes for flaming/non-flaming replicates within levels of radiant energy in the validation dataset, and separation issues (where the model is unable to calculate standard errors due to all observations for a factor level being either zero or one). Differences in accuracy within radiant energy levels were instead compared qualitatively. Overall, this approach allowed me to test (a) the relative accuracy of the models; (b) the accuracy of the model when applied to new samples of a subset of the same species used to build the models; (c) the accuracy of the model predictions when applied to species which were not used in the modelling process, and (d) the accuracy of the models when interpolation was performed.

All analyses and graphical presentation were performed with R (R Core Team 2017), and the packages emmeans (Lenth 2019), and multcomp (Hothorn *et al.* 2008).

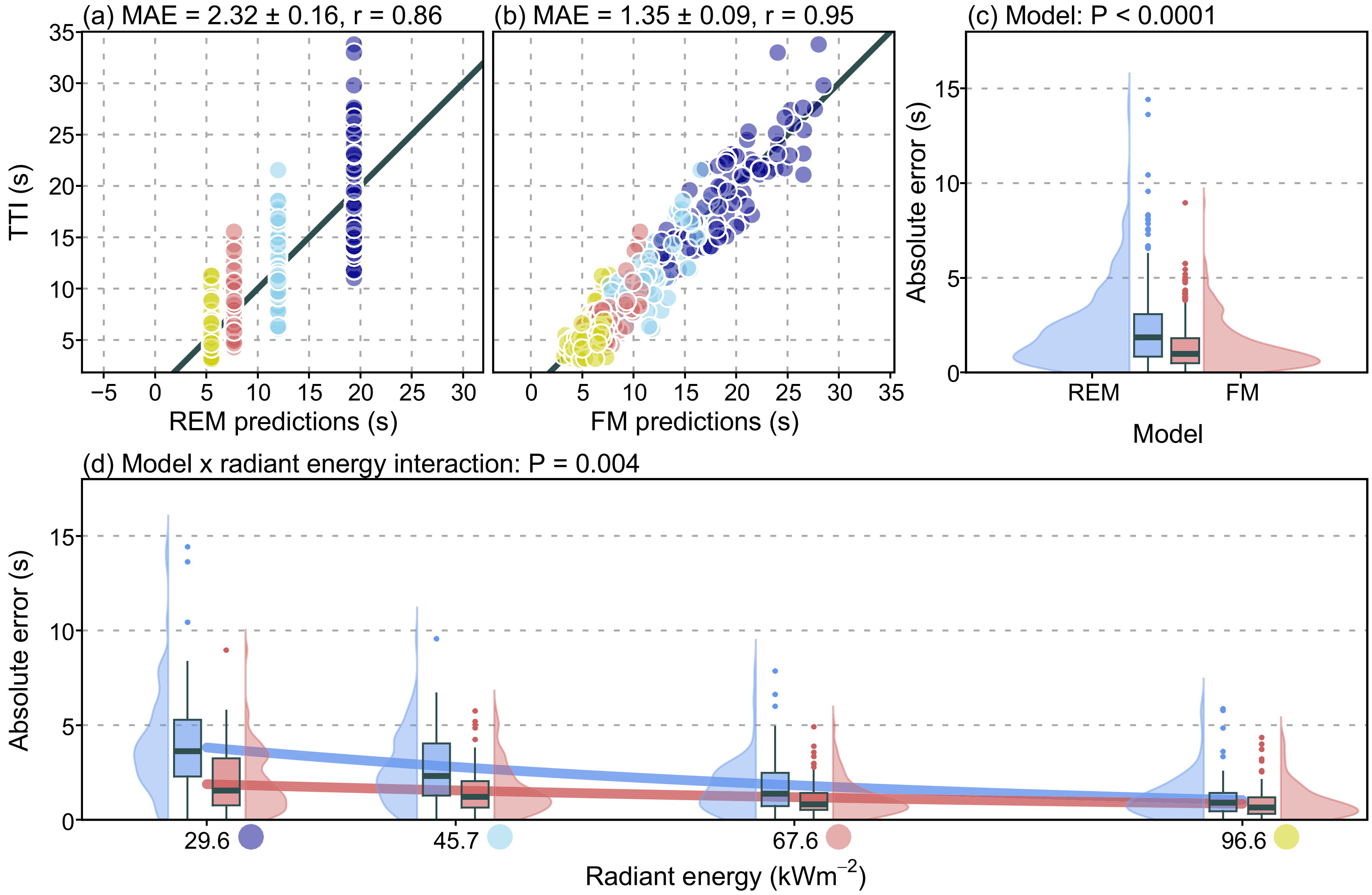
5.3 Results

5.3.1 The importance of including leaf traits in predictive modelling

The inclusion of leaf traits as explanatory variables in predictive models lowered the mean absolute error in predicting TTI by 42%, and strengthened the fit of the predictive models from $r = 0.86$ to $r = 0.95$ (Fig. 5.5a, b). Comparison between the REM and the FM showed that absolute error values were significantly lower in the FM model ($\chi^2_{1,768} = 89.34$, $P < 0.0001$; Fig. 5.5c). There was a significant relationship between absolute error and radiant energy ($\chi^2_{1,768} = 190.37$, $P < 0.0001$) with lower error significantly related to higher radiant energy, and a significant model x radiant energy interaction ($\chi^2_{1,768} = 8.33$, $P = 0.004$; Fig. 5.5d). This interaction was driven by error remaining similar and relatively low across levels of radiant energy in the FM, while error in the REM decreased with increasing radiant energy.

The inclusion of leaf traits as explanatory variables in predictive models lowered the mean absolute error in predicting ID by 70%, and strengthened the fit of the predictive models from $r = 0.44$ to $r = 0.92$ (Fig. 5.6a, b). Comparison between the REM and the FM showed that absolute error values were significantly lower in the FM model ($\chi^2_{1,768} = 327.48$, $P < 0.0001$; Fig. 5.6c), with lower error significantly related to higher radiant energy ($\chi^2_{1,768} = 93.41$, $P < 0.0001$). There was a significant model x radiant energy interaction ($\chi^2_{1,768} = 8.38$, $P = 0.004$; Fig. 5.6d). Error remained comparatively low across levels of radiant energy in the

Fig. 5.5 (following page) Comparing mean absolute error (MAE ± SE, Pearson correlation coefficient) between TTI models with (a) radiant energy as the sole explanatory variable (REM) and (b) radiant energy in conjunction with leaf traits (FM) as explanatory variables. Point colours correspond to levels of radiant energy, with a colour key shown on the x-axis of (d). The distribution of absolute error values across all observations are shown for the REM in blue and for the FM in red in (c), and for each model at each level of radiant energy in (d). Data are presented as boxplots and associated probability distributions (shaded areas). Coloured lines in (d) are the absolute error and model x radiant energy coefficients from the generalised linear model (Poisson distribution).


(a) MAE = 2.32 ± 0.16, r = 0.86

(b) MAE = 1.35 ± 0.09, r = 0.95

(c) Model: P < 0.0001

(d) Model x radiant energy interaction: P = 0.004

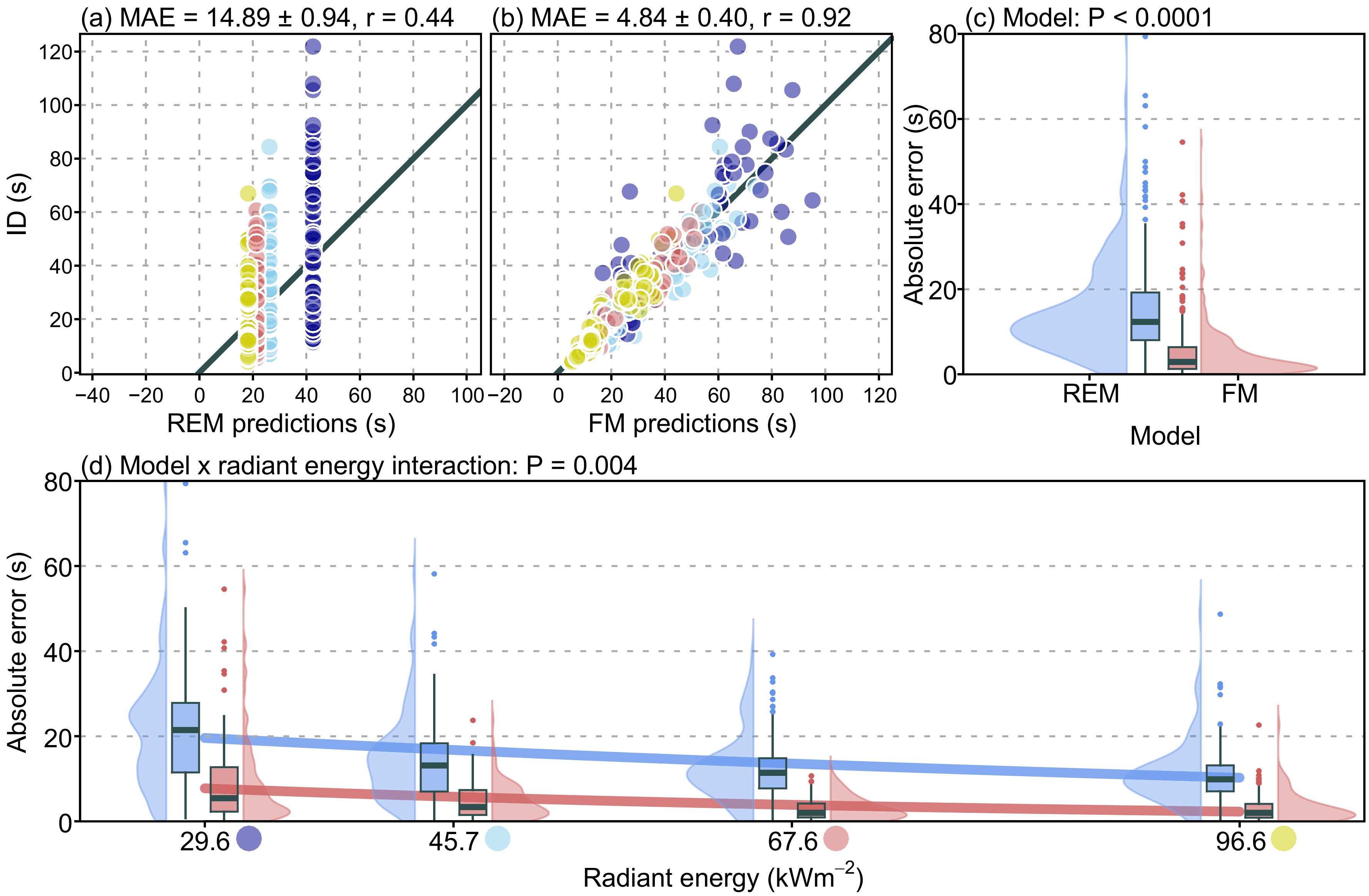

(a) MAE = 14.89 ± 0.94, r = 0.44
(b) MAE = 4.84 ± 0.40, r = 0.92
(c) Model: P < 0.0001
ID (s)
120
100
80
60
40
20
0
−40
−20
0
20
40
60
80
100
REM predictions (s)
−20
0
20
40
60
80
100
120
FM predictions (s)
Absolute error (s)
REM
FM
Model
(d) Model x radiant energy interaction: P = 0.004
Absolute error (s)
29.6
45.7
67.6
96.6
Radiant energy (kWm^{-2})

Fig. 5.6 (previous page) Comparing mean absolute error (MAE ± SE, Pearson correlation coefficient) between ID models with (a) radiant energy as the sole explanatory variable (REM) and (b) radiant energy in conjunction with leaf traits (FM) as explanatory variables. Point colours correspond to levels of radiant energy, with a colour key shown on the x-axis of (d). The distribution of absolute error values across all observations are shown for the REM in blue and for the FM in red in (c), and for each model at each level of radiant energy in (d). Data are presented as boxplots and associated probability distributions (shaded areas). Coloured lines in (d) are the absolute error and model x radiant energy coefficients from the generalised linear model (Poisson distribution).

REM, while error decreased more steeply with increasing radiant energy in the FM, generating a significant model x radiant energy interaction ($\chi^2_{1,768}$ = 8.38, P = 0.004. Fig. 5.6d).

In the REM, all leaves that did not flame were correctly predicted at 29.6 and 45.7 kWm^{-2}, and all leaves that flamed were correctly predicted at 67.6 and 96.6 kWm^{-2} (Fig. 5.7a). However, all leaves which flamed at 29.6 and 45.7 kWm^{-2} and all leaves which didn't flame at 67.6 and 96.6 kWm^{-2} were misclassified by this model as non-flaming and flaming respectively (Fig. 5.7a). This arose from the model simply predicting for all leaves in each radiant energy level the most prevalent response within a given radiant energy level, due to the mechanics of the logistic regression model returning a probability equal to the proportion of samples flaming within each level of radiant energy. In the FM, and accepting model predictions > 0.5 as indication of flaming balanced this effect, the inclusion of leaf traits increased the proportion of correctly classified flaming leaves at 45.7 kWm^{-2}, and non-flaming leaves at 67.6 and 96.6 kWm^{-2} (Fig. 5.7b). These increases in accuracy were

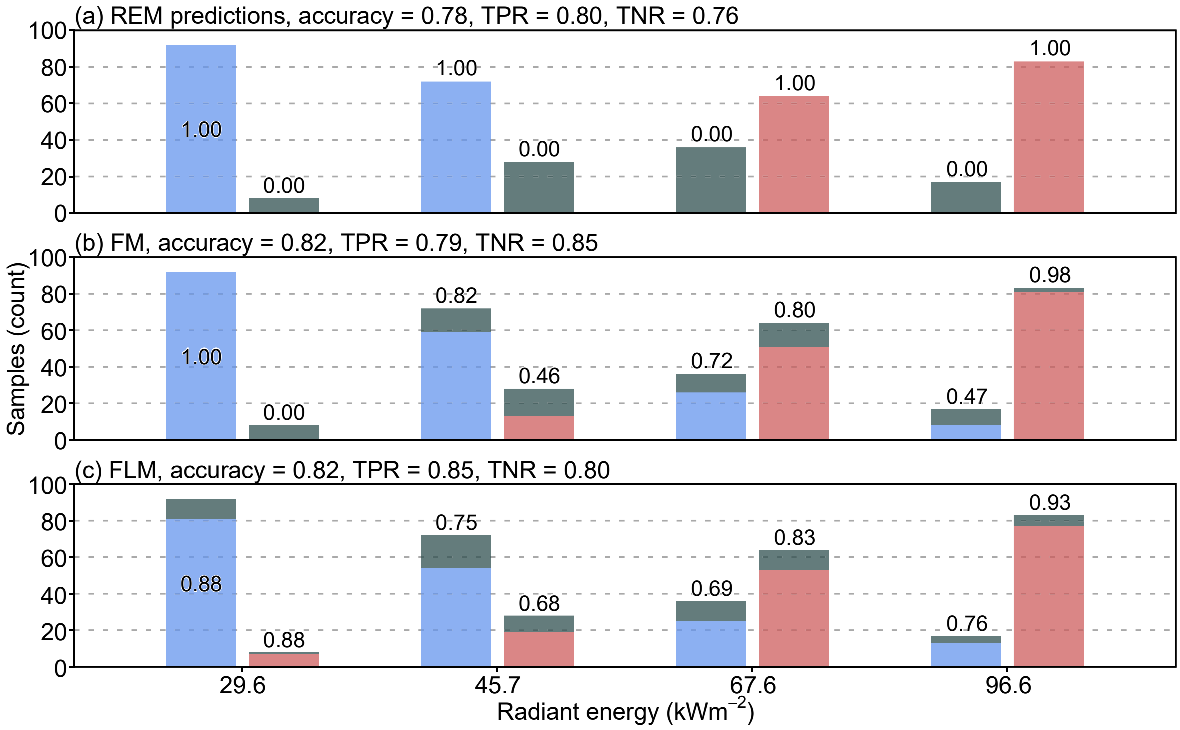


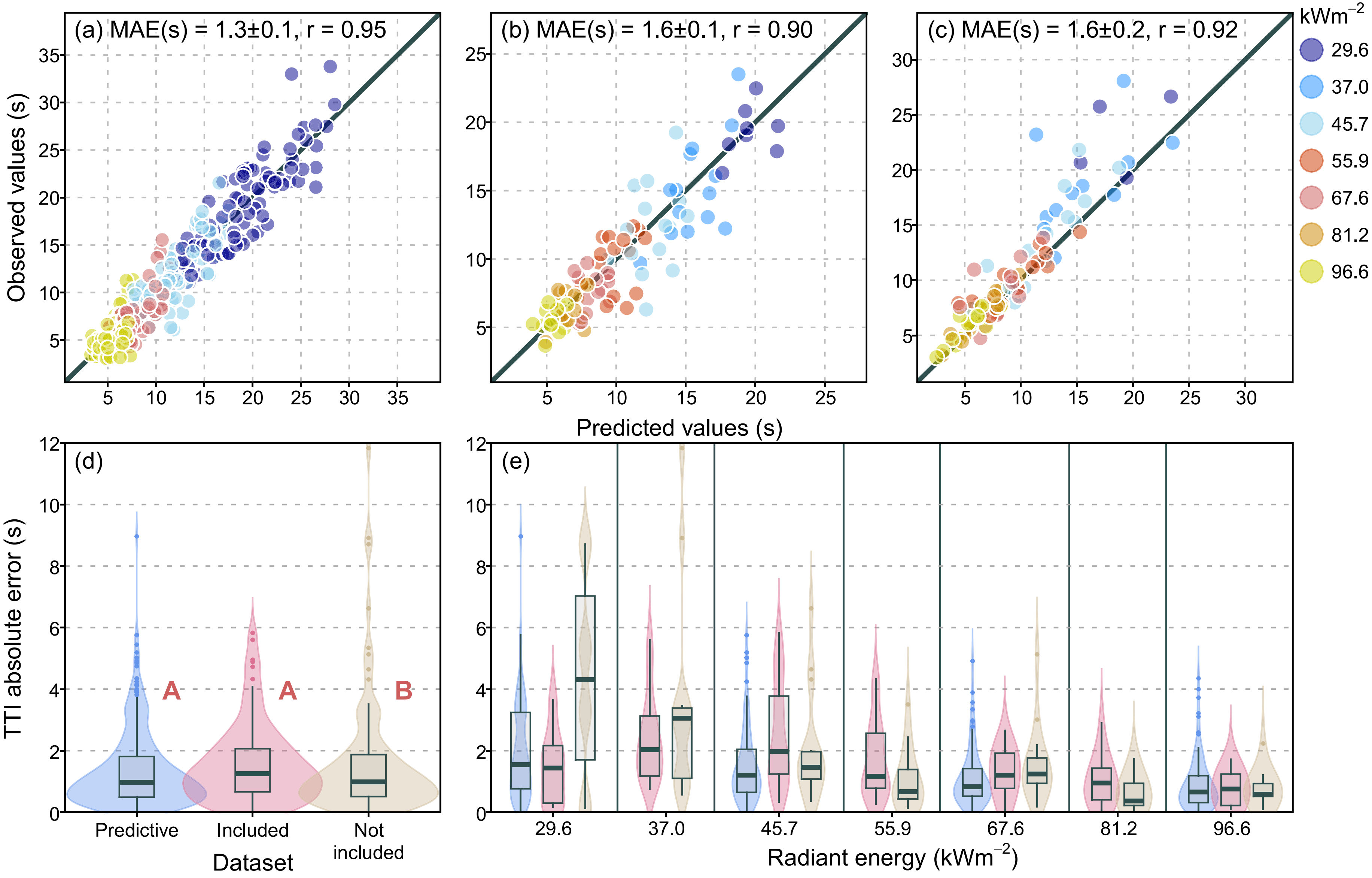
Fig. 5.7 Barcharts of classification accuracy of the (a) REM, (b) the FM, and (c) the FLM with the application of the $P_{flaming}$ approach. Bars to the left of the x-axis divisions show the counts of non-flaming samples, and flaming samples to the right. The blue and red shaded sections of these bars indicate the counts of samples which were correctly predicted (also shown as numeric proportions above or within bars).

attended by relative decreases in the TNR at 45.7 kWm^{-2}, and in the TPR at 67.6 and 96.6 kWm^{-2}, while flaming leaves at the lowest level of radiant energy remained misclassified as non-flaming. Flaming leaves at 45.7 kWm^{-2}, and non-flaming leaves at 96.6 kWm^{-2} were also classified no more accurately than would be expected from random chance (i.e., approximately 0.5) by the FM model. Application of the $P_{flaming}$ approach in the FLM allowed a compromise between the two types of classification errors (false positive and false negative) within each level of radiant energy (Fig. 5.7c). Where a decrease in a category of classification resulted, it was balanced by an increase in the other, e.g. at 29.6 kWm^{-2}, the TNR dropped from one to 0.88, while the TPR rose from zero to 0.88. Across all levels of radiant energy, TPR and TNR were also substantially above what would be expected from chance alone.

5.3.2 Comparison of prediction error in TTI between the predictive and validation datasets

Absolute error differed significantly as a function of dataset, with error significantly higher in the species not included in the predictive dataset compared to both error in the original predictive dataset and error in the species included in the predictive dataset ($\chi^2_{2,567} = 9.47$, P = 0.009; Fig. 5.8d). Error decreased significantly with higher radiant energy ($\chi^2_{1,567} = 94.88$, P < 0.0001; Fig. 5.8e), and there was a significant dataset x radiant energy interaction ($\chi^2_{2,567} = 13.95$, P = 0.0009; Fig. 5.9). Error in prediction for species not included in the predictive dataset decreased significantly more rapidly with increasing radiant energy when compared to both the predictive dataset and to the species included in the predictive dataset (Fig. 5.9).

Fig. 5.8 (following page) Plots of observed values against predicted values of TTI for the (a) predictive dataset, (b) species in the validation dataset included in the predictive dataset, and (c) species in the validation dataset not included in the predictive dataset. Points in (a) to (c) are coloured by radiant energy level, with a key shown at the right of (c). Absolute error values across all observations for each dataset's predictions are shown in (d), with red letters indicating significant differences among the groups. Absolute error values within each radiant energy level and dataset are shown in (e). Data are presented as boxplots with shaded density distributions in (d) and (e).


(a) MAE(s) = 1.3±0.1, r = 0.95
(b) MAE(s) = 1.6±0.1, r = 0.90
(c) MAE(s) = 1.6±0.2, r = 0.92
Observed values (s)
Predicted values (s)
5
10
15
20
25
30
35
kWm^{-2}
29.6
37.0
45.7
55.9
67.6
81.2
96.6
(d)
(e)
TTI absolute error (s)
0
2
4
6
8
10
12
A
A
B
Predictive
Included
Not included
Dataset
Radiant energy (kWm^{-2})

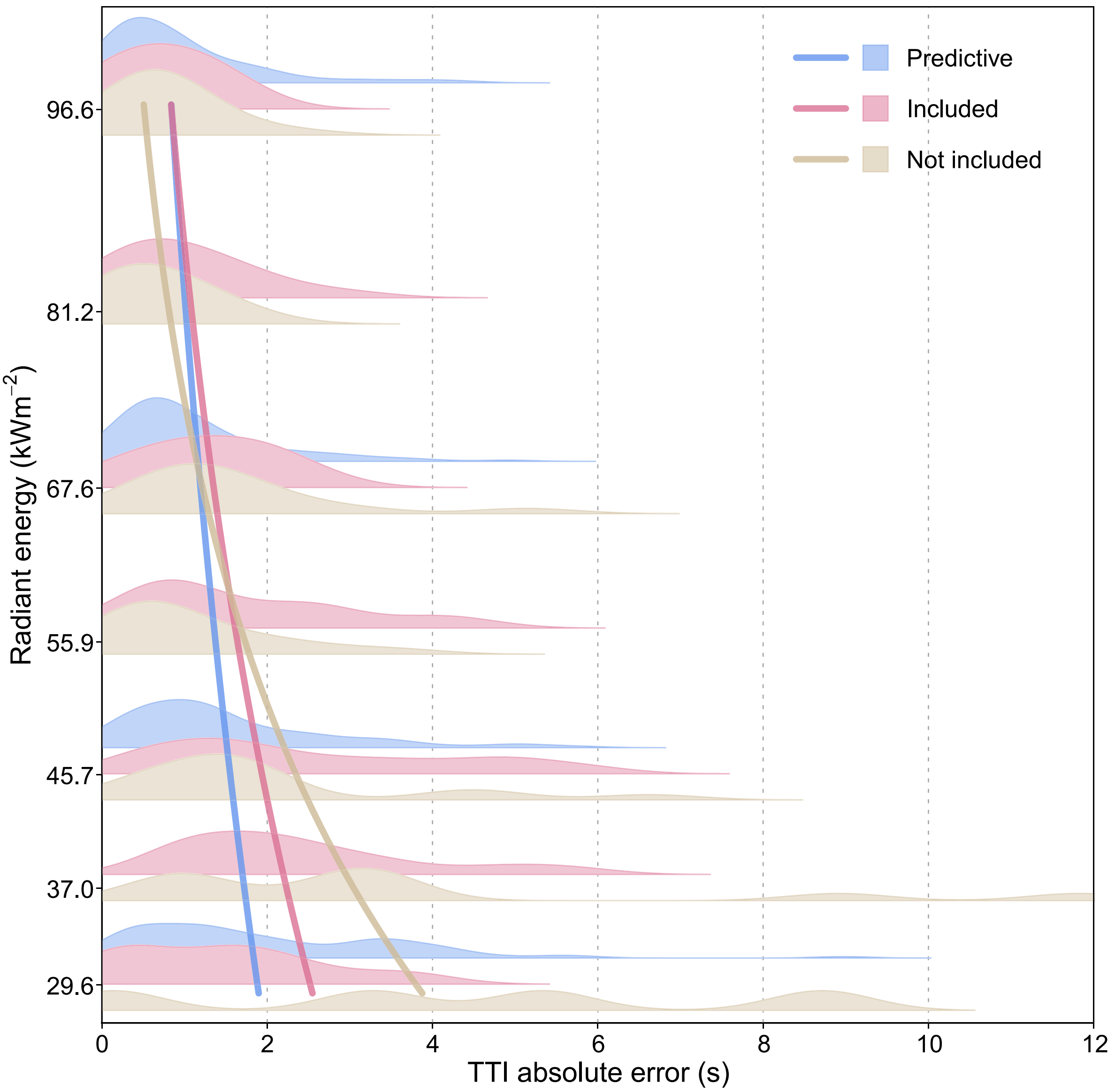
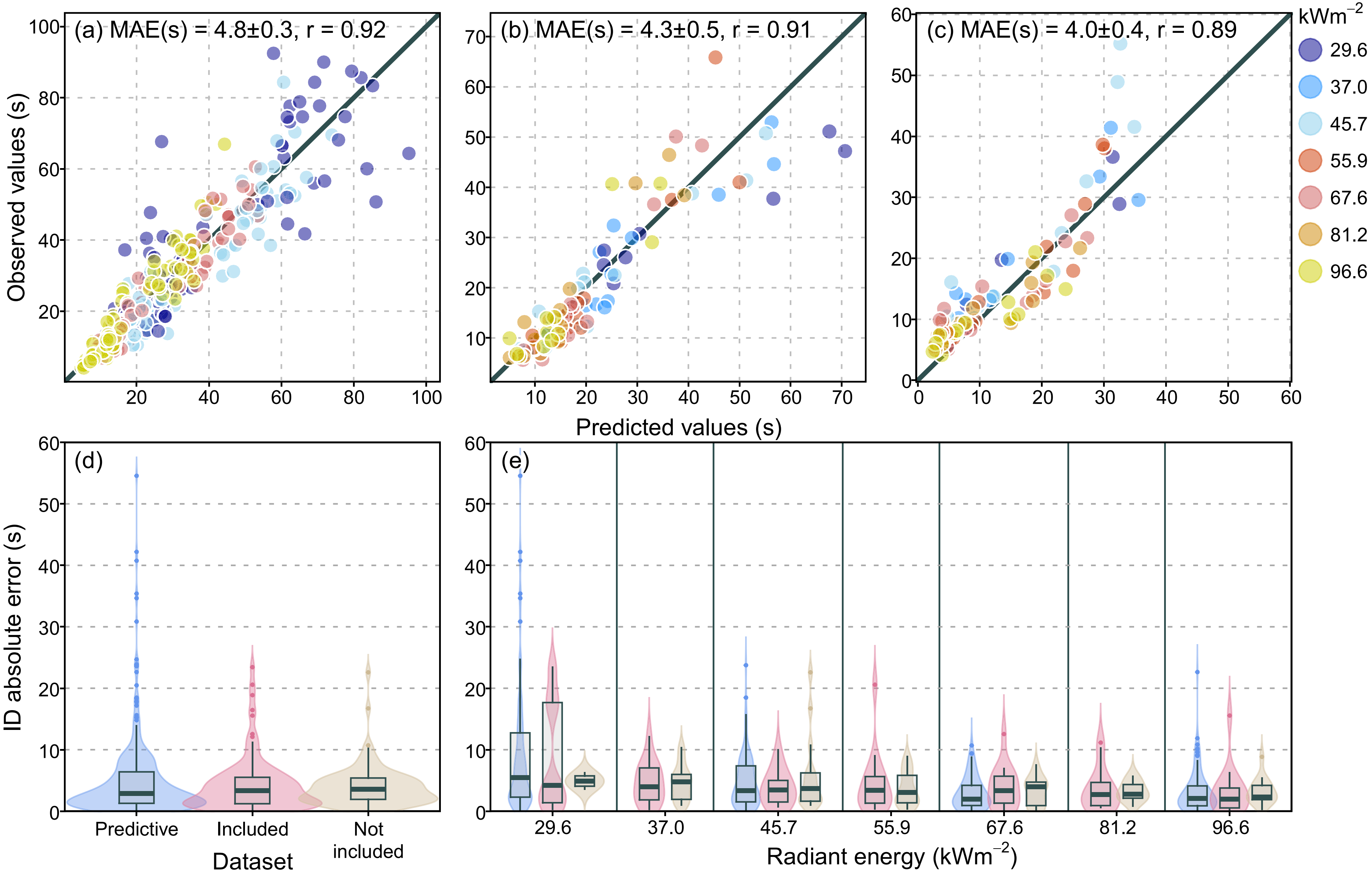


Fig. 5.9 Absolute error values of TTI for each of the three datasets shown as separate probability density distributions for each level of radiant energy. Lines are the TTI absolute error by dataset x radiant energy coefficient from the generalised linear model (Poisson). A colour key to the datasets is shown at top right.

5.3.3 Comparison of prediction error in ID between the predictive and validation datasets

There was no significant effect of dataset on absolute error ($\chi^2_{2,567} = 1.28$, $P = 0.50$; Fig. 5.10d). However, absolute error decreased significantly with increasing radiant energy ($\chi^2_{1,567} = 67.94$, $P < 0.0001$; Fig. 5.10e). There was no significant dataset x radiant energy interaction ($\chi^2_{2,567} = 3.03$, $P = 0.2$; Fig. 5.11).

Fig. 5.10 (following page) Plots of observed values against predicted values of ID for the (a) predictive dataset, (b) species in the validation dataset included in the predictive dataset, and (c) species in the validation dataset not included in the predictive dataset. Points in (a) to (c) are coloured by radiant energy level, with a key shown at the right of (c). Absolute error values across all observations for each dataset's predictions are shown in (d), with red letters indicating significant differences among the groups. Absolute error values within each radiant energy level and dataset are shown in (e). Data are presented as boxplots with shaded density distributions in (d) and (e).


(a) MAE(s) = 4.8±0.3, r = 0.92
(b) MAE(s) = 4.3±0.5, r = 0.91
(c) MAE(s) = 4.0±0.4, r = 0.89
Observed values (s)
Predicted values (s)
20
40
60
80
100
10
30
50
70
0
kWm^{-2}
29.6
37.0
45.7
55.9
67.6
81.2
96.6
(d)
(e)
ID absolute error (s)
Predictive
Included
Not included
Dataset
Radiant energy (kWm^{-2})

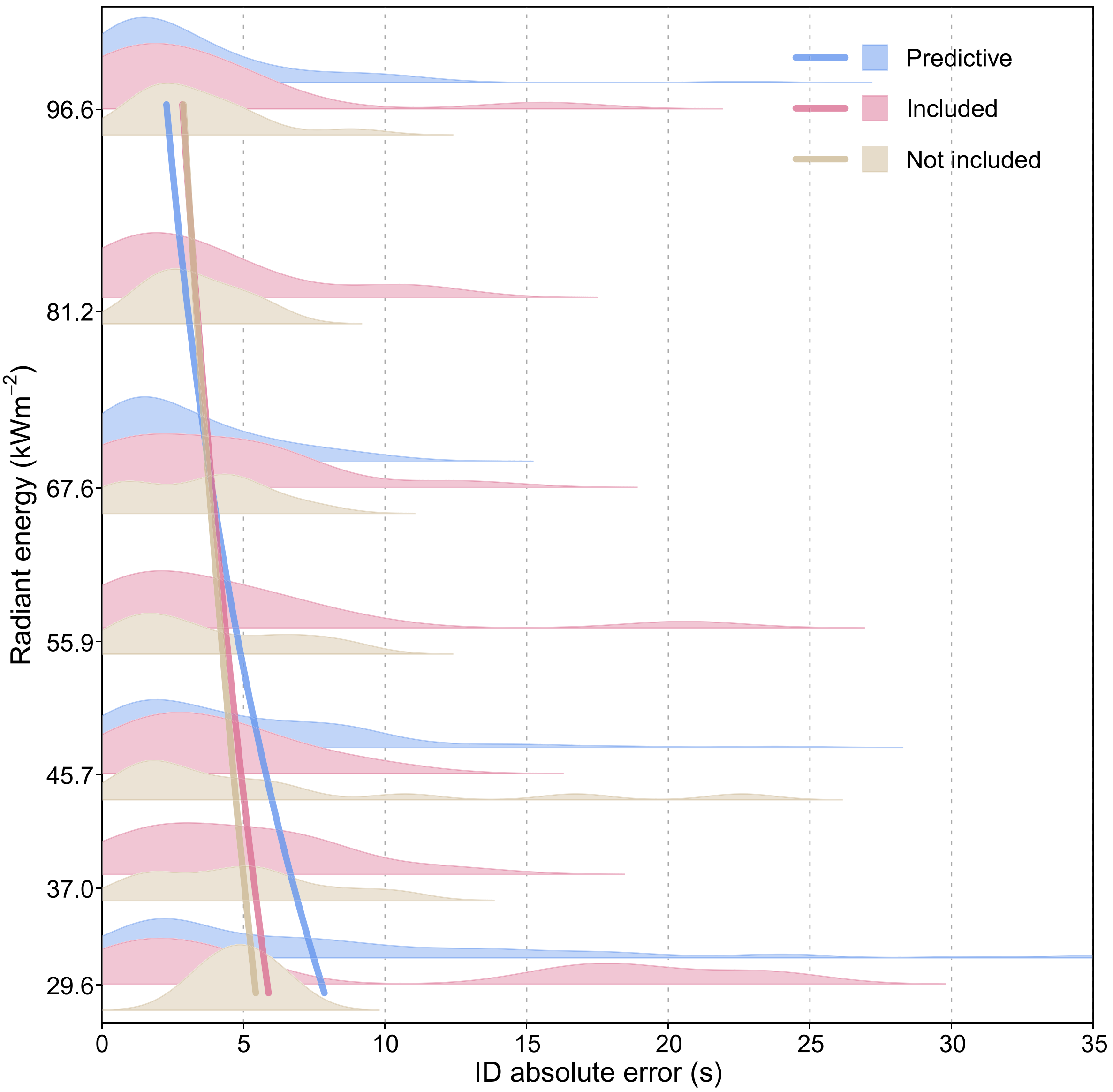


Fig. 5.11 Absolute error values of ID for each of the three datasets shown as separate probability density distributions for each level of radiant energy. Lines are the ID absolute error by dataset x radiant energy coefficient from the generalised linear model (Poisson). A colour key to the datasets is shown at top right.

5.3.4 Comparison of classification accuracy of leaf flaming between the predictive and validation datasets

Overall accuracy for prediction of leaf flaming did not differ significantly among the datasets ($\chi^2_{2,604}$ = 1.32, P = 0.50; Fig. 5.12a), and was balanced across the datasets in predicting both flaming and non-flaming samples ($\chi^2_{1,604}$ = 2.99, P = 0.08). No significant dataset x flaming behaviour effect was found ($\chi^2_{2,604}$ = 0.18, P = 0.90; Fig. 5.12b), with accuracy for predicting non-flaming samples and flaming samples similar across the datasets. The largest divergence from the modelled data accuracy was for non-flaming samples in the species not included in the predictive dataset (0.75 of samples correctly predicted as non-flaming vs 0.80 in the modelled data; Fig. 5.12b). Within and across levels of radiant energy, accuracy among the models was broadly similar (Fig. 5.13), with only the classification of flaming samples at 29.6, 37.0 kWm^{-2} (misclassifying two flaming samples), non-flaming samples at 81.2 kWm^{-2}, and 96.6 kWm^{-2} (six and two samples respectively), falling below 50% accuracy (representing model accuracy no better than chance; Fig. 5.13b). The model maintained discriminatory power to identify non-flaming samples of species not included in the predictive dataset at higher temperatures (Fig. 5.13c), and high accuracy in identifying flaming samples above 55.9 kWm^{-2} in the validation dataset species (Fig. 5.13b and 5.13c).

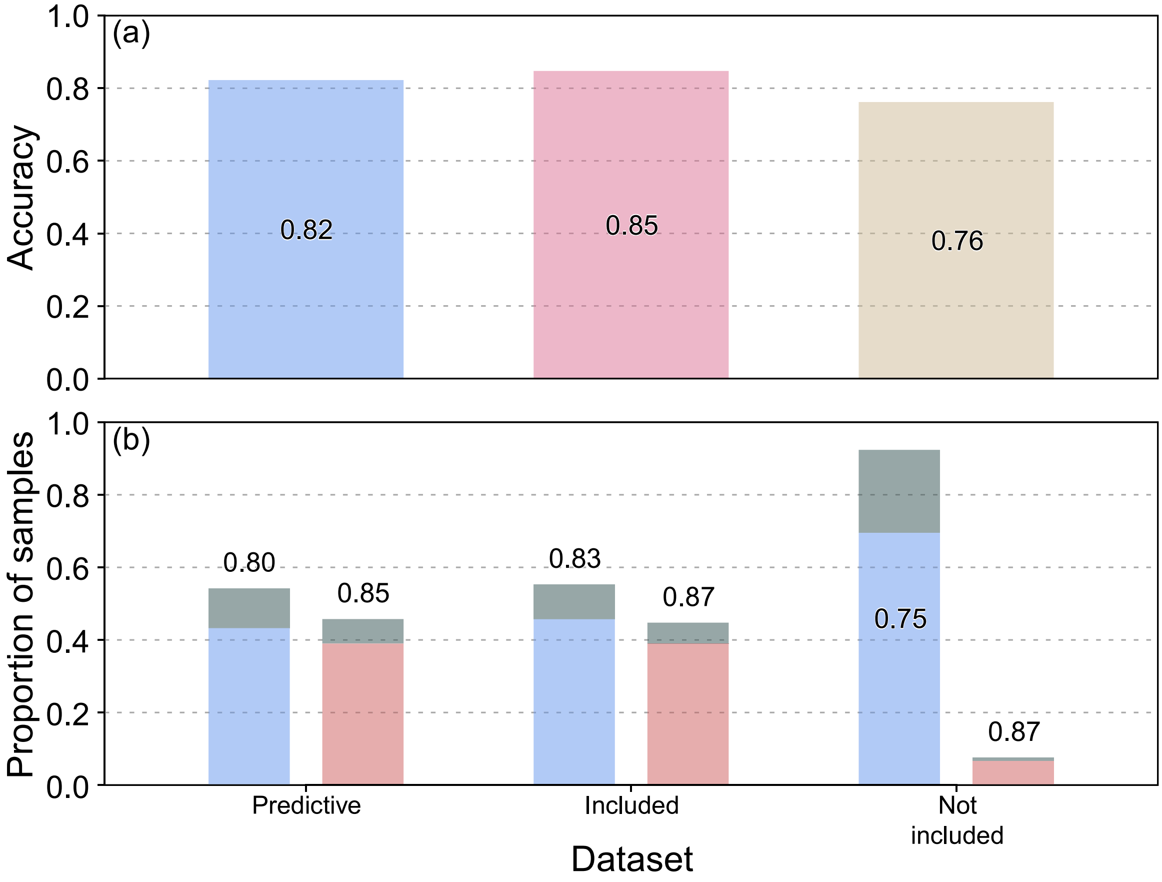


Fig. 5.12 (a) Overall accuracy of predictions for leaf flaming (or not) for the three datasets and (b) classification accuracy for samples which flamed and did not by dataset. In (b), bars to the left of the x-axis divisions show the proportion of non-flaming samples, and bars to the right show the proportion of flaming samples. The blue and red shaded sections of these bars indicate the proportions of samples which were correctly predicted. Numbers above or within bars indicate the proportion of samples correctly predicted.

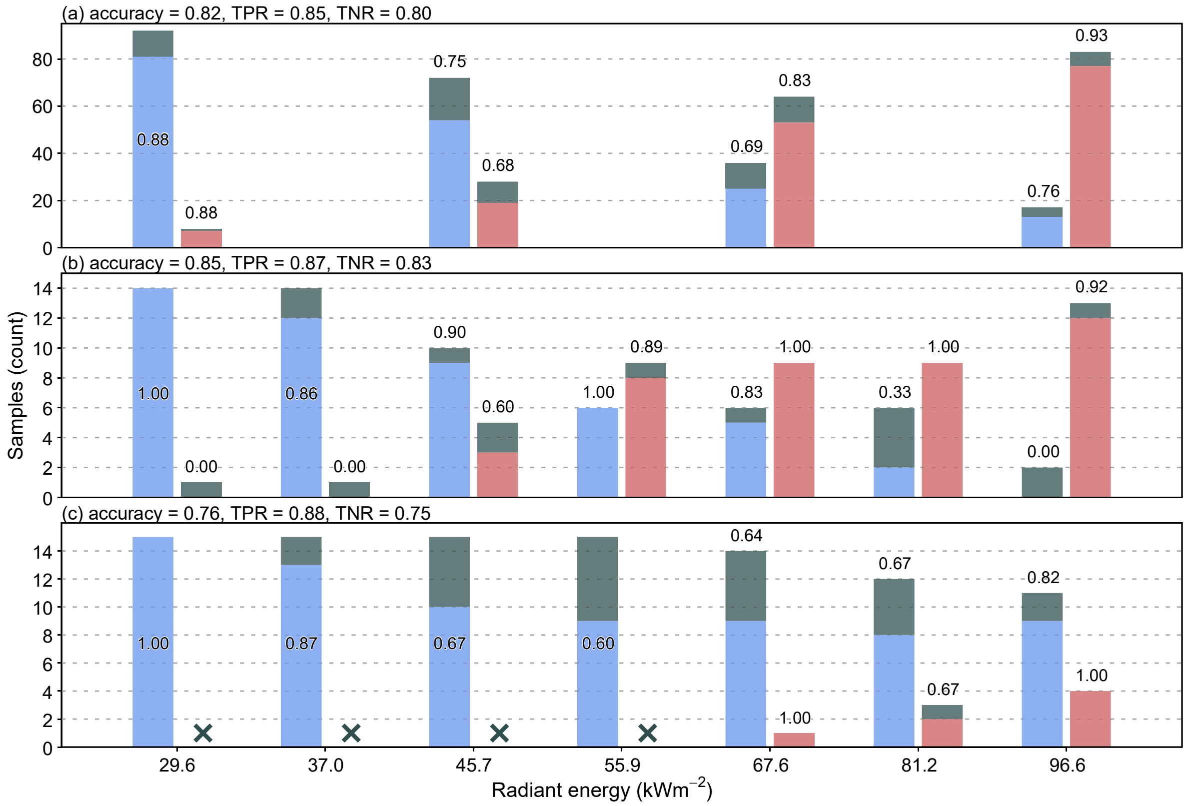


Fig. 5.13 Classification accuracy by radiant energy level for the predictive dataset (a), the species included (b), and the species not included in the predictive dataset (c). Bars to the left of the x-axis divisions show the counts of non-flaming samples, and flaming samples to the right. The blue and red shaded sections of these bars indicate the counts of samples which were correctly predicted. Numbers above or within bars indicate the proportion of samples correctly predicted.

5.4 Discussion

Leaf traits were shown to be an important dimension in the prediction of leaf flammability, with their inclusion in modelling leading to a considerable decrease in absolute error of prediction for TTI, ID and leaf flaming. As other authors, and Chapter 2 of this thesis have demonstrated, strong relationships exist between leaf traits and flammability attributes (Gill & Moore 1996, Murray *et al.* 2013, Grootemaat *et al.* 2015), which underpins this finding.

The increase in accuracy overall was greatest for ID and leaf flaming. As explored in further detail in Chapter 4, TTI shortens and leaf flaming becomes more prevalent with increasing radiant energy, while ID shows relatively smaller changes. This explains to some degree why the inclusion of leaf traits in predicting TTI results in relatively smaller changes in the accuracy of prediction, being more strongly determined by radiant energy. For ID, leaf traits, particularly LA (shown in Chapter 2 of this thesis) have a very strong effect on interspecific differences in ID. Addition of the $P_{flaming}$ approach further improved accuracy of the model predictions, important in correctly classifying flaming leaves at low radiant energy, and non-flaming leaves at high radiant energy. This is a crucial consideration, given that plant species chosen on the basis of low leaf-flammability might be rejected for flaming at low fire intensity, or selected for being unlikely to flame at higher fire intensity.

Overall the predictive models for TTI and ID performed well, returning small absolute errors of comparable size between the predictive and validation datasets. Importantly, absolute error between the species included and not included in the predictive dataset were of similar size, illustrating the utility in applying the models to species not included in the predictive dataset, while maintaining accuracy. While a significant difference was found for absolute error for TTI between the validation dataset species not included in the predictive dataset and the absolute error in the predictive dataset and validation dataset species included in the predictive dataset, the difference was relatively small. Across both datasets for TTI and ID, absolute error was lower at higher radiant energy, and higher for the validation dataset species not included in the predictive dataset. Interpolation between the levels of radiant energy used in the predictive dataset also showed similar errors relative to the adjacent levels of radiant energy in the predictive dataset. For use in estimating relative flammability of plant leaves, an intermediate level of radiant energy might be used for higher accuracy (e.g. 50 to 60 kWm^{-2}, a furnace temperature of approximately 670°C to 740°C), avoiding lower values of radiant energy where absolute error is greater, and higher levels of radiant energy where differences in TTI and ID among species are smaller and modelling error may confound interspecific differences. Classification of flaming was relatively accurate, maintaining accuracy above that expected by chance, with interpolated prediction in the validation dataset showing similar accuracy to adjacent levels of radiant energy in the predictive dataset. The accuracy of this model might be improved further with data on the presence of volatile oils in species leaves, although laboratory determination of this is likely to be time consuming (Llusià *et al.* 2006, McKiernan *et al.* 2014, Pausas *et al.* 2016), with direct flammability testing possibly a faster alternative. A further consideration, not captured in this experimental approach, is how the flaming response of leaves within the flame plume of adjacent leaves, or leaves undergoing ember attack may be affected. If the underlying leaf trait and leaf flaming relationship found here for spontaneous flaming due to radiant energy hold, these differences may be minor. However, leaf volatiles in the case of leaves within the flame plume, or leaf traits such as cuticle thickness which may act as a buffer to heating of the leaf at a point source during ember attack may play a larger role in these circumstances.

The use of leaf trait databases could be used to generate relative flammability ratings for both wild occurring and decorative plant species. In selection of 'green firebreak' species (Curran *et al.* 2018, Murray *et al.* 2018), these models could be applied to select for low-leaf flammability species, with results from the models possibly passed on to a compound flammability rating (e.g. the overall leaf flammability index presented in Chapter 3, see also Pérez-Harguindeguy *et al.* 2013). In the case of green firebreaks or garden plantings at fire prone wildland-urban interfaces, several calculations of TTI and ID could be made across a range of radiant energy values reflecting the possible fire intensities likely to be experienced at the planting site, and mean values (the geometric mean, rather than the arithmetic mean, may be more accurate where a wide range of radiant energies is used) taken to provide a more accurate prediction of flammability. For predicted leaf flaming, it may be most useful to score plant species on the lowest radiant energy that they are predicted to flame. As these models may be applied for any fire intensity within the range of radiant energy that was tested experimentally, there may be applications in fire behaviour models which explicitly include fire intensity. Fire movement, particularly at lower intensities might be most affected by leaves flaming and spreading fire to adjacent leaves (Bradstock & Gill 1993, Zylstra *et al.* 2016), or neighbouring plants. Accurate predictions of which plant species leaves are likely to flame at a given fire intensity might be incorporated into current models to provide more accurate predictions of fire spread.

Chapter 6

General discussion

6.1 Were the aims of this thesis met?

Broadly, the aims of this thesis were to explore interspecific patterns and processes in leaf flammability attributes, the relation between habitat, leaf traits and flammability attributes, and the effect radiant energy has on flammability attributes. This thesis has met these aims by showing landscape differences in plant species leaf flammability, quantifying relationships among flammability attributes, demonstrating the effect that increasing radiant energy has on flammability attributes, and building predictive models of leaf flammability that account for radiant energy, with leaf traits being a common element to the various components of the research. The broad focus of the thesis was addressed with these specific aims being met:

1. *To quantify interspecific patterns in leaf flammability attributes in woodland and forest plant species.*

Chapter 2 of this thesis presented data for TTI, ID[BD] and MLR for 92 species (57 species from woodland, 35 species from forest). These plant communities are separated geographically by short distances, experience the same rainfall and weather patterns, and exist on the same geological substrate (Hawkesbury Sandstone), so can be taken to represent a good model system to quantify differences due to habitat. During data analysis, a phylogenetically informed approach (PGLS) was used to control for possible similarities in flammability attributes that may have arisen due to shared ancestry. Overall, my results showed considerable variation among species in flammability attributes, with TTI ranging from 2 s to 31 s (mean: 10 s), ID[BD] from 2 s to 60 s (mean: 19 s), and MLR from 0.2 mgs^{-1} to 20.5 mgs^{-1} (mean: 5.3 mgs^{-1}).

2. *To compare leaf flammability attributes between two contrasting habitats.*

In Chapter 2 TTI, ID[BD] and MLR of leaves from woodland (exposed habitat) and forest species (sheltered habitat) were compared. Sheltered forest plant species were found to begin incandescent combustion significantly more quickly, and burn at a significantly higher rate (MLR) compared to species from exposed woodland, which tends to be more fire-prone (Bradstock *et al.* 2010, Hammill & Tasker 2010). This finding shows that the plant species from less fire-prone habitats may have equal or higher flammability than species from more fire-prone habitats, demonstrating that at leaf level, these species do not appear to have evolved flammability in these flammability attributes, but that is has arisen through other leaf trait adaptations. Sheltered habitat is cooler and wetter relative to exposed habitat, through receiving lowered amounts of direct sunlight and protection from wind by surrounding topography, and proximity to water sources at gully bottoms, factors which are also largely responsible for spatial patterns in fire (Bradstock *et al.* 2010, Hammill & Tasker 2010). With climate change, changes in rainfall may lead to a ‘drying out’ of sheltered habitat, and also change patterns in fire behaviour, given that the available fuels are at least as flammable as those in exposed habitats. Given the physiological importance of the leaf traits driving leaf flammability, it appears unlikely that plant species in the more fire-prone habitat would evolve higher leaf flammability through leaf trait adaptations as the specific relationships (larger LA and lower LMA) which results in higher ignitibility (lower TTI) and combustibility (higher MLR) are a poor fit for the drier, brighter conditions in exposed woodland habitats. However, it does remain conceivable that certain combinations of life history traits (e.g., quick recruitment after fire in obligate seeding species) and ecological conditions (e.g., flammable species with fire survival adaptations coexisting with species with less effective fire survival strategies, Bond & Midgley 1995), might favour evolution towards higher flammability, to 'kill thy neighbour'. Disentangling patterns such as these would require careful work in an appropriate model ecosystem and carefully chosen species.

3. *To explore the relationships among leaf flammability attributes, and identify plant species with low-leaf-flammability.*

In Chapter 3, a range of flammability attributes representing ignitibility and sustainability were defined in the flammability temporal pathway, and showed strong inter-correlations. However, the nature of these correlations confounded simple identification of low-leaf-flammability species, with faster ignitibility associated with shorter sustainability, and higher combustibility (presence of flaming), related to longer sustainability. The OLFI flammability metric attempts to score species' leaf flammability by giving equal weight to ignitibility and sustainability processes (through the use of scaled and centred values of each flammability attribute), and classifying high combustibility species. Smaller leafed species were found to have slow ignitibility, shorter sustainability and lower combustibility. This relationship between leaf size and flammability might be usefully tested at larger scale by burning plant shoots (Calitz *et al.* 2015, Wyse *et al.* 2016, Battersby *et al.* 2017, Wyse *et al.* 2018) to determine if this relationship is consistent at plant branch scale. Other considerations to be made, beyond leaf level flammability are: resistance to desiccation to avoid plants becoming a more flammable through water stress; low or no retention of dead branches; absence of bark shedding, and possibly being non-deciduous to avoid accumulation of leaf litters. While water stress in garden plants can be avoided with manual watering, water restrictions during fire season weather may preclude this. Garden maintenance, pruning of dead branches and removal of accumulated litter may ameliorate other factors, however homeowners may not necessarily be relied upon to undertake this.

4. *To provide further insight into the relationship between leaf flammability attributes and leaf traits.*

In Chapter 2, partial linear regression was used to disentangle the relationships between LA, LMA and FMC, and the flammability attributes TTI, ID[BD] and MLR, identifying strong relationships between leaf flammability and leaf traits. This was extended in Chapter 3 where the ignitibility, sustainability and OLFI indices were used as responses in multiple linear regression with LA, LMA and LWC as predictors. For the sustainability index, the occurrence of leaf flaming, and OLFI, LA emerged as a key leaf trait, with larger leaves being associated with greater leaf flammability in each instance. For the ignitibility index, LMA was found to be the most important single predictor. For all three indices and also leaf combustibility, large amounts of the variation among species was explained by leaf traits. Chapter 5 further expanded on this, showing the importance of leaf traits in prediction of flammability attributes, their inclusion vastly improved the accuracy of predictions of TTI, ID and the flaming behaviour of individual samples above that for models using radiant energy alone.

5. *To examine the effect fire intensity may have on flammability attributes.*

In Chapter 4, inclusion of a radiant energy gradient in experimentation showed that with increasing radiant energy, species identity remained relatively more important for sustainability than for ignitibility, with interspecific differences in ignitibility being much smaller in magnitude. Species maintained their distinctiveness in particular for ID, and to a lesser degree in FD. Patterns in flaming behaviour were found to differ widely among species, which may be of key importance for fire behaviour given that flaming leaves might more easily spread fire to adjacent leaves. Use of leaves maintained at field LWC levels in this experiment may have underestimated the convergence in TTI and TTF that would be experienced in fire-cured fuels, given that LWC (the related measure FMC was used in Chapter 2), was found to be important in slowing TTI, and likely has the same effect on TTF. Conversely, the lack of association found between LWC and ID[BD], is less likely to have affected the transferability of these findings to wildfire conditions.

6. *To build predictive models of flammability attributes.*

In chapter 5 I built predictive models of TTI, ID and leaf flaming, and used a separate dataset to test the accuracy of these predictions. Building the models using leaf traits and radiant energy as predictors allows the models to be applied to new datasets of leaf traits within the range of radiant energy included in the modelling. I also demonstrated that the inclusion of leaf traits in the modelling produced far more accurate predictions than those that could be made using radiant energy alone. These models may potentially have application in estimating leaf flammability from leaf trait databases, or in fire modelling.

6.2 Future research directions

This thesis has focussed exclusively on single leaf flammability, a useful next step would be to test the relationship between single leaf flammability and scale up to branch level flammability using methods such as those outlined by Jaureguiberry *et al.* (2011) and implemented by Calitz *et al.* 2015, Wyse *et al.* 2016, Battersby *et al.* 2017, Wyse *et al.* 2018, among others. Recent research on New Zealand endemic plants (Alam *et al.* 2019) has shown a decoupling between single leaf flammability and flammability at branch level. Further investigation may clarify the relationship between flammability at these two levels of plant architecture, and if Australian native plants, which likely exhibit differing ranges of leaf traits, display the same patterns in flammability. The muffle furnace method of flammability testing remains relatively fast (approximately five minutes per sample) compared to other methods (e.g. calorimetry), and requires simple equipment available in most environmental science laboratories, and may be the least time consuming and simplest method for determining plant flammability without specialised equipment. Phylogenetic patterns in leaf flammability might also be further examined, applying more complicated phylogenetic methods such as Ornstein-Uhlenbeck models of evolution (Butler & King 2004), or modelling accounting for convergent evolution towards higher or lower flammability at leaf level (SURFACE; Ingram & Mahler 2013). Examination of species from areas with differing fire risk using these methods, may go some way towards answering the

Mutch (1970) hypothesis. If the modelling were to show a convergence of disparate plant lineages from highly fire prone habitats towards higher flammability, and no convergence, or convergence towards lower flammability for species from habitat experiencing infrequent fire, it would confirm this hypothesis at leaf level. Relationships between leaf flammability and fire survival adaptations (obligate seeding vs resprouting species) might also be tested, to explore the ‘kill thy neighbour’ hypothesis (Bond & Midgley 1995). Further research into volatile oils and their relationship with leaf flaming may provide more accurate predictions of leaf flaming, as effects on flammability have been found in other research (Alessio *et al.* 2008, Pausas *et al.* 2016).

6.3 Conclusion

This thesis has provided further understanding of leaf flammability in an ecological context, the relationships between leaf flammability attributes, defined the importance of species distinctiveness in leaf flammability, the possible relationships of flammability components with fire intensity and thus species distributions may be in fire behaviour in relation to leaf flammability, and provided models to predict flammability attributes which may provide reliable estimates of leaf flammability from plant traits. I believe these findings have provided information which further the understanding of plant flammability both ecologically and mechanistically, and may contribute usefully to fire behaviour modelling.

Thesis appendices

Appendix 2.1 List of study species from the two habitats separated into strata.

Habitat	**Stratum**	**Family**	**Species**
Sheltered habitat	Overstory	Myrtaceae	*Backhousia myrtifolia*
		Cunoniaceae	*Callicoma serratifolia*
		Cunoniaceae	*Ceratopetalum apetalum*
		Cunoniaceae	*Ceratopetalum gummiferum*
		Proteaceae	*Lomatia myricoides*
		Oleaceae	*Notelaea venosa*
		Proteaceae	*Persoonia linearis*
		Proteaceae	*Persoonia mollis*
		Rhamnaceae	*Pomaderris elliptica*
		Proteaceae	*Stenocarpus salignus*
		Myrtaceae	*Syncarpia glomulifera*
		Myrtaceae	*Tristaniopsis collina*
	Understory	Ericaceae	*Acrotriche divaricata*
		Pteridaceae	*Adiantum aethiopicum*
		Pteridaceae	*Adiantum hispidulum*

Araliaceae	*Astrotricha latifolia*
Myrtaceae	*Austromyrtus tenuifolia*
Blechnaceae	*Blechnum cartilagineum*
Blechnaceae	*Blechnum nudum*
Dicksoniaceae	*Calochlaena dubia*
Vitaceae	*Cissus hypoglauca*
Sapindaceae	*Dodonaea triquetra*
Proteaceae	*Grevillea mucronulata*
Dilleniaceae	*Hibbertia saligna*
Cyperaceae	*Lepidosperma filiforme*
Ericaceae	*Leucopogon lanceolatus*
Lomandraceae	*Lomandra montana*
Fabaceae	*Podolobium ilicifolium*
Lamiaceae	*Prostanthera incisa*
Fabaceae	*Pultenaea flexilis*
Smilacaceae	*Smilax australis*
Smilacaceae	*Smilax glyciphylla*
Gleicheniaceae	*Sticherus flabellatus*

		Winteraceae	*Tasmannia insipida*
		Osmundaceae	*Todea barbara*
Exposed habitat	Overstory	Proteaceae	*Banksia serrata*
		Myrtaceae	*Corymbia gummifera*
		Myrtaceae	*Eucalyptus burgessiana*
		Myrtaceae	*Eucalyptus piperita*
		Myrtaceae	*Eucalyptus punctata*
		Myrtaceae	*Eucalyptus sparsifolia*
		Proteaceae	*Hakea dactyloides*
		Myrtaceae	*Leptospermum trinervium*
		Proteaceae	*Persoonia levis*
		Proteaceae	*Xylomelum pyriforme*
	Understory	Fabaceae	*Acacia myrtifolia*
		Fabaceae	*Acacia suaveolens*
		Fabaceae	*Acacia terminalis*
		Apiaceae	*Actinotus helianthi*
		Apiaceae	*Actinotus minor*
		Euphorbiaceae	*Amperea xiphoclada*

Proteaceae	*Banksia spinulosa*
Rutaceae	*Boronia ledifolia*
Fabaceae	*Bossiaea ensata*
Fabaceae	*Bossiaea heterophylla*
Fabaceae	*Bossiaea rhombifolia*
Ericaceae	*Brachyloma daphnoides*
Cyperaceae	*Caustis flexuosa*
Cyperaceae	*Caustis pentandra*
Proteaceae	*Conospermum longifolium*
Cyperaceae	*Cyathochaeta diandra*
Goodeniaceae	*Dampiera stricta*
Fabaceae	*Daviesia corymbosa*
Phormiaceae	*Dianella caerulea*
Phormiaceae	*Dianella prunina*
Fabaceae	*Gompholobium grandiflorum*
Fabaceae	*Gompholobium latifolium*
Goodeniaceae	*Goodenia decurrens*
Proteaceae	*Grevillea phylicoides*

Proteaceae	*Grevillea sericea*
Proteaceae	*Hakea sericea*
Dilleniaceae	*Hibbertia bracteata*
Dilleniaceae	*Hibbertia obtusifolia*
Proteaceae	*Isopogon anemonifolius*
Proteaceae	*Lambertia formosa*
Ericaceae	*Leucopogon ericoides*
Ericaceae	*Leucopogon setiger*
Lomandraceae	*Lomandra longifolia*
Lomandraceae	*Lomandra multiflora*
Fabaceae	*Mirbelia rubiifolia*
Ericaceae	*Monotoca scoparia*
Iridaceae	*Patersonia glabrata*
Iridaceae	*Patersonia sericea*
Proteaceae	*Petrophile pulchella*
Rutaceae	*Philotheca hispidula*
Thymelaeaceae	*Pimelea linifolia*
Fabaceae	*Pultenaea scabra*

	Cyperaceae	*Schoenus imberbis*
	Elaeocarpaceae	*Tetratheca rupicola*
	Ericaceae	*Woollsia pungens*
	Apiaceae	*Xanthosia pilosa*
	Apiaceae	*Xanthosia tridentata*

Appendix 2.2 We used a measure of combustibility referred to as mean MLR (mass loss rate in mg/s) which expresses rate of loss in terms of leaf dry mass consumed per second. This differs from intrinsic MLR which represents the rate that a leaf burns at expressed in terms of the percentage of total leaf mass consumed per second. Intrinsic MLR can be calculated as 100 x (initial leaf dry mass – final leaf dry mass)/BD, which simplifies to 100/BD for leaves that are totally (or almost completely) consumed. Here, we present results from multiple regressions (see Methods for a description of this regression approach) of intrinsic MLR as the response variable against ln-transformed leaf trait predictors to show that mean MLR and intrinsic MLR differ in how they relate to the three leaf traits. Higher intrinsic MLR was significantly and uniquely related to both smaller leaf area and lower LMA, indicating that leaves with smaller area and lower LMA are consumed at a higher rate than leaves that are larger with a higher LMA when controlling for leaf mass. The results for intrinsic MLR are simply the inverse of the results for BD shown in Fig. 4d to Fig. 4f.

Predictor	**Coefficient (SE)**	$t_{3,88}$	**P value**	**Partial r^2**
LA	-0.32 (0.02)	-16.9	< 0.0001	0.76
LMA	-0.64 (0.07)	-9.6	< 0.0001	0.51
FMC	0.11 (0.11)	1.0	0.3	0.01

Appendix 2.3 AIC values for GLMs and PGLS models with BM or OU error structure.

Model	**GLM**	**PGLS (OU)**	**PGLS (BM)**
Ignitibility ~ Habitat + Stratum + Habitat x Stratum	- 60.4	- 41.0	27.0
Sustainability ~ Habitat + Stratum + Habitat x Stratum	42.8	59.1	94.1
Combustibility ~ Habitat + Stratum + Habitat x Stratum	131.4	143.8	131.7
LA ~ Habitat + Stratum + Habitat x Stratum	188.6	198.5	181.7
LMA ~ Habitat + Stratum + Habitat x Stratum	- 38.8	- 18.9	16.2
FMC ~ Habitat + Stratum + Habitat x Stratum	- 112.1	- 89.1	19.5
Ignitibility ~ Habitat + Stratum + Habitat x Stratum + LA + LMA + FMC	- 168.0	- 128.6	- 1.2
Sustainability ~ Habitat + Stratum + Habitat x Stratum + LA + LMA + FMC	- 99.7	- 65.5	27.9
Combustibility ~ Habitat + Stratum + Habitat x Stratum + LA + LMA + FMC	- 136.0	- 99.0	- 5.1

Appendix 3.1 Inventory of the study species with taxonomic family, growth form, and flammability attribute data. Mean ± standard deviations are presented for the attributes TTS, time to smoking; SD, smoke duration; TTI, time to ignition; ID, ignition duration; TTF, time to flaming; FD, flaming duration. NA, leaves did not begin flaming combustion.

Family	Species	Growth form	TTS (s)	SD (s)	TTI (s)	ID (s)	TTF (s)	FD (s)
Fabaceae	*Acacia myrtifolia*	Shrub	7.2 (0.5)	8.3 (2.3)	9.5 (1.2)	20.9 (3.8)	NA	NA
Fabaceae	*Acacia suaveolens*	Shrub	9.3 (1.4)	11.2 (1.3)	13.8 (1.8)	20.2 (6.1)	NA	NA
Ericaceae	*Acrotriche divaricata*	Shrub	3.2 (0.6)	1.4 (0.5)	4.3 (0.8)	4.5 (1.0)	NA	NA
Apiaceae	*Actinotus helianthi*	Herb	5.1 (1.7)	5.2 (1.1)	6.4 (1.3)	11.2 (4.1)	9.7 (1.9)	2.8 (0.7)
Araliaceae	*Astrotricha latifolia*	Shrub	4.4 (0.8)	3.0 (0.3)	4.5 (1.8)	23.6 (3.4)	4.7 (1.9)	10.1 (12.9)
Myrtaceae	*Austromyrtus tenuifolia*	Shrub	4.7 (0.4)	4.2 (0.6)	7.4 (0.3)	6.9 (1.6)	NA	NA
Myrtaceae	*Backhousia myrtifolia*	Tree	5.1 (0.5)	4.6 (1.4)	7.8 (0.4)	18 (2.8)	9 (0)	3.3 (0)
Proteaceae	*Banksia serrata*	Tree	8.5 (0.4)	7.8 (3.0)	12.9 (1.5)	49.9 (5.6)	13.7 (2.9)	12.4 (5.2)
Proteaceae	*Banksia spinulosa*	Shrub	7.1 (1.9)	6.0 (2.3)	11.8 (0.8)	11.4 (3.6)	13.0 (0.9)	0.8 (0.6)
Rutaceae	*Boronia ledifolia*	Shrub	10.4 (2.4)	4.6 (0.7)	13.7 (3.1)	12.7 (2.9)	11.5 (0)	1.4 (0)
Fabaceae	*Bossiaea heterophylla*	Shrub	6.0 (0.6)	4.1 (0.8)	12.0 (4.4)	7.8 (0.7)	NA	NA

Fabaceae	*Bossiaea rhombifolia*	Shrub	3.8 (0.3)	3.7 (0.5)	7.2 (1.1)	8.5 (1.4)	NA	NA
Ericaceae	*Brachyloma daphnoides*	Shrub	5.7 (1.5)	3.0 (1.0)	8.8 (1.5)	9.8 (3.0)	NA	NA
Cunoniaceae	*Callicoma serratifolia*	Tree	4.5 (0.8)	4.6 (0.8)	7.3 (1.4)	34.6 (5.5)	7.8 (1.7)	13.4 (2.8)
Cunoniaceae	*Ceratopetalum apetalum*	Tree	6.2 (0.6)	4.9 (1.3)	9.1 (0.4)	34.9 (6.4)	9.8 (0.9)	10.8 (6.5)
Cunoniaceae	*Ceratopetalum gummiferum*	Tree	4.9 (0.8)	6.0 (1.0)	8.5 (1.3)	14.6 (4.1)	10.8 (1.9)	1.6 (0.6)
Vitaceae	*Cissus hypoglauca*	Climber	5.4 (0.3)	4.0 (0.4)	7.1 (0.9)	18.4 (3.2)	NA	NA
Myrtaceae	*Corymbia gummifera*	Tree	7.3 (0.9)	9.5 (4.5)	10.9 (1.4)	53.7 (7.6)	12.8 (2.9)	6.2 (1.1)
Goodeniaceae	*Dampiera stricta*	Herb	7.9 (1.5)	5.9 (3.6)	12.2 (2.0)	9.5 (3.7)	NA	NA
Fabaceae	*Daviesia corymbosa*	Shrub	8.1 (2.1)	8.0 (2.1)	11.9 (2.0)	21.8 (5.4)	NA	NA
Sapindaceae	*Dodonaea triquetra*	Shrub	6.9 (0.9)	5.2 (1.6)	8.9 (1.4)	26.8 (1.0)	8.3 (0)	2 .0 (0)
Myrtaceae	*Eucalyptus burgessiana*	Tree	9.1 (3.4)	12.3 (1.3)	11.2 (4.5)	58.0 (9.1)	12.9 (5.4)	9.0 (4.6)
Myrtaceae	*Eucalyptus piperita*	Tree	8.0 (2.4)	11.4 (3.9)	11.3 (3.1)	48.7 (8.9)	12.0 (5.1)	8.9 (4.1)
Myrtaceae	*Eucalyptus punctata*	Tree	5.2 (0.6)	9.6 (3.1)	8.2 (1.1)	36.2 (4.5)	7.2 (0.5)	4.7 (1.0)
Myrtaceae	*Eucalyptus sparsifolia*	Tree	8.2 (2.3)	15.2 (1.9)	11.7 (3.9)	46.5 (10.0)	15.1 (7.5)	9.2 (5.6)
Goodeniaceae	*Goodenia decurrens*	Herb	10.5 (0.6)	10.9 (1.5)	15.3 (0.7)	26.7 (7.4)	NA	NA

Proteaceae	*Grevillea mucronulata*	Shrub	4.4 (0.2)	3.4 (0.8)	6.3 (0.6)	7.6 (1.4)	NA	NA
Proteaceae	*Grevillea phylicoides*	Shrub	4.8 (1.0)	4.1 (1.0)	7.8 (1.9)	7.9 (1.3)	NA	NA
Proteaceae	*Grevillea sericea*	Shrub	7.2 (0.5)	4.9 (1.2)	10.9 (1.0)	11.1 (5.7)	11.6 (0.5)	1.6 (0.8)
Proteaceae	*Hakea dactyloides*	Shrub	6.5 (0.7)	7.3 (1.2)	10.7 (1.3)	16.0 (3.1)	NA	NA
Dilleniaceae	*Hibbertia bracteata*	Shrub	5.9 (0.5)	3.1 (0.2)	9.0 (0.9)	12.2 (1.6)	NA	NA
Dilleniaceae	*Hibbertia saligna*	Shrub	6.4 (0.9)	6.0 (2.2)	9.0 (1.4)	15.9 (5.0)	10.2 (0)	1.3 (0)
Proteaceae	*Isopogon anemonifolius*	Shrub	9.6 (1.8)	11.0 (2.7)	16.3 (2.5)	36.2 (12.1)	13.4 (0)	3.2 (0)
Proteaceae	*Lambertia formosa*	Shrub	8.3 (0.9)	6.7 (0.8)	13 (1.7)	14.6 (1.8)	NA	NA
Ericaceae	*Leucopogon lanceolatus*	Shrub	4.4 (0.8)	3.7 (1.2)	6.6 (1.4)	9.0 (3.1)	NA	NA
Ericaceae	*Leucopogon setiger*	Shrub	4.3 (2.1)	3.0 (0.5)	6.8 (2.3)	6.2 (3.9)	NA	NA
Proteaceae	*Lomatia myricoides*	Shrub	4.8 (0.7)	6.7 (1.9)	7.2 (0.4)	22.8 (3.4)	9.2 (0)	3.4 (0)
Fabaceae	*Mirbelia rubiifolia*	Shrub	6.1 (0.7)	5.2 (0.8)	10.1 (1.7)	6.2 (1.1)	NA	NA
Ericaceae	*Monotoca scoparia*	Shrub	5.9 (1.2)	4.0 (0.6)	9.2 (1.8)	6.1 (1.0)	NA	NA
Oleaceae	*Notelaea venosa*	Tree	4.4 (0.4)	6.7 (5.1)	7.1 (1.2)	29.4 (8.8)	8.3 (3.8)	5.8 (1.8)
Proteaceae	*Persoonia levis*	Shrub	9.3 (1.3)	9.1 (0.6)	12.9 (2.5)	28.9 (4.0)	14 (4.9)	5.6 (2.6)

Proteaceae	*Persoonia linearis*	Shrub	10.0 (1.0)	5.5 (1.1)	15.6 (2.0)	9.9 (2.5)	NA	NA
Proteaceae	*Persoonia mollis*	Shrub	5.3 (0.9)	5.9 (1.0)	8.0 (0.3)	10.4 (1.9)	NA	NA
Rutaceae	*Philotheca hispidula*	Shrub	10.6 (1.0)	8.0 (2.7)	14.3 (3.2)	12.5 (3.8)	NA	NA
Thymelaeaceae	*Pimelea linifolia*	Shrub	6.5 (1.1)	2.0 (0.7)	8.8 (2.6)	4.1 (0.8)	NA	NA
Fabaceae	*Podolobium ilicifolium*	Shrub	5.4 (0.4)	3.7 (0.7)	6.7 (0.7)	6.7 (0.6)	NA	NA
Rhamnaceae	*Pomaderris elliptica*	Shrub	4.2 (0.3)	8.3 (3.6)	6.4 (0.4)	25.5 (1.0)	7.2 (0.1)	5.3 (3.1)
Fabaceae	*Pultenaea flexilis*	Shrub	6.6 (2.1)	5.0 (3.5)	10.4 (4.7)	6.0 (1.6)	NA	NA
Fabaceae	*Pultenaea scabra*	Shrub	4.5 (0.8)	4.5 (0.6)	7.2 (0.5)	7.5 (0.7)	NA	NA
Smilacaceae	*Smilax australis*	Climber	8.3 (0.8)	9.2 (3.0)	11.1 (1.1)	27.3 (4.9)	13.8 (0)	3.5 (0)
Smilacaceae	*Smilax glyciphylla*	Climber	5.7 (1.4)	5.1 (1.4)	7.5 (1.8)	14.9 (4.3)	NA	NA
Proteaceae	*Stenocarpus salignus*	Tree	4.7 (0.4)	5.1 (1.9)	6.5 (1.1)	18.6 (3.0)	7.8 (3.9)	6.1 (2.5)
Myrtaceae	*Syncarpia glomulifera*	Tree	5.0 (0.8)	7.8 (1.7)	8.1 (1.3)	28.3 (10.4)	10.1 (1.7)	4.5 (1.6)
Winteraceae	*Tasmannia insipida*	Shrub	5.0 (0.1)	10.3 (2.4)	8.4 (0.9)	27 (8.5)	NA	NA
Elaeocarpaceae	*Tetratheca rupicola*	Herb	7.0 (1.3)	3.9 (1.4)	11.0 (2.4)	4.9 (0.5)	NA	NA
Myrtaceae	*Tristaniopsis collina*	Tree	7.8 (0.6)	10.8 (7.0)	11.0 (1.9)	30.5 (7.7)	10.2 (2.2)	10.1 (1.1)

Ericaceae	*Woollsia pungens*	Shrub	3.0 (0.6)	3.5 (1.3)	5.6 (1.0)	5.9 (1.4)	NA	NA
Apiaceae	*Xanthosia pilosa*	Herb	5.2 (0.8)	2.9 (0.6)	7.1 (1.0)	4.9 (0.8)	NA	NA
Apiaceae	*Xanthosia tridentata*	Herb	6.8 (0.7)	3.8 (0.7)	10.6 (1.4)	7.0 (1.6)	NA	NA
Proteaceae	*Xylomelum pyriforme*	Shrub	7.2 (1.8)	5.8 (2.3)	9.3 (1.2)	44.7 (4.9)	10.6 (3.8)	7.6 (3.8)

Appendix 3.2 Ranking of study species by the Overall Leaf Flammability Index (OLFI) from least to most flammable. Species' data for OLFI, ignitibility index (reverse sign values, used in calculating the OLFI), sustainability index, and combustibility ('low', leaves did not begin flaming combustion; 'high', leaves began flaming combustion)

Species	**Rank**	**OLFI**	**Ignitibility index**	**Sustainability index**	**Combustibility**
Persoonia linearis	1	-2.42	-2.13	-0.44	low
Philotheca hispidula	2	-1.74	-2.03	0.19	low
Tetratheca rupicola	3	-1.34	-0.44	-0.98	low
Pimelea linifolia	4	-1.26	0.08	-1.41	low
Dampiera stricta	5	-1.22	-0.92	-0.37	low
Xanthosia tridentata	6	-1.16	-0.32	-0.92	low
Lambertia formosa	7	-1.12	-1.19	0.00	low
Bossiaea heterophylla	8	-1.11	-0.37	-0.81	low
Pultenaea flexilis	9	-0.88	-0.23	-0.71	low
Goodenia decurrens	10	-0.75	-2.18	1.38	low
Monotoca scoparia	11	-0.69	0.17	-0.90	low

Mirbelia rubiifolia	12	-0.69	-0.06	-0.66	low
Brachyloma daphnoides	13	-0.63	0.30	-0.96	low
Hibbertia bracteata	14	-0.58	0.22	-0.84	low
Xanthosia pilosa	15	-0.42	0.74	-1.19	low
Acacia suaveolens	16	-0.41	-1.59	1.16	low
Daviesia corymbosa	17	-0.29	-0.89	0.58	low
Podolobium ilicifolium	18	-0.16	0.78	-0.95	low
Hakea dactyloides	19	-0.08	-0.27	0.19	low
Grevillea phylicoides	20	-0.07	0.74	-0.82	low
Leucopogon setiger	21	-0.06	1.05	-1.11	low
Austromyrtus tenuifolia	22	0.01	0.84	-0.83	low
Grevillea mucronulata	23	0.15	1.12	-0.96	low
Pultenaea scabra	24	0.16	0.91	-0.74	low
Persoonia mollis	25	0.20	0.54	-0.33	low
Leucopogon lanceolatus	26	0.20	1.06	-0.84	low

Smilax glyciphylla	27	0.22	0.54	-0.31	low
Bossiaea rhombifolia	28	0.23	1.11	-0.86	low
Acrotriche divaricata	29	0.29	1.81	-1.50	low
Cissus hypoglauca	30	0.29	0.69	-0.38	low
Acacia myrtifolia	31	0.36	-0.23	0.61	low
Woollsia pungens	32	0.57	1.62	-1.01	low
Tasmannia insipida	33	1.72	0.56	1.27	low
Boronia ledifolia	34	-2.02	-1.38	-0.77	high
Banksia spinulosa	35	-1.35	-0.75	-0.68	high
Grevillea sericea	36	-1.15	-0.48	-0.75	high
Isopogon anemonifolius	37	-0.78	-1.80	0.97	high
Persoonia levis	38	-0.60	-1.41	0.77	high
Smilax australis	39	-0.46	-0.99	0.50	high
Hibbertia saligna	40	-0.38	0.09	-0.49	high
Ceratopetalum gummiferum	41	-0.15	0.34	-0.50	high

Dodonaea triquetra	42	0.06	0.29	-0.22	high
Actinotus helianthi	43	0.13	0.71	-0.57	high
Backhousia myrtifolia	44	0.21	0.64	-0.41	high
Banksia serrata	45	0.63	-1.24	1.91	high
Lomatia myricoides	46	0.72	0.74	0.03	high
Xylomelum pyriforme	47	0.78	-0.14	0.97	high
Syncarpia glomulifera	48	0.87	0.47	0.45	high
Corymbia gummifera	49	0.89	-0.64	1.59	high
Stenocarpus salignus	50	0.95	1.03	-0.03	high
Ceratopetalum apetalum	51	1.02	0.17	0.91	high
Tristaniopsis collina	52	1.06	-0.40	1.52	high
Eucalyptus sparsifolia	53	1.20	-1.22	2.49	high
Eucalyptus piperita	54	1.20	-0.72	2.00	high
Eucalyptus burgessiana	55	1.30	-1.02	2.40	high
Notelaea venosa	56	1.34	0.95	0.48	high

Pomaderris elliptica	57	1.63	1.20	0.52	high
Eucalyptus punctata	58	1.65	0.81	0.94	high
Astrotricha latifolia	59	1.88	1.74	0.27	high
Callicoma serratifolia	60	2.01	0.97	1.16	high

Appendix 3.3 Ranking of study species by flammability attributes and the ignitibility and sustainability indices

Rankings based on mean values of flammability attributes (s) and indices for each species. For ignitibility, the rankings are from quickest (most flammable) to slowest to ignite. For sustainability, the rankings are from longest duration (most flammable) to shortest duration.

Family	**Species**	**Ignitibility**	**Sustainability**	**TTS**	**SD**	**TTI**	**ID**	**TTF**	**FD**
Fabaceae	*Acacia myrtifolia*	36	16	43	13	35	23	NA	NA
Fabaceae	*Acacia suaveolens*	56	9	55	4	56	24	NA	NA
Ericaceae	*Acrotriche divaricata*	1	60	2	60	1	59	NA	NA
Apiaceae	*Actinotus helianthi*	19	37	20	30	5	37	10	21
Araliaceae	*Astrotricha latifolia*	2	22	9	55	2	20	1	4
Myrtaceae	*Austromyrtus tenuifolia*	13	46	12	42	18	50	NA	NA
Myrtaceae	*Backhousia myrtifolia*	21	33	19	40	20	27	8	19
Proteaceae	*Banksia serrata*	53	4	52	18	53	3	24	2
Proteaceae	*Banksia spinulosa*	46	39	40	24	48	36	22	27
Rutaceae	*Boronia ledifolia*	54	43	58	39	55	33	17	25
Fabaceae	*Bossiaea heterophylla*	40	44	30	43	50	46	NA	NA

Fabaceae	*Bossiaea rhombifolia*	6	49	3	49	15	44	NA	NA
Ericaceae	*Brachyloma daphnoides*	27	53	27	57	28	41	NA	NA
Cunoniaceae	*Callicoma serratifolia*	10	10	10	38	17	10	5	1
Cunoniaceae	*Ceratopetalum apetalum*	30	14	32	37	32	9	11	3
Cunoniaceae	*Ceratopetalum gummiferum*	26	36	16	25	26	32	16	23
Vitaceae	*Cissus hypoglauca*	20	32	25	46	12	26	NA	NA
Myrtaceae	*Corymbia gummifera*	44	5	44	10	40	2	20	10
Goodeniaceae	*Dampiera stricta*	48	31	46	27	51	42	NA	NA
Fabaceae	*Daviesia corymbosa*	47	17	48	16	49	22	NA	NA
Sapindaceae	*Dodonaea triquetra*	28	28	38	32	29	17	6	22
Myrtaceae	*Eucalyptus burgessiana*	50	2	53	2	45	1	21	7
Myrtaceae	*Eucalyptus piperita*	45	3	47	3	46	4	19	8
Myrtaceae	*Eucalyptus punctata*	14	13	21	9	24	7	2	15
Myrtaceae	*Eucalyptus sparsifolia*	52	1	49	1	47	5	27	6
Goodeniaceae	*Goodenia decurrens*	60	7	59	6	58	18	NA	NA

Proteaceae	*Grevillea mucronulata*	5	54	7	53	4	47	NA	NA
Proteaceae	*Grevillea phylicoides*	17	45	14	44	21	45	NA	NA
Proteaceae	*Grevillea sericea*	43	42	41	36	41	38	18	24
Proteaceae	*Hakea dactyloides*	38	23	34	19	39	28	NA	NA
Dilleniaceae	*Hibbertia bracteata*	29	47	28	54	31	35	NA	NA
Dilleniaceae	*Hibbertia saligna*	32	35	33	23	30	29	14	26
Proteaceae	*Isopogon anemonifolius*	57	11	56	5	60	8	23	20
Proteaceae	*Lambertia formosa*	51	26	51	22	54	31	NA	NA
Ericaceae	*Leucopogon lanceolatus*	7	48	8	50	8	43	NA	NA
Ericaceae	*Leucopogon setiger*	8	57	5	56	10	53	NA	NA
Proteaceae	*Lomatia myricoides*	16	25	15	21	14	21	9	18
Fabaceae	*Mirbelia rubiifolia*	34	38	31	31	36	52	NA	NA
Ericaceae	*Monotoca scoparia*	31	50	29	45	33	54	NA	NA
oleaceae	*Notelaea venosa*	11	20	6	20	11	12	7	12
Proteaceae	*Persoonia levis*	55	15	54	12	52	13	26	13

Proteaceae	*Persoonia linearis*	59	34	57	29	59	40	NA	NA
Proteaceae	*Persoonia mollis*	24	30	23	26	22	39	NA	NA
Rutaceae	*Philotheca hispidula*	58	24	60	15	57	34	NA	NA
Thymelaeaceae	*Pimelea linifolia*	33	59	35	59	27	60	NA	NA
Fabaceae	*Podolobium ilicifolium*	15	52	24	51	9	51	NA	NA
Rhamnaceae	*Pomaderris elliptica*	4	18	4	14	6	19	3	14
Fabaceae	*Pultenaea flexilis*	37	40	36	35	37	55	NA	NA
Fabaceae	*Pultenaea scabra*	12	41	11	41	16	48	NA	NA
Smilacaceae	*Smilax australis*	49	19	50	11	44	15	25	17
Smilacaceae	*Smilax glyciphylla*	23	29	26	33	19	30	NA	NA
Proteaceae	*Stenocarpus salignus*	9	27	13	34	7	25	4	11
Myrtaceae	*Syncarpia glomulifera*	25	21	18	17	23	14	12	16
Winteraceae	*Tasmannia insipida*	22	8	17	8	25	16	NA	NA
Elaeocarpaceae	*Tetratheca rupicola*	42	55	39	47	43	58	NA	NA
Myrtaceae	*Tristaniopsis collina*	41	6	45	7	42	11	13	5

Ericaceae	*Woollsia pungens*	3	56	1	52	3	56	NA	NA
Apiaceae	*Xanthosia pilosa*	18	58	22	58	13	57	NA	NA
Apiaceae	*Xanthosia tridentata*	39	51	37	48	38	49	NA	NA
Proteaceae	*Xylomelum pyriforme*	35	12	42	28	34	6	15	9

Appendix 4.1 Results of general linear models of TTI, ID, TTF and FD, and binomial models of samples flaming, as a proportion calculated for each species within each level of radiant energy. Models used radiant energy (categorical factor), species (categorical factor) and a radiant energy x species interaction. For the general linear models, SS and F statistic values are given, and deviance and χ^2 statistics for the binomial model.

Flammability attribute	**Factor**	**SS (deviance)**	**d.f.**	**F (χ^2)**	**P**
TTI	radiant energy	81.11	1	2866.01	< 0.0001
	species	16.83	9	66.09	< 0.0001
	radiant energy x species	1.16	9	4.56	< 0.0001
	residuals	10.30	364		
ID	radiant energy	30.56	1	598.77	< 0.0001
	species	155.30	9	338.05	< 0.0001
	radiant energy x species	3.21	9	6.99	< 0.0001
	residuals	18.58	364		
TTF	radiant energy	20.35	1	821.23	< 0.0001
	species	5.20	6	34.99	< 0.0001
	radiant energy x species	0.50	6	3.33	0.004
	residuals	3.67	148		
FD	radiant energy	0.02	1	0.19	0.7
	species	135.51	6	197.81	< 0.0001
	radiant energy x species	1.29	6	1.89	0.09
	residuals	16.90	148		

Flaming	radiant energy	3.87	1	338.07	< 0.0001
(proportion)	species	2.52	9	279.02	< 0.0001
	radiant energy x species	2.75	9	21.26	0.012
	residuals	1.26	20		

Appendix 4.2 Results from models fitted to individual species for TTI, ID, TTF, FD and flaming as a function of sqrt transformed values of radiant energy. Linear models were used for TTI, ID, TTF, and FD, and binomial logistic regression for flaming. For TTF and FD, data were omitted within levels of radiant energy where fewer than four samples flamed. ‘NA’ values in the table indicate species which only flamed consistently (i.e. four or more times) at the highest radiant energy level (96.6 kWm^{-2}) which did not allow the regression model to be fitted.

Flammability attribute	**Species**	**Coefficient (SE)**	**d.f.**	**t**	**P**
TTI	*A. myrtifolia*	-0.311(0.026)	1,38	-12.18	< 0.0001
	A. suaveolens	-0.243(0.019)	1,38	-12.85	< 0.0001
	B. serrata	-0.277(0.014)	1,38	-20.28	< 0.0001
	B. spinulosa	-0.266(0.017)	1,28	-16.05	< 0.0001
	C. citrinus	-0.272(0.013)	1,38	-21.68	< 0.0001
	C. gummifera	-0.289(0.017)	1,38	-17.48	< 0.0001
	E. sparsifolia	-0.367(0.019)	1,38	-19.77	< 0.0001
	G. phylicoides	-0.296(0.017)	1,35	-17.94	< 0.0001
	L. formosa	-0.292(0.011)	1,37	-27.82	< 0.0001
	P. mollis	-0.248(0.013)	1,36	-18.55	< 0.0001
ID	*A. myrtifolia*	-0.190(0.018)	1,38	-10.73	< 0.0001
	A. suaveolens	-0.084(0.022)	1,38	-3.91	0.0004
	B. serrata	-0.091(0.019)	1,38	-4.68	< 0.0001
	B. spinulosa	-0.178(0.041)	1,28	-4.34	0.0002

	C. citrinus	-0.171(0.019)	1,38	-8.89	< 0.0001
	C. gummifera	-0.191(0.021)	1,38	-8.99	< 0.0001
	E. sparsifolia	-0.181(0.025)	1,38	-7.1	< 0.0001
	G. phylicoides	-0.229(0.020)	1,35	-11.3	< 0.0001
	L. formosa	-0.286(0.028)	1,37	-10.21	< 0.0001
	P. mollis	-0.178(0.020)	1,36	-8.87	< 0.0001
TTF	*A. myrtifolia*	NA	NA	NA	NA
	A. suaveolens	-0.178(0.046)	1,15	-3.92	0.001
	B. serrata	-0.340(0.020)	1,36	-17.41	< 0.0001
	B. spinulosa	-0.262(0.022)	1,21	-11.82	< 0.0001
	C. citrinus	-0.197(0.028)	1,16	-7.17	< 0.0001
	C. gummifera	-0.295(0.025)	1,23	-11.71	< 0.0001
	E. sparsifolia	-0.330(0.064)	1,17	-5.14	< 0.0001
	G. phylicoides	NA	NA	NA	NA
	L. formosa	-0.281(0.018)	1,20	-15.99	< 0.0001
	P. mollis	NA	NA	NA	NA
FD	*A. myrtifolia*	NA	NA	NA	NA
	A. suaveolens	-0.247(0.094)	1,15	-2.63	0.019
	B. serrata	0.044(0.039)	1,36	1.12	0.3
	B. spinulosa	-0.080(0.059)	1,21	-1.36	0.2
	C. citrinus	0.009(0.061)	1,16	0.16	0.9
	C. gummifera	0.074(0.058)	1,23	1.27	0.2
	E. sparsifolia	0.077(0.116)	1,17	0.67	0.5

	G. phylicoides	NA	NA	NA	NA
	L. formosa	-0.030(0.053)	1,20	-0.57	0.6
	P. mollis	NA	NA	NA	NA
Flaming (proportion)	*A. myrtifolia*	1.312(0.234)	1,38	5.61	< 0.0001
	A. suaveolens	1.525(0.299)	1,38	5.11	< 0.0001
	B. serrata	0.398(0.232)	1,38	1.72	0.09
	B. spinulosa	1.233(0.352)	1,38	3.5	0.001
	C. citrinus	1.768(0.293)	1,38	6.03	< 0.0001
	C. gummifera	1.489(0.302)	1,38	4.94	< 0.0001
	E. sparsifolia	1.985(0.225)	1,38	8.82	< 0.0001
	G. phylicoides	0.569(0.246)	1,38	2.32	0.026
	L. formosa	1.439(0.295)	1,38	4.88	< 0.0001
	P. mollis	0.414(0.222)	1,38	1.87	0.07

Appendix 5.1 Mean absolute error (MAE) from models excluding a given leaf trait (LMA, LA, or LWC) built using the predictive dataset. Four non-linear regression models were fitted using the same approach outlined in Chapter 5, with the exclusion of a single leaf trait in turn (LMA, LA, or LWC) in addition to the full model including all leaf traits Using the predictions from these models, values for MAE were calculated over all samples, and for each level of radiant energy individually. Where the MAE of a given model is greater than the MAE of the full model, the values are shown in bold.

Attribute	Trait	Overall	29.6 kWm^{-2}	45.7 kWm^{-2}	67.6 kWm^{-2}	96.6 kWm^{-2}
TTI	Full	1.3	2.0	1.5	1.1	0.9
	LMA	**2.3**	**3.9**	**2.6**	**1.7**	**1.1**
	LA	**1.5**	**2.3**	**1.6**	1.1	0.9
	LWC	**1.7**	**2.7**	**1.8**	**1.4**	**1.1**
ID	Full	4.8	9.2	4.7	2.9	3.1
	LMA	**6.3**	**11.1**	**6.1**	**4.2**	**4.4**
	LA	**9.6**	**12.7**	**10.4**	**8.5**	**7.4**
	LWC	**4.9**	9.2	**4.8**	**3.1**	**3.2**

Appendix 5.2 True positive (TPR) and true negative (TNR) rates for predictive models of flaming excluding a single leaf trait. Four logistic regression models were fitted using the same approach outlined in Chapter 5, with the exclusion of a single leaf trait in turn (LMA, LA, or LWC) in addition to the full model including all leaf traits. For the models excluding a leaf trait, a separate $P_{flaming}$ coefficient was calculated for each model (see chapter 5 for details) Where TPR or TNR is lower than the relevant value for the full model, the value is shown in bold.

Model	**Error**	**Overall**	29.6 kWm^{-2}	45.7 kWm^{-2}	67.6 kWm^{-2}	96.6 kWm^{-2}
Full	TPR	0.85	0.88	0.68	0.80	0.95
	TNR	0.80	0.88	0.75	0.72	0.76
LMA	TPR	**0.74**	0.88	**0.61**	**0.73**	**0.78**
	TNR	0.81	0.88	0.75	0.78	0.76
LA	TPR	**0.83**	**0.62**	0.68	0.81	**0.90**
	TNR	**0.75**	**0.84**	**0.71**	**0.67**	**0.65**
LWC	TPR	0.85	0.88	**0.64**	0.80	0.95
	TNR	**0.79**	**0.87**	**0.71**	0.72	0.82

References

Abatzoglou JT, Williams AP (2016) Impact of anthropogenic climate change on wildfire across western US forests. *Proceedings of the National Academy of Sciences of the United States of America* **113**, 11770–11775.

Alam MA, Wyse SV, Buckley HL, Perry GLW, Sullivan JJ, *et al*. (2019) Shoot flammability is decoupled from leaf flammability, but controlled by leaf functional traits. *Journal of Ecology* **00,** 1–13.

Alessio GA, Peñuelas J, Llusià J, Ogaya R, Estiarte M, De Lillis M (2008) Influence of water and terpenes on flammability in some dominant Mediterranean species. *International Journal of Wildland Fire* **17**, 274–286.

Alexander ME (2010). Surface fire spread potential in trembling aspen during summer in the Boreal Forest Region of Canada. *Forestry Chronicle* **86**, 200–212.

Anderson HE (1970) Forest fuel ignitibility. *Fire Technology* **6**, 31–319.

Australian Bureau of Meteorology (2014) Climate data online. http://www.bom.gov.au/climate/data/.

Banks SC, Dujardin M, McBurney L, Blair D, Barker M, Lindenmayer DB (2011) Starting Points for Small Mammal Population Recovery After Wildfire: Recolonisation Or Residual Populations? *Oikos* **120**, 26–37.

Battersby PF, Wilmshurst JM, Curran TJ, McGlone MS, Perry GL (2017) Exploring fire adaptation in a land with little fire: serotiny in *Leptospermum scoparium* (Myrtaceae). *Journal of Biogeography* **44**, 1306–1318.

Behm AL, Duryea ML, Long AJ, Zipperer WC (2004) Flammability of native understory species in pine flatwood and hardwood hammock ecosystems and implications for the wildland–urban interface. *International Journal of Wildland Fire* **13**, 355-365.

Bianchi LO, Defossé GE (2015) Live Fuel Moisture Content and Leaf Ignition of Forest Species in Andean Patagonia, Argentina. *International Journal of Wildland Fire* **24**, 340–348.

Blackhall M, Raffaele E, Veblen TT (2012) Is foliar flammability of woody species related to time since fire and herbivory in northwest Patagonia, Argentina? *Journal of Vegetation Science* **23**, 931-941.

Boer MM, Nolan RH, Resco De Dios V, Clarke H, Price OF, Bradstock RA (2017) Changing Weather Extremes Call for Early Warning of Potential for Catastrophic Fire. *Earth's Future* **5**, 1196-1202.

Bond WJ, Midgley JJ (1995) Kill Thy Neighbour: An Individualistic Argument for the Evolution of Flammability. *Oikos* **73**, 79–85.

Bowman DMJS, French BJ, Prior LD (2014) Have plants evolved to self-immolate? *Frontiers in Plant Science* **5**, 590.

Bradshaw SD, Dixon KW, Hopper SD, Lambers H, Turner SR (2011) Little evidence for fire-adapted plant traits in Mediterranean climate regions. *Trends in Plant Science* **16**, 69–76.

Bradstock RA, Gill AM (1993). Fire in semi-arid, mallee shrublands: Size of flames from discrete fuel arrays and their role in the spread of fire. *International Journal of Wildland Fire* **3**, 3–12.

Bradstock RA, Hammill KA, Collins L, Price O (2010) Effects of Weather, Fuel and Terrain on Fire Severity in Topographically Diverse Landscapes of South-Eastern Australia. *Landscape Ecology* **25**, 607–619.

Bragg JG, Westoby M (2002) Leaf size and foraging for light in a sclerophyll woodland. *Functional Ecology* **16**, 633–639.

Breshears DD, McDowell NG, Goddard KL, Dayem KE, Martens SN, Meyer CW, Brown KM (2008) Foliar absorption of intercepted rainfall improves woody plant water status most during drought. *Ecology* **89**, 41–47.

Brooks ML, D'Antonio CM, Richardson DM, Grace JB, Keeley JE, DiTomaso JM, Hobbs RJ, Pellant M, Pyke D (2004) Effects of invasive alien plants on fire regimes. *BioScience* **54**, 677–688.

Brouillette LC, Mason CM, Shirk RY, Donovan LA (2014). Adaptive differentiation of traits related to resource use in a desert annual along a resource gradient. *New Phytologist,* **201**, 1316–1327.

Butler MA, King AA (2004) Phylogenetic Comparative Analysis: A Modeling Approach for Adaptive Evolution. *The American Naturalist* **164**, 683–695.

Calitz W, Potts AJ, Cowling RM (2015) Investigating species-level flammability across five biomes in the Eastern Cape, South Africa. *South African Journal of Botany* **101**, 32–39

Castro-Díez P, Villar-Salvador P, Pérez-Rontomé C, Maestro-Martínez M, Montserrat-Martí G (1997) Leaf Morphology and Leaf Chemical Composition in Three Quercus (Fagaceae) Species Along a Rainfall Gradient in NE Spain. Trees – Structure and Function **11**, 127–134.

Curran TJ, Perry GLW, Wyse SV, Alam MA (2018) Managing fire and biodiversity in the wildland-urban interface: A role for green firebreaks. *Fire* **1**, 3.

Curt T, Schaffhauser A, Borgniet L, Dumas C, Estève R, Ganteaume A, *et al.* (2011) Litter flammability in oak woodlands and shrublands of south-eastern France. *Forest Ecology and Management* **12**, 2214-2222.

Chia EK, Bassett M, Nimmo DG, Leonard SWJ, Ritchie EG, Clarke MF, Bennett AF, Peters DPC (2015) Fire Severity and Fire-Induced Landscape Heterogeneity Affect Arboreal Mammals in Fire-Prone Forests. *Ecosphere* **6**, 1–14.

Clarke HG, Smith PL, Pitman AJ (2011) Regional Signatures of Future Fire Weather Over Eastern Australia from Global Climate Models. *International Journal of Wildland Fire* **20**, 550–562.

Clarke PJ, Prior LD, French BJ, Vincent B, Knox KJE, Bowman DMJS (2014) Using a rainforest-flame forest mosaic to test the hypothesis that leaf and litter fuel flammability is under natural selection. *Oecologia* **176**, 1123-1133.

Clarke H (2015) The impact of climate change on bushfire weather conditions and fuel load, PhD Thesis, UNSW Australia, Sydney.

Collins L, Bradstock RA, Tasker EM, Whelan RJ (2012) Can Gullies Preserve Complex Forest Structure in Frequently Burnt Landscapes? *Biological Conservation* **153**, 177–186.

Cornwell WK, Ackerly DD (2009) Community assembly and shifts in plant trait distributions across and environmental gradient in coastal California. *Ecological Monographs* **79**, 109–126.

Cui X, Alam MA, Perry GLb, Paterson AM, Wyse SV, Curran TJ (2019) Green firebreaks as a management tool for wildfires: Lessons from China. Journal of Environmental Management 233, 329-336.

Dai A (2013) Increasing drought under global warming in observations and models. *Nature Climate Change* **3**, 52–58.

de Magalhaes RMQ, Schwilk DW (2012) Leaf traits and litter flammability: Evidence for non-additive mixture effects in a temperate forest. *Journal of Ecology* **100**, 1153–163.

Della Rocca G, Hernando C, Madrigal J, Danti R, Moya J, Guijarro M, Pecchioli A, Moya B (2015) Possible land management uses of common cypress to reduce wildfire initiation risk: a laboratory study. *Journal of Environmental Management* **15**, 68–77

Della Rocca G, Madrigal J, Marchi E, Michelozzi M, Moya B, Danti R (2017) Relevance of terpenoids on flammability of Mediterranean species: an experimental approach at a low radiant heat flux. *iForest* **10**, 766–775.

Dimitrakopoulos AP, Mitsopoulos ID, Kaliva A (2011) Short communication comparing flammability traits among fire-stricken (low elevation) and non fire- stricken (high elevation) conifer forest species of Europe: A test of the Mutch hypothesis. *Forest Systems* **22**, 134-137.

Dufresne JL, Foujols MA, Denvil S, Caubel A, Marti O, Aumont O, *et al.* (2013) Climate change projections using the IPSL-CM5 Earth System Model: from CMIP3 to CMIP5. *Climate* dynamics **40**, 2123–2165.

Engber E, Varner J (2012) Patterns of flammability of the California oaks: The role of leaf traits. *Canadian Journal of Forest Research* **42**, 1965–1975.

Engstrom JD, Butler JK, Smith SG, Baxter LL, Fletcher TH, Weise DR (2004) Ignition behaviour of California chaparral leaves. *Combustion Science and Technology* **176**, 1577–1591.

Enright NJ, Fontaine JB, Bowman D, Bradstock RA, Williams RJ (2015) Interval squeeze: altered fire regimes and demographic responses interact to threaten woody species persistence as climate changes. *Frontiers in Ecology and the Environment* **13**, 265–272.

Etlinger MG, Beall FC (2004) Development of a laboratory protocol for fire performance of landscape plants. *International Journal of Wildland Fire* **13**, 479–488.

Fairley A, Moore P (2010) Native Plants of the Sydney Region third edition. Sydney: Jacana

Fairman TA, Bennett LT, Nitschke CR (2019) Short-interval wildfires increase likelihood of resprouting failure in fire-tolerant trees. *Journal of Environmental Management* **231**, 59–65.

Fares S, Bajocco S, Salvati L, Camarretta N, Dupuy J, Xanthopoulos G, Guijarro M, Madrigal J, Hernando C, Corona P (2017) Characterizing potential wildland fire fuel in live vegetation in the Mediterranean region. *Annals of Forest Science* **74**, 1.

Flannigan MD, Krawchuk MA, de Groot WJ, Wotton BM, Gowman LM (2009) Implications of changing climate for global wildland fire. *International Journal of Wildland Fire* **18**, 483–507.

Fletcher TH, Pickett BM, Smith SG, Spittle GS, Woodhouse MM, Haake E, Weise DR (2007) Effects of moisture on ignition behavior of moist California Chaparral and Utah leaves. *Combustion Science and Technology* **6**, 1183-1203.

Fox J, Weisberg S (2011) An {R} Companion to Applied Regression, Second Edition. Thousand Oaks CA: Sage.

Friedman R (1998) Principles of Fire Protection Chemistry and Physics. Third Edition. National Fire Protection Association. Jones and Bartlett Publishers, Inc. Sudbury, USA.

Fuentes-Ramirez, A, Veldman JW, Holzapfel C, Moloney KA (2016), Spreaders, igniters, and burning shrubs: plant flammability explains novel fire dynamics in grass-invaded deserts. *Ecological Applications* **26**, 2311-2322.

Gagnon PR, Passmore HA, Platt WJ, Myers JA, Paine CET, Harms KE (2010) Does Pyrogenicity Protect Burning Plants? *Ecology* **91**, 3481–3486.

Gallacher JR, Lansinger V, Smith S, Doll A, Weise DR, Fletcher TH (2015) The ignition and burning of live fuels studied using natural variation in fuel characteristics. 2015 Fall Meeting of the Western States Section of the Combustion Institute.

Ganteaume A, Jappiot M, Lampin C (2013a) Assessing the flammability of surface fuels beneath ornamental vegetation in wildland–urban interfaces in Provence (south-eastern France). *International Journal of Wildland Fire* **22**, 333–342.

Ganteaume A, Jappiot M, Lampin C, Guijarro M, Hernando C (2013b) Flammability of some ornamental species in wildland-urban interfaces in southeastern France: Laboratory assessment at particle level. *Environmental Management* **52**, 467–480.

Ganteaume A (2018) Does plant flammability differ between leaf and litter bed scale? Role of fuel characteristics and consequences for flammability assessment. *International Journal of Wildland Fire* **27**, 342–352.

Ghermandi L, Beletzky NA, de Torres Curth MI, Oddi FJ (2016) From leaves to landscape: A multiscale approach to assess fire hazard in wildland-urban interface areas. *Journal of Environmental Management* **183**, 925-937.

Gibbons P, van Bommel L, Gill AM, Cary GJ, Driscoll DA, Bradstock RA, *et al*. (2012) Land Management Practices Associated with House Loss in Wildfires. *PLoS ONE* **7**, e29212.

Gill AM, Moore PHR (1996) ‘Ignitability of leaves of Australian plants.’ (CSIRO Plant Industry: Canberra)

Gill AM, Zylstra P (2005) Flammability of Australian forests. *Australian Forestry* **68**, 87–93.

Grootemaat SI, Wright J, van Bodegom PM, Cornelissen JHC, Cornwell WK (2015) Burn or rot: Leaf traits explain why flammability and decomposability are decoupled across species. *Functional Ecology* **29**, 1486–1497.

Grootemaat SI, Wright IJ, van Bodegom PM, Cornelissen JHC (2017) Scaling up flammability from individual leaves to fuel beds. Oikos **126**, 1428–1438.

Gubareff GG, Janssen JE, Torborg RH (1960) Thermal Radiation Properties Survey, Honeywell Research Centre, Minneapolis, Minnesota.

Hammill K, Tasker E (2010) 'Vegetation, fire and climate change in the greater Blue Mountains World Heritage Area.' (NSW Department of Environment, Climate Change and Water: Sydney)

Harrell Jr FE (2014) Hmisc: Harrell Miscellaneous. R package version 3.14-6.

Ingram T, Mahler D (2013) SURFACE: detecting convergent evolution from comparative data by fitting Ornstein-Uhlenbeck models with stepwise Akaike Information Criterion. *Methods in Ecology and Evolution* **4**, 416–425.

Jaureguiberry P, Bertone G, DÍAz S (2011) Device for the standard measurement of shoot flammability in the field. *Austral Ecology* **36**, 821–829.

Jolly WM, Cochrane MA, Freeborn PH, Holden ZA, Brown TJ, Williamson GJ, Bowman DMJS (2015) Climate-induced variations in global wildfire danger from 1979 to 2013. *Nautre Communications* **6**, 7537.

Kampstra P (2008) Beanplot: A Boxplot Alternative for Visual Comparison of Distributions. *Journal of Statistical Software*, Code *Snippets*, **28**, 1–9.

Kattge J, Diaz S, Lavorel S, Prentice IC, Leadley P, Bönisch G *et al.* (2011) TRY – a global database of plant traits. *Global Change Biology*, **17**, 2905–2935.

Kauf Z, Fangmeier A, Rosavec R, Španjol Ž (2014) Testing vegetation flammability: The problem of extremely low ignition frequency and overall flammability score. *Journal of Combustion* **2014**, e970218.

Kramer HA, Mockrin MH, Alexandre PM, Stewart SI, Radeloff VC (2018) Where wildfires destroy buildings in the US relative to the wildland–urban interface and national fire outreach programs. *International Journal of Wildland Fire* **27**, 329–341.

Krawchuk MA, Moritz MA, Parisien MA, Van Dorn J, Hayhoe K (2009) Global Pyrogeography: The Current and Future Distribution of Wildfire. *PLoS ONE* **4**, e5102.

Kreye JK, Varner JM, Hamby GW, Kane JM (2018) Mesophytic litter dampens flammability in fire-excluded pyrophytic oak-hickory woodlands. *Ecosphere* **9**, e02078.

Krix DW, Murray BR (2018) Landscape variation in plant leaf flammability is driven by leaf traits responding to environmental gradients. *Ecosphere* **9**, e02093.

Krix DW, Phillips ML, Murray BR. (2019) Relationships among leaf flammability attributes and identifying low-leaf-flammability species at the wildland–urban interface. *International Journal of Wildland Fire* **28**, 295-307.

Leigh A, Sevanto S, Ball M, Close JD, Ellsworth DS, Knight CA, Nicotra AB, Vogel S (2012) Do thick leaves avoid thermal damage in critically low wind speeds? *New Phytologist* **194**, 477–487.

Leigh A, Sevanto S, Close JD, Nicotra AB (2017) The influence of leaf size and shape on leaf thermal dynamics: does theory hold up under natural conditions? *Plant Cell and Environment* **40**, 237–248.

Leonard SWJ, Bennett AF, Clarke MF (2014) Determinants of the Occurrence of Unburnt Forest Patches: Potential Biotic Refuges within a Large, Intense Wildfire in South-Eastern Australia. *Forest Ecology and Management* **314**, 85–93

Llusià J, Peñuelas J, Alessio GA, Estiarte M (2006) Seasonal contrasting changes of foliar concentrations of terpenes and other volatile organic compound in four dominant species of a Mediterranean shrubland submitted to a field experimental drought and warming. *Physiologia Plantarum* **127**, 632–649.

Luke RH, McArthur AG (1978) Bushfires in Australia. Canberra: Australian Government Publishing Service.

Mason NWH, Frazao C, Buxton RP, Richardson SJ (2016) Fire Form and Function: Evidence for Exaptive Flammability in the New Zealand Flora. *Plant Ecology* **217**, 645–659.

McCaw WL, Neal JE, Smith RH (1996) Fuel accumulation following prescribed burning in young even-aged stands of karri (*Eucalyptus diversicolor*). *Journal Australian Forestry* **59**, 171–177.

McGill BJ, Enquist BJ, Weiher E, Westoby M (2006) Rebuilding community ecology from functional traits. *Trends in Ecology and Evolution* **21**, 178–185.

McKiernan AB., Hovenden MJ, Brodribb TJ, Potts BM, Davies NW, O'Reilly-Wapstra JM (2014) Effect of limited water availability on foliar plant secondary metabolites of two eucalyptus species. *Environmental and Experimental Botany* **105**, 55–64.

Mell WE, Manzello SL, Maranghides A, Butry D, Rehm RG (2010) The wildland–urban interface fire problem – current approaches and research needs. *International Journal of Wildland Fire* **19**, 238–251.

Midgley JJ (2013) Flammability is not selected for, it emerges. *Australian Journal of Botany* **61**, 102–106.

Moritz MA, Batllori E, Bradstock RA, Gill AM, Handmer J, Hessburg PF, Leonard J, McCaffrey S, Odion DC, Schoennagel T (2014) Learning to coexist with wildfire. *Nature* **515**, 58–66.

Murray BR, Rice B, Keith D, Myerscough PJ, Howell J, Floyd A, Mills K, Westoby M (1999) Species in the tail of rank-abundance curves. *Ecology* **80**, 1806–1816.

Murray BR, Hardstaff LK, Phillips ML (2013) Differences in leaf flammability, leaf traits and flammability-trait relationships between native and exotic plant species of dry sclerophyll forest. *PLOS ONE* **8**, e79205.

Murray BR, Martin LJ, Brown C, Krix DW, Phillips ML (2018) Selecting low-flammability plants as green firebreaks within sustainable urban garden design. *Fire* **1**, 15.

Mutch RW (1970) Wildland Fires and Ecosystems - A Hypothesis. *Ecology* **51**, 1046–1051.

Nelson KC, Monroe MC, Fingerman J, Bowers A (2004) Living with fire: homeowner assessment of landscape values and defensible space in Minnesota and Florida, USA. *International Journal of Wildland Fire* **13**, 413–425.

Nolan RH, Sinclair J, Waters CM, Mitchell PJ, Eldridge DJ, Paul KI, *et al.* (2019) Risks to carbon dynamics in semi-arid woodlands of eastern Australia under current and future climates. *Journal of Environmental Management* **235**, 500–510.

Ordonez A, Olff H (2013) Do alien plant species profit more from high resource supply than natives? A trait-based analysis. *Global Ecology and Biogeography* **22**, 648–658.

Paradis E, Claude J, Strimmer K (2004) APE: analyses of phylogenetics and evolution in R language. *Bioinformatics* **20**, 289–290.

Parsons AL, Balch JK, de Andrade RB, Brando PM (2015) The role of leaf traits in determining litter flammability of south-eastern Amazon tree species. *International Journal of Wildland Fire* **24**, 1143-1153.

Pausas JG, Alessio GA, Moreira B, Segarra-Moragues JG (2016) Secondary compounds enhance flammability in a Mediterranean plant. *Oecologia* **180**, 103–110.

Pausas JG, Keeley JE, Schwilk DW (2017) Flammability as an ecological and evolutionary driver. *Journal of Ecology* **105**, 289–297.

Pechony O, Shindell DT (2010) Driving forces of global wildfires over the past millennium and the forthcoming century. *Proceedings of the National Academy of Sciences* **107**, 19167–19170.

Penman TD, Kavanagh RP, Binns DL, Melick DR (2007) Patchiness of Prescribed Burns in Dry Sclerophyll Eucalypt Forests in South-Eastern Australia. *Forest Ecology and Management* **252**, 24–32.

Penman TD, Collins L, Syphard AD, Keeley JE, Bradstock RA (2014) Influence of fuels, weather and the built environment on the exposure of property to wildfire. *PLOS ONE* **9**, e111414.

Penman TD, Eriksen C, Horsey B, Green A, Lemcke D, Cooper P, Bradstock RA (2017) Retrofitting for wildfire resilience: What is the cost? *International Journal of Disaster Risk Mitigation* **21**, 1–10.

Pérez-Harguindeguy N, Díaz S, Garnier E, Lavorel S, Poorter H, Jaureguiberry P, Bret-Harte MS, *et al.* (2013) New handbook for standardised measurement of plant functional traits worldwide. *Australian Journal of Botany* **61**, 167–234.

Petit JR, Jouzel J, Raynaud D, Barkov NI, Barnola M, Basile I, *et al.* (1999) Climate and atmospheric history of the past 420,000 years from the Vostok ice core, Antarctica. *Nature* **399**, 429–436.

Pickett BM, Isackson C, Wunder R, Fletcher TH, Butler BW, Weise DR (2009) Flame interactions and burning characteristics of two live leaf samples. *International Journal of Wildland Fire* **18**, 865–874.

Pinheiro J, Bates D, DebRoy S, Sarkar D, R Core Team (2017) nlme: Linear and Nonlinear Mixed Effects Models.

Pitman AJ, Narisma GT, McAneney J (2007) The Impact of Climate Change on the Risk of Forest and Grassland Fires in Australia. *Climatic Change* **84**, 383–401.

Poorter H, Niinemets U, Poorter L, Wright IJ, Villar R (2009) Causes and consequences of variation in leaf mass per area (LMA): a meta-analysis. *New Phytologist* **182**, 565–588.

Prince D, Shen C, Fletcher T (2017) Semi-empirical Model for Fire Spread in Shrubs with Spatially-Defined Fuel Elements and Flames. *Fire Technology* **53**, 1439-1469.

Prior LD, Murphy BP, Williamson GJ, Cochrane MA, Jolly WM, Bowman DMJS (2017) Does inherent flammability of grass and litter fuels contribute to continental patterns of landscape fire activity? *Journal of Biogeography* **44**, 1225–1238.

R Core Team (2017) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Reich PB, Walters MB, Ellsworth DS (1992) Leaf life span in relation to leaf, plant and stand characteristics among diverse ecosystems. *Ecological Monographs* **62**, 365–392.

Reich PB, Wright IJ, Cavender-Bares J, Craine JM, Oleksyn J, Westoby M, Walters MB (2003) The evolution of plant functional variation: Traits, spectra, and strategies. *International Journal of Plant Sciences* **164**, 143–164.

Revell LJ (2012) phytools: An R package for phylogenetic comparative biology (and other things). *Methods in Ecology and Evolution* **3**, 217–223.

Roberts SL, Kelt DA, Wagtendonk JWVan, Miles AK, Meyer MD (2015) Effects of Fire on Small Mammal Communities in Frequent-Fire Forests in California. *Journal of Mammalogy* **96**, 107–119.

Robinson NM, Leonard SWJ, Bennett AF, Clarke MF (2014) Refuges for Birds in Fire-Prone Landscapes: The Influence of Fire Severity and Fire History on the Distribution of Forest Birds. *Forest Ecology and Management* **318**, 110–121.

Rothermel RC (1972) A mathematical model for predicting fire spread in wildland fuels. Res. Pap. INT115. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station.

Scarff FR, Westoby M (2006) Leaf litter flammability in some semi-arid Australian woodlands. *Functional Ecology* **20**, 745–752.

Schneider CA, Rasband WS, Eliceiri KW (2012) NIH Image to ImageJ: 25 years of image analysis. *Nature Methods* **9**, 671–675.

Schulz A (2014) pBrackets: Plot Brackets. R package version 1.0. https://CRAN.R-project.org/package=pBrackets

Schwilk DW (2003) Flammability is a niche construction trait: canopy architecture affects fire intensity. *The American Naturalist* **162**, 725–733.

Schwilk DW (2015) Dimensions of plant flammability. *New Phytologist* **206**, 486–488.

Scott JH, Burgan RE (2005) "Standard Fire Behavior Fuel Models: A Comprehensive Set for Use with Rothermel's Surface Fire Spread Model." USDA Forest Service. General Technical Report RMRS-GTR-153.

Simpson KJ, Ripley BS, Christin PA, Belcher CM, Lehmann CER, Thomas GH, Osborne CP (2016) Determinants of flammability in savanna grass species. *Journal of Ecology* **104**, 138-148.

Smith AMS, Kolden CA, Paveglio T, Cochrane MA, Moritz MA, Bowman DMJS, *et al.* (2016) The science of firescapes: Achieving fire resilient communities. *Bioscience* **66**, 130–146.

Swan M, Galindez-Silva C, Christie F, York A, Di Stefano J (2016) Contrasting Responses of Small Mammals to Fire and Topographic Refugia. *Austral Ecology* **41**, 443–451.

Syphard AD, Brennan TJ, Keeley JE (2014) The role of defensible space for residential structure protection during wildfires. *International Journal of Wildland Fire* **23**, 1165–1175.

Trenberth KE (2011) Changes in precipitation with climate change. *Climate Research*, **47**, 123–128.

Venables WN, Ripley BD (2002) ‘Modern Applied Statistics with S.’ Fourth Edition. (Springer: New York)

Vendramini F, Díaz S, Gurvich DE, Wilson PJ, Thompson K, Hodgson JG (2002) Leaf traits as indicators of resource-use strategy in floras with succulent species. *New Phytologist* **154**, 147–157.

Webb CO, Donoghue MJ (2005) Phylomatic: Tree assembly for applied phylogenetics. *Molecular Ecology Notes* **5**, 181–183.

Weiher E, Van Der Werf A, Thompson K, Roderick M, Garnier E, Eriksson O (1999). Challenging Theophrastus: A common core list of plant traits for functional ecology. *Journal of Vegetation Science* **10**, 609–620.

Weise DR, Wotton BM (2010) Wildland-urban interface fire behaviour and fire modelling in live fuels. *International Journal of Wildland Fire* **19**, 149-152.

Westerling AL, Bryant BP, Preisler HK, Holmes TP, Hidalgo HG, Das T, Shrestha SR (2011) Climate change and growth scenarios for California wildfire. *Climatic Change* **109**, 445-463.

White RH, Zipperer WC (2010) Testing and classification of individual plants for fire behaviour: plant selection for the wildland-urban interface. *International Journal of Wildland Fire* **19**, 213–227.

Wotton MB, Gould JS, McCaw LW, Cheney PN, Taylor WS (2011) Flame temperature and residence time of fires in dry eucalypt forest. *International Journal of Wildland Fire* **21**, 270–281.

Wright IJ, Reich PB, Westoby M (2001) Strategy Shifts in Leaf Physiology, Structure and Nutrient Content between Species of High- and Low-Rainfall and High- and Low-Nutrient Habitats. *Functional Ecology* **15**, 423–434.

Wright IJ, Reich PB, Westoby M, Ackerly DD, Baruch Z, Bongers F, *et al.* (2004) The worldwide leaf economics spectrum. *Nature* **428**, 821–827.

Wright SJ, Kitajima K, Kraft NJB, Reich PB, Wright IJ, Bunker DE, *et al.* (2010) Functional Traits and the Growth-Mortality Trade-Off in Tropical Trees. *Ecology* **91**, 3664–3674.

Wyse SV, Perry GLW, O’Connell DM, Holland PS, Wright MJ, Hosted CL, et al. (2016) A quantitative assessment of shoot flammability for 60 tree and shrub species supports rankings based on expert opinion. *International Journal of Wildland Fire* **25**, 466-477.

Wyse SV, Perry GLW, Curran TJ (2018) Shoot-level flammability of species mixtures is driven by the most flammable species: implications for vegetation-fire feedbacks favouring invasive species. *Ecosystems* **21**, 886–900.

Yates MJ, Anthony Verboom G, Rebelo AG, Cramer MD (2010) Ecophysiological significance of leaf size variation in Proteaceae from the Cape Floristic Region. *Functional Ecology* **24**, 485–492.

Zanne AE, Tank DC, Cornwell WK, Eastman JM, Smith SA, Fitzjohn RG, McGlinn DJ, *et al.* (2014) Three Keys to the Radiation of Angiosperms into Freezing Environments. *Nature* **506**, 89–92.

Zhang D (2018) rsq: R-Squared and Related Measures. R package version 1.0.1. https://CRAN.R-project.org/package=rsq

Zhao W, Cornwell WK, van Pomeren M, van Logtestijn RSP, Cornelissen JHC (2016) Species mixture effects on flammability across plant phylogeny: The importance of litter particle size and the special role for non-*Pinus* Pinaceae. *Ecology and Evolution* **6**, 8223–8234.

Zylstra P, Bradstock RA, Bedward M, Penman TD, Doherty MD, Weber RO, Gill AM, Cary GJ (2016) Biophysical mechanistic modelling quantifies the effects of plant traits on fire severity: Species, not surface fuel loads, determine flame dimensions in eucalypt forests. *PLOS ONE* **11**, e0160715.