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Leaf traits predict global patterns in the structure and flammability of forest litter beds

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Abstract

1. Fallen plant material such as leaves, needles and branches form litter beds which strongly influence fire ignition and spread. Traits of the dominant species influence litter flammability directly by determining how individual leaves burn and indirectly through the structure of the litter bed. However, we are yet to determine the relative importance of these different drivers across a range of plant species from different biomes.
2. We undertook a meta-analysis, combining leaf trait, litter structure and flammability data for 106 species from North America, South America, Europe, Asia and Australia. The dataset encompassed broad-leaved and coniferous species from seven different experimental studies. Relationships between leaf traits, litter structure and key flammability metrics—sustainability, combustibility and consumability—were analysed using bivariate and piecewise structural equation modelling (SEM).
3. Traits which characterise the three-dimensional nature of the leaf and how much space a leaf occupies showed much stronger associations to litter structure and flammability than other morphological traits. Leaf curl, surface area to volume ratio (SAV) and SLA predominately influence litter flammability indirectly via litter structure with SLA being the only leaf trait which had a negative direct effect on flame duration. Packing ratio and bulk density were influenced by different combinations of leaf traits and, in turn, they aligned with different flammability metrics. Bulk density predicted flame spread rate and flame duration whereas packing ratio predicted consumption.
4. *Synthesis*. We identified key leaf and litter traits which influence different components of litter bed flammability. Importantly, we show that the effects of these leaf and litter traits are consistent across a wide range of taxa and biomes. Our study represents a significant step towards developing trait-based models for predicting surface wildfire behaviour. Such models will more flexibly accommodate future shifts in the composition of plant species triggered by altered fire regimes and climate change.

KEYWORDS
fire behaviour, flammability, leaf traits, litter properties, meta-analysis, surface fuel

1 | INTRODUCTION

Wildfires are a major disturbance that shape the distribution and structure of plant communities across the globe (Bond & Keeley, 2005). Plants are not only affected by wildfire but, as fuel, they influence how wildfires behave (Pausas et al., 2017; Schwilk & Caprio, 2011). Plant species differ in their flammability (ability to burn) as a function of their physical and chemical traits (Pausas et al., 2017; White & Zipperer, 2010). Whilst the number of studies examining relationships between plant traits and flammability is growing, the generality of these relationships has not been evaluated.

Identifying the underlying traits responsible for interspecific variation in flammability is important. Models that incorporate plant traits can be used to predict fire behaviour (Morvan & Dupuy, 2004; Zylstra et al., 2016) and evaluate vegetation management strategies (McColl-Gausden & Penman, 2019). Studies that rank species flammability can be used to identify low flammable species for planting in fire-prone areas (Dimitrakopoulos & Panov, 2001; Krix et al., 2019; Murray et al., 2018). Additionally, knowledge linking plant traits to flammability can help explain the evolution and function of plant species in fire-prone environments (Pausas et al., 2017; Pausas & Moreira, 2012) and provides insight into how changes in the distribution and abundance of plant species may affect future wildfire behaviour (Babl et al., 2020; Stevens et al., 2020).

Recent studies have quantified interspecific variation in flammability at the leaf-level and shoot-level for a range of plant species (Alam et al., 2020; Cui et al., 2020). However, an equivalent examination of patterns at the litter bed-scale has not yet been made. Identifying what drives flammability at different scales is critical as the results from one scale may not be transferable to another scale (Ganteaume, 2018; Grootemaat et al., 2017a). This is particularly important for litter beds which contain senesced, fallen leaves rather than green leaves. In litter beds, the effect of plant traits on flammability is mediated by trait afterlife effects (Cornelissen et al., 2017). Understanding trait afterlife effects on litter flammability is especially important as most wildfires ignite and initially spread in the litter bed (Burrows, 2001; Curt et al., 2011). Moreover, a fire in the litter bed promotes and sustains burning of upper fuel layers, allowing fire to spread vertically (Plucinski et al., 2010).

Litter flammability is multidimensional and encompasses four components—ignitability, sustainability, combustibility and consumability—which associate with different aspects of fire behaviour (Anderson, 1970; Martin et al., 1994). Each of these components are not necessarily positively related and may be driven by different traits or factors (Varner et al., 2015). Ignitability refers to the ability of a litter bed to ignite and spread a certain distance and is commonly measured as ignition success or time to ignition once exposed to a heat source (Anderson, 1970). Sustainability describes how long litter continues to burn once ignited and is commonly measured as the duration of flaming combustion (Martin et al., 1994). Combustibility represents how rapidly or intensely litter burns, generally measured as the flame spread rate (Martin et al., 1994). Finally, consumability captures how much litter is consumed (Martin et al., 1994).

Studies linking leaf and litter bed traits to flammability have been conducted in different fire-prone ecosystems across the world using mostly experimental laboratory approaches (Cornwell, Elvira, van Kempen, van Logtestijn, Aptroot, et al., 2015; de Magalhães & Schwilk, 2012a; Engber & Varner, 2012; Fonda, 2001; Grootemaat et al., 2017a; Parsons et al., 2015; Scarff & Westoby, 2006; Zhao et al., 2016) but also some field-based approaches (Schwilk & Caprio, 2011). These studies focused on the flammability of leaf litter beds, owing to the dominance of leaves in the litter bed and the propensity of leaves to ignite due to their fineness and high surface area (Zhao et al., 2019). Each study focused on local species or species from a single forest biome. To date, no study has quantitatively evaluated whether the trends observed in these individual studies are globally consistent across a range of plant species, encompassing both conifers and broad-leaves.

A range of leaf morphological traits which are important to flammability have been identified in these studies (Table 1). We focus only on morphological traits as they have been found to be a stronger driver of litter bed flammability in experimental manipulations (Cornwell, Elvira, van Kempen, van Logtestijn, Aptroot, et al., 2015; Scarff & Westoby, 2006), although we acknowledge leaf chemistry (e.g. terpene content) may also be important (Dewhirst et al., 2020; Ormeño et al., 2009; Romero et al., 2019). Leaf size and shape influence flammability indirectly via litter structure and thus litter bed aeration (Scarff & Westoby, 2006). Additionally, leaf size and shape can influence litter bed flammability directly by determining how individual leaves burn and so how quickly fire can spread from leaf to leaf in the litter bed (Martin et al., 1994). Thinner leaves with higher surface area to volume ratio (SAV) and SLA are quicker to ignite, which can lead to faster fire spread and shorter burning times (Grootemaat et al., 2015; Murray et al., 2013; Rothermel, 1972).

Litter structure is a well-established driver of litter fire behaviour, influencing fire spread rate and combustion duration (Rothermel, 1972). Various methods are used to report litter structure such as bulk density (mass of litter per litter bed volume), packing ratio (volume of litter per litter bed volume) or porosity (the fraction of void space in the litter bed). Multiple traits related to the size and shape of leaves have been found to influence both the packing ratio and bulk density of litter beds by different studies (Table 1). For example, larger (as quantified by size, SLA, SAV) and curlier leaves create a more aerated structure (lower packing ratio) which at low moisture contents burns more rapidly and leads to greater consumption (Engber & Varner, 2012; Grootemaat et al., 2017a). A variety of leaf traits have been found to be associated with bulk density, including length, leaf curl, SLA, thickness and leaf area (Table 1).

Exploring the patterns between leaf traits, litter structure and litter flammability provides fundamental information for understanding how plant species influence wildfire behaviour. In this study, we combined the results of several key experimental studies on litter

TABLE 1 Summary of morphological leaf traits and their influence on litter bed structure and flammability

Leaf trait	Definition	Effect on litter bed structure[a]	Association with litter flammability[a]	Studies observing relationship
Length (mm)	Length of leaf	Bulk density (−)	Combustibility (+) Consumability (+)	de Magalhães and Schwilk (2012a), Engber and Varner (2012), Scarff and Westoby (2006), Schwilk and Caprio (2011)
Leaf curl (mm)	Maximum absolute height of leaf when positioned on a flat surface	Bulk density (−) Packing ratio (−)	Combustibility (+) Sustainability (−) Consumability (+)	Engber and Varner (2012), Grootemaat et al. (2017a)
Surface area to volume ratio (SAV, cm^{-1})	Two-sided leaf area per leaf volume	Packing ratio (−)	Ignitability (−) Consumability (+)	Parsons et al. (2015) and Rothermel (1972)
SLA (cm^2/g) Inverse is leaf mass per area (LMA, g/cm^2)	One-sided leaf area per leaf dry mass	Bulk density (−)	Ignitability (−) Sustainability (−) Combustibility (+)	de Magalhães and Schwilk (2012a), Ganteaume (2018), Grootemaat et al. (2017a), Murray et al. (2013) and Parsons et al. (2015)
Area (cm^2)	One-sided leaf area	Packing ratio (−) Bulk density (−)	Combustibility (+) Sustainability (−)	Cornwell, Elvira, van Kempen, van Logtestijn, Aptroot, et al. (2015), de Magalhães and Schwilk (2012a), Murray et al. (2013) and Scarff and Westoby (2006)
Thickness (mm)	Thickness of leaf at intermediate position between border and midrib	Packing ratio (+) Bulk density (+)	Ignitability (+) Sustainability (+)	Ganteaume (2018), Parsons et al. (2015), Plucinski and Anderson (2008)
Tissue density (g/cm^3)	Leaf dry mass per leaf dry volume		Sustainability (+) Combustibility (−)	Grootemaat et al. (2017a) and van Altena et al. (2012)

[a] + or − indicate the direction of influence of leaf trait on litter structure or flammability metric, e.g. leaf length has a negative influence on bulk density, longer leaves create lower bulk density litter beds.

flammability and asked: how do plant species' leaf traits determine litter bed properties and thereby flammability across a wide range of taxa from different biomes?

2 | MATERIALS AND METHODS

2.1 | Literature review and data compilation

A structured literature review was conducted using the Web of Science database (all databases). Document types were restricted to published journal articles and the time span included all years (1900–2019). Keywords required were 'litter', 'flammability' and 'traits'. This search yielded 55 potential articles for the analysis. From an initial screening of the literature, the following criteria were developed and then applied to select appropriate studies to include in the analysis:

1. Laboratory studies testing the flammability of single-species leaf litter beds (not individual leaves);
2. Measured at least two of three flammability components: sustainability (flame duration, seconds), combustibility (flame spread rate, cm/s) and consumability (consumption, % mass consumed), ignitability was not included as it was not measured in a consistent way across studies;
3. Litter structure was measured as either litter depth, bulk density or packing ratio; and
4. At least one leaf trait was measured.

Seven studies were selected based on the above criteria, creating a final dataset that consisted of 109 observations from 106 unique woody species across four forest biomes (Figure 1; Tables S1 and S2). Africa and Asia were not well-represented in the dataset as no comparable studies have been conducted in these regions. All studies contained multiple species, ranging from three (Kauf et al., 2019) to 33 species (Cornwell, Elvira, van Kempen, van Logtestijn, Aptroot, et al., 2015). Three plant species were measured across multiple studies (*Calocedrus decurrens*, *Quercus kelloggii* and *Sequoiadendron giganteum*). The Cornwell, Elvira, van Kempen, van Logtestijn, Aptroot, et al. (2015) dataset comprised conifer litter from different regions including Europe, Asia, South Africa, South America, North America and Australia and was collected from several temperate arboretums, botanic gardens and greenhouses in the Netherlands. Similarly, the Kauf et al. (2018) comprised litter collected from botanic gardens in Germany. Although environmental conditions in the botanic gardens may differ from the native environment of a given species, in this study, we were interested in general trait-flammability relationships, so the use of material from botanic gardens is justified. See Table S2 for the full list of

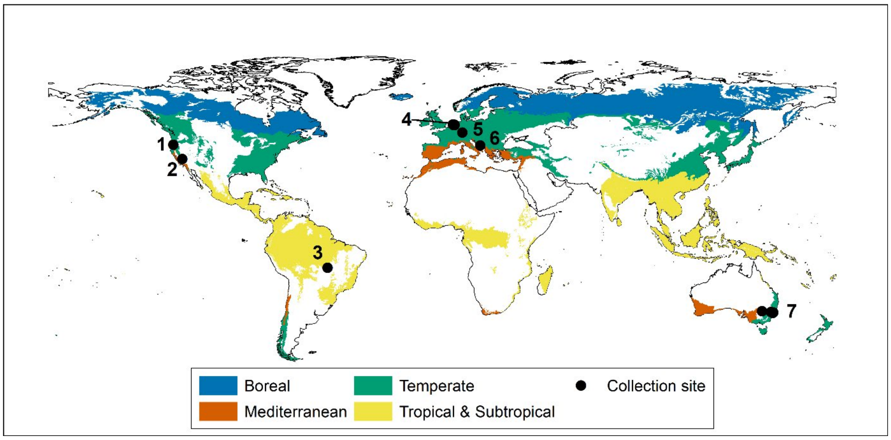

FIGURE 1 Location of studies included in the meta-analysis. Colours represent different forest biomes (from WWF Terrestrial Ecoregions https://www.worldwildlife.org). Black circles indicate collection sites. Studies are as follows: (1) Engber and Varner (2012); (2) de Magalhães and Schwilk (2012a); (3) Parsons et al. (2015); (4) Cornwell, Elvira, van Kempen, van Logtestijn, Aptroot, et al. (2015)), Zhao et al. (2016); (5) Kauf et al. (2018); (6) Kauf et al. (2019) and (7) Grootemaat et al. (2017a). Note Study 4 includes species from multiple biomes but collected from temperate aboretums, botanic gardens and subtropical greenhouses

plant species across all studies. Data were extracted from online repositories for most studies (Cornwell et al., 2015; de Magalhães, & Schwilk, 2012b; Grootemaat et al., 2017b; Parsons & Balch, 2015a, 2015b). For the remaining studies, data were extracted from the main text, tables and/or digitised graphs of primary references. Where data were collected but not reported, the authors were contacted and data incorporated if they were made available. All experiments were conducted on dry (<10% moisture content) litter beds. Details of experimental set-up and flammability metrics are in Table S1. Plant species litter was categorised into four groups based on litter type: leaf (flattened leaf, includes both conifer and broadleaf species), short-needle, long-needle and branch. Branch litter included coniferous species from Cupressaceae and Araucariaceae which typically do not shed individual leaves but small branches with leaves attached. However, for simplicity, we use the term 'leaf' to describe any of the litter types.

Litter structure was measured as packing ratio and bulk density. In cases where bulk density was not reported it was calculated from sample mass and fuel bed volume based on litter depth and sample tray area. This was necessary for species reported in Engber and Varner (2012) and Parsons et al. (2015). Where packing ratio was not recorded it was calculated by dividing bulk density by particle density as was done for the Parsons et al. (2015) dataset. Supplementary leaf trait data for the species from the Cornwell, Elvira, van Kempen, van Logtestijn, Aptroot, et al. (2015) dataset were sourced from the TRY database (Kattge et al., 2020) and The Gymnosperm Database (Earle, 2020).

2.2 | Data analysis

All leaf trait, litter structure data and flammability metrics were log-transformed to meet assumptions of normality and homogeneity of residuals prior to analysis. The only exception was consumption for which we used raw values for the analysis because a non-normal distribution was observed.

We first tested how leaf traits influence both litter structure and flammability. Seven leaf traits were identified as important based on previous studies (Table 1). Initially, we used Pearson correlation to test for relationships between the seven leaf traits, litter structure and flammability (Figure S1). From this, we selected key traits which had a strong ($r > 0.7$) correlation to either litter structure or flammability. This led us to choose three leaf traits for inclusion in further analysis; leaf curl, SAV and SLA. Relationships between selected leaf traits, litter structure and flammability metrics were then assessed using linear regression with a gaussian error distribution. For the relationship between packing ratio and consumption we used logistic regression with a binomial distribution, following Cornwell, Elvira, van Kempen, van Logtestijn, Aptroot, et al. (2015) with consumption treated as a proportion. We evaluated the strength of linear regressions using R^2 values and for the logistic regression we used log likelihood. All bivariate analyses were performed in R version 3.6.2 (R Core Team, 2016).

Piecewise Structural Equation Modelling (SEM) was used to disentangle the effects of different leaf traits and litter structure on litter flammability. SEM can incorporate multiple predictors and response variables in a single causal network, allowing direct and indirect effect pathways to be evaluated (Grace, 2006; Grace et al., 2010). Piecewise SEM is an extension of the traditional SEM approach. Here, the SEM is translated into a set of linear models which are evaluated individually or locally and then combined to make inferences about the entire SEM (Lefcheck, 2016). This allows the source of the data to be included as a random effect to account for the effect of different experimental approaches and conditions. Model conceptualisation and parametrisation was based on a priori knowledge and our bivariate analysis. Leaf traits which had a moderately strong relationship ($R^2 \geq 0.50$) with litter structure or flammability were chosen as predictors. Thus, SLA and leaf curl were chosen as predictors of bulk density. SAV and leaf curl were chosen as predictors of packing ratio. Leaf curl and SLA were chosen as predictors of flame duration. SLA was chosen as a predictor of flame spread rate. For flame spread rate and flame duration, both packing ratio and bulk density were chosen as predictors, in addition to selected leaf traits. Only packing ratio was selected for consumption with no leaf traits selected as predictors due to the lack of strong associations.

Each component model of the piecewise SEM was set-up as a linear mixed effect model (LMM), with errors estimated using restricted maximum likelihood and study number included as a random effect. As the variables measured differed between studies, the number of observations and studies included in each LMM differed from 44 observations (four studies) to 83 observations (five studies). Variables were scaled and centred prior to analysis. We report the standardised path coefficient for each path, which indicates the relative strength of the different predictors on litter structure or flammability. We also report two different R^2 for each response variable, the marginal R^2 (R^2_m, based on the variance of the fixed effects only) and the conditional R^2 (R^2_c, based on the variance of both the fixed and random effects). We evaluated the fit of the entire SEM using the Fisher's C test, with small Fisher's C and $p > 0.05$ indicating good model fit. Piecewise SEM was performed in R version 3.6.2 (R Core Team, 2016), using the packages LME4 (Bates et al., 2015) and PIECEWISESEM (Lefcheck, 2016). Code and data are available via Figshare (Burton et al., 2020).

3 | RESULTS

3.1 | Interspecific differences in litter structure and flammability

Litter structure and flammability varied among the 106 shrub and tree species in the dataset (Table 2; Figure 2). There was little variation in consumption for most species, short-needle conifers had the lowest amount of material burnt (<10% consumed). Flame spread rate and flame duration were significantly negatively correlated ($r = -0.78$, $p < 0.001$; Figure S1), meaning that when flames spread more slowly through the litter bed, the burning was sustained for longer. Consumption was not significantly correlated with neither flame spread rate nor flame duration (Figure S1).

Flame duration was better predicted by bulk density (slope = 1.04, $R^2 = 0.73$, $p < 0.05$) than packing ratio (slope = 0.74, $R^2 = 0.53$, $p < 0.05$; Figure 2a,b). Litter beds that were more aerated (lower packing ratios and lower bulk densities) had shorter flame durations. Flame spread rate declined with increasing bulk density (slope = −0.95, $R^2 = 0.63$, $p < 0.05$) and packing ratio (slope = −1.13, $R^2 = 0.63$, $p < 0.05$; Figure 2c,d). There was no relationship between bulk density and consumption (Figure 2e). However, packing ratio had a significant relationship with consumption (slope = −1.17, $p = 0.01$, log likelihood = 0.57). Consumption decreased with increasing packing ratio, with substantially lower consumption observed beyond 0.15 cm^3/cm^3 (Figure 2f). Litter derived from short-needle coniferous plant species (*Picea* sp., *Abies* sp., *Tsuga* sp. and *Larix* sp.) did not conform to the general trends observed for other litter types. Short-needle litter was characterised by higher bulk densities and packing ratios and lower litter consumption.

TABLE 2 Summary statistics for litter structure and flammability components

Variable	Mean (min–max)	x-fold variance
Litter structure		
Packing ratio (cm^3/cm^3)	0.06 (0.005–0.39)	74.3
Bulk density (g/cm^3)	0.02 (0.003–0.10)	28.0
Flammability		
Sustainability, flame duration (s)	258 (21–1,880)	90.5
Combustibility, flame spread rate (cm/s)	0.5 (0.05–3.7)	79.7
Consumability, consumption (%)	85 (3–100)	38.1

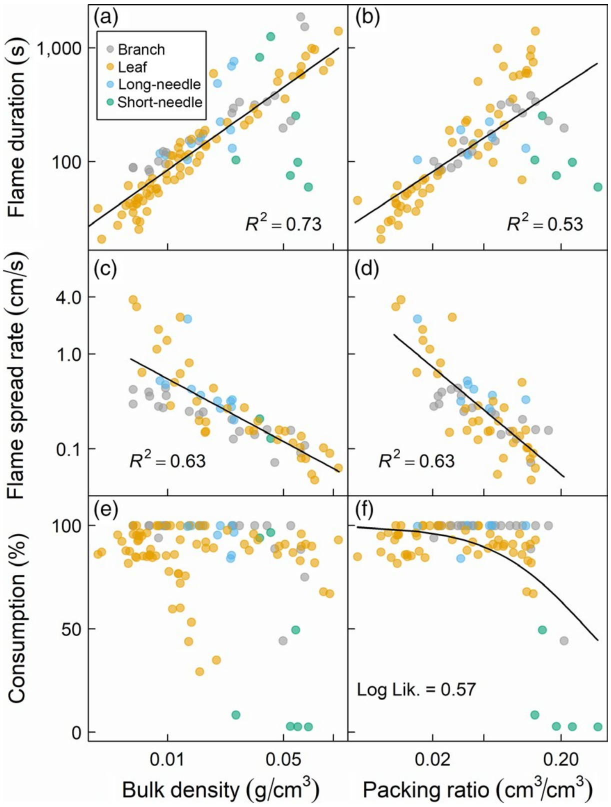

FIGURE 2 Relationships between litter structure and flammability from experimental burns. Each dot represents a species mean. Significant ($p < 0.001$) relationships from linear (a–d) and logistic (f) regression are represented with solid lines and corresponding R^2 (linear) and Log Likelihood values (Log Lik, logistic regression). All axes are log-transformed except for consumption

3.2 | Which leaf traits are most important for litter structure and flammability?

Leaf area, length, thickness and density were not strongly related to litter bed structure or flammability (Figure S1). In contrast, leaf curl, SLA and SAV showed stronger associations with litter bed structure and some flammability metrics (Figure S1).

The strongest predictors of flame duration were SLA (slope = −1.38, R^2 = 0.63, $p < 0.05$) and leaf curl (slope = −1.19, R^2 = 0.60, $p < 0.05$; Figure 3a,c). Leaves with higher SLA and greater leaf curl had shorter burning times than leaves that had lower SLA and leaf curl. SLA was also the best predictor of flame spread rate, explaining 60% of the variation in flame spread rate (slope = 1.05, R^2 = 0.60, $p < 0.05$; Figure 3f). Litter beds composed of leaves with greater SLA had faster flame spread rates. Consumption did not have a strong relationship to any of the leaf traits, being only weakly positively related to leaf curl (Figure 3g–i).

Bulk density was negatively related to SLA, leaf curl and SAV (Figure 3j–l). Leaf curl (slope = −0.98, R^2 = 0.57, $p < 0.05$) and SLA (slope = −0.96, R^2 = 0.50, $p < 0.05$) were the strongest drivers of bulk density, explaining 57% and 50% of the variation in bulk density respectively. Packing ratio exhibited similar trends to leaf traits as bulk density (Figure 3m–o). However, leaf curl (slope = −1.02, R^2 = 0.57, $p < 0.05$) and SAV (slope = −1.25, R^2 = 0.52, $p < 0.05$) were the strongest drivers of packing ratio, explaining 57% and 52% of the variation in packing ratio respectively.

3.3 | Influence of leaf traits and litter structure on flammability

The Piecewise Structural Equation Model was a good fit to the data (Fisher's C = 30.87, p = 0.23, df = 26). There was a difference

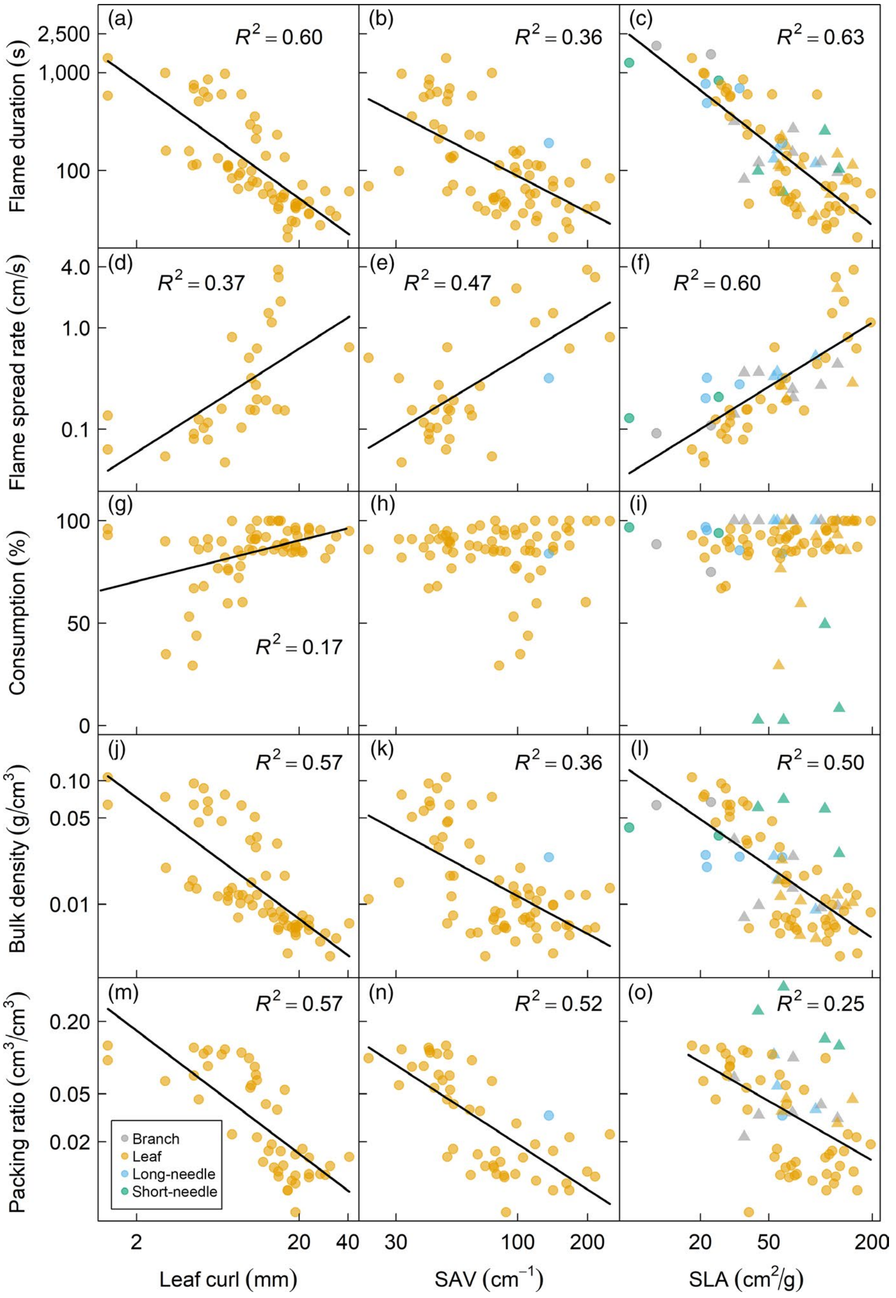

FIGURE 3 Relationship between selected leaf traits and flame duration (a–c), flame spread rate (d–f), consumption (g–i), bulk density (j–l) and packing ratio (m–o). Each symbol represents a species mean. Shapes denote whether leaf trait (SLA) was measured within the study (circle) or sourced from an alternative source (triangle). Significant ($p < 0.001$) relationships are represented with solid lines and corresponding R^2 values. All axes are log-transformed except for consumption. SAV, surface area to volume ratio

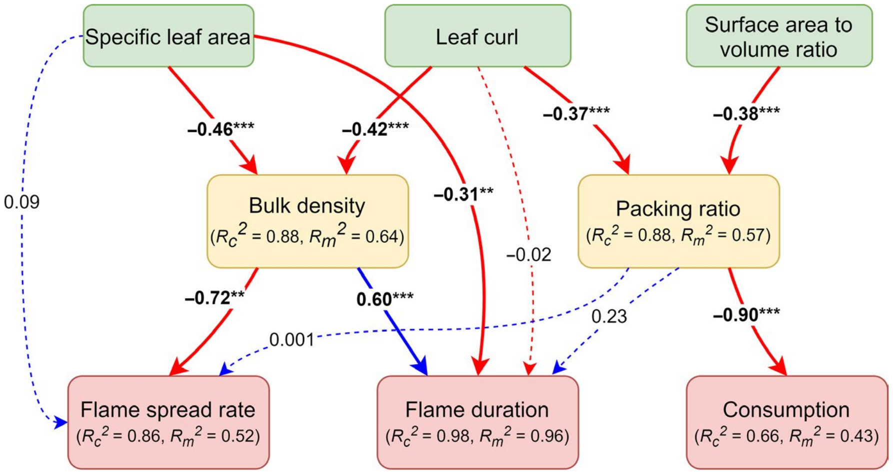

FIGURE 4 Piecewise Structural Equation Model for the effect of leaf traits on litter structure and flammability. Solid arrows indicate significant relationships between variables, and dashed arrows indicate non-significant relationships. Blue arrows indicate positive relationships and red arrows indicate negative relationships. Numbers on arrows show standardised path coefficients. Significant values are indicated by $^{*}p < 0.05$, $^{**}p < 0.01$ and $^{***}p < 0.001$. Conditional R^2 and marginal R^2 values shown in the boxes of the response variables

between the conditional R^2 and marginal R^2 for flame spread rate and consumption but not flame duration. Hereafter, we refer to the marginal R^2 only as this represents the effects of predictor variables only. Leaf curl and SAV explained 57% of the variation in packing ratio (Figure 4). SAV and leaf curl both had a negative effect on packing ratio, with similar path coefficients (SAV, coefficient = −0.38, $p < 0.001$ and curl, coefficient = −0.37, $p < 0.001$). Leaf curl and SLA explained 64% of the variation in bulk density, with SLA and curl both having a negative effect (coefficient = −0.46, $p < 0.001$ vs. coefficient = −0.42, $p < 0.001$).

Leaf curl did not have a significant influence on flame duration despite being strongly related in bivariate analysis (coefficient = −0.02, $p = 0.65$). SLA did have a significant negative effect on flame duration (coefficient = −0.31, $p = 0.003$) but not flame spread rate (coefficient = 0.09, $p = 0.59$). Bulk density significantly positively influenced flame duration (coefficient = 0.60, $p < 0.001$) and negatively influenced flame spread rate (coefficient = −0.72, $p = 0.003$). Packing ratio had a significant negative effect consumption (coefficient = −0.90, $p < 0.001$) but was not significantly related to flame duration (coefficient = 0.23, $p = 0.06$) nor flame spread rate (coefficient = 0.001, $p = 0.99$) in the piecewise SEM. Packing ratio explained 43% of the variation in consumption. The combination of leaf traits and litter structure explained 52% and 96% of the variation in flame spread rate and flame duration respectively.

4 | DISCUSSION

4.1 | Importance of leaf traits to litter bed structure and flammability

We quantified relationships between leaf traits, litter structure and flammability for a wide range of plant species (and litter types) across multiple forest biomes. Despite some differences in experimental design, we found consistent significant effects of leaf traits on litter structure and flammability. Specifically, we found traits which characterise the three-dimensional nature of the leaf and how much space a leaf occupies (namely leaf curl, SAV and SLA) showed much stronger associations to litter structure and flammability than other morphological traits (thickness, length, area and tissue density).

Leaf curl influences both packing ratio and bulk density. Leaves with greater curl allow more air spaces in the litter bed leading to lower packing ratios and bulk densities (Engber & Varner, 2012; Grootemaat et al., 2017a). In addition to leaf curl, SAV drove variation in packing ratio, with larger leaves resulting in more aerated litter (lower packing ratio), as previously found (Grootemaat et al., 2017a). Leaf curl and SLA were strongly associated with bulk density. Leaves which were less curled and had lower SLA created denser litter beds (higher bulk density). Leaf curl covaries with leaf length and size such that larger leaves also have greater curl. Thus, it is possible that the relationship between curl and litter bed packing may be also be related to differences in leaf length and size. Isolating the effect of leaf curl would require experimental manipulations standardising curl relative to leaf size. In addition, leaf curl data were available for leaf litter beds only, not needle or branch litter. For needle and branch litter, litter particle size (measured as litter particle length × width × height) which also indicates the three-dimensional nature of the litter particle, may be a better determinant of packing ratio (Zhao et al., 2016).

Morphological leaf traits were not related to consumption in contrast to previous studies that showed consumption to be positively related to both SAV (Parsons et al., 2015) and community-weighted mean leaf length (Schwilk & Caprio, 2011). It is possible that traits related to chemical composition rather than morphology may be more important for driving differences in consumption. Grootemaat et al. (2017a) found that for sclerophyllous south-eastern Australian species, higher tannin and lower lignin concentrations were associated with lower consumption. Insufficient data about the chemical traits across the range of plant species in our study meant we could not test for the effect of these on flammability, making it a worthwhile avenue for further exploration.

Morphological leaf traits were strongly associated with flame spread rate and duration, consistent with previous studies (de Magalhães & Schwilk, 2012a; Engber & Varner, 2012; Grootemaat et al., 2017a). Flame duration was most strongly negatively related to leaf curl and SLA. Litter composed of curlier particles with greater SLA flamed for shorter periods. Flame spread rate was strongly positively related to SLA. Faster flame spread rates were observed in litter composed of leaves with greater SLA. However, due to the interrelatedness between leaf traits, litter structure and flammability, it is not possible to determine whether these associations are from a direct effect or indirect effect via litter structure or a combination of both. By using piecewise SEM, we were able to quantify the direct and indirect effect (via litter structure) of leaf traits on litter bed flammability, the results of which are discussed below.

4.2 | Direct and indirect effects of leaf traits on flammability

Litter bed flammability is driven largely by litter structure. Flame duration was the only flammability metric to be influenced by both leaf traits and litter structure in the SEM, being negatively related to SLA and positively related to bulk density. The direct effect of SLA on flame duration is likely related to the influence of SLA on leaf ignitability. Leaves with higher SLA have been found to ignite more quickly owing to the greater surface area exposed to heat and flames (Ganteaume, 2018; Grootemaat et al., 2015; Murray et al., 2013). The spread of fire in the litter depends on the successive ignitions of individual leaves (Grootemaat et al., 2017a; Martin et al., 1994). Thus, the more easily leaves ignite, the faster flames can spread from leaf to leaf, leading to shorter flame durations overall.

Bulk density emerged as the most important predictor of flame spread rate and flame duration. Litter beds with higher bulk density have more fuel available to burn but longer flame durations and slower flame spread rates. This is likely due to variation in the penetration distance of radiant heat. At higher bulk densities radiative heat transfer through the fuel bed is lower, leading to longer burning times and slower spread rates (Bartoli et al., 2011). Unlike flame duration, flame spread rate was not significantly related to any leaf traits in the SEM. In addition, leaf curl did not have a significant effect on flame duration, despite being strongly negatively related in the bivariate analysis. Thus, we suggest the strong associations between SLA and flame spread rate and leaf curl and flame duration in bivariate analysis is an artefact of their influence on bulk density rather than a direct effect on flammability.

Packing ratio is a strong driver of consumption, explaining 43% of the variation in consumption. At low packing ratios air can easily flow into the litter bed providing well-ventilated combustion conditions, which results in greater consumption as downwards heat transfer is not limited. At higher packing ratios and no-wind conditions, combustion becomes increasingly limited in oxygen supply (El Houssami et al., 2018). This results in lower amounts of material consumed, as observed in our dataset. There was a sharp decline in consumption at higher packing ratios (0.15 cm^3/cm^3), which is consistent with previous studies (Cornwell, Elvira, van Kempen, van Logtestijn, Aptroot, et al., 2015; Zhao et al., 2016). This decline was driven by the presence of a few short-needle conifers (*Larix* sp., *Abies* sp., *Tsuga* sp. and *Picea* sp.), making it difficult to confirm whether the patterns observed are due to packing ratio alone or some other unquantified trait potentially related to litter chemistry as previously outlined (see section 4.1). However, there is qualitative evidence of broad-leaf litter, similar in size and shape to the short-needle coniferous species, failing to ignite at high packing ratios. Plucinski and Catchpole (2001) who used the same methods as (Cornwell, Elvira, van Kempen, van Logtestijn, Aptroot, et al., 2015; Grootemaat et al., 2017a) reported that litter from *Banksia ericifolia* L.f. (packing ratio = 0.284, leaf area = 0.242 cm^2) and *Leptospermum laevigatum* (Gaertn.) F. Muell. (packing ratio = 0.202, leaf area = 0.576 cm^2) failed to ignite and spread at low moisture contents. This suggests that the packing ratio-consumption relationship may be relevant to both broad-leaf and conifer species.

It is important to note that all experiments in our meta-analysis were conducted in controlled conditions with no effect of wind or radiant heat. It would be interesting to explore under what ambient conditions ignition is successful and if the effect of packing ratio becomes less influential. For example, the presence of wind may support ignition and burning rate by supplying oxygen, mixing pyrolysis gases with air (El Houssami et al., 2018) and increasing flame contact from the ignition source to the fuel (Plucinski & Catchpole, 2001; Rothermel, 1972). Another important consideration is the influence of variation in experimental design on the results. It is possible that difference in burning methods, such as tray shape (e.g. square, rectangle and circle) and ignition source contributed to some of the variation observed in flame spread rate and consumption. To this end, it is important that any future studies follow consistent methods, perhaps following methods in Cornwell, Elvira, van Kempen, van Logtestijn, Aptroot, et al. (2015) as this methodology represented half of the dataset in our study (56 out of 109 observations).

4.3 | Applications and next steps

Our study provides insight into how flammability and the traits which drive flammability differ across taxa. Two genera which occur in fire-prone environments, *Eucalyptus* and *Pinus*, create litter with low packing ratios and high flammability. However, they produce contrasting litter particles, large curled leaves versus long thin needles grouped in fascicles. In comparison the non-*Pinus* Pinaceae create litter which is distinct from any of the other species in the dataset as highlighted by Cornwell, Elvira, van Kempen, van Logtestijn, Aptroot, et al. (2015). Future studies could integrate the flammability data synthesised in this study with species phylogeny to explore the evolutionary patterns of litter bed flammability, similar to the approach of Cui et al. (2020) for shoot flammability and expanding on the analysis of Zhao et al. (2016).

Identifying the underlying traits responsible for variation in flammability can allow the prediction of flammability using species-specific traits. Although there are models for live plants (Forest Flammability Model, Zylstra et al., 2016), there is currently no equivalent model for litter beds. This study represents a significant step towards developing trait-based empirical models for litter beds. Such models could be incorporated into exisiting models which use plant traits (e.g. Forest Flammability Model) to improve the estimation of surface fire behaviour. Trait-based models could also be developed to predict the ecological effects of wildfires. For example, flame spread rate in addition to flame duration, influences soil temperatures and thus soil heating. The degree of soil heating influences physical soil properties (Certini, 2005), the mortality of soil organisms (Pingree & Kobziar, 2019) and the germination of buried dormant seeds (Bradstock et al., 1992; Burrows, 1999; Penman & Towerton, 2008). In addition, flame spread rate and fuel consumption are sub-components of fire intensity (Bryam, 1959) which is important for understanding wildfire effects above-ground. Fire intensity and flame duration influence plant mortality, with longer flame durations and higher fire intensities causing greater damage (Gagnon et al., 2010; Neary et al., 1999).

Trait-based models require information on both senesced and green leaf traits, as leaf traits most important to flammability in a living plant differ from those most important in a litter bed. However, the collection of trait data to understand flammability is heavily skewed towards traits that are important for living vegetation (Pérez-Harguindeguy et al., 2013). SLA is an important trait for the ignitability of green leaves (Grootemaat et al., 2015; Murray et al., 2013) and here we show it affects flammability directly (flame duration) and indirectly via litter structure (bulk density). However, green leaf SLA may not be the same as senesced leaf SLA due to carbon and nutrient resorption before abscission (Vergutz et al., 2012). Thus, there is a need to measure SLA of both green and freshly senesced leaves. Another trait for which there is no protocol for measurement in the handbook for leaf traits is leaf curl. As the value of leaf curl may change with moisture or decomposition stage, measurements should be taken from dried freshly senesced, undecomposed leaves. This would also reflect the maximum potential leaf curl of a species. An interesting avenue for future research could be exploring what influences the tendency for leaves to curl when senesced. If curl can be associated with green leaf traits, predictions of curl (and thus packing ratio) could then be made using green leaf traits for which there is greater data availability.

Another important consideration is the temporal variability of leaf trait effects on litter bed flammability. The relationships we identified are most relevant for freshly senesced dry (<10% moisture content) leaf litter. However, leaf traits and litter beds are not static and are continually changing over time. Thus, the influence of these traits on flammability may fluctuate due to changes in moisture, decomposition and fragmentation. Exposure to moisture can reduce leaf curl and increase compaction of the litter bed, which increases bulk density (Kauf et al., 2018; Weir & Limb, 2013). Decomposition and fragmentation affect the size, shape and chemical composition of the leaves in the litter bed which changes litter structure and flammability (Cornwell et al., 2009; Kauf et al., 2015; Zhao et al., 2014). The temporal variability of leaf trait effects on flammability is an interesting question for future studies.

The amount and composition of the litter bed are also important determinants of litter flammability, in addition to leaf traits and litter structure (Varner et al., 2015). Thus, any possible trait-based model of litter flammability needs to include these effects. The amount of litter depends on the rate of litterfall and decomposition which varies with site productivity and climate (Facelli & Pickett, 1991). In natural forests litter beds are rarely homogenous and are usually composed of more than one species or component (e.g. leaf, twig, bark). Several studies have investigated the effect of compositional variation by sampling intact samples (Ganteaume et al., 2014) or by artificially creating leaf litter mixtures of two or more species (van Altena et al., 2012; Della Rocca et al., 2018; de Magalhães & Schwilk, 2012a; Zhao et al., 2016). There is growing evidence that litter mixtures can behave non-additively, that is the flammability of the mixture differs markedly from expected flammability based on the flammability of the species when burnt in isolation. Moreover, moisture content can influence the magnitude and direction of non-additivity (Blauw et al., 2015; de Magalhães & Schwilk, 2020). However, the majority of these studies have used mixtures made up of the same litter component (leaves, needles) from different plant species, with fewer studies using mixtures made up of different litter components e.g. leaves, bark and twigs (but see Gormley et al., 2020; Zhao et al., 2019)). Further research into the flammability of mixed litter beds (species and components) is required to better understand litter bed flammability.

We show that trait-flammability relationships previously identified in individual studies are maintained for a wide range of plant species across multiple forest biomes. Our synthesis represents a crucial first step towards developing empirical models of litter bed flammability using leaf traits. Such models will be useful for understanding flammability in plant communities now and into the future as altered fire regimes and climate change trigger shifts in plant species composition and leaf traits.

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AUTHORS' CONTRIBUTIONS

J.E.B. conceptualised the meta-analysis; J.E.B. designed the methodology, collated the data and performed the analysis; J.E.B. led the writing of the manuscript; T.D.P., J.G.C. and A.I.F. are supervisors of J.E.B. PhD project and as such made substantial contributions to project design and the writing and revision of the manuscript. They approved the final version for publication.

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DATA AVAILABILITY STATEMENT

Data and code associated with this manuscript are archived and made publicly available on Figshare https://doi.org/10.6084/m9.figshare.13218836.v3 (Burton et al., 2020).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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