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ORIGINAL ARTICLE

Does inherent flammability of grass and litter fuels contribute to continental patterns of landscape fire activity?

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ABSTRACT

Aims To (1) identify the trade-offs among flammability attributes within grass and litter fuel types; (2) determine how flammability attributes of grass and litter fuels vary across macro-ecological gradients; and (3) test our hypothesis that inherent flammability attributes of grass and litter fuels scale to satellite-derived proxies for fire frequency and intensity.

Location Continent of Australia.

Methods Samples of litter and grass fuels collected from 133 sites across Australia were oven dried, then burnt under controlled conditions. Measurements of ignitability, combustibility and sustainability were made. Estimates of fire frequency and fire radiative power (a proxy for intensity) were derived from satellite imagery. Multivariate analyses were used to identify inter-relationships among variables and trends across macro-ecological gradients.

Results Flammability was best described by two axes: high rate of combustion versus long duration of burning, and fast rate of spread versus high maximum temperature. As expected, our study confirmed that grass and litter fuel types have inherently differently flammability attributes whereby grass samples burn more quickly, with a higher rate of spread, than litter samples. However, there were also smaller differences in flammability attributes within fuel types, which scaled to rainfall, temperature and soil phosphorus concentrations. In keeping with our hypothesis, we found correlations between inherent fuel flammability attributes and landscape fire activity across the Australian continent. Fire frequency and rate of combustion of grass fuels were both highest in the tropics, and fire intensity and maximum temperature during combustion of litter fuels were highest in temperate areas.

Main conclusions At a continental scale, we found landscape fire activity was correlated with inherent flammability of grass and litter fuels. This inherent flammability contributes to observed pyrogeographical patterns that are shaped by climate through its known effects on plant productivity, the abundance of cured grass biomass and fire weather.

Keywords
Australia, biogeographical patterns, fire frequency, fire intensity, fire radiative power, grass fuels, litter fuels, MODIS active fire detections, pyrogeography

INTRODUCTION

A fundamental, unresolved question in fire ecology is the extent to which fuel characteristics influence fire regimes. It is well understood that there are clear geographical patterns in fire activity as a result of differences in climate and short-term fire weather, topography, fuel load (biomass), ignition rates and fire management practices (Russell-Smith *et al.*, 2007; Bradstock, 2010; Krawchuk & Moritz, 2011; Pausas & Ribeiro, 2013; Parisien *et al.*, 2014; Williamson *et al.*, 2016). Fuel type is also important; in Australia, grassy surface fuels are associated with high fire frequencies, while litter

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surface fuels tend to burn less frequently, but with high maximum intensities (Murphy *et al.*, 2013). These differences are also apparent at a local scale; a conspicuous feature of savanna–forest boundaries is an abrupt change in fire regime corresponding with the switch from grass fuels to litter fuels (Bowman & Wilson, 1988; Hoffmann *et al.*, 2012). However, whether variations in intrinsic flammability within grass or litter fuels also contribute to continental-scale differences in fire regimes has not been explored. A possible example is the notoriously flammable spinifex (*Triodia* spp., Poaceae) hummock grasslands, which occur across vast areas of Australia's continental interior and are one of Australia's most frequently burnt ecosystems (Russell-Smith *et al.*, 2007; Burrows & Ward, 2009; Murphy *et al.*, 2013). It is unclear whether this high fire frequency is simply a product of an arid climate with extended periods of high fire danger, or possibly also reflects spinifex's exceptionally high inherent flammability. Thus, differences in fire frequency and intensity at the regional to continental scale could conceivably reflect the intrinsic flammability of plant species as well as extrinsic climatic and edaphic factors. To explore this conjecture, we undertook a biogeographical fuel survey across Australia, collecting litter and grass fuels from sites spanning a broad climatic gradient and measuring their flammability. Australia is an ideal study system for such an analysis because virtually the entire continent is fire-prone, and has a mix of grass- and litter-dominated ecosystems which span temperate, arid and tropical climates.

Flammability is multi-dimensional, with four commonly recognized components: ignitability (short ignition delay, rapid rate of spread), combustibility (high rate of consumption, high flame temperature and tall flames), sustainability (long time to flame extinction and long residence time) and consumability (high proportion of biomass consumed) (Anderson, 1970; Gill & Zylstra, 2005; White & Zipperer, 2010). While some of these attributes are positively inter-correlated, others are independent or negatively correlated (Curt *et al.*, 2011; Frejaville *et al.*, 2013; Cornwell *et al.*, 2015; Varner *et al.*, 2015). For instance, flame height is typically positively related to fuel consumption but negatively related to flaming duration (Varner *et al.*, 2015). These differences are apparent when comparing different fuel types: grass is highly ignitable and burns rapidly, whereas litter fires spread more slowly but are likely to be of longer duration (Bradstock & Auld, 1995; Ganteaume *et al.*, 2009; Collins *et al.*, 2015). However, there can also be substantial variation within these fuel types (Curt *et al.*, 2011; Frejaville *et al.*, 2013; Clarke *et al.*, 2014; Cornwell *et al.*, 2015; Simpson *et al.*, 2016). Another consideration is that flammability attributes are strongly affected by fuel moisture content (Bowman *et al.*, 2014a and references therein), which varies continuously in space and time and is driven primarily by recent weather conditions. Determining temporal patterns in fuel moisture at each site as well as the flammability response of each sample to moisture content was beyond the scope of this study. Rather, we aimed to describe the inherent flammability of fuel independent of recent weather, and used dried samples to standardize the moisture content. Our measurements therefore represent the maximum potential flammability of litter and grass fuels at each site. It has also been suggested that soil nutrients, especially phosphorus, could influence flammability through their effects on plant growth, as well as phosphate being a fire retardant (Scarff *et al.*, 2012).

Knowing the flammability of fuel types is essential for testing and parameterizing landscape to global level models of fire risk and behaviour, smoke emissions and vegetation dynamics, as well as understanding the biogeography of flammable biomes and the role of fire in controlling of forest–savanna boundaries (Pettinari & Chuvieco, 2015). Surprisingly, there have been no previous studies explicitly investigating the linkages between inherent fuel flammability and measures of landscape fire activity such as frequency and intensity. Satellites can provide estimates of area burnt and fire radiative power (FRP: the measured radiant heat output of detected fires, in units MW) at landscape to global scales (Giglio *et al.*, 2006; Roy & Boschetti, 2009), enabling such comparisons. The different components of flammability must be considered when attempting to relate experimental measurements of flammability to regional or landscape fire activity. In principle, it is likely that at a landscape scale, area burnt is positively correlated with rate of spread of the fire, and that fire intensity is positively correlated with flame temperature and the duration of flaming combustion.

The overarching aim of our study was to test our hypothesis that intrinsic differences in flammability of grass and litter fuels contribute to the biogeographical patterns of fire observed across the Australian continent. To do this, we first analysed the inter-relationships among flammability attributes of dried fuels. Next, we examined biogeographical patterns in the intrinsic flammability of grass and litter fuels in relation to climate and soil fertility. Finally, we determined whether flammability of grass and litter samples was correlated with satellite-derived estimates of area burnt and FRP in the region surrounding the sample site.

MATERIALS AND METHODS

Field sites and sample collection

Grass and litter fuels were sampled from 133 sites (41 tropical, 27 arid and 65 temperate) spanning a broad environmental gradient across Australia (Fig. 1). Mean annual temperature ranged from 7 to 29 °C, and mean annual precipitation was between 192 and 1796 mm (Fig. 2), according to climatic data obtained from the WORLDCLIM data set (Hijmans *et al.*, 2005). Vegetation type was simplified from the National Vegetation Inventory System 4.1 (Department of the Environment, 2012). The work was part of a broader study examining consumption of fuels by wildfires, so field sites were located where it was possible to pair recently burnt areas with adjacent, similar unburnt areas. Here, we consider only the unburnt sites, which characterize fuels across a spectrum of flammable environments.

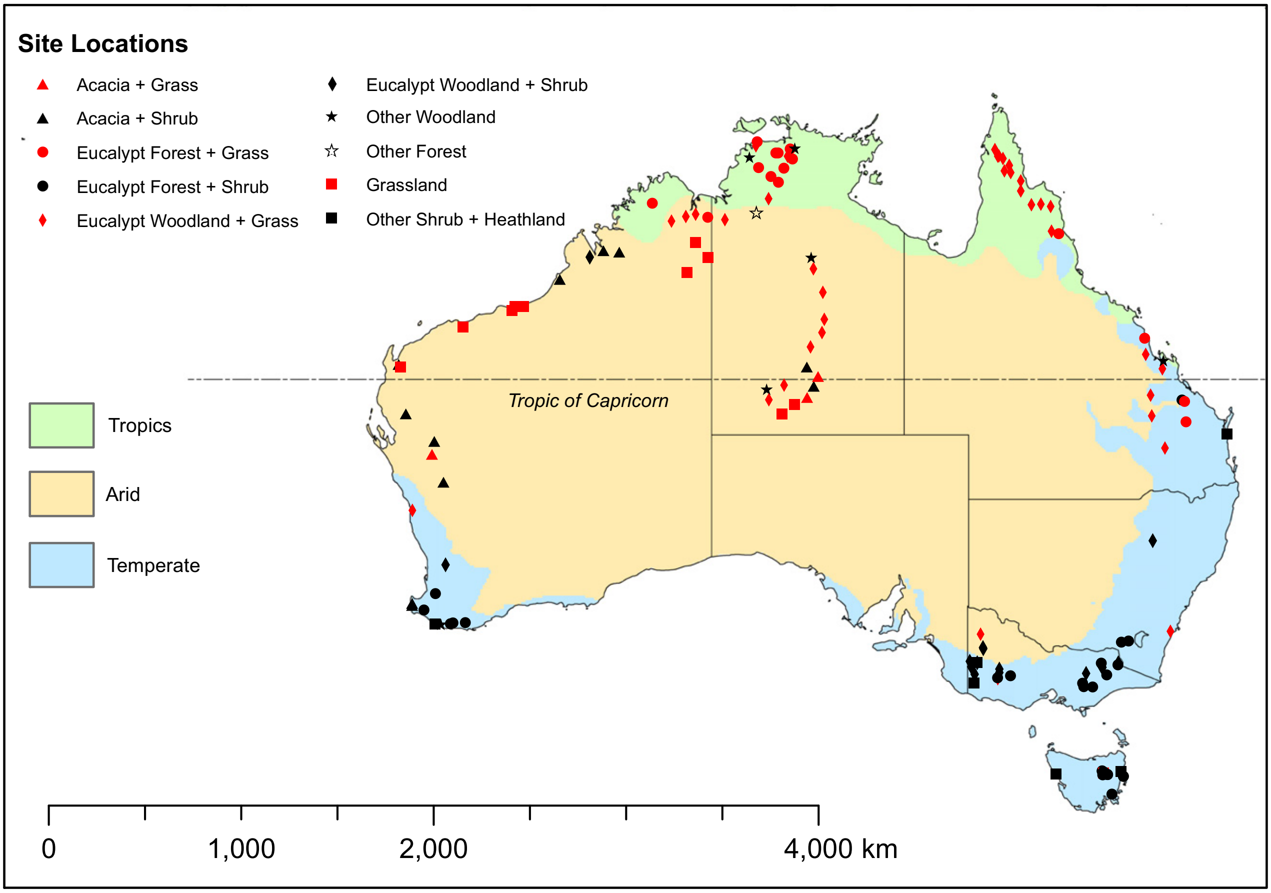

Figure 1 Location of sample sites, which span the tropical, arid, and temperate climate zones of Australia, according to the Koppen-Geiger major classes (Kottek *et al.*, 2006). The vegetation type at each site is indicated by the symbols.

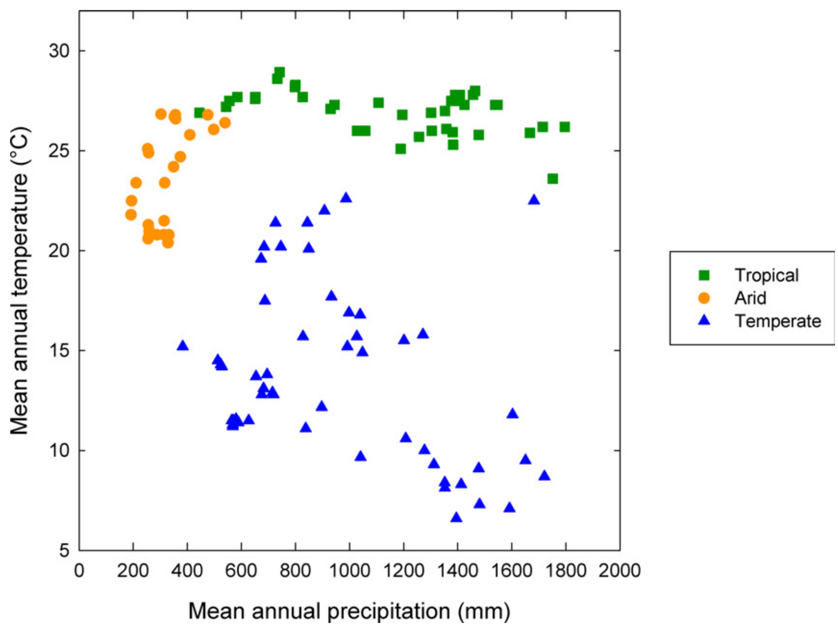

Figure 2 The climate space covered in our study. Climate at each site in Australia was classified as tropical, arid or temperate according to the Koppen-Geiger system (Kottek *et al.*, 2006). Climatic data were obtained from the WORLDCLIM data set (Hijmans *et al.*, 2005).

Each site comprised three transects, 30 m in length, established at a semi-random location by throwing a stick backwards over the shoulder. Transects were situated *c.* 100 m from fire boundaries and at least 100 m apart. Samples of fine litter (< 6 mm) and standing grass were collected separately in 1 m^2 quadrats, then weighed. It was impractical to identify individual species that comprised the fuels because samples were desiccated and from mixed communities. Biomass of standing herbs was so small it is not considered here. Litter and grass were collected in at least two quadrats on each transect (at 0 and 14 m), but at some sites, where fuels were very patchy, three or four quadrats were measured. Grass as a percentage of fine fuel at each transect was calculated as (grass mass)/(grass mass + litter mass) × 100, then averaged for the site. Canopy cover was measured using a convex spherical crown densiometer (Forestry Suppliers, Jackson, MS, USA) at the start of and 15 m along each transect, and averaged for the site. At each site, the fine litter and grass samples from all quadrats were pooled and a subsample of *c.* 100 g was collected for flammability measurements in the laboratory.

To investigate whether flammability was related to soil fertility, soil nitrogen (N) and phosphorus (P) were measured in surface soils (0–10 cm depth) from 77 of the sites. Samples were taken from each of the three transects and bulked for each site. Soil samples were analysed for total organic N content using an Automated N/C Analyser-Mass Spectrometer consisting of a Roboprep connected with a Tracermass isotope ratio spectrometer (Europa Scientific Ltd, Crewe, UK). Total P was measured by digesting soil in concentrated H_2SO_4 for 4 h at 320 °C, then analysing the digest using a modified ascorbic acid method (Kuo, 1996). Analyses were performed at the Western Australian Biogeochemistry Centre at the University of Western Australia.

Landscape fire activity

In order to test our hypothesis that landscape fire activity is correlated with fuel flammability attributes, we characterized recent fire activity at each field site using remotely sensed proxies for fire intensity and area burnt, as follows. For each site, we identified the approximate date of the most recent fire using the MODIS collection 5 MCD45 burnt area product (Roy & Boschetti, 2009). Each site was then attributed with the sum of FRP for all MODIS collection 5 MCD14DL active fire detections (Giglio *et al.*, 2006) for a window spanning 16 days before to 16 days after the fire day, within a 4 km radius of the site. This window allowed for possible inaccuracies in the fire date and the potential for smouldering fires to continue to burn for an extended period, as well as measuring the broader-scale total energy emission of the fire in the vegetation surrounding the sample site. To determine fire frequency, we sampled a 50 km radius around our sites. This was considered representative of the surrounding landscape, given much of Australia has few marked topographic features and limited spatial turnover in species composition (Woinarski *et al.*, 2005). The AVHRR satellite data identified areas burnt during the period 1997–2010. The average area burnt per year was calculated and expressed as a percentage of the sample area to provide a measure of fire frequency (www.firenorth.org.au; Russell-Smith *et al.*, 2007; Murphy *et al.*, 2013).

Fuel flammability measurements

Grass and litter samples were oven dried at 60 °C for at least 48 h before combustion. Following an approach similar to that used by Plucinski & Anderson (2008), a fixed mass of dried fuel was placed in a circular tray 26 cm in diameter and 4.6 cm high, with a tile base and wire mesh sides. As found by Plucinski & Anderson (2008), each sample naturally packed to a characteristic bulk density, which could not be increased without crushing the fuel. A greater mass of litter (70 g) than grass (30 g) was used to achieve complete coverage of the tray by litter fuels and avoid overflow of grass fuels, and create a fuel bed of similar depth for each fuel type (average 5.8 cm for grass and 4.2 cm for litter). In order to compare grass and litter fuels *post hoc*, we investigated how flammability attributes were affected by these differences in sample mass by comparing eight pairs of 70 and 30 g litter subsamples. Full details of this comparison are presented in Appendix S1 in Supporting Information.

Samples were burned under ambient conditions (see Appendix S2). During the combustion measurements the tray was placed in a small, open-fronted shed with a fibre-cement shelf to minimize air movement. Fuel height was measured at four positions within the sample tray and the pre-burn mass was recorded. Fuel bulk density was calculated as the pre-burn dry fuel mass divided by fuel volume (tray area × fuel mean height). A cotton ball, wetted with 1 mL of denatured ethanol, was placed on the fuel at the centre of the tray and used as an ignition source (Plucinski & Anderson, 2008). Time to ignition was recorded as the time delay between ignition of the cotton ball and visible ignition of the fuel sample (Ganteaume *et al.*, 2009; Curt *et al.*, 2011) and flame duration was measured as the length of time from fuel ignition to flame extinction (Ormeño *et al.*, 2009). Rate of spread was determined by measuring the time it took for flames to reach the edge of the tray after ignition and dividing that time by the tray radius. A video camera recorded the combustion of each sample, so that flame height could be determined from a reference scale visible in the image. Flame height was measured every 3 s from the video recording, and maximum and mean flame heights were calculated. One thermocouple was placed 5 cm above the base of the sample (i.e. very close to the sample without compressing it), and another at 30 cm height, to measure the temperature once per second during combustion. Mean and maximum temperatures during combustion were calculated for both the 5 and 30 cm heights during each experimental burn. The remaining biomass was then weighed and post-burn mass was recorded. Rate of flaming combustion was calculated as the mass combusted) divided by the flame duration.

Statistical analyses

Principal components analysis (PCA) was done on the flammability variables, to examine patterns in these data, using the statistical software R 3.1.1 (R Core Team 2015).

The analyses were performed separately on grass and litter measurements, because different masses were used. Analysis of variance and Tukey's honestly significant difference test were used to identify significant differences ($P < 0.05$) among climate zones in PC1 and PC2 for both grass and litter fuels. We used *t*-tests to compare flammability of grass and litter samples; full details of the grass and litter comparison, accounting for differences in fuel masses used, are presented in Appendix S1. We also used *t*-tests to compare flammability of spinifex with that of other tropical grass samples.

Inspection of the raw correlation coefficients suggested some likely influences of rainfall, temperature and soil P (but not soil N) on individual flammability variables (see Appendix S3). These influences were tested for both grass and litter fuels using complete subsets regressions. We constructed candidate sets of linear models containing the eight possible additive combinations of the three explanatory variables, mean annual temperature (MAT), mean annual precipitation (MAP: log transformed) and soil P. Interactions were not included because that would have significantly increased the number and complexity of possible models. The best model was selected according to Akaike's information criterion adjusted for small sample size (AICc), which balances model fit and parsimony (Burnham & Anderson, 2002). Bulk density was affected by climate and it was therefore added to the best model, to determine whether the environmental effects on the flammability variable were still important, or were mediated through an effect on bulk density. The same approach was used to evaluate the influence of MAP, MAT and soil P on area burnt and FRP, except that bulk density was not added to the models.

RESULTS

Inter-relationships among flammability attributes

Both grass and litter had similar inter-relationships among flammability attributes (see Appendix S3). For instance, rate of combustion and mean flame height (combustibility attributes) were positively correlated with each other, and negatively correlated with duration of flaming (sustainability attribute) (see Appendix S3). Percentage combusted (consumability) was positively correlated with combustibility attributes, especially in litter fuels (see Appendix S3). Rate of combustion, mean flame height and duration of flaming were also strongly correlated with fuel bulk density, especially in litter fuels (see Appendix S3). The two ignitability attributes, rate of spread and time to ignition, were not closely correlated ($|r| > 0.60$) with any other flammability attributes (see Appendix S3).

Within each fuel type, principal components analysis revealed close alignment of both sustainability (duration of flaming) and the ignitability attributes (time to ignition and rate of spread) with fuel bulk density. The combustibility attributes also formed a cluster, but there was some divergence among them (Fig. 3). Percentage combusted

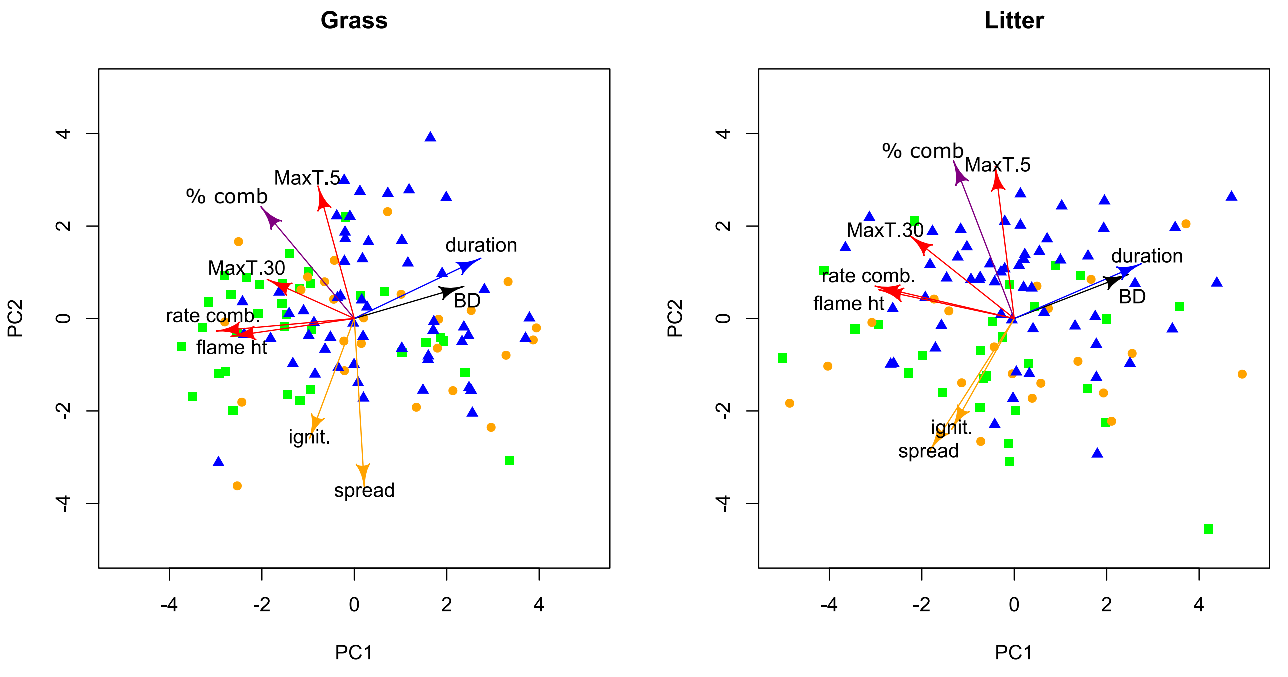

Figure 3 Principal components analysis of flammability attributes for grass and litter samples. Ignitability attributes are shown by orange arrows, combustibility attributes in red, consumability in purple, sustainability in blue and fuel bulk density in black. $MaxT._5$ and $MaxT._{30}$ are maximum temperature at 5 and 30 cm height, % comb is percentage mass combusted, rate comb is rate of combustion, flame ht is mean flame height, and ignit. is the inverse of time to ignition. Tropical sites are represented by green squares, arid sites by orange circles and temperate sites by blue triangles.

(consumability) was embedded between the combustibility attributes maximum temperature at 5 cm and maximum temperature at 30 cm (Fig. 3). Only the first two principal components (PC) of the PCA had eigenvalues > 1, considered important in describing the data (Quinn & Keogh, 2002). These first two PCs together explained 60% of the variation in the flammability attributes for grass (PC1 = 40%, PC2 = 20%), and 70% for litter (PC1 = 46%, PC2 = 24%). PC1 represented the spectrum of rapid combustion/high flames versus long duration of flaming/high bulk density, while PC2 represented the spectrum of rapid rate of spread versus high maximum temperature (5 cm height) and high percentage combusted.

Variability within grass and litter fuels in relation to environment

There was substantial variability in the flammability attributes within grass and litter fuels. Some of these flammability attributes were weakly correlated with environmental variables (see Appendix S3). PCA revealed distinct patterns in flammability in relation to climate (Fig. 3). Tropical grasses had a significantly lower PC1 ($P < 0.001$) than arid or temperate ones, while temperate litter had significantly higher PC2 ($P < 0.001$) than tropical or arid litter.

The association of many flammability attributes with climate, demonstrated by PCA, was confirmed by linear modelling (Table 1). In grass, for example, high MAT and MAP (i.e. tropical grasses) were associated with low bulk density, low duration of flaming, rapid rate of combustion and high flames (Table 1; Figs 4 & 5). The MAT effects appeared to be mediated through bulk density, because they were no longer important when bulk density was added to the models (Table 1). However, MAP effects on grass flammability attributes appeared independent of bulk density, except for percentage mass combusted. In litter samples, high MAT was associated with low bulk density, low duration of flaming, low percentage mass combusted, low time to ignition and rapid rate of spread (Table 1; Fig. 4). These associations appeared independent of bulk density, except for duration of flaming (Table 1). The only litter flammability attribute correlated with MAP was duration of flaming, and this effect was subsumed by bulk density.

Soil P (but not soil N) was also correlated with some grass and litter flammability variables (Table 1). Linear modelling showed that soil P was positively correlated with rate of spread, and negatively correlated with percentage mass combusted and temperature at 5 cm in both grass and litter fuels. These effects were independent of bulk density.

The comparison of spinifex with other tropical grasses showed that spinifex took longer to ignite, spread more slowly but burned for slightly longer than the other tropical grasses (Table 2). Sites with spinifex were drier, and had lower soil N, but similar soil P, to other tropical sites (Table 2).

Table 1 Summary of results of linear modelling, showing statistically important correlations of mean annual temperature (MAT), mean annual precipitation (MAP) and soil phosphorus with flammability attributes for litter and grass samples, and also for landscape fire activity* in Australia. The '+' and '–' symbols indicate directions of all important effects. We also tested whether environmental effects on flammability were mediated through bulk density (BD) by adding this term to the model containing all the supported climate terms†. Summaries of individual models this table is based on are given in Appendix S4.

Attribute	MAT	MAP	Soil P	Adding bulk density
Grass				
Bulk density	–	–		n.a.
Time to ignition				
Rate of spread		+	+	
Duration	–	–		BD subsumes MAT
% combusted		+	–	BD subsumes MAP
Rate of combustion	+	+		BD subsumes MAT
Max temp at 30 cm				
Max temp at 5 cm			–	
Mean flame height	+	+		BD subsumes MAT
Litter				
Bulk density	–			n.a.
Time to ignition	–		–	
Rate of spread	+		+	
Duration	–	–		BD subsumes MAT and MAP
% combusted	–		–	
Rate of combustion				
Max temp at 30 cm				
Max temp at 5 cm	–		–	
Mean flame height				
Landscape fire activity				
Area burnt	+	+	–	n.a.
FRP	–	–	–	n.a.

*Importance values (w+) > 0.73 were considered to indicate substantial support for an effect (Richards, 2005).

†We considered bulk density subsumed an environmental effect if the model was improved by adding bulk density (delta AICc lowered by > 2), and the AICc was further improved or unaffected (delta AICc < 2) when the original environmental term(s) were then dropped.

Comparison of grass and litter fuels

Grass and litter fuels displayed different flammability attributes (Fig. 4), even allowing for differences in mass of grass and litter fuels (see Appendix S1). Bulk density appeared an important driver of these differences: it was approximately three times higher for litter than grass fuels, and there was almost no overlap between the fuel types (Fig. 5; see Appendix S1). Grass was generally more ignitable and more combustible, but combustion sustainability was lower than for litter (Fig. 4). The grass samples produced a higher rate of spread, a higher rate of combustion a greater flame height than litter samples, and a lower duration of flaming combustion (Fig. 4; see Appendix S1).

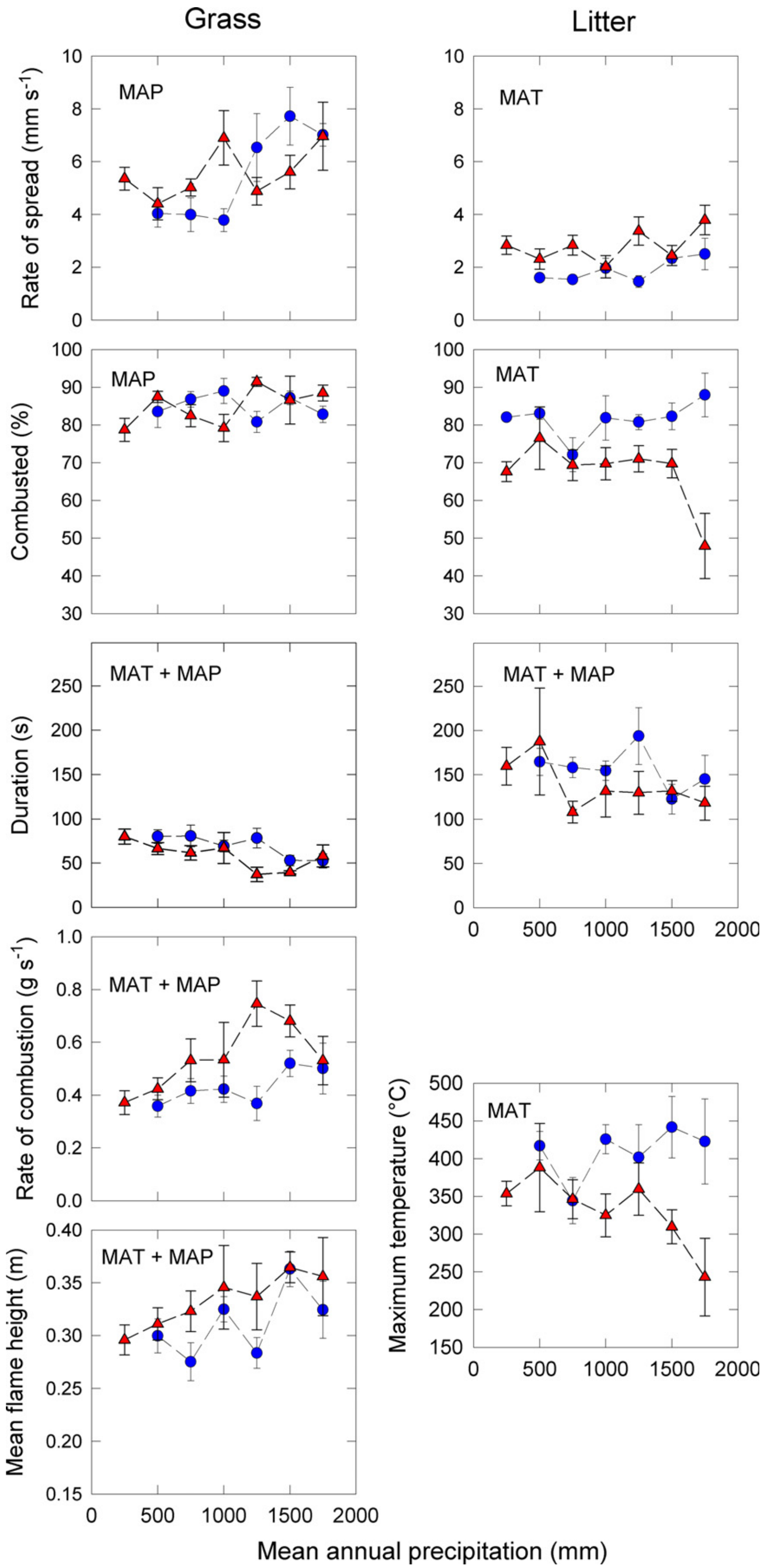

Figure 4 Statistically important climatic trends in fuel attributes: rate of spread, percentage mass combusted and duration of flaming combustion for both grass and litter fuels; rate of combustion and mean flame height for grass fuels only; and maximum temperature at 5 cm for litter fuels only in Australia. The statistically important climatic variables (mean annual temperature, MAT, and mean annual precipitation, MAP) are listed on each panel. Sites are binned into 250-mm precipitation categories for presentation, and red triangles indicate sites ≥ 20 °C mean annual temperature (MAT), and blue circles, sites < 20 °C MAT. Bars represent SE.

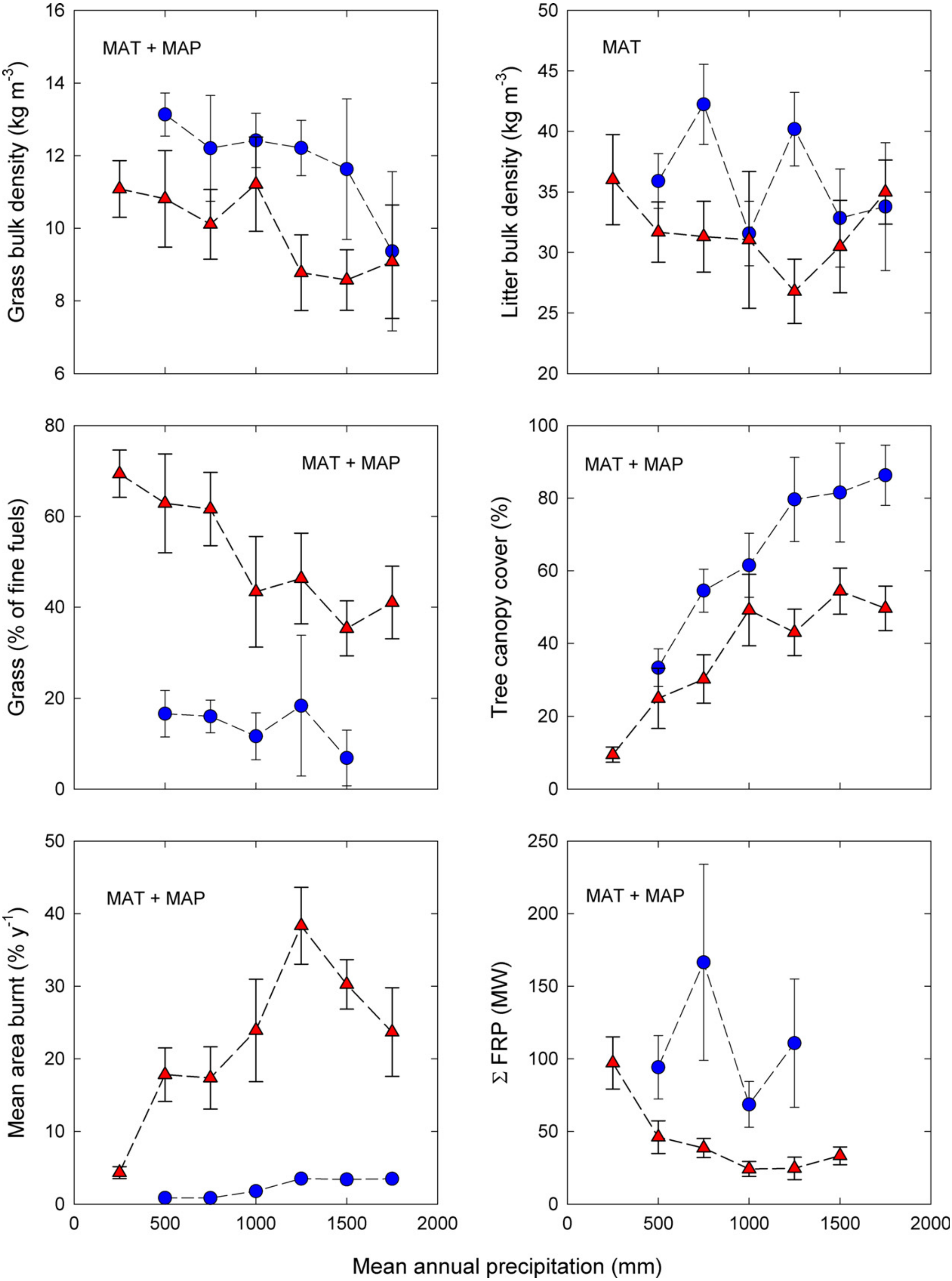

Figure 5 Climatic trends in bulk density of grass and litter fuels, grass fuels (as a percentage of grass and litter), tree canopy cover and remotely sensed area burnt (from AVHRR), and summed fire radiative power, ΣFRP (from MODIS) in Australia. Sites are binned into 250-mm precipitation categories for presentation, and red triangles indicate sites ≥ 20 °C mean annual temperature, MAT), and blue circles, sites < 20 °C MAT. Bars represent SE. The statistically important climatic variables are listed on each panel.

Table 2 Comparison of flammability of spinifex (*Triodia* spp.) and other tropical grasses, and environmental conditions at the sample sites in Australia. A *t*-test was used to determine whether differences between the grass types were significant.

		Spinifex (n = 15)		Other tropical grasses (n = 45)		
	Unit	Mean	SE	Mean	SE	P
Fuel bulk density	kg m^{-3}	9.9	0.8	10.3	0.5	NS
Duration	s	64	4	59	5	< 0.05
Time to ignition	s	1.7	0.3	1.2	0.1	< 0.05
Rate of spread	mm s^{-1}	3.8	0.3	6.0	0.3	< 0.001
Rate of combustion	g s^{-1}	0.42	0.03	0.56	0.04	NS
Mass combusted	%	86	4	83	2	NS
Max temp 30 cm	°C	119	12	100	5	NS
Max temp 5 cm	°C	290	17	288	12	NS
Mean flame height	m	0.32	0.01	0.33	0.01	NS
Environmental variables						
Mean annual precipitation	mm	455		966		< 0.00001
Mean annual temperature	°C	25.7		25.4		NS
Soil N	mg g^{-1}	0.26		0.45		< 0.05
Soil P	mg g^{-1}	0.09		0.12		NS

Landscape fire activity in relation to experimental flammability and climate

We found relationships between experimental flammability measurements and landscape fire activity. There was a negative correlation between fire frequency and FRP (r = −0.55), reflecting the high fire frequency in grass-dominated ecosystems and often high fire intensity in litter-dominated ones (Table 3). Fire frequency showed some weak associations with litter but not grass loads, and was positively correlated with percentage grass. Conversely, FRP was negatively correlated with % grass but not with grass load, and was positively correlated with litter load. There was little relationship between tree canopy cover and either FRP or area burnt, despite the strong association of all three with climate (Fig. 5).

Landscape-scale fire activity showed strong climatic trends, with a possible association with soil P (Table 1). Both the raw correlation coefficients and linear modelling indicated that average area burnt each year was positively correlated with both mean annual temperature and mean annual precipitation (Tables 1 & 3), reflecting the high fire frequency in the tropical zone. Conversely, FRP was negatively correlated with mean annual temperature and mean annual precipitation, reflecting frequent, low intensity fires in the tropical savannas (Tables 1 & 3; Fig. 5). Despite their strong association with climate, neither landscape fire variable was closely correlated with mean annual FFDI (Table 3). Linear modelling suggested that both area burnt and FRP were negatively correlated with soil P when mean annual rainfall and temperature were controlled for (Table 1; see Appendix S3).

There were weaker associations of landscape fire activity with fuel flammability attributes. Fire frequency was most closely associated with grass flammability. Specifically, it was positively correlated with grass flame height and rate of combustion, and negatively correlated with duration of flaming and bulk density (Table 3). There were some weaker correlations with litter flammability (Table 3). On the other hand, FRP was more closely associated with litter flammability attributes. It was positively correlated with percentage of litter consumed and maximum temperature at 5 cm height, and negatively correlated with the rate of spread.

DISCUSSION

Our study has documented biogeographical patterns in the flammability of grass and litter fuels across Australia. This continent is a powerful model system given the ubiquity and ecological importance of landscape fire across climatic gradients and among diverse vegetation types (Bradstock, 2010; Murphy *et al.*, 2013). Accordingly, our results provide insights into the role of fuels in driving regional to continental level pyrogeographical patterns, as we discuss below.

What is flammability?

This study showed consistent inter-relationships of flammability attributes within both grass and litter fuels, similar to those reported for litter and bark fuels in a range of other ecosystems (Curt *et al.*, 2011); de Magalhães & Schwilk, 2012; Frejaville *et al.*, 2013; Cornwell *et al.*, 2015).

Our flammability attributes broadly segregated according to the three components of flammability (ignitability and sustainability, and combustibility) recognized by Anderson (1970) (Fig. 3). The consumability variable (percentage combusted) was embedded among the combustibility variables. Consumability is likely to be a more important component of flammability with coarser fuels, or those with higher water content, than the fine, dry fuels used in our experiment. In

Table 3 Correlation coefficients for the landscape fire activity attributes, fire frequency and summed FRP, versus environmental and flammability variables of grass and litter fuels in Australia. Values where $P < 0.01$ are shown in bold.

	Fire frequency (from AVHRR)	ΣFRP (MW) (from MODIS)
Environmental variables		
MAT	**0.71**	**−0.59**
MAP	**0.41**	**−0.25**
Mean annual FFDI	0.14	−0.06
Soil P	0.00	−0.22
Soil N	−0.03	−0.13
Canopy cover	−0.06	0.01
Grass load	0.07	−0.08
Litter load	**−0.28**	**0.26**
Percentage grass	**0.30**	**−0.27**

	Fire frequency		ΣFRP	
	Grass	Litter	Grass	Litter
Flammability variables				
Bulk density	**−0.45**	**−0.33**	0.22	**0.27**
Duration	**−0.49**	**−0.29**	0.20	**0.26**
Ignitability	0.19	0.18	0.02	**−0.25**
Rate of spread	0.17	**0.31**	−0.05	**−0.31**
% combusted	0.16	−0.14	0.07	**0.32**
Rate of combustion	**0.44**	0.18	−0.13	−0.09
Maximum T_{30}	0.14	−0.04	0.05	0.17
Maximum T_5	0.08	**−0.24**	0.07	**0.32**
Mean flame height	**0.45**	0.09	−0.18	0.03

Percentage grass is (grass/(grass + litter) × 100). Ignitability is (1/time to ignition), MAT is mean annual temperature, MAP is mean annual precipitation, FFDI is forest fire danger index, Soil P and N are soil phosphorus and nitrogen concentrations, area burnt is mean proportion burnt each year (within a 100-km radius of site). Fire frequency is based on mean percentage area burnt per year and ΣFRP is the summed fire radiative power (representing the total intensity of the fire line). Variables were log or arcsin transformed as appropriate.

fact, we found that flammability of both our grass and litter fuels could be adequately described using just two principal axes (high rate of combustion versus long duration of burning and fast rate of spread versus high maximum temperature). These two axes correspond broadly to rate of spread and total heat release, the two dimensions of flammability proposed by Schwilk (2015) in his recent, conceptually appealing model. Our two axes are ecologically important because they shape fire regimes and affect plants in contrasting ways. The axis representing high rate of spread affects area burnt and the maximum temperatures to which plants are exposed. The axis representing high rate of combustion versus long duration of burning affects the exposure times of plants, seeds and soils to lethal temperatures (Bradstock & Auld, 1995; Stoof *et al.*, 2013). Bulk density was a convenient proxy for the rate of combustion–duration axis of flammability, directly influencing the rate of combustion through its effect on airflow (Varner *et al.*, 2015).

The multi-dimensionality of flammability needs to be considered when discussing its evolution. Proponents of the Mutch (1970) hypothesis assert that flammability can be selected for in fire-dependent communities. However, to test this hypothesis it is critical to specify which flammability components are under selective pressure (e.g. ignitability, combustibility or sustainability). Researchers must also consider the inherent trade-offs among these components. For instance, the strong, negative correlations between some flammability attributes, such as duration and rate of combustion, mean it would be difficult to envision, even in theory, how evolution could select for high levels of all flammability components simultaneously. Future studies of the evolution of 'flammability' need to explicitly state whether they are focusing on ignitability, combustibility, sustainability and/or consumability. Our study provides evidence of the degree to which these various flammability components are related, and how this varies among fuel types.

Although our study highlights trade-offs among flammability attributes within grass and litter fuels, it is important to acknowledge that landscape flammability is far more complex than can be captured by a standardized sample of a single fuel type (Gill & Zylstra, 2005; de Magalhães & Schwilk, 2012; Varner *et al.*, 2015). There is a strong influence of packing and fuel arrangement on landscape flammability (de Magalhães & Schwilk, 2012; Ganteaume *et al.*, 2014). While it is difficult to envisage a particular fuel that is highly ignitable, combustible and sustainable, this might be possible for a landscape with a mix of fine and coarse fuels, suitably arranged to facilitate a 'combustion cascade', whereby the grass fuels are ignitable, litter fuels are combustible and coarse fuels sustain combustion over a long duration.

Biogeographical variability in intrinsic flammability of grass and litter fuels

There was geographical patterning in the flammability of both grass and litter fuels after oven drying. Both MAP and MAT were correlated with important grass flammability attributes, reflecting lower bulk density and duration of flaming, and higher rate of combustion and flame height, in tropical grasses. Litter flammability was generally more closely correlated with MAT, reflecting the lower rate of spread and higher bulk density and duration of flaming in temperate compared with tropical or arid zone litter. Bulk density appeared to drive much of the variability in flammability, and subsumed most MAT effects on grass flammability attributes. This was similar to other findings that an open litter bed structure with low bulk density burns more rapidly than tightly packed ones (Scarff & Westoby, 2006; Cornwell *et al.*, 2015). Grass flammability is affected by canopy architecture (Simpson *et al.*, 2016) and in our experiment, grass fuels were laid horizontally, with no major gaps, unlike the more variable, generally vertical arrangement of grasses in the field.

[Other researchers have similarly placed shoots horizontally to measure shoot flammability (Jaureguiberry *et al.*, 2011; Wyse *et al.*, 2016)]. We also found some flammability attributes differed according to fuel load, and this needs to be further investigated at a larger experimental scale.

It has been proposed that impoverished soils can lead to rapid accumulation of nutrient-poor biomass, which provides fuel for intense fire (Orians & Milewski, 2007). Conversely, phosphates are used as fire retardants and in aerial suppression of wildfires (Bell *et al.*, 2005), so high soil and therefore foliar P concentrations could plausibly be linked to lower flammability (Scarff *et al.*, 2012). We detected a weak positive correlation between soil P and the rate of spread of flames in both grass and litter fuels, but when climate was controlled for in our modelling, there was a negative relationship between soil P and both area burnt and FRP. Our results concur with the conclusion of Scarff *et al.* (2012), that effects of P on flammability are likely to be modest relative to those of leaf moisture content. They are also consistent with findings in southern Australian woodlands, that soil fertility could weakly influence fuel accumulation and flammability, but that rainfall was the dominant influence on fire regimes (Gibson *et al.*, 2015).

Fuel loads and fuel moisture were factored out of our study by using a standardized mass of oven-dried samples. This avoided the complication of temporal and spatial variation in fuel moisture content, which strongly influences flammability (Gill & Moore, 1996; Alessio *et al.*, 2008; De Lillis *et al.*, 2009). It is possible that oven drying could influence flammability by driving off volatile flammable compounds in leaves of plants such as eucalypts and spinifex. However, this effect was not apparent in the Clarke *et al.* (2014) study, which found similar rankings for fresh and dry leaves of rain forest and eucalypt species using the same techniques employed in this study. Obviously, comparisons of landscape flammability across regions must consider the spatial and temporal patterns of fuel moisture content (Bradstock, 2010). These patterns of fuel moisture are partially captured by indices such as FFDI, which includes an antecedent drought or soil moisture term (Dowdy *et al.*, 2009). Additional information is needed about how these changes in fuel moisture affect the flammability of grass, litter and woody fuels across the continent, but determining this would be a massive undertaking, made increasingly difficult by stricter quarantine regulations.

Grass versus litter flammability

Our study confirmed there are large differences between grass and litter fuels for many flammability attributes. This was particularly striking for rate of spread (faster in grass) and duration of flaming combustion (longer in litter), which represent both the major axes of flammability identified in our analysis, and broadly correspond with Schwilk's (2015) two-dimensional model. Thus, our study highlights the important role of fuel type (grass versus litter) in shaping fire regimes, as illustrated by the need for separate fire danger indices for grasslands and forests (Noble *et al.*, 1980). Our study also supports the notion that changes in grass abundance can drive state shifts in plant communities and their fire regimes (Bowman *et al.*, 2014b). Examples of such shifts are overgrazing leading to the dominance of woody plants (Asner *et al.*, 2004) or conversely, the proliferation of flammable grasses causing degradation of forests and woodlands (D'Antonio & Vitousek, 1992).

Landscape level fire activity

Our study has shown that satellite estimates of landscape fire activity across Australia were closely related to climate. This is not surprising, given the many influences of climate, both direct, in determining fuel moisture content and in generating fire weather, and indirect, in influencing the quantities and types of fuel produced (Russell-Smith *et al.*, 2007; Bradstock, 2010; Murphy *et al.*, 2013; Bowman *et al.*, 2014a and references therein). More surprisingly, our study has shown that climate may also influence the properties of grass and litter fuels in a way that reinforces patterns of fire activity driven by well-recognized factors such as biological productivity and fire weather. We found a relationship between satellite estimates of landscape fire activity across Australia and experimentally determined flammability attributes. This biogeographical relationship was apparent despite differences in fuel moisture between our experimental samples (which were oven dried) and fuels burnt by management burns and uncontrolled landscape fires, which occurred under a variety of fuel moisture and weather conditions. Grass fuels from the tropical savannas were extremely ignitable, matching the high fire frequency of these systems (Russell-Smith *et al.*, 2007; Murphy *et al.*, 2013). By contrast, forested Australian temperate areas have some of the highest intensity fires in Australia, and we found the litter fuels from these systems have higher bulk density, and produce hotter flames which burn for longer than the litter fuels from tropical Australia.

The fundamental difference in grass and litter fuels has long been understood by fire managers, yet there have been few attempts to quantify these differences, particularly at macro-ecological scales as we have done here. It is clear that differences among grass and litter fuels are far smaller than the differences between them, which helps to simplify pyrogeographical models seeking to explain fire activity at both local and continental scales.

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REFERENCES

Alessio, G.A., Penuelas, J., Llusia, 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.

Anderson, H.E. (1970) Forest fuel ignitibility. *Fire Technology*, **6**, 312–319.

Asner, G.P., Elmore, A.J., Olander, L.P., Martin, R.E. & Harris, A.T. (2004) Grazing systems, ecosystem responses, and global change. *Annual Review of Environment and Resources*, **29**, 261–299.

Bell, T., Tolhurst, K. & Wouters, M. (2005) Effects of the fire retardant Phos-Chek on vegetation in eastern Australian heathlands. *International Journal of Wildland Fire*, **14**, 199–211.

Bowman, D.M.J.S. & Wilson, B.A. (1988) Fuel characteristics of coastal monsoon forests, Northern Territory, Australia. *Journal of Biogeography*, **15**, 807–817.

Bowman, D.M.J.S., French, B.J. & Prior, L.D. (2014a) Have plants evolved to self-immolate? *Frontiers in Plant Science*, **5**, Article 590.

Bowman, D.M.J.S., MacDermott, H.J., Nichols, S.C. & Murphy, B.P. (2014b) A grass-fire cycle eliminates an obligate-seeding tree in a tropical savanna. *Ecology and Evolution*, **4**, 4185–4194.

Bradstock, R.A. (2010) A biogeographic model of fire regimes in Australia: current and future implications. *Global Ecology and Biogeography*, **19**, 145–158.

Bradstock, R.A. & Auld, T.D. (1995) Soil temperatures during experimental bushfires in relation to fire intensity – consequences for legume germination and fire management in south-eastern Australia. *Journal of Applied Ecology*, **32**, 76–84.

Burnham, K.P. & Anderson, D.R. (2002) *Model selection and multimodel inference. A practical information-theoretic approach*, 2nd edn. Springer, New York.

Burrows, N.D. & Ward, B. (2009) Fuel dynamics and fire spread in spinifex grasslands of the Western Desert. *Proceedings of the Royal Society of Queensland*, **115**, 69–76.

Clarke, P.J., Prior, L.D., French, B.J., Vincent, B., Knox, K.J.E. & Bowman, D.M.J.S. (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.

Collins, L., Penman, T.D., Price, O.F. & Bradstock, R.A. (2015) Adding fuel to the fire? Revegetation influences wildfire size and intensity. *Journal of Environmental Management*, **150**, 196–205.

Cornwell, W.K., Elvira, A., van Kempen, L., van Logtestijn, R.S.P., Aptroot, A. & Cornelissen, J.H.C. (2015) Flammability across the gymnosperm phylogeny: the importance of litter particle size. *New Phytologist*, **206**, 672–681.

Curt, T., Schaffhauser, A., Borgniet, L., Dumas, C., Esteve, R., Ganteaume, A., Jappiot, M., Martin, W., N'Diaye, A. & Poilvet, B. (2011) Litter flammability in oak woodlands and shrublands of southeastern France. *Forest Ecology and Management*, **261**, 2214–2222.

D'Antonio, C.M. & Vitousek, P.M. (1992) Biological invasions by exotic grasses, the grass/fire cycle, and global change. *Annual Review of Ecology and Systematics*, **23**, 63–87.

De Lillis, M., Bianco, P.M. & Loreto, F. (2009) The influence of leaf water content and isoprenoids on flammability of some Mediterranean woody species. *International Journal of Wildland Fire*, **18**, 203–212.

de Magalhães, R.M.Q. & Schwilk, D.W. (2012) Leaf traits and litter flammability: evidence for non-additive mixture effects in a temperate forest. *Journal of Ecology*, **100**, 1153–1163.

Department of the Environment (2012) *Australia – Present Major Vegetation Groups – NVIS Version 4.1*. Australian Government, Canberra. Available at: http://www.environment.gov.au/land/native-vegetation/national-vegetation-information-system. Accessed 14 September 2016.

Dowdy, A.J., Mills, G.A., Finkele, K. & de Groot, W. (2009) *Australian fire weather as represented by the McArthur Forest Fire Danger Index and the Canadian Forest Fire Weather Index*. Technical Report No. 10. Centre for Australian Weather and Climate Research, Melbourne.

Frejaville, T., Curt, T. & Carcaillet, C. (2013) Bark flammability as a fire-response trait for subalpine trees. *Frontiers in Plant Science*, **4**, article 466.

Ganteaume, A., Marielle, J., Corinne, L.M., Thomas, C. & Laurent, B. (2009) Fuel characterization and effects of wildfire recurrence on vegetation structure on limestone soils in southeastern France. *Forest Ecology and Management*, **258**, S15–S23.

Ganteaume, A., Jappiot, M., Curt, T., Lampin, C. & Borgniet, L. (2014) Flammability of litter sampled according to two different methods: comparison of results in laboratory experiments. *International Journal of Wildland Fire*, **23**, 1061–1075.

Gibson, R.K., Bradstock, R.A., Penman, T., Keith, D.A. & Driscoll, D.A. (2015) Climatic, vegetation and edaphic influences on the probability of fire across mediterranean woodlands of south-eastern Australia. *Journal of Biogeography*, **42**, 1750–1760.

Giglio, L., Csiszar, I. & Justice, C.O. (2006) Global distribution and seasonality of active fires as observed with the Terra and Aqua Moderate Resolution Imaging Spectroradiometer (MODIS) sensors. *Journal of Geophysical Research: Biogeosciences*, **111**, article G02016.

Gill, A.M. & Moore, P.H.R. (1996) *Ignitability of leaves of Australian Plants*. CSIRO, Canberra.

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

Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G. & Jarvis, A. (2005) Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, **25**, 1965–1978.

Hoffmann, W.A., Jaconis, S., McKinley, K.L., Geiger, E.L., Gotsch, S.G. & Franco, A.C. (2012) Fuels or microclimate? Understanding the drivers of fire feedbacks at savanna-forest boundaries. *Austral Ecology*, **37**, 634–643.

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

Kottek, M., Grieser, J., Beck, C., Rudolf, B. & Rubel, F. (2006) World map of the Koppen-Geiger climate classification updated. *Meteorologische Zeitschrift*, **15**, 259–263.

Krawchuk, M.A. & Moritz, M.A. (2011) Constraints on global fire activity vary across a resource gradient. *Ecology*, **92**, 121–132.

Kuo, S. (1996) Phosphorus. *Soil analysis, part 3: chemical methods* (ed. by D. Sparks, A. Page, P. Helmke and R. Loeppert), pp. 869–919. Soil Science Society of America, Madison, WI.

Murphy, B.P., Bradstock, R.A., Boer, M.M., Carter, J., Cary, G.J., Cochrane, M.A., Fensham, R.J., Russell-Smith, J., Williamson, G.J. & Bowman, D. (2013) Fire regimes of Australia: a pyrogeographic model system. *Journal of Biogeography*, **40**, 1048–1058.

Mutch, R.W. (1970) Wildland fires and ecosystems – a hypothesis. *Ecology*, **51**, 1046–1051.

Noble, I.R., Bary, G.A.V. & Gill, A.M. (1980) McArthur fire-danger meters expressed as equations. *Australian Journal of Ecology*, **5**, 201–203.

Orians, G.H. & Milewski, A.V. (2007) Ecology of Australia: the effects of nutrient-poor soils and intense fires. *Biological Reviews*, **82**, 393–423.

Ormeño, E., Cespedes, B., Sanchez, I.A., Velasco-Garcia, A., Moreno, J.M., Fernandez, C. & Baldy, V. (2009) The relationship between terpenes and flammability of leaf litter. *Forest Ecology and Management*, **257**, 471–482.

Parisien, M.A., Parks, S.A., Krawchuk, M.A., Little, J.M., Flannigan, M.D., Gowman, L.M. & Moritz, M.A. (2014) An analysis of controls on fire activity in boreal Canada: comparing models built with different temporal resolutions. *Ecological Applications*, **24**, 1341–1356.

Pausas, J.G. & Ribeiro, E. (2013) The global fire-productivity relationship. *Global Ecology and Biogeography*, **22**, 728–736.

Pettinari, M.L. & Chuvieco, E. (2015) Generation of a global fuel dataset using the Fuel Characteristic Classification System. *Biogeosciences Discussions*, **12**, 17245–17284.

Plucinski, M.P. & Anderson, W.R. (2008) Laboratory determination of factors influencing successful point ignition in the litter layer of shrubland vegetation. *International Journal of Wildland Fire*, **17**, 328–637.

Quinn, G.P. & Keogh, M.J. (2002) *Experimental design and data analysis for biologists*. Cambridge University Press, Cambridge, UK.

R Core Team (2015) *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria.

Richards, S.A. (2005) Testing ecological theory using the information-theoretic approach: examples and cautionary results. *Ecology*, **86**, 2805–2814.

Roy, D.P. & Boschetti, L. (2009) Southern Africa validation of the MODIS, L3JRC, and GlobCarbon burned-area products. *IEEE Transactions on Geoscience and Remote Sensing*, **47**, 1032–1044.

Russell-Smith, J., Yates, C.P., Whitehead, P.J., Smith, R., Craig, R., Allan, G.E., Thackway, R., Frakes, I., Cridland, S., Meyer, M.C.P. & Gill, M. (2007) Bushfires 'down under': patterns and implications of contemporary Australian landscape burning. *International Journal of Wildland Fire*, **16**, 361–377.

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

Scarff, F.R., Gray, B.F. & Westoby, M. (2012) Exploring phosphate effects on leaf flammability using a physical chemistry model. *International Journal of Wildland Fire*, **21**, 1042–1051.

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

Simpson, K.J., Ripley, B.S., Christin, P.-A., Belcher, C.M., Lehmann, C.E.R., Thomas, G.H. & Osborne, C.P. (2016) Determinants of flammability in savanna grass species. *Journal of Ecology*, **104**, 138–148.

Stoof, C.R., Moore, D., Fernandes, P.M., Stoorvogel, J.J., Fernandes, R.E.S., Ferreira, A.J.D. & Ritsema, C.J. (2013) Hot fire, cool soil. *Geophysical Research Letters*, **40**, 1534–1539.

Varner, J.M., Kane, J.M., Kreye, J.K. & Engber, E. (2015) The flammability of forest and woodland litter: a synthesis. *Current Forestry Reports*, **1**, 91–99.

White, R.H. & Zipperer, W.C. (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.

Williamson, G.J., Prior, L.D., Jolly, W.M., Cochrane, M.A., Murphy, B.P. & Bowman, D.M.J.S. (2016) Measurement of inter- and intra-annual variability of landscape fire activity at a continental scale: the Australian case. *Environmental Research Letters*, **11**, 035003.

Woinarski, J.C.Z., Williams, R.J., Price, O. & Rankmore, B. (2005) Landscapes without boundaries: wildlife and their environments in northern Australia. *Wildlife Research*, **32**, 377–388.

Wyse, S.V., Perry, G.L.W., O'Connell, D.M., Holland, P.S., Wright, M.J., Hosted, C.L., Whitelock, S.L., Geary, I.J., Maurin, K.J.L. & Curran, T.J. (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.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Comparison of grass and litter fuels, accounting for different masses used.
Appendix S2 Weather conditions during measurement of flammability attributes.
Appendix S3 Additional statistical analyses.

BIOSKETCH

The Environmental Change Biology group in the School of Biological Sciences at the University of Tasmania is led by Professor David Bowman, and studies the effects of global environmental change, climate variability and Aboriginal and contemporary fire management on vegetation and bushfire activity across the Australian continent.

Author contributions: D.M.J.S.B. conceived and M.A.C. facilitated the project; L.D.P. analysed the data and led the writing; G.J.W. and B.P.M. provided the spatial analyses; all authors contributed to the writing.

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