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From plant traits to fire behavior: scaling issues in flammability studies

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[Last revised 27 October 2020.]

Dear American Journal of Botany,

We thank the reviewers for their thoughtful and helpful comments. We've made changes in response to these comments and our responses are below.

Special Issue Editor:

> *We have now received two reviews for your manuscript entitled "How plant traits shape flammability from leaf to landscape scales". They are both supportive of accepting a revised version for publication at AJB, provided that the authors address their suggestions for improvement. I also enjoyed reading this manuscript and I think it will be a good addition to the reading list of plant biology/ecology courses.*
>
> *Please go through the reviewers' comments carefully and make the necessary changes in the text as needed. When submitting the revised version, please highlight in both the text and response letter where modifications were made. Also please upload the most up to date version of Figure 1 with your revisions. Also, for Box 1, shouldn't all fields in column "How is it measured?" be completed?*

Thank you for your comments. We've included a version of revised manuscript with Microsoft word "track changes" indicating our edits. We now have a complete Figure 1 and thank the editor and reviewers for their understanding. We've edited Box 1 to complete all fields.

Reviewer #1:

> *I appreciate the opportunity to review this manuscript. I want to see this in print and the topic moved forward. The ms is well-written and touches on key aspects that tie this sometimes disparate field together. That said, there are some weaknesses that are pretty substantial, barring me from recommending acceptance. My comments here are to improve this work.*

Thank you for your thoughtful comments. The reviewer was especially helpful in suggestions for improving how we addressed the relationship between traits and "fuel models". The reviewer also rightly corrected and gave suggestions for our discussion of dead fuels and fuel moisture.

> *Title: This is more of a "we need to know more" paper, so I would add this somehow to the title.*

We've proposed a new title: "From plant traits to fire behavior: scaling issues in flammability studies"

> *Abstract: L44: Insert "structural" before "characteristics"*

Fixed.

> *L51: This is relevant to all "wildland fires" encompassing wildfires and prescribed and cultural burning.*

Fixed. We have edited wording throughout in light of this comment.

> *L55: Include humans here.*

Edited to include: "...and may have been used by hominids as early as 1.5 MYA (Brain and Sillent, 1988)" (line 56).

L60: refine this choppy sentence to flow.

Edited to "Although fire regimes have an intrinsic range of natural variation, rapid changes in climate and land use are leading to unprecedented extreme fire events" (line 59)

L63: Add wet Tropics and citation(s) here as a startling example.

We added a citation for Amazonia, line 65.

L65: It is worthwhile when discussing fire-vegetation feedbacks globally to reference mesophication as related to widespread fire exclusion, particularly in the Temperate Zone (Nowacki and Abrams 2008 BioScience) since that model is also driven by flammability changes (multiple citations).

Good point. We added this example and citation: "or experience community composition and subsequent fuel changes (e.g. "mesophication", Nowacki and Abrams, 2008) (line 68).

L67: This section generally needs more text toward "fuel models" from the US as coalescing ideas for ecosystems as fuel. The classic Anderson (1981, USDA Gen Tech Rep INT-122; the same Anderson who conceptualized the 1970 flammability metrics) is notable for its classifying ecosystems in a functional group way. I would cite that here, along with Anderson 1970 and expand a little more.

We've edited this section to be more specific and cite the fuels literature directly. We are still attempting to keep this background brief without being misleading (lines 69-75). We made more edits regarding fuel models in later sections in response to the reviewer's concerns. See extensive changes on lines 120-152

L69: Important to note that they are dynamic from a fuel moisture standpoint.

True. We now address this and the reviewer's detailed comments on fuel moisture in that section. here we are only introducing the idea of fuel types and prefer to keep it brief.

L70: cite the "challenging" statement.

We disagree that this needs a citation as it is introducing the thesis statement for the entire review which we then argue in more detail throughout the manuscript.

L96: The exceptions to fuel models behaving poorly outside of the fuels they were developed for is not widespread nor universal. I would tone down this sentence so as not to overdo this idea.

We'll need help to understand this suggestion. We don't list exceptions here so how are we overdoing the idea of "exceptions to fuel models behaving poorly outside of the fuels they were developed." Perhaps the reviewer is suggesting that fuel models generally *do* translate well across systems? That would be keeping with the previous comments. Assuming the latter, we've edited this to better isolate what we see as the knowledge gap and to not downplay the enormous history of fuel research. We've added text to later paragraphs to better recognize that the history of fuel characterization involved much "bottom up" work characterizing mechanisms of fuel moisture dynamics, etc. See extensive changes and additions to lines 120-153.

L103 and elsewhere: "ground" fuels are organic, below-ground fuels such as peats, mucks, and humus. These should all be categorized as "surface" fuels. See also L 187, 332, 357, 358, etc...

Yes, agreed. We missed this terminology disparity across continents in our earlier editing. This is now corrected here (line 198) and at the other locations. We disagree with change at previous line 332 because that is not referring to a fuel type.

L114-124: This paragraph is important in the paper; as written it falls short. Top-down fuels would be squarely within US fuel model assignment (the Anderson 1981 and later Scott and Burgan 2005 versions) that is done similarly around the world. In the US, this assignment is accomplished with RS crosswalks like LANDFIRE (Rollins 2009 Int J Wild. Fire). Fuel model assignment is primarily based on functional groups (grass-dominated, shrub, tree litter, and woody for Anderson 1981 and similar, albeit finer for Scott & Burgan 2005) and emergent traits of the communities- for example, herbaceous savannas, whether pine-dominated (as P. ponderosa and P. palustris and others in the US) or oak-dominated (Q. garryana or Q. stellata in the US) are all categorized as the same model. These focus on vegetation structure (open canopies), traits of trees (flammable litter), grassy and herbaceous dominance (similarly flammable, well-aerated), etc ,,. To me, this section is too harsh on our current state of understanding.

We agree that in our desire to keep this introduction to the idea of top-down assessment brief, we left out much detail. We have made edits to avoid giving the impression that we are criticizing the state of knowledge about fuels. Rather, we are examining gaps between how traits are handled in plant physiological ecology and how fuel characteristics are described in the fire hazard and fire behavior models. See extensive edits to lines 120-152.

L129: This area, too, is too harsh. Both Schwilk and Varner work on western and eastern pine ecosystems, respectively, have lab based litter flammability findings that track field based measures.

We agree that litter fuels have the best track record in terms of successful scaling from traits to fire behavior and cover this in more detail on lines [144-148]. We've edited here to soften this statement in recognition of this criticism.

Flammability is multidimensional: L175-184: See Figure 1 in Varner et al 2015 (Curr For Reports) that is relevant to much of this section and others.

Yes, this paper is useful and we have cited it in lines 169, 256, and 375.

L242-305: This section is far too skewed to live plant moisture. Dead fuel moisture drives surface and ground fires, with some surface fires having a LFMC role. Crown ignition (as precursor to canopy fires, whether in shrubs or trees) can be important, but the emphasis in the text (3 paragraphs and 52 lines to LFMC and only 1 paragraph and 8 lines for dead fuels) is far too live fuel heavy. Live fuels vary within a narrow (from an ignition standpoint) range from 40% (in freak examples) to 300% (as a wet leaf develops) but under the vast majority of field case, live foliage ranges between 80-110%, effectively the same from an energy required to ignition standpoint. Dead fuels vary from 1% to saturated, from a low threshold for ignition to one that extinguishes spreading fire. I would reduce the LFMC section to at most a 1:1 ratio, simultaneously enabling expansion of the dead fuel section.

The reviewer's point regarding the range of variability being narrow in live fuels is well taken and we made edits in light of this by moving the section on dead fuels to come first, and by expanding that section. Our uneven treatment arose from our desire to focus on areas that are more poorly understood; this gave the incorrect impression that dead fuel moisture was less important. We've added caveats regarding the absolute range of live fuel moisture as you suggest, but we note that water loss from live plants may behave differently than water loss from dead and dry material. This is an active area of research and we aim to point out knowledge gaps. See new material lines 253-270

> *L244: Dead plants vary in their moisture content, and this variation is tied to leaf traits and fuelbed traits (see Kreye work and others).*

Agreed. We've expanded this section as requested.

> *L255: "sized"*

> *Fixed.*

> *L256: "can produce"*

Typo fixed.

> *L268: The list provided is exhaustive; it would be good to add a line that either says that one of these is the real driver or that "more research that does X is needed..."*

We added a sentence to accommodate the latter suggestion (line 396).

> *L276: The dynamic fuel models enable variation in fuel moisture and plant curing.*

We've added text to mention that some fuel models include plant curing (lines 314-315).

> *L296: See my rant for L242-305 suggesting expanding this subsection.*

Rant well taken. We've edited this section in response to the reviewer's comments, lines 243-270.

> *L325: Do you mean "on" the stem?*

Fixed.

> *L327, 329, 332, and elsewhere: a plant has a crown and a collection of crowns is a canopy.*

Edited to be consistent as requested throughout.

> *L340: Do you mean "grass crown"?*

Sentence removed.

> *L377: say FARSITE and then the spelled out version.*

Added on line 396.

L380s and 90s: This section is also too long for the mostly marginal importance of chemistry, save for terpenes, fats, and waxes.

Here the reviewer requests the trimming of the first two paragraphs of this section on the grounds that chemistry is relatively unimportant in determining flammability, except for compounds such as terpenes. We respectfully disagree with this suggestion and here outline why we should retain these existing first two paragraphs, while taking on board the reviewer's suggestion to expand the discussion on terpenes.

The first paragraph (lines 380s in the original MS) outlines the structure of what is to follow in this whole section, identifying the three main groups of chemicals that have been studied for their links to flammability: essential elements, primary metabolites and secondary metabolites. When reviewing the literature on plant chemistry and flammability we noted just how fragmentary this is; few studies look at more than one group of chemicals. Indeed, to our knowledge there is no over-arching review of the role of plant chemistry in determining flammability, and one of us (TJC) is supervising a PhD student who plans to fill this gap with a systematic review.

Therefore, we believe that this first paragraph serves as an important first step in laying the foundation for such a review by identifying the different chemical groups that have been associated with flammability. Consequently, we would prefer to keep it intact, along with the amendments suggested by Reviewer #2 (lines 415-419):

'While the term 'secondary metabolites' is widely used in the literature, and we have retained it here for consistency with previous work, we prefer the term 'specialized metabolites' as these are compounds derived from primary metabolism to fulfill specific functions, essentially adaptations which enhance survival. 'Specialized metabolites' avoids the connotations of 'secondary' being a less important function.'

The second paragraph (lines 390s in the original MS) summarizes the literature that has examined links between essential elements (C, N, K, P, Ca, Ma, S) and flammability. As pointed out in this paragraph, a number of studies have found significant correlations between various essential elements and flammability, though these relationships are rarely consistent across studies. Hence, we consider it is important to point this out to the reader. Furthermore, we have now added the crucial point, demonstrated in very recent work by some of us (TJC and DWS) that these significant correlations between flammability and essential elements are often less strong than those between flammability and other traits (lines 428-433):

'although Budha-Magar et al. (2024) found negative relationships between shoot flammability and various leaf nutrients (Mg, K, S, Ca, but not P). While essential elements may be correlated with flammability, these relationships are often weaker than those between flammability and other traits (e.g. leaf moisture content, twig dry matter content and retained dead material; Budha-Magar et al. 2024).'

Again, we would argue for keeping this paragraph intact.

There is old research (e.g., Philpot 1971 For Sci, Broido and Nelson 1964 Science) that shows some of the work on ash-generators.

Thank you for pointing these out. We have now added a sentence and references (lines 407-409)

The text on terpenes on the other hand should be much expanded. Terpenes show clear and measurable differences in flammability for several taxa and are also interesting to the AJB readership. Pinus is such a clear example and recent flammability work (Varner et al. 2022 Sci Reports) follows other pine work of the lead author and others on the variation in this genus.

Thank you for this suggestion and for the accompanying references. We have now expanded this section: lines 450-465.

L485: Insert Genus and species for "cheatgrass"

Fixed.

L487: Unclear what a "biographic" model is-

Oops. Missed during proofreading. Thanks.

L487-490s: This section seems oversold.

We've slightly reduced this section (lines 534-545).

L498-530 is important. Given the length of this text, it would be good to spell out (more explicitly) the potential mechanism(s) at the plant and fuelbed level.

We expanded this and added a sentence on potential mechanism (lines 564-581).

L525: see also Varner et al. 2017 Biol Invasions

Good point! We added citation (lines 573-574).

L546: all wildland fires, not just wildfires

Rephrased as suggested here and elsewhere.

Reviewer #2:

Thank you for inviting me to review this manuscript. The authors of the manuscript "How plant traits shape flammability from leaf to landscape scales" provide a literature review of different approaches in flammability research with a critical overview of key knowledge gaps and directions for future multi-scale designed studies using comparable measures for different dimensions of flammability and consistently used terminologies to describe traits, plant and community architecture. The manuscript is well written and clearly presented. It provides a general overview of the state of the art and can serve as a guide for future research. The topic is suitable for the American Journal of Botany.

Specific comments:

At a finer scale, the flammability of plants is determined by a combination of plant traits (moisture content, chemistry, morphology, geometry) and landscape features (amount and continuity of vegetation, fuel distribution pattern). The moisture content of living and dead fuels is the most important factor and can be held responsible for the transition of landscapes from non-flammable to highly flammable. Although empirical evidence suggests that low moisture content of fuels favours the development, the MC *must exceed certain thresholds for fires to occur. Are there attempts to identify such thresholds (at different scales)? This could help in effectively assessing the landscape-scale potential for wildfire.*

This is an excellent point. We've expanded our discussion of dead fuel moisture (lines 256-270) in response to suggestions by Reviewer #1. We now mention specific thresholds for dead fuels and recent work on live fuels as well Boving et al. (2023) and Sultana (2022). See lines 251-255.

Plant traits that contribute to the ignition and maintenance of fire (chemistry, morphology, geometry) are often discussed as fire-promoting or fire-adaptive traits. When referring to "secondary metabolites", I would prefer the term "specialized metabolites". Essentially, they are derived from primary metabolism to fulfill a specific function - to enhance adaptation and survival. The widespread use of the term "secondary" suggests a less important function.

We agree that this terminology is misleading; however, we feel confined by the widespread use of the term secondary metabolites in the literature (in both phytochemistry and fire ecology papers). To aid the reader's interpretation we have kept the term secondary metabolites throughout our paper, but have made the following acknowledgment (lines 415-419):

While the term 'secondary metabolites' is widely used in the literature, and we have retained it here for consistency with previous work, we prefer the term 'specialized metabolites' as these are compounds derived from primary metabolism to fulfill specific functions, essentially adaptations which enhance survival. 'Specialized metabolites' avoids the connotations of 'secondary' being a less important function.

Sincerely,

Dylan W. Schwilk

From plant traits to fire behavior: scaling issues in flammability studies

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Abstract

Despite fire being one of the oldest and most important ecological disturbance processes on Earth, many aspects of fire-vegetation feedbacks are poorly understood, limiting their accurate representation in predictive models. Translating plant flammability traits to fire behavior and fire effects on ecosystems has proven a challenge with different disciplines approaching the problem at widely different scales. One approach has been a top-down assessment of ecosystem-level effects of vegetation structural characteristics and plant physiology on fuel properties such as fuel moisture. This has had some success, but is often forced to collapse species-specific variation into a small number of functional types and, as a practical necessity, usually focuses on highly plastic traits (e.g. moisture content) that can be modeled across an ecosystem without the need to characterize species-specific characteristics. The other approach grew out of trait-centric comparative ecology and focused on how traits might influence individual plant flammability. However, the degree to which such lab-based flammability trials reflect real species-specific differences maintained during wildland fires has been questioned. We review the history of these approaches, discuss where each has succeeded, and identify areas of research aimed at closing the apparent gap in scale.

Background

Fire has been a key component of the Earth system for hundreds of millions of years (Glasspool et al., 2004) and may have been used by hominids as early as 1.5 MYA (Brain and Sillent, 1988). In addition to atmospheric oxygen and background ignitions, such as lightning, wildland fuels (e.g., living plants and their associated litter and debris) are a fundamental determinant of fire occurrence and behavior. Although fire regimes have an intrinsic range of natural variation, rapid changes in climate and land use are leading to unprecedented extreme fire events (French et al., 2015; Cunningham et al., 2024). In many regions, fire seasons are lengthening and are associated with elevated risks of extreme fire behavior and occurrence of fire events (Jolly et al., 2015). These effects are not only amplifying fire activity in fire-prone landscapes; some ecosystems where fire has historically been extremely rare are also predicted to experience increased fire activity (e.g., Aoteaora New Zealand, Melia et al., 2022; Arctic tundra, French et al., 2015; Amazonia, Brando et al 2020). Furthermore, some ecosystems maintained by fire may experience reduced fire activity as systems move below critical biomass thresholds (Krawchuk and Moritz, 2011; McWethy et al., 2013) or experience community composition and subsequent fuel changes (e.g. "mesophication", Nowacki and Abrams, 2008). Highly flammable dead plant matter, especially leaf litter and dry graminoid cover, shaped by plant traits and phenology patterns, has been the traditional focus of fire hazard and fuel load assessments with fuel models used to characterize ecosystems in terms of plant functional groups and structure (Anderson, 1981). Plant characteristics, especially the characteristics of live plants, are important controls of landscape flammability (Anderson, 1971), and fire behavior models have been successfully grounded in the categorization of fuel types. However, parametrization of plant flammability in terms of traits important to ecological strategies remains challenging. Consequently, critical uncertainties regarding how climate change will impact plant community composition and hence the relative flammability of fuel assemblages, limit our ability to predict future changes in fire regimes.

In an era of extreme fires, much attention has been paid to the direct effects of climate change on fire weather and fuel dryness (Ellis et al., 2022) with less consideration of the abundance of different fuel types. Living and dead fuels link fire science and plant ecology, therefore plant traits provide an important conceptual framework for fire ecology; they provide a way to predict how individual plants and their components will ignite, burn, and influence fire behavior, broadly captured by the concept of plant 'flammability' (Box 1) (Cornelissen et al. 2017; Pausas et al., 2017). For example, the quantitative description of traits such as leaf mass per area, maximum moisture content, and concentration of volatile organic compounds can inform our understanding of fine-scale fire dynamics (Murray et al., 2013; Alam et al., 2020; Burton et al., 2021; Popović et al., 2021). However, scaling from individual plants to stand-level characteristics is challenging because the interplay between plant traits and fire behavior is also shaped by environmental conditions and interactions with pathogens, herbivores, and non-fire disturbances (Younes et al., 2024; Oliveras et al., this issue). This spatio-temporal context-dependence limits the ability to scale up assessments of flammability conducted on plant components (Fernandes and Cruz, 2012; Pausas and Moreira, 2012).

The multi-scale nature of flammability (Figure 1) and the tremendous multi-scale trait diversity in plant communities resulting from variation in species composition, individual age and size, and phenotypic plasticity challenges integrating functional ecology with fire science (Grootemaat et al., 2017a; Ganteaume, 2018; Tumino et al., 2019). Different vegetation types in the same climate can show different fire behaviors (van Wilgen et al., 1990; Odion et al., 2010; Archibald et al., 2018), indicating that emergent properties of living plants can shape fire. Furthermore, several biogeographical conundrums point to a possible role for lineage-specific species traits as influencing fire regimes (Rogers et al., 2015; Archibald et al., 2018; Simpson et al., 2022). Scaling from plant traits to fire behavior at landscape scales remains challenging, with fire behavior models sometimes performing poorly when used outside of the ecosystems or climatic conditions for which they were developed (Sullivan et al., 2009a–c). Moreover, there is little overlap in traits considered between the fuel modeling of fire scientists and the functional trait measurements of ecologists.

There are two contrasting, but complementary approaches to understanding the role of plant traits in influencing fire hazard and fire behavior. One approach focuses on gross plant or fuel characteristics that are amenable to landscape-scale remote sensing or modeling from vegetation maps (Abdollahi and Yebra, 2023). We call this the “top-down” approach. The second approach is the assessment of species-specific flammability traits in laboratory trials: the “bottom-up” approach. A barrier to establishing general flammability relationships is that individual studies usually focus on a single fuel type such as surface fuels measured by fire spread through artificial fuel beds, crown fire fuels measured on shoots of woody plants, or graminoid fuels with flammability measured at the whole plant scale. Different plant traits appear to affect different dimensions of flammability among these fuel types (Schwilk, 2015). The top-down and bottom-up approaches considersharply contrasting spatial grains and extents with limited overlap (but see exceptions e.g. Prior et al., 2017), which has inhibited the development of cross-scale integrated approaches to quantifying plant flammability. Additionally, it is important to note that this dichotomization breaks down under more extreme fire behavior and extreme fuel drying, where fuel characteristics maycease to be important because all biomass becomes available to burn (Cruz et al., 2022). For instance, extreme fires can burn tropical rainforests that are typically considered pyrophobic communities.

The top-down assessment of fuels, often using remote sensing or vegetation mapping, aims to assess ecosystem level effects of plant characteristics on stand, community, and landscape fuel properties (Figure 1). This approach is well-integrated with fire behavior models and forms the basis of tools used by fire incident teams during active fires (eg LANDFIRE, Rollins et al. 2017). These assessments generally require collapsing species-specific variation into functional types (Anderson, 1982; Scott and Burgan, 2005). The fuel model approach has underpinned fire hazard and behavior prediction particularly in the US and Europe (Cruz et al. 2025) where such fuel models combining plant traits of dominant species and ecosystem level vegetation structural characteristics are widely used. More recently, there has been increasing interest in including physiological traits in the assessment of flammability (Jolly and Johnson, 2018) and examining traits such as those regulating plant water use and carbon dynamics that can be modeled across an ecosystem (e.g., Drucker et al., 2023). In ecosystems dominated by one or a few species, this approach is essentially species-specific, as in chamise-dominated California chaparral where live fuel moisture content has been shown to predict fire hazard (Park et al., 2022).

The “bottom” up approach has involved laboratory experiments and has been integrated into wildland fire science for decades especially in the vast literature on measuring and modeling fuels (e.g. Anderson, 1970, Rothermel, 1986 and many others). However, such work was rarely explicitly linked with plant morphological or physiological traits. A trait-based “bottom-up” approach has the potential to link well-studied ecological strategies of plants with fire and vegetation feedback processes. However, it is uncertain how well individual-level measures of plant flammability predict fire behavior in wildland fires, or how these effects vary with fire weather conditions. Lab-based flammability trials of leaves, litter, and detached branches have demonstrated extensive variation in multiple dimensions of flammability (Varner et al., 2015; Cui et al., 2020; Popović et al., 2021). However, there is a gap between these flammability parameters usually measured at the organ or partial plant level and the emergent flammability of actual plant communities. In litter fuels, plant traits show both additive and non additive effects that extrapolate well to local fire behavior (Schwilk and Caprio, 2011, de Magalhães and Schwilk, 2012; van Altena et al 2012; Kane et al., 2021). However, there is debate about how trait variation influences wildfire relative to climate, weather, and topography, especially for crown fire. Nevertheless, there have been successful attempts to use traits in fire behavior assessment (Cardoso et al., 2018), modeling (Zylstra et al., 2016), and hazard prediction (Balaguer-Romano et al., 2022). This scaling challenge is not unique to fire ecology and is an example of a broader debate in functional ecology regarding how well plant traits predict ecosystem-level processes (van der Plas et al., 2020; Gornish et al., 2022; Hagan et al., 2023).

In this review, we examine the efficacy of trait-based bottom-up approaches and top-down landscape flammability assessment across four important fuel characteristics (fuel moisture, fuel chemistry, fuel architecture, and fuel load). This review addresses two main questions:

1. How well do traits measured at the organism-level match fuel characteristics measured at broader scales?

2. How well do species-specific traits predict fire behavior?

Finally, we identify approaches that can advance the field of plant flammability from plant to landscape scales.

Flammability is multidimensional

The dimensions of intrinsic plant flammability

Whole plant flammability is a compound functional trait (Jaureguiberry et al., 2011), and can be assessed using different variables of measurement (Pérez-Harguindeguy et al., 2013), across a range of scales of organization from plant tissues and excised parts to organs, shoots, and entire individuals (White and Zipperer, 2010; Younes et al., 2024), and for live, dry, or dead fuel (Boving et al., 2023; Melnik et al., 2024). Common to these multiple dimensions, scales, and fuel types is the measurement of intrinsic plant flammability, a multivariate concept that represents the inherent burning properties of plants as determined by their physico-chemical traits (Varner et al., 2015). Anderson (1970) established three intrinsic flammability variables that are widely used in fire ecology research: ignitibility, sustainability, and combustibility (Box 1).

Ignitibility is the ease with which a plant begins to burn when exposed to an ignition source (Gill and Moore, 1996), most frequently measured as either the time to ignition (Murray et al., 2013) or the frequency of ignition events among a set of samples exposed to an ignition source (Wyse et al., 2016). *Sustainability* is how long a plant burns after ignition, with or without an external heat source (White and Zipperer, 2010; Jaureguiberry et al., 2011). Sustainability is most frequently measured as the duration of combustion and can include durations of incandescence, flaming, and smoldering (Ormeño et al., 2009). *Combustibility* refers to the intensity of burning, measured variously as the highest temperature measured during burning (Alam et al., 2020), flame height (de Magalhães and Schwilk, 2012), flame spread rate (Ganteaume et al., 2011b), and mass loss rate (Simpson et al., 2016). Martin et al. (1993) considered consumability as a fourth dimension of intrinsic plant flammability, representing how much of a plant is consumed by fire. *Consumability* is commonly measured as the percentage of burnt biomass once combustion has finished (Burger and Bond, 2015; Zanzarini et al., 2022).

Relationships among dimensions of flammability

Comparative flammability studies have explored inter-species relationships between the four intrinsic flammability dimensions (i.e., ignitibility, sustainability, combustibility, and consumability). A key goal of such investigations has been to determine whether there are species for which all four flammability variables are aligned\ (Murray et al., 2023). In this context, some evidence exists for correlations between intrinsic flammability variables. Previous work has shown that leaf ignitibility and sustainability are negatively correlated, such that species with leaves that take a long time to ignite also possess leaves that burn for a long time (Krix et al., 2019; but see Grootemaat et al., 2015). Cawson et al. (2023) showed that shoot sustainability is positively correlated with shoot combustibility. Further evidence that some flammability variables are correlated is provided by studies requiring the use of dimensionality reduction methods (e.g., principal component analysis) to consider collinearity among ignitibility, sustainability, combustibility, and consumability (Prior et al., 2017; Wyse et al., 2018).

Relationships among variables differ when measured on different fuel types. Flammability studies of surface fuels (leaf and twig litter) tend to show two relatively equal and orthogonal axes of variation with one axis representing flame duration and/or total heat released and another axis associated with ignitability and spread rate (de Magalhaes and Schwilk, 2012; Engber et al., 2012; Prior et al., 2018). In well-aerated fuels such as grasses, on the other hand, flammability measures are often more strongly correlated, suggesting a single major axis of variation (Simpson et al, 2016; Gao and Schwilk, 2018; Padullés Cubino et al., 2018). In addition to differences across fuel types, another possible explanation for differing results is differences in how flammability is measured (Younes et al., 2024). There is a need to develop globally consistent methodologies of assessment and analysis of intrinsic plant flammability (Ocampo-Zuleta et al., 2024), to allow robust conclusions about the nature of inter-relationships among flammability variables.

Relationships between plant flammability variables and fire behavior descriptors

Theoretical frameworks suggest that each dimension of a plant's intrinsic flammability corresponds to a specific aspect of fire behavior and ecosystem processes (Box 1). For example, Gill and Zylstra (2005) propose that ignitability, combustibility, and sustainability at the individual plant level are linked to the rate of fire spread, flame length, and fire residence time, respectively. Conversely, Pausas et al. (2017) argue that the rate of fire spread is more closely related to combustibility. The consumability axis, is theoretically aligned with fire severity at the ecosystem level, often measured by the amount of above- and below-ground organic matter consumed by fire (Gill and Zylstra, 2005; Keeley, 2009). There are few empirical test theoretical models of landscape flammability, with one study from the Australian monsoon tropics supporting two axes: total heat release and rate of spread (Prior et al., 2018).

Researchers have also attempted to connect these dimensions of flammability with flammability metrics at different scales to better predict fire behavior. For instance, Grootemaat et al. (2017b) investigated the relationship between individual leaf flammability and fuel bed flammability, finding that the time-to-ignition of individual leaves was correlated with several flammability parameters in fuel beds, including the rate of fire spread. Consequently, fire spread can be understood as a sequence of ignition events, where the ease of ignition of individual leaves accelerates the spread of fire from one leaf to another (Grootemaat et al., 2017b).

Plant traits to fuel characteristics across scales

Given the multidimensionality of flammability, predicting fire behavior at community and ecosystem scales based on bottom-up approaches is extraordinarily difficult (Loudermilk et al., 2022). To examine flammability across scales, we consider four major categories of fuel characteristics likely to be influenced by plant traits: fuel moisture, fuel architecture, fuel chemistry, and fuel load (Box 1). These are not independent, for example architecture can influence moisture dynamics and fuel load, and leaf chemistry interacts with leaf moisture. Each of these categories also encompasses mixtures of live and dead fuel components and how they interact with the fuel complex. Below we discuss how different plant traits in each category impact flammability across ecological scales and identify the challenges in bridging scales and their causes.

Fuel moisture across scales

Fuel moisture content, whether of dead or live fuels, has long been recognized to affect time to ignition (Rothermel, 1972). Water acts as a heat sink, thus, a high moisture content requires more energy to evaporate water before ignition can occur and the amount of water in the fuel impacts the effective heat of combustion as well as the rate and form of heat released (Smith et al., 2013; Campos-Ruiz et al., 2022). The relationship between fuel moisture and flammability has been extensively studied in the laboratory, and there is strong evidence that this association is negative (Bowman et al., 2014; Popović et al., 2021). Fuel moisture content is negatively correlated with ignitibility at a range of fuel scales, including leaf (Murray et al., 2013; Grootemaat et al., 2015; Simpson et al., 2016; Krix et al., 2019; Younes et al., 2024), litter (Plucinski and Anderson, 2008; Blauw et al., 2015; Burton et al., 2023), shoot (Wyse et al., 2018; Murray et al., 2023) and the whole plant (shrubs, Weise et al., 2005; grasses, Simpson et al., 2016; forbs and shrubs, Zanzarini et al., 2022). However, the relationships between moisture content and sustainability (negative, positive and neutral) and consumability (negative and neutral) are ambiguous (Popović et al., 2021; Younes et al., 2024). Associations with fuel moisture content are the best studied of all trait-flammability relationships, and the effect of moisture content may outweigh that of other traits, such as phytochemistry (Alessio et al., 2008). Moisture content can exhibit thresholds that delineate flammable and non flammable vegetation. Thresholds for dead fuels ("moisture of extinction" values) depend upon fuel type and wind speed (Matthews, 2013), but often range from 15-40% (Scott and Burgan. 2005; Smith et al., 2013). Recent research has also identified thresholds in live fuels (Sultana, 2022; Boving et al. ,2023).

Fuel moisture in dead and excised fuels

Dead fuel moisture is a strong driver of litter flammability (Varner et al., 2015; Kreye et al., 2018, de Magalhães and Schwilk, 2021). Dead fuel moisture can vary from 1% to saturated and accordingly can create fuels with low energy thresholds for ignition to levels that extinguish spreading fire and is driven by driven by relative humidity, solar radiation, wind, and microclimate conditions, as well as by plant traits that influence surface area to volume ratios, litter packing, and bulk density (Rothermel, 1986, Kreye et al., 2018, 2023).

Dead fuel moisture is represented explicitly in US fire behavior models, but this is largely in terms of atmospheric effects on wetting and drying (Rothermel, 1986; Viney, 1991; Nelson, 2000). Species-specific characteristics are included only through the fuel-type specifications. However, in systems where leaf litter drives surface fire, inter-specific differences can result in differing litter flammability where part of the species effect is realized through different moisture absorption/adsorption dynamics and drying rates (Kreye et al., 2018, 2023; Talhelm and Smith, 2018; de Magalhães and Schwilk, 2021; Kane et al., 2021). Additionally, canopy cover and soil moisture influence the litter microenvironment, affecting drying rates and flammability (Kreye et al., 2020; Zhao et al., 2022).

Fuel moisture in living plants

Moisture of live fuels is much more complex to understand than moisture in dead fuels.. Live fuel moisture depends on plant physiology and plants can transport water and nutrients across their tissues on short time scales (Nolan et al. 2022). Live fuel moisture content (LFMC) is the ratio of water mass (g) to dry mass (g) in fresh biomass and is commonly quantified in small branches. It is tightly correlated with other measures of plant water content such as leaf relative water content (proportion of water content relative to saturated condition) and can vary with plant water potential (Boving et al., 2021; Mahmud and Schwilk, this issue). In laboratory studies, the relationship between LFMC and time to ignition has been described as a linear relationship or a threshold relationship (Xanthopoulos and Wakimoto, 1993; Terrah et al., 2020). Such discrepancies potentially result from the heat flux applied or the mode of heat transfer (i.e., convective versus radiative), as radiant heating will take substantially longer to ignite small fuel pieces than similarly sized pieces heated by convection (Cohen and Finney, 2023) and radiant heaters can produce both types of heat flux depending on sample positioning. Despite laboratory studies demonstrating a negative relationship between LFMC and flammability, the importance of LFMC in field studies is debated (Alexander and Cruz, 2013; Rossa and Fernandes, 2018). There are multiple, not mutually exclusive, potential reasons for the discrepancy between laboratory and field studies: (1) the challenges of isolating the effect of LFMC from other variables (e.g., wind speed, solar radiation, topographic slope, dead fuel moisture) in the field; (2) the higher heat fluxes in wildfires than laboratory studies may mask any effect of LFMC on time to ignition (Alexander and Cruz, 2013); (3) the relatively low variation in LFMC observed in field studies may be insufficient to induce an effect on time to ignition (Pimont et al., 2019); (4) the moister conditions of vegetation during field experiments, since field experiments are often conducted under mild conditions for safety reasons (Fernandes and Cruz, 2012; Alexander and Cruz, 2013; Rossa and Fernandes, 2018; Pimont et al., 2019); (5) differences in vegetation structure that may affect the relative importance of LFMC; and, (6) errors in estimates of LFMC in the field (Pimont et al., 2019). Further field-based studies are required to examine the relative importance on LFMC on fire behavior.

This ongoing debate leads to differences in how LFMC is included in fire behavior models across different systems. For example, in Australia, fire behavior models for short stature or highly horizontally connected vegetation, such as grasslands and shrublands, require inputs of LFMC or proxies for LFMC, such as plant curing (Cruz et al., 2015). In contrast, fire behavior models for taller eucalypt forests do not consider LFMC (Cruz et al., 2015). Live fuel moisture is not explicitly included in US fire behavior models based on the Rothermel (1972) fire behavior equations (reviewed in Sullivan 2009a–c); however, LFMC is implicitly included in such models through dead to live fuel biomass ratios or as constants in fuel type categories (known as "fuel models," Finney, 1998). It has been proposed that failures of the Rothermel (1972) equations to predict fire spread in shrub fuels may arise from how moisture effects are parameterized (Weise et al., 2016; García et al., 2020). Despite the inconsistent consideration of LFMC in models, there is growing evidence that low LFMC is associated with wildfire extent (Dennison et al., 2008; 2009; Chuvieco et al., 2009; Nolan et al., 2016; Argañaraz et al., 2018; Luo et al., 2019; Park et al., 2022, Rao et al., 2022) and increased receptivity of landscapes to lightning ignitions (Rao et al., 2023; Wickramasinghe et al., 2024).

There are multiple challenges to estimating LFMC across broad spatial scales. Top-down approaches may not characterize fine-scale spatial patterns in LFMC. Perhaps most importantly, LFMC is temporally dynamic. Remote sensing methods are used to assess hazard (e.g., Fuelcast, https://www.fuelcast.net/); however, such methods struggle to forecast temporal changes in fuel moisture (but see Miller et al., 2023). Ongoing efforts to link top-down with bottom-up approaches that use correlated plant traits to predict leaf flammability traits, including LFMC (Nolan et al., 2018; Balaguer-Romano et al., 2022). Recent research has attempted to predict fuel moisture and flammability from hydraulic traits such leaf saturated moisture content and leaf capacitance (Scarff et al., 2021; Nolan et al., 2022). Within and between some species, water status measured as leaf water potential predicts ignitibility (Boving et al., 2023) or integrated measures of flammability (Sultana et al. this issue), however the degree of sensitivity to water potential can vary across species and may depend not just on water content but on the rate of water loss during preheating (Mahmud and Schwilk, this issue).

Fuel architecture across scales

Fuel architecture refers to the size, shape, volumetric arrangement, and distribution of fuel materials that burn during wildfires (Box 1). Although fuel architecture is often quantified based on the volumetric arrangement of assemblages of different live and dead fuel components, with metrics such as compaction, bulk density, ladder fuel presence, among others (Kreye et al., 2014), some studies have addressed the architecture of individual plants (White and Zipperer, 2010). Fuel architecture influences flammability by affecting variables such as ignition, combustion, heat transfer, wind patterns and the airflow across fuel scales (Papió and Trabaud, 1990; Zylstra et al., 2016). Architecture also influences the flammability of smaller fuel particles that are routinely examined in the laboratory (Alam et al., 2024), such as leaves, litter, and shoots, and the larger fuels and mixtures of fuels in the field, such as surface fuels (e.g., grasses, leaves, litter), ladder fuels (e.g., shrubs, small trees), and canopy fuels (e.g., tree crown).

Fuel architecture of live plants

Fuel architecture is an important determinant of flammability at larger fuel scales, such as the shoot and whole plant. For shoots, the physical arrangement of leaves in the branches likely plays a more important role in influencing flammability than leaf size and shape (Perez-Harguindeguy et al., 2016; Alam et al., 2020). However, some work has found architectural traits less important in determining flammability than leaf traits such as leaf dry matter content and leaf thickness (Alam et al. 2024). Key architectural traits at the shoot-level include branch ramification, leaf and twig fraction mass and fuel bulk density, with species with more fine branches, higher leaf fraction mass, and higher bulk density being more flammable (Santacruz-García et al., 2019; Alam et al., 2024). At the whole-plant level, especially for trees and shrubs, the spatial arrangement and density of leaves and branches on the stem, the vertical and horizontal distribution of the fine fuels, and the retention of dead fuels in the crown or around the base of the plant determine flammability (Mitsopoulos and Dimitrakopoulos, 2007). For example, manipulative field experiments demonstrate that the canopy architecture of dead fuel retention in the shrub *Adenostoma fasciculatum* was more important than total fuel load in enhancing fire intensity (Schwilk, 2003). A tree crown structure with closely connected leaves and branches is more likely to carry a fire than a crown with sparse branches, due to more efficient heat transfer in the former (Saura-Mas et al., 2010; Schwilk, 2015). Also, plants with continuous vertical fuel from the ground to the crown (ladder fuels) are more likely to propagate a surface fire into the tree crown, producing crown fires, which are more intense (Graham et al., 2004; Menning and Stephens, 2007; Mitsopoulos and Dimitrakopoulos, 2007). Likewise, dense lateral branching in the crown and well-connected aerial branching between adjacent trees help spread and sustain a fire more than those with gaps in fuel continuity (Graham et al., 2004; Menning and Stephens, 2007; Mitsopoulos and

Dimitrakopoulos, 2007). Fire ecologists have often assumed that architectural differences across herbaceous species are less important than are differences in biomass to fire behavior, supported by studies of grassland fuels indicating that flammability strongly depends on fuel load (Simpson et al., 2016; Padulles Cubino et al., 2018). However, there are some indications of other architectural effects on flammability in grasses related to the positioning of biomass (Gao and Schwilk, 2018; 2022).

Fuel architecture in dead and litter fuels

Extrapolating flammability across scales is challenging (Fernandes and Cruz, 2012). A striking example of the decoupling between the flammability of individual fuel elements and their corresponding fuel beds is seen in small, thin shrub leaves. These leaves ignite easily as individual plant parts or when attached to a shoot but, when organized as litter, produce low heat release rates due to poor ventilation (Scarff and Westoby, 2006). Leaf litter fuel beds possess emergent properties, such as packing ratio and bulk density, which influence airflow and can override the effects of individual leaf flammability (Grootemaat et al., 2017b). A litter layer with larger leaves and other materials facilitates ventilation and ensures more oxygen availability, resulting in fires that burn more rapidly, whereas small leaves tend to produce a compacted litter structure that can restrict airflow and so burn slowly or rarely (de Magalhaes and Schwilk, 2012; Van Altena et al., 2012; Ganteaume, 2018). Consequently, litter flammability is aeration-limited, while canopy flammability, where fuels are usually well-ventilated, is not (Schwilk, 2015; Varner et al., 2015).

Although leaf-level flammability measurements do not predict flammability of surface fuels composed of leaf litter, ground fuels do provide an example where extrapolating from fine to coarser scales has succeeded: surface fire behavior in one temperate forest was predicted by the abundance-weighted leaf traits known to influence fuel aeration (Schwilk and Caprio, 2011). At the extreme of oxygen limitation, organic soils and peat bogs can exhibit extensive fuel consumption under smoldering combustion (Turetsky et al., 2015; Walker et al., 2019, Prior et al., 2024). In addition to natural fuel beds, forest management practices can lead to large areas of masticated (i.e., chipped or shredded) material as a part of fuels thinning operations, a practice that has increased over time particularly in the wildland urban interface (Reed et al., 2020). The size, shape, and chemistry of these masticated materials, as well as material depth, can affect how tightly they pack and how long they retain moisture and therefore flammability and fire spread rates. Fuel bed characteristics in this case depend upon species composition and the machinery used to create masticated material (Kreye et al., 2014).

Elevated dead fine fuels, such as fibrous and ribbon barks, are a unique, albeit important, type of wildfire fuels. Some species, particularly many eucalypts, have a comparatively high biomass of this fuel type that is often specifically measured in hazard assessments (Pickering et al., 2023). These fuels are important in generating embers and fire brands which can spread wildfires over long (> 30 km) distances through a process known as 'spotting' (Tarifa, 1965; Manzello et al., 2007) and can depend on both plant traits that facilitate brand formation (Pickett et al., 2005; Penman et al., 2017) and the receptivity of the fuel bed to ignition by lofted brands (Ganteaume et al., 2011a). Spotting is included in simulated fire spread models such as FARSITE (Fire Area Simulator, Finney, 1998, 2004), but such models struggle to predict fire perimeters accurately under conditions favorable to spotting (Zigner et al., 2022). Further work on factors influencing the likelihood that a spot fire will lead to an ignition and subsequent fire spread is needed from both top-down and bottom-up perspectives. The development of spatial vegetation flammability datasets are needed to enable utility, municipal, and land management planners to target, remove, or reduce certain vegetation types or debris identified to exhibit a higher probability of promoting spot-fire ignitions.

Fuel chemistry across scales

Plant tissues contain numerous chemical elements and compounds, many of which have been linked to plant flammability across fuel scales. The most important of these is water (see section "Fuel moisture across scales"), although plant water content is traditionally (as it is herein) considered separately from plant chemistry (Younes et al., 2024). Some of the earliest research into plant traits associated with flammability focused on chemistry, such as mineral ash content (Broido and Nelson 1964; Mutch and Philpot, 1970; Philpot 1970). Chemicals that affect flammability fall into the following main groups: essential elements, e.g., C, N, K, P, Ca, Ma, S (Salisbury and Ross, 1992); primary metabolites, which are plant-produced chemicals essential for growth, development and reproduction, e.g., carbohydrates, amino acids, fatty acids and vitamins (Schlaeppi et al., 2021); and secondary metabolites, which are plant-produced chemicals that have no direct role in this primary function but are useful in other ways, such as plant defense against herbivores (Neilson et al., 2013). While the term 'secondary metabolites' is widely used in the literature, and we have retained it here for consistency with previous work, we prefer the term 'specialized metabolites' as these are compounds derived from primary metabolism to fulfill specific functions, essentially adaptations which enhance survival. 'Specialized metabolites' avoids the connotations of 'secondary' being a less important function.

The relationship between certain essential elements and flammability has received some attention. For instance, there is evidence for a negative relationship between P and leaf and litter flammability (Scarff and Westoby, 2008; Grootemaat et al., 2015), although this is not universal across fuel scales (Mason et al., 2016; Grootemaat et al., 2017b; Alam et al., 2020), and P may influence flammability less than traits such as moisture content and leaf morphology (Turner, 1994; Scarff et al., 2012). Nitrogen is another essential element that has been linked to flammability, although again results have been mixed across fuel scales (Grootemaat et al., 2015, 2017b; Mason et al., 2016; Gowda et al., 2022). Other essential elements, such as K, Ca, and Mg, have rarely been investigated in relation to their impact on flammability (Popović et al., 2021; Rahman et al., 2023), although Budha-Magar et al. (2024) reported negative relationships between shoot flammability and various leaf nutrients (Mg, K, S, Ca, but not P). While essential elements may be correlated with flammability, these relationships are often weaker than those between flammability and other traits (e.g. leaf moisture content, twig dry matter content and retained dead material; Budha-Magar et al. 2024).

Primary metabolites, such as carbohydrates and fatty acids, may be positively correlated with different flammability traits at leaf, litter and bark scales (Mason et al., 2016; Grootemaat et al., 2017b), likely due to their low relative molecular mass and high volatility (Page et al., 2012). Non-structural carbohydrates, such as sugars and starches, enhanced the sustainability of living needles of *Pinus banksiana*, and foliar chemistry had a greater influence on flammability than moisture content (Campos-Ruiz et al., 2022). Further research into primary metabolite-flammability relationships should prove fruitful.

Secondary metabolites are the most extensively studied group of chemicals in relation to their influence on flammability across fuel scales, and include volatile organic compounds such as phenolics and terpenes, as well as lignins and tannins (Owens et al., 1998; Ormeño et al., 2009; Pausas et al., 2016; Ganteaume et al., 2021; Guerrero et al., 2022). Of these chemical groups, terpenes have received the most attention at both the leaf and litter scales for trees (Popović et al., 2021) and are considered in more detail below. The relationships between secondary metabolites and flammability are complex and can be idiosyncratic, depending on the type of fuel examined, the level at which chemical compounds are studied (e.g., at broad group, subgroup or molecular levels), and the diversity of compounds examined. As with other chemical traits, the effect of secondary compounds on flammability may be less important than that of water content (Alessio et al., 2008).

Terpenes are unsaturated hydrocarbons comprised of isoprene units (C_5) and are known to be flammable due to their high heating value and low flash point (Ormeño et al., 2009). While terpene content was by far the most frequently studied chemical trait on both live leaves and litter for trees, its relationship with flammability was inconsistent across studies (Popović et al., 2021). For instance, for combustibility, 8 out of 10 studies reported a positive relationship with leaf terpene content, and one study each reported a neutral and a negative relationship. For ignitibility and leaf terpene the ratios were 5:3:1 for positive:neutral:negative relationships, while for sustainability five out of six studies reported a negative relationship, with the other a positive relationship (Popović et al., 2021). While general patterns between terpene content and flammability may be lacking, there is evidence to suggest that terpenes drive flammability in particular species and groups. For instance, in *Rosmarinus officinalis* high terpene content increased ignitability, and genetic differences between individuals hinted that such differences in flammability were heritable (Pausas et al. 2016). Furthermore, in the genus *Pinus*, in which flammability (He et al. 2012; Varner et al. 2022) and terpenes (Mitić et al. 2017) have been shown to be phylogenetic conserved and terpenes drive differences in the flammability of leaf litter (Ormeño et al., 2009), it has been suggested that differences in terpene content could be behind unexplained variation in litter flammability (Varner et al. 2022).

There is a paucity of research into the effect of chemistry on fire at community and landscape scales, although the widely used Rothermel fire spread equations include a mineral content damping coefficient which can be set to vary across fuel types (Rothermel, 1972). Fuel chemistry likely influences flammability at landscape scales through interactions between soil chemistry and plant traits and herbivory-induced defenses. Plants from low-fertility ecosystems tend to have traits (e.g., small sclerophyllous leaves, high leaf dry matter content) that make them more flammable (Ojeda et al., 2010; Gibson et al., 2015; Paula et al., 2024). In Australian Mediterranean-climate mallee ecosystems, soil fertility had a strong influence on the probability of fire estimated based on fire interval data, although this was dependent on vegetation type, and the effect of rainfall was stronger (Gibson et al., 2015). In a continental-wide examination of fire activity in Australia, there was a negative relationship between soil P and both area burned and fire radiative power, after controlling for climate (Prior et al., 2017). Unexpectedly, there was a weak positive relationship between soil P and flame rate of spread in grass and litter fuels, which was attributed to the influence of soil P on flammability being less than that of leaf moisture content (Scarff et al., 2012; Prior et al., 2017). In a global study of drivers of fire activity in Mediterranean-type climate regions, low-fertility soils (lower pH and higher concentration of exchangeable aluminum) were positively associated with higher fire activity, although other measures of soil fertility (P, N, C:N) were not related to fire activity (Paula et al., 2024). Intriguingly, these relationships between low soil fertility and higher fire activity may be maintained via positive feedbacks mediated by high-flammability plant species: low soil fertility selects species with traits (small leaves, high leaf dry matter content) that promote high flammability and these species burn readily, resulting in frequent fires that deplete soil nutrient pools, favoring species with traits associated with high flammability (Wood and Bowman, 2012; Hinojosa et al., 2021; Paula et al., 2024). While more work is needed to disentangle how soil chemistry influences flammability, these studies show the value of incorporating soil fertility in models predicting future fire regimes.

Fuel load across scales

Fuel load, the total combustible material, is usually defined as mass/area and is often estimated through top-down approaches. Interactions between fuel load and fuel structure across multiple scales make it difficult to isolate the effects of each driver. At the finest scales, fuel load is determined by the density of plant biomass. Leaf dry matter content (LDMC) is related to the amount of carbon in a leaf available for combustion and is calculated as the ratio of dry mass to water-saturated fresh mass (Perez-Harguindeguy et al., 2013), so is related to live fuel moisture content. At the individual leaf level, higher LDMC has shown a negative relationship with different flammability axes. For instance, Rahman (2018) reported that leaves with higher LDMC required higher ignition temperatures. Similarly, Mason et al. (2016) reported a negative correlation between the rate of temperature increase and LDMC, indicating that higher LDMC is associated with lower combustibility. In contrast, at the shoot level, higher LDMC is associated with increased flammability, demonstrating a decoupling of flammability between leaf and shoot levels (Alam et al., 2020). Alam et al. (2020) and Potts et al. (2022) further demonstrated that LDMC significantly influenced shoot flammability measures connected to all axes of flammability (ignition percentage, burnt biomass, burn time, and maximum temperature) across growth forms and families. Ortiz et al. (2023) corroborated these findings, showing that LDMC positively influenced burn time and maximum temperature. Importantly in the context of isolating fuel load versus fuel structural effects, Alam et al. (2024) demonstrated that LDMC was a better predictor of shoot flammability than various architectural traits. Finally, at the global scale, patterns in LDMC have been linked to fire activity, especially among plants with postfire regeneration abilities (resprouting or reseeding), that have higher LDMC (Dai et al. 2025).

As the scale of analysis expands to include not only shoot characteristics but also individual crowns, fuel density is another important predictor of flammability. At fine scales, fuel load is often measured as mass per unit volume, and at the broadest scales, as mass per unit area. As fuel density increases, fire spread rate tends to decrease while burning time increases (Grootemaat et al., 2017; Prior et al., 2017). However, an important point of distinction regarding fuel bed density (or litter-bed density) is that it may have starkly different influences on flammability/fire behavior in canopies versus litter (see section "Fuel architecture across scales"). Furthermore, herbivores and fire interact (Bond, 2005), and the flammability of vegetation on nutrient-poor soils may in part result from relatively lower herbivory pressure (Archibald and Hempson, 2015).

A central element of predicting fire behavior at broad scales is characterizing the crown size of individual trees and shrubs. In fire behavior models, crown size is often represented by canopy bulk density and canopy height (from canopy base height to top of canopy). Both are seen as essential predictors of wildland fire behavior (Affleck et al., 2012), with greater canopy sizes leading to increased fire intensity in the presence of vertical fuel continuity (Agee, 1996). Keyser and Smith (2010) demonstrated that these metrics of canopy size were insufficient without including the context of vertical structure; even after accounting for vertical structure, the relationship between fuel load and fire behavior is complex and dynamic across stand-to-landscape scales. Vegetation cover affects fuel loads, thereby reducing fire spread rate, heat release, and area burned as the distance between the crowns of neighboring individuals increases. However, horizontal variability in fuel load can lead to increased spread rate, heat release, and area burned (Atchley et al., 2021). LiDAR technology facilitates efficient assessment of fuel architecture with great precision across broad scales (e.g., Price and Gordon, 2016), and methods such as structure-from-motion imaging may continue to make this possible at lower cost (Reilly et al., 2024).

Within a fuel of similar architecture such as grass fuels, biomass strongly influences fire behavior and grassland fire regimes often show effects of previous season growth conditions that influence fire season fuel loads. For example, invasive *Bromus tectorum* in the Great Basin of the western US, which has altered fire regimes, exhibits multi-year effects of past precipitation on current season fire extent (Pilliod et al., 2017). Biomass and net primary productivity have often been used as proxies for fuel density to predict landscape flammability (Bradstock et al., 2010; Pausas et al., 2017). Both these metrics can be estimated across very broad extents through remote sensing or modeling (Tsitsi, 2016), and thus biomass can be readily scaled across. Distinctions between separate categories of biomass can be important to retain even at the broadest scales; for example, Newberry et al. (2020) found grass biomass to be the primary driver of landscape flammability across savanna-forest transition zones in Brazil, although Cardoso et al. (2018) found grass species flammability to be more important than biomass in such ecosystem boundaries in Gabon.

Interactions across fuel characteristics and non-additive effects

When considering the scaling of flammability from the leaf to organism to community scale, it is important to consider how interactions between adjacent fuel components influence whether fire will propagate from one fuel element to another (Finney et al., 2010). If the first fuel element ignites, the probability of the adjacent elements also igniting will depend on intrinsic properties such as fuel moisture and chemical composition. Additionally, this probability is influenced by extrinsic properties, both inherently non-static—such as the distance between elements, which affects the degree of pre-heating and airflow (e.g., wind, air entrainment) that can supply oxygen or cool the elements through convection (Sullivan, 2009a)—and static, such as topography (Finney et al., 2010). Under non-extreme fire conditions, even in the presence of significant pre-heating, element-to-element propagation generally occurs following direct flame contact, with factors such as slope and wind increasing this degree of flame contact (Finney et al., 2010). Under extreme fire conditions (i.e., Forest Fire Danger Index (FFDI) >50), fire propagation and spread becomes independent of fuel conditions (Cruz et al., 2022), and there is evidence from a range of vegetation types (forests, shrublands) that the relevance of species-level fuel characteristics on fire behavior in the field decreases directly as a function of the Forest Fire Danger Index (Bessie and Johnson, 1995; Cruz et al., 2022). However, further work to determine thresholds where trait-based differences in fuels are relevant is warranted, especially in light of models that highlight the importance of convection for fire propagation (Cohen and Finney, 2023).

Non-additive effects challenge the extrapolation of individual plant flammability to the flammability of mixed-species communities. These effects, which arise from emergent physico-chemical properties in fuel mixtures, lead to outcomes that cannot be accurately predicted by simply considering the flammability of individual species. When plants of differing flammability burn together, they can exhibit one of two effects: an additive effect, where the flammability of the mixture reflects the average of the individual species; or a non-additive effect, where the most or least flammable species may dominate, resulting in a net flammability higher or lower than expected (van Altena et al., 2012; de Magalhães and Schwilk, 2012; Della Rocca et al., 2018). This phenomenon of non-additivity has been documented in several studies assessing the flammability of surface fuel beds (van Altena et al., 2012; de Magalhães and Schwilk, 2012; Della Rocca et al., 2018; Varner et al., 2017, Bowman et al., 2018) and shoots (Wyse et al., 2018, Wei et al., 2025). Non-additive effects are most common for fire spread and duration, which likely reflects flames propagating via the most flammable components of a fuelbed (van Altena et al. 2012). These non-additive effects indicate that it is challenging to predict the flammability of a plant community solely based on aggregating the flammability of its individual species, although attempts have been made to do this using community-weighted means of flammability (Padullés Cubino et al., 2018). Given the complexity introduced by non-additive effects, there is a pressing need to better understand how these interactions occur when mixtures of species are burned, particularly using leaves, shoots or whole individuals.

Conclusions

Although some tissue and organismal scale plant traits influence flammability and hence fire behavior, their effect size remains unresolved as is how their influences vary among different vegetation types and changes with fire weather. Live fuel moisture is one fuel characteristic where scaling from leaf to landscapes has been most successfully established, with work from both approaches linking trait investigations with remotely sensed data (e.g., Scarff et al., 2021; Griebel et al., 2023). There is evidence that some plant traits (e.g., leaf traits that control ground fuel litter flammability, Schwilk and Caprio, 2011) influence patterns of local fire severity such that they drive fire behavior at landscape scales. For other fuel characteristics such as architecture, there is potential to link trait measurements with newly available three-dimensional remotely sensed information, although the mechanistic connections need better study.

There has been progress in assessing which leaf-level traits matter for shoot-level flammability, but there are still gaps in extrapolating from shoot to individual up to the community and landscape scales, despite the use of broader scale methods such as wind tunnels (e.g., Marino et al., 2014). This paucity of studies linking lab-based measurements of flammability and plant traits with wildland fire, has reinforced a conceptual disconnection between top-down and bottom-up approaches. Research that directly addresses the criticisms of trait-centric approaches (e.g., that flammability measured at low heat fluxes does not inform stand level fire, Fernandes and Cruz, 2012) is also sorely needed. To bridge this conceptual gap demands carefully designed multi-scale studies that use comparable measures of different dimensions of flammability and consistently used terminologies to describe traits, plant and community architecture. Of prime importance are experimental tests of flammability at the species-level that predict fire behavior at the stand and community levels. Putting aside the mechanistic understanding of how plant traits influence fire, evaluating if abundance-weighted averages of species-level shoot or individual level measurements of flammability can predict fire behavior is a key contribution. Finally, a critical applied research question is identifying how different traits affect fire weather thresholds (e.g., fire weather indices) when variation in fuel characteristics is overwhelmed by climatic factors in determining fire behavior (Cruz et al., 2022).

While in this review we have highlighted many areas where there are empirical and theoretical discrepancies between top-down and bottom-up approaches to predicting flammability, we remain hopeful that these can be overcome. Indeed, having researchers from both schools-of-thought working together will help mitigate the increasing impacts of changing fire regimes on human society (Bowman et al., 2020) and global biodiversity (Kelly et al., 2020).

Author Contributions

D.W.S. conceived the review and wrote the first outline, D.W.S., T.J.C., M.A.A., N.G., B.R.M., R.H.N., G.L.W.P., and A.M.S.S. drafted major text sections, S.O., N.G. TJ.C. an D.W.S. designed the figure, and all authors contributed text and comments to multiple drafts of the manuscript.

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References

Abdollahi, A. and M. Yebra. 2023. Forest fuel type classification: Review of remote sensing techniques, constraints and future trends. *Journal of Environmental Management 342:* 118315.

Affleck, D. L., C. R. Keyes, and J. M. Goodburn. 2012. Conifer crown fuel modeling: current limits and potential for improvement. *Western Journal of Applied Forestry* 27: 65-169.

Agee, J. K. 1996. The influence of forest structure on fire behavior. In: *Proceedings of the 17th Annual Forest Vegetation Management Conference* 52-68.

Alam, M. A. 2019. Plant functional traits associated with shoot flammability. Unpublished PhD thesis, Lincoln University, Lincoln, New Zealand.

Alam, M. A., S. V. Wyse, H. L. Buckley, G. L. W. Perry, J. J. Sullivan, N. W. H. Mason, R. Buxton, et al. 2020. Shoot flammability is decoupled from leaf flammability, but controlled by leaf functional traits. *Journal of Ecology* 108: 641–653.

Alam M. A., S. V. Wyse, H. L. Buckley, G. L. W. Perry, X. Cui, J. J. Sullivan, D. W. Schwilk, T. J. Curran. In press. Fuel architecture influences interspecific variation in shoot flammability, but not as much as leaf traits. Journal of Ecology

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

Alexander, M. E. and M. G. Cruz. 2013. Corrigendum to: Assessing the effect of foliar moisture on the spread rate of crown fires. *International Journal of Wildland Fire*, 22: 869-870.

Anderson, H. E., 1970. Forest fuel ignitibility. *Fire Technology* 6: 312-319.

Archibald, S., and G. P. Hempson. 2016. Competing consumers: contrasting the patterns and impacts of fire and mammalian herbivory in Africa. *Philosophical Transactions of the Royal Society B: Biological Sciences* 371: 20150309.

Anderson, H. E. 1982. Aids to Determining Fuel Models for Estimating Fire Behavior. USDA Forest Service General Technical Report INT-122. Intermountain Forest and Range Experiment Station, Ogden, Utah.

Archibald, Sally, et al. 2018. Biological and geophysical feedbacks with fire in the Earth system.

Environmental Research Letters 13: 033003.

Argañaraz, J. P., M. A. Landi, C. M. Scavuzzo, and L. M. Bellis. 2018. Determining fuel moisture thresholds to assess wildfire hazard: A contribution to an operational early warning system. *PloS One:* 13: e0204889.

Atchley, A. L., R. Linn, A. Jonko, C. Hoffman, J. D. Hyman, F. Pimont, C. Sieg, and R. S. Middleton. 2021. Effects of fuel spatial distribution on wildland fire behaviour. *International Journal of Wildland Fire* 30: 179-189.

Balaguer-Romano, R., R. Díaz-Sierra, M. De Cáceres, À. Cunill-Camprubí, R. H. Nolan, M. M. Boer, J. Voltas, and V. R. de Dios. 2022. A semi-mechanistic model for predicting daily variations in species-level live fuel moisture content. A*gricultural and Forest Meteorology* 323: p.109022.

Bessie, W. C. and E. A. Johnson. 1995. The relative importance of fuels and weather on fire behavior in subalpine forests. *Ecology* 76: 747-762.

Blauw, L. G., N. Wensink, L. Bakker, R. S. P. Van Logtestijn, R. Aerts, N. A. Soudzilovskaia, and J. H. C. Cornelissen. 2015. Fuel moisture content enhances nonadditive effects of plant mixtures on flammability and fire behavior. *Ecology and Evolution* 5: 3830–3841.

Bond, W. J. 2005. Large parts of the world are brown or black: A different view on the 'Green World' hypothesis. *Journal of Vegetation Science* 16: 261–266.

Boving, I., J. Celebrezze, R. Salladay, A. Ramirez, L. D. Anderegg, and M. Moritz. 2023. Live fuel moisture and water potential exhibit differing relationships with leaf-level flammability thresholds. *Functional Ecology* 37: 2770-2785.

Bowman, D. M. J. S., B. J. French, and L. D. Prior. 2014. Have plants evolved to self-immolate? *Frontiers in Plant Science* 5: 590.

Bowman, D. M., C. A. Kolden, J. T. Abatzoglou, F. H. Johnston, G. R. van der Werf, and M. Flannigan. 2020. Vegetation fires in the Anthropocene. *Nature Reviews Earth & Environment* 1: 500-515.

Bowman, D. M. J. S., C. Haverkamp, K. D. Rann, and L. D. Prior. 2018. Differential demographic filtering by surface fires: How fuel type and fuel load affect sapling mortality of an obligate seeder savanna tree. *Journal of Ecology* 106: 1010–1022.

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

Brain, C.K. and A. Sillent. 1988. Evidence from the Swartkrans cave for the earliest use of fire. *Nature* 336: 464-466

Brando, P., M. Macedo, D. Silvério, L. Rattis, L. Paolucci, A. Alencar, M. Coe, and C. Amorim. 2020. Amazon wildfires: Scenes from a foreseeable disaster. *Flora* 268: p.151609.

Broido A. and M. A. Nelson. 1964. Ash content: its effect on combustion of corn plants. *Science* 46: 652–3.

Burger, N. and W. Bond. 2015. Flammability traits of Cape shrubland species with different post-fire recruitment strategies. *South African Journal of Botany* 101: 40–48.

Burton, J. E., J. G. Cawson, A. I. Filkov, and T. D. Penman. 2021. Leaf traits predict global patterns in the structure and flammability of forest litter beds. *Journal of Ecology* 109: 1344-1355.

Burton, J. E., T. D. Penman, A. I. Filkov, and J. G. Cawson. 2023. Multi-scale investigation of factors influencing moisture thresholds for litter bed flammability. *Agricultural and Forest Meteorology* 337: 109514.

Campos-Ruiz, R., M. A. Parisien, and M. D. Flannigan. 2022. Physicochemical characteristics controlling the flammability of live *Pinus banksiana* needles in central Alberta, Canada. *International Journal of Wildland Fire* 31: 857–870.

Cardoso, A. W., I. Oliveras, K. A. Abernethy, K. J. Jeffery, D. Lehmann, J. Edzang Ndong, I. McGregor, C. M. Belcher, W. J. Bond, and Y. S. Malhi. 2018. Grass species flammability, not biomass, drives changes in fire behavior at tropical forest-savanna transitions. *Frontiers in Forests and Global Change* 1: 14.

Cawson, J.G., J.E. Burton, B.J. Pickering, V. Demetriou, and A.I. Filkov. 2023. Quantifying the flammability of living plants at the branch scale: which metrics to use? *International Journal of Wildland Fire* 32: 1404-1421.

Chuvieco, E., I. González, F. Verdú, I. Aguado, and M. Yebra. 2009. Prediction of fire occurrence from live fuel moisture content measurements in a Mediterranean ecosystem. *International Journal of Wildland Fire* 18: 430–441.

Cohen, J., and M. Finney. 2023. Fuel Particle Heat Transfer Part 2: Radiation and Convection during Spreading Laboratory Fires. *Combustion Science and Technology* 195: 3122-3147.

Cornelissen, J. H. C., S. Grootemaat, L. M. Verheijen, W. K. Cornwell, P. M. Van Bodegom, R. Van Der Wal, and R. Aerts. 2017. Are litter decomposition and fire linked through plant species traits? *New Phytologist* 216: 653–669.

Cornelissen, J. H., S. Lavorel, E. Garnier, S. Díaz, N. Buchmann, D. E. Gurvich, P. B. Reich, H. Ter Steege, H. D. Morgan, M. G. A. Van Der Heijden, and J. G. Pausas. 2003. A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Australian Journal of Botany:* 51 335-380.

Cruz, M. G., J. S. Gould, M. E. Alexander, A. L. Sullivan, W. L. McCaw, and S. Matthews. 2015. Empirical-based models for predicting head-fire rate of spread in Australian fuel types. *Australian Forestry:* 78: 118-158.

Cruz, M. G., C. M. Hoffman, and P. M. Fernandes. 2025. Global synthesis of quantification of fire behaviour characteristics in forests and shrublands: recent progress. *Current Forestry Reports* 11:8.

Cruz, M. G., M. E. Alexander, and P. M. Fernandes. 2022. Evidence for lack of a fuel effect on forest and shrubland fire rates of spread under elevated fire danger conditions: implications for modelling and management. *International Journal of Wildland Fire* 31: 471-479.

Cui X, A. P. Paterson, S. V. Wyse, M. A. Alam, K. Maurin, R. Pieper, J. Padullés Cubino, D. O'Connell, D. Donkers, J. Bréda, H. L. Buckley, G. L. W. Perry, and T. J. Curran. 2020. Shoot flammability of vascular plants is phylogenetically conserved and related to habitat fire-proneness and growth form. *Nature Plants* 6: 355-359

Cunningham, C. X., G. J. Williamson, R. H. Nolan, L. Teckentrup, M. M. Boer, and D. M. Bowman. 2024. Pyrogeography in flux: Reorganization of Australian fire regimes in a hotter world. *Global Change Biology 3*0: e17130.

Curran, T. J., G. L. Perry, S. V. Wyse, and M. A. Alam. 2017. Managing fire and biodiversity in the wildland-urban interface: A role for green firebreaks. *Fire*1: 3.

Dai, D., Yu, D., Gao, W., Perry, G. L. W., Paterson, A. M., You, C., Zhou, S., Xu, Z., Huang, C., Cao, D., Curran, T. J. and Cui, X. (2025), Leaf dry matter content Is phylogenetically conserved and related to environmental conditions, especially wildfire activity. *Ecology Letters*, 28: e70056.

Della Rocca, G., R. Danti, C. Hernando, M. Guijarro, and J. Madrigal. 2018. Flammability of two Mediterranean mixed forests: study of the non-additive effect of fuel mixtures in laboratory. *Frontiers in Plant Science* 9: 825.

Dennison, P. E., and M. A. Moritz. 2009. Critical live fuel moisture in chaparral ecosystems: a threshold for fire activity and its relationship to antecedent precipitation. *International Journal of Wildland Fire* 18: 1021–1027.

Dennison, P. E., M. A. Moritz, and R. S. Taylor. 2008. Evaluating predictive models of critical live fuel moisture in the Santa Monica Mountains, California. *International Journal of Wildland Fire* 17: 18–27.

Drucker, J. R., A. Farguell, C. B. Clements, and A. K. Kochanski. 2023. A live fuel moisture climatology in California. *Frontiers in Forests and Global Change* 6: 1203536.

Ellis, T. M., D. M. Bowman, D. M., P. Jain, M. D. Flannigan, and G. J. Williamson. 2022. Global increase in wildfire risk due to climate-driven declines in fuel moisture. *Global Change Biology* 28: 1544-1559.

Engber, E. A. and J. M. Varner III. 2012. Patterns of flammability of the California oaks: the role of leaf traits. *Canadian Journal of Forest Research* 42: 1965-1975.

Finney, M. A. 1998. FARSITE: Fire Area Simulator - model development and evaluation. Research Paper RMRS-RP-4. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Ft. Collins, CO.

Finney, M. A., J.D. Cohen, S. S. McAllister, and W. M. Jolly. 2012. On the need for a theory of wildland fire spread. *International Journal of Wildland Fire* 22: 25-36.

French, N. H. F., L. K. Jenkins, T. V. Loboda, M. Flannigan, R. Jandt, L. L. Bourgeau-Chavez, and M. Whitley. 2015. Fire in arctic tundra of Alaska: past fire activity, future fire potential, and significance for land management and ecology. *International Journal of Wildland Fire* 24: 1045–1061.

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

Ganteaume, A., M. Guijarro, M. Jappiot, C. Hernando, C. Lampin-Maillet, P. Pérez-Gorostiaga, and

J. A. Vega. 2011a. Laboratory characterization of firebrands involved in spot fires. *Annals of Forest Science* 68: 531–541.

Ganteaume, A., J. Marielle, L.-M. Corinne, C. Thomas, and B. Laurent. 2011b. Effects of vegetation type and fire regime on flammability of undisturbed litter in Southeastern France. *Forest Ecology and Management* 261: 2223–2231.

Ganteaume, A., B. Romero, C. Fernandez, E. Ormeño, and C. Lecareux. 2021. Volatile and semi-volatile terpenes impact leaf flammability: differences according to the level of terpene identification. *Chemoecology* 31: 259–275.

Gao, X., and D. W. Schwilk. 2022. Burn hot or tolerate trees: flammability decreases with shade tolerance in grasses. *Oikos* 2022: e08930.

Gao, X., and D. W. Schwilk. 2018. Grass canopy architecture influences temperature exposure at soil surface. *Fire* 1: 35.

García, M., D. Riaño, M. Yebra, J. Salas, A. Cardil, S. Monedero, J. Ramirez, M.P. Martín, L. Vilar, J. Gajardo, and S. Ustin. 2020. A live fuel moisture content product from Landsat TM satellite time series for implementation in fire behavior models. *Remote Sensing*12: 1714.

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

Gill, A. M. and P. H. Moore.1996. *Ignitibility of Leaves of Australian Plant*s (Vol. 34). Canberra: CSIRO. 34pp.

Gill, A. M. and P. Zylstra. 2005. Flammability of Australian forests. *Australian Forestry* 68: 87-93.

Glasspool, I.J., D. Edwards, and L. Axe. 2004. Charcoal in the Silurian as evidence for the earliest wildfire. *Geology* 32: 381-383.

Gornish, E. S., C. Campbell, L. Svejcar, S.M. Munson, K. Vaughn, M.K. Spaeth, S.G. Yelenik, A. Wolf, and R. Mitchell. 2023. Functional traits are used in restoration practice: a response to Merchant et al. (2022). *Restoration Ecology* 31: e13880.

Gowda, J. H., M. Blackhall, L. Shipley, T. Kitzberger, and F. Tiribelli. 2022. Are digestibility and flammability related? Two variables shaping landscape dynamics of Northwestern Patagonian forests. *Forest Ecology and Management* 503: 119810.

Graham, R. T., S. McCaffrey, and T. B. Jain. 2004. Science basis for changing forest structure to modify wildfire behavior and severity. General Technical Report RMRS-GTR-120, U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Ft. Collins, CO.

Griebel, A., M. M. Boer, C. Blackman, B. Choat, D. S. Ellsworth, P. Madden, B. Medlyn, V. Resco de Dios, A. Wujeska-Klause, M. Yebra, and N. Younes Cardenas. 2023. Specific leaf area and vapour pressure deficit control live fuel moisture content. *Functional Ecology* 37: 719-731.

Grootemaat, S., I. J. Wright, P. M. Van Bodegom, and J. H. C. Cornelissen. 2017a. Scaling up flammability from individual leaves to fuel beds. *Oikos* 126: 1428–1438.

Grootemaat, S., I. J. Wright, P. M. Van Bodegom, J. H. C. Cornelissen, and W. K. Cornwell. 2015. Burn or rot: leaf traits explain why flammability and decomposability are decoupled across species. *Functional Ecology* 29: 1486–1497.

Grootemaat, S., I. J. Wright, P. M. Van Bodegom, J. H. C. Cornelissen, and V. Shaw. 2017b. Bark traits, decomposition and flammability of Australian forest trees. *Australian Journal of Botany* 65: 327–338.

Guerrero, F., L. Espinoza, C. Carmona, M. Blackhall, C. Quintero, K. Ocampo-Zuleta, S. Paula, J. Madrigal, M. Guijarro, Y. Carrasco, and M. A. Bustamante-Sánchez. 2024. Unraveling the chemistry of plant flammability: Exploring the role of volatile secondary metabolites beyond terpenes. *Forest Ecology and Management* 572: 122269.

Hagan, J. G., J. J. Henn, and W. H. Osterman. 2023. Plant traits alone are good predictors of ecosystem properties when used carefully. *Nature Ecology & Evolution* 7: 332-334.

He, T., J. G. Pausas, C. M. Belcher, D. W. Schwilk, and B. B. Lamont. 2012. Fire-adapted traits of *Pinus* arose in the fiery Cretaceous. New Phytologist 194: 751–759.

Hinojosa, M. B., E. Albert-Belda, B. Gómez-Muñoz, and J. M. Moreno. 2021. High fire frequency reduces soil fertility underneath woody plant canopies of Mediterranean ecosystems. *Science of the Total Environment* 752, 141877.

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

Jolly, W. M., and D. M. Johnson. 2018. Pyro-Ecophysiology: Shifting the Paradigm of Live Wildland Fuel Research. *Fire* 1: 8.

Kane, J. M., J. K. Kreye, R. Barajas-Ramirez, and J. M. Varner. 2021. Litter trait driven dampening of flammability following deciduous forest community shifts in eastern North America. *Forest Ecology and Management* 489: 119100.

Keeley, J. E. 2009. Fire intensity, fire severity and burn severity: a brief review and suggested usage. *International Journal of Wildland Fire* 18: 116-126.

Kelly, L. T., K. M. Giljohann, A. Duane, N. Aquilué, S. Archibald, E. Batllori, A.F. Bennett, S. T. Buckland, Q. Canelles, M. F. Clarke, and M. J. Fortin. 2020. Fire and biodiversity in the Anthropocene. *Science* 370: eabb0355.

Keyser, T. and F. W. Smith. 2010. Influence of crown biomass estimators and distribution on canopy fuel characteristics in ponderosa pine stands of the Black Hills. *Forest Science* 56: 156-165.

Krawchuk, M. A. and M. A. Moritz. 2011. Constraints on global fire activity vary across a resource gradient. *Ecology* 92: 21-132.

Kreye, J. K., N. W. Brewer, P. Morgan, J. M. Varner, A. M. S. Smith, C. M. Hoffman, and R. D. Ottmar. 2014. Fire behavior in masticated fuels: A review. *Forest Ecology and Management* 314: 193–207.

Kreye, J. K., J. K. Hiers, J. M. Varner, B. Hornsby, S. Drukker, and J. J. O'Brien. 2018. Effects of solar heating on the moisture dynamics of forest floor litter in humid environments: composition, structure, and position matter. *Canadian Journal of Forest Research* 48: 1331– 1342.

Kreye, J. K., J. M. Kane, and J. M. Varner. 2023. Multivariate roles of litter traits on moisture and flammability of temperate northeastern North American tree species. *Fire Ecology* 19: 21.

Kreye, J. K., J. M. Kane, J. M. Varner, and J. K. Hiers. 2020. Radiant heating rapidly increases litter flammability through impacts on fuel moisture. *Fire Ecology* 16: 8.

Krix, D. W., M. L. Phillips, and B. R. Murray. 2019. Relationships among leaf flammability attributes and identifying low-leaf-flammability species at the wildland–urban interface. *International Journal of Wildland Fire* 28: 295–307.

Loudermilk, E. L., J. J. O'Brien, S. L. Goodrick, R. R. Linn, N. S. Skowronski, and J. K. Hiers. 2022. Vegetation's influence on fire behavior goes beyond just being fuel. *Fire Ecology* 18: 9.

Luo, K., X. Quan, B. He, and M. Yebra. 2019. Effects of live fuel moisture content on wildfire occurrence in fire-prone regions over Southwest China. *Forests* 10: 887.

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

de Magalhães, R. Q. and D. W. Schwilk. 2021. Moisture absorption and drying alter nonadditive litter flammability in a mixed conifer forest. J*ournal of Ecology* 109: 234-245.

Manzello, S. L., Maranghides, A., Mell, and W. E. 2007. Firebrand generation from burning vegetation. *International Journal of Wildland Fire* 16: 458-462.

Martin R. E., D. A. Gordon, M.E. Gutierrez, D. S. Lee, D. M. Molina, R. A. Schroeder, D. B. Sapsis, S. L. Stephens, and M. Chambers. 1993. Assessing the flammability of domestic and wildland vegetation. In *Proceedings of the 12th Conference on Fire and Forest Meteorology*. pp. 130–137. Society of American Foresters Publication 94-02: Bethesda, MD, USA

Marino, E., C. Hernando, J. Madrigal, and M. Guijarro. 2014. Short-term effect of fuel treatments on fire behaviour in a mixed heathland: a comparative assessment in an outdoor wind tunnel. *International Journal of Wildland Fire* 23: 1097–1107.

Mason, N. W. H., C. Frazao, R. P. Buxton, and S. J. Richardson. 2016. Fire form and function: evidence for exaptive flammability in the New Zealand flora. *Plant Ecology* 217: 645–659.

Matthews, S., 2013. Dead fuel moisture research: 1991–2012. *International Journal of Wildland Fire* 23: 78-92.

Melia, N., S. Dean, H. G. Pearce, L. Harrington, D. J. Frame, and T. Strand. 2022. Aotearoa New Zealand's 21st-century wildfire climate. *Earth's Future* 10: e2022EF002853.

Melnik, O. M., S. A. Paskaluk, M. Y. Ackerman, K. O. Melnik, D. K. Thompson, S. S. McAllister, and M. D. Flannigan. 2021. New in-flame flammability testing method applied to monitor seasonal changes in live fuel. *Fire* 5: 1.

McWethy, D. B., P. E. Higuera, C. Whitlock, T. T. Veblen, D. M. J. S. Bowman, G. J. Cary, S. G. Haberle, R. E. Keane, B. D. Maxwell, M. S. McGlone, and G. L. W. Perry. 2013. A conceptual framework for predicting temperate ecosystem sensitivity to human impacts on fire regimes. *Global Ecology and Biogeography* 22: 900-912.

Menning, K. M., and S. L. Stephens. 2007. Fire climbing in the forest: a semiqualitative, semiquantitative approach to assessing ladder fuel hazards. *Western Journal of Applied Forestry*

22: 88–93.

Miller, L., L. Zhu, M. Yebra, C. Rüdiger, and G. I. Webb. 2023. Projecting live fuel moisture content via deep learning. *International Journal of Wildland Fire* 32: 709-727.

Mitić, Z. S., S. Č Jovanović, B. K. Zlatković, B. M. Nikolić, G. S. Stojanović, and P. D. Marin. 2017. Needle terpenes as chemotaxonomic markers in *Pinus*: Subsections Pinus and Pinaster. *Chemistry & Biodiversity* 14: e1600453.

Mitsopoulos, I. D., and A. P. Dimitrakopoulos. 2007. Canopy fuel characteristics and potential crown fire behavior in Aleppo pine (*Pinus halepensis* Mill.) forests. *Annals of Forest Science* 64: 287–299.

Murray, B. R., L. K. Hardstaff, and M. L. Phillips. 2013. Differences in leaf flammability, leaf traits and flammability-trait relationships between native and exotic plant species of dry sclerophyll forest. *PLoS One* 8: e79205.

Murray B. R., T. Hawthorne, T. J. Curran, D. W. Krix, M. I. Wallace, K. Young, M. L. Murray, E. Morley, N. Huber-Smith, J. K. Webb. 2023. Shoot flammability patterns among plant species of the wildland-urban interface in the fire-prone Greater Blue Mountains World Heritage Area. *International Journal of Wildland Fire* 32: 1119–1134.

Mutch, R. W. and Philpot, C. W., 1970. Relation of silica content to flammability in grasses. *Forest Science* 16: 64-65.

Neilson, E. H., J. Q. D. Goodger, I. E. Woodrow, and B. L. Møller. 2013. Plant chemical defense: at what cost? *Trends in Plant Science* 18: 250–258.

Nelson Jr, R. M. 2000. Prediction of diurnal change in 10-h fuel stick moisture content. *Canadian Journal of Forest Research* 30: 1071–1087.

Newberry, B. M., C. R. Power, R. C. Abreu, G. Durigan, D. R. Rossatto, and W. A. Hoffmann. 2020. Flammability thresholds or flammability gradients? Determinants of fire across savanna–forest transitions. *New Phytologist* 228: 910-921.

Nolan, R. H., M. M. Boer, V. Resco De Dios, G. Caccamo, and R. A. Bradstock. 2016. Large-scale, dynamic transformations in fuel moisture drive wildfire activity across southeastern Australia. *Geophysical Research Letters* 43: 4229–4238.

Nolan, R. H., B. Foster, A. Griebel, B. Choat, B. E. Medlyn, M. Yebra, N. Younes, and M. M. Boer.

2022. Drought-related leaf functional traits control spatial and temporal dynamics of live fuel moisture content. *Agricultural and Forest Meteorology* 319: 108941.

Nolan, R. H., J. Hedo, C. Arteaga, T. Sugai, and V. Resco De Dios. 2018. Physiological drought responses improve predictions of live fuel moisture dynamics in a Mediterranean forest. *Agricultural and Forest Meteorology* 263: 417–427.

Nowacki, G. J. and M. D. Abrams,. 2008. The demise of fire and "mesophication" of forests in the eastern United States. *BioScience* 58: 123-138.

Ocampo-Zuleta, K., J. G. Pausas, and S. Paula. 2024. FLAMITS: A global database of plant flammability traits. *Global Ecology and Biogeography* 33: 412-425.

Odion, D. C., M. A. Moritz, and D. A. DellaSala. 2010. Alternative community states maintained by fire in the Klamath Mountains, USA. *Journal of Ecology* 98: 96-105.

Ojeda, F., J. G. Pausas, and M. Verdú. 2010. Soil shapes community structure through fire. *Oecologia* 163: 729–735.

Ormeño, E., J. Ruffault, C. Gutigny, J. Madrigal, M. Guijarro, C. Hernando, and C. Ballini. 2020. Increasing cuticular wax concentrations in a drier climate promote litter flammability. *Forest Ecology and Management* 473: 118242.

Owens, M. K., C. D. Lin, C. A. Taylor, and S. G. Whisenant. 1998. Seasonal patterns of plant flammability and monoterpenoid content in *Juniperus ashei*. *Journal of Chemical Ecology* 24: 2115-2129.

Padullés Cubino, J., H. L. Buckley, N. J. Day, R. Pieper, and T. J. Curran. 2018. Community-level flammability declines over 25 years of plant invasion in grasslands. *Journal of Ecology* 106: 1582–1594.

Pagadala, T., M. A. Alam, T. M. Maxwell, and T. J. Curran. 2024. Measuring flammability of crops, pastures, fruit trees, and weeds: A novel tool to fight wildfires in agricultural landscapes. *Science of the Total Environment* 906: 167489.

Page, W. G., M. J. Jenkins, and J. B. Runyon. 2012. Mountain pine beetle attack alters the chemistry and flammability of lodgepole pine foliage. *Canadian Journal of Forest Research* 42: 1631–1647.

Papió, C., and L. Trabaud. 1990. Structural characteristics of fuel components of five Meditarranean shrubs. *Forest Ecology and Management* 35: 249–259.

Park, I., K. Fauss, and M.A. Moritz. 2022. Forecasting live fuel moisture of *Adenostema fasciculatum* and its relationship to regional wildfire dynamics across Southern California shrublands. *Fire* 5: 110.

Paula, S., D. P. Ramírez, S. Estay, and J. G. Pausas. 2024. Soil fertility shapes fire activity across Mediterranean-type climate regions. *Global Ecology and Biogeography* 33: 400–411.

Pausas, J. G., G. A. Alessio, B. Moreira, and J. G. Segarra-Moragues. 2016. Secondary compounds enhance flammability in a Mediterranean plant. *Oecologia* 180: 103–110.

Pausas, J. G., J. E. Keeley, and D. W. Schwilk. 2017. Flammability as an ecological and evolutionary driver. *Journal of Ecology* 105: 289-297.

Pausas, J. G. and B. Moreira. 2012. Flammability as a biological concept. *New Phytologist* 194: 610-613.

Penman, T. E., J. G. Cawson, S. Murphy, and T. J. Duff. 2017. Messmate stringybark: bark ignitability and burning sustainability in relation to fragment dimensions, hazard score and time since fire. *International Journal of Wildland Fire* 26: 866–876.

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

Philpot C. W. 1970. Influence of mineral content on the pyrolysis of plant materials. *Forest Science.* 16: 461–71.

Pickett, B. M., Smith, S. G., Fletcher, T. H. and D. R. Weise 2005, October. Burning characteristics of live California chaparral and Utah leaf samples. In Sixth Symposium on Fire and Forest Meteorolo, J. L. Welty, and R. S. Arkle. 2017. Refining the cheatgrass–fire cycle in the Great Basin: Precipitation timing and fine fuel composition predict wildfire trends. *Ecology and Evolution* 7: 8126–8151.

Pickering, B. J., L. T. Bennett, and J. G. Cawson. 2023. Extending methods for assessing fuel hazard in temperate Australia to enhance data quality and consistency. *International Journal of Wildland Fire* 32: 1422-1437.

Pilliod, D. S., J. L. Welty, and R.S. Arkle. 2017. Refining the cheatgrass–fire cycle in the Great

Basin: Precipitation timing and fine fuel composition predict wildfire trends. *Ecology and Evolution* 7: 8126-8151.

Pimont, F., J. Ruffault, N. K. Martin-StPaul, and J. L. Dupuy. 2019. Why is the effect of live fuel moisture content on fire rate of spread underestimated in field experiments in shrublands?. *International Journal of Wildland Fire* 28: 127-137.

Plucinski, M. P., and W. R. Anderson. 2008. Laboratory determination of factors influencing successful point ignition in the litter layer of shrubland vegetation. *International Journal of Wildland Fire* 17: 628–637.

Popović, Z., S. Bojović, M. Marković, and A. Cerdà. 2021. Tree species flammability based on plant traits: A synthesis. *Science of The Total Environment* 800: 149625.

Potts, E., D. Tng, D., D. Apgaua, T. J. Curran, J. Engert, and S. G. Laurance. 2022. Growth form and functional traits influence the shoot flammability of tropical rainforest species. *Forest Ecology and Management* 522: 120485.

Price, O. F., and C. E. Gordon. 2016. The potential for LiDAR technology to map fire fuel hazard over large areas of Australian forest. *Journal of Environmental Management* 181: 663–673.

Prior, L. D., B. P. Murphy, and D. M. Bowman. 2018. Conceptualizing ecological flammability: An experimental test of three frameworks using various types and loads of surface fuels. *Fire* 1:14.

Prior, L. D., B. P. Murphy, G. J. Williamson, M. A. Cochrane, W. M. Jolly, and D. M. J. S. Bowman. 2017. Does inherent flammability of grass and litter fuels contribute to continental patterns of landscape fire activity? *Journal of Biogeography* 44: 1225–1238.

Prior, L. D., K. Storey, G. J. Williamson, and D. M. J. S. Bowman. 2024. When soil becomes fuel: identifying a safe window for prescribed burning of Tasmanian vegetation growing on organic soils. *International Journal of Wildland Fire* 33: WF24061.

Pyne, S. J. Introduction to Wildland Fire: Fire Management in the United States. John Wiley & Sons: New York, NY, USA, 1984.

Rahman, N. E. B., S. W. Smith, W. N. Lam, K. Y. Chong, M. S. E. Chua, P. Y. Teo, D. W. J. Lee, et al. 2023. Leaf decomposition and flammability are largely decoupled across species in a tropical swamp forest despite sharing some predictive leaf functional traits. *New Phytologist* 238: 598–611.

Rao, K., Williams, A. P., Diffenbaugh, N. S., Yebra, M. and Konings, A.G., 2022. Plant-water sensitivity regulates wildfire vulnerability. *Nature Ecology & Evolution* 6: 332-339.

Rao, K., A.P. Williams, N. S. Diffenbaugh, M. Yebra, C. Bryant, and A. G. Konings. 2023. Dry live fuels increase the likelihood of lightning-caused fires. *Geophysical Research Letters* 50: p.e2022GL100975.

Rossa, C. G. and P. M. Fernandes. 2018. Live fuel moisture content: The ‘pea under the mattress’ of fire spread rate modeling? *Fire* 1: 43.

Reed, W. P., J. M. Varner, E. E. Knapp, and J. K. Kreye. 2020. Long-term changes in masticated woody fuelbeds in northern California and southern Oregon, USA. *International Journal of Wildland Fire* 29: 807-819.

Reilly, S., M. L. Clark, L. Loechler, J. Spillane, M. Kozanitas, P. Krause, D. Ackerly, et al. 2024. Unoccupied aerial system (UAS) Structure-from-Motion canopy fuel parameters: Multisite area-based modelling across forests in California, USA. *Remote Sensing of Environment* 312: 114310.

Rogers, B. M., A. J. Soja, M. L. Goulden, and J. T. Randerson. 2015. Influence of tree species on continental differences in boreal fires and climate feedbacks. *Nature Geoscience* 8: 228–234.

Rollins, M. G., C. Rodriguez-Franco, T. Haan, and S. Conard. 2017. Research and development wildland fire and fuels accomplishments and outcomes. U.S.D.A. Forest Service report FS-1086. Washington, DC.

Rothermel, R. C. 1972. A mathematical model for predicting fire spread in wildland fuels. USDA Forest Service, Intermountain Forest and Range Experiment Station, Research Paper RP-INT-15. Ogden, UT)

Rothermel, R. C., R. A. Wilson, G. A. Morris, and S. S. Sackett. 1986. Modeling moisture content of fine dead wildland fuels: input to the BEHAVE fire prediction system. USDA Forest Service, Intermountain Forest and Range Experiment Station, Research Paper RP-INT-359. Ogden, UT.

Salisbury, F. B., and C.W. Ross. 1992. Plant physiology. Fourth edition. Wadsworth, California.

Santacruz-García, A. C., S. Bravo, F. del Corro, F. and Ojeda. 2019. A comparative assessment of plant flammability through a functional approach: The case of woody species from Argentine Chaco region. *Austral Ecology* 44: 1416-1429.

Saura-Mas, S., S. Paula, J. G. Pausas, and F. Lloret. 2010. Fuel loading and flammability in the

Mediterranean Basin woody species with different post-fire regenerative strategies. *International Journal of Wildland Fire* 19: 783–794.

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

Scarff, F. R., T. Lenz, A. E. Richards, A. E. Zanne, I. J. Wright, and M. Westoby. 2021. Effects of plant hydraulic traits on the flammability of live fine canopy fuels. *Functional Ecology* 35: 835–846.

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

Scarff, F. R., and M. Westoby. 2008. The influence of tissue phosphate on plant flammability: A kinetic study. *Polymer Degradation and Stability* 93: 1930–1934.

Schlaeppi, K., J. J. Gross, S. Hapfelmeier, and M. Erb. 2021. Plant chemistry and food web health. *New Phytologist* 231: 957–962.

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

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

Schwilk, D. W. and A. C. Caprio. 2011. Scaling from leaf traits to fire behaviour: community composition predicts fire severity in a temperate forest. J*ournal of Ecology* 99: 970-980.

Scott, J. H. and R. E. Burgan. 2005. Standard fire behavior fuel models: a comprehensive set for use with Rothermel's surface fire spread model. General Technical Report RMRS-GTR-153. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fort Collins, CO.

Simpson, K. J., S. Archibald, and C. P. Osborne. 2022. Savanna fire regimes depend on grass trait diversity. *Trends in Ecology & Evolution* 37: 749–758.

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

Smith, A. M. S., W. T. Tinkham, D. P. Roy, L. Boschetti, R. L. Kremens, S. S. Kumar, A. M. Sparks, and M. J. Falkowski. 2013. Quantification of fuel moisture effects on biomass consumed derived from fire radiative energy retrievals. *Geophysical Research Letters* 40: 6298–6302.

Stenzel. J. E., K. J. Bartowitz, M. D. Hartman, J. A. Lutz, A. M. S. Smith, C. A. Kolden, B. E. Law, M. E. Swanson, A. J. Larson, W. J. Parton. and T. W. Hudiburg. 2019. Fixing a snag in estimating carbon emissions from wildfires. *Global Change Biology* 25: 3985-3994.

Sullivan, A. L. 2009a. Wildland surface fire spread modelling, 1990 - 2007. 1: Physical and quasi-physical models. *International Journal of Wildland Fire* 18: 349–368.

Sullivan, A. L. 2009b. Wildland surface fire spread modelling, 1990 - 2007. 2: Empirical and quasi-empirical models. *International Journal of Wildland Fire* 18: 369–386.

Sullivan, A. L. 2009c. Wildland surface fire spread modelling, 1990 - 2007. 3: Simulation and mathematical analogue models. *International Journal of Wildland Fire* 18: 387–403.

Terrah, S. M., F. Z. Sabi, O. Mosbah, A. Dilem, N. Hamamousse, A. Sahila, O. Harrouz, H. Boutchiche, F. Chaib, N. Zekri, and A. Kaiss. 2020. Nonexistence of critical fuel moisture content for flammability. *Fire Safety Journal* 111: 102928.

Talhelm, A. F., and A. M. S. Smith. 2018. Litter moisture adsorption is tied to tissue structure, chemistry, and energy concentration. *Ecosphere* 9: e02198.

Tarifa, C. S., P. P. Del Notario, and F. G. Moreno. 1965. On the flight paths and lifetimes of burning particles of wood. In: *Symposium (International) on Combustion* 10,1:1021-1037. https://doi.org/10.1016/S0082-0784(65)80244-2

Tumino, B. J., T. J. Duff, J. Q. D. Goodger, and J. G. Cawson. 2019. Plant traits linked to field-scale flammability metrics in prescribed burns in Eucalyptus forest. *PLoS One* 14: e0221403.

Turetsky, M. R., B. Benscoter, S. Page, G. Rein, G. R. Van Der Werf, and A. Watts. 2015. Global vulnerability of peatlands to fire and carbon loss. *Nature Geoscience* 8: 11–14.

Turner, I. M. 1994. Sclerophylly: Primarily Protective? *Functional Ecology* 8: 669–675.

Van Altena C., R. S. van Logtestijn, W. K. Cornwell, and J. H. Cornelissen. 2012. Species composition and fire: non-additive mixture effects on ground fuel flammability. *Frontiers in Plant Science* 3: 63.

Van Der Plas, F., T. Schröder-Georgi, A. Weigelt, K. Barry, S. Meyer, A. Alzate, R. L. Barnard, et al. 2020. Plant traits alone are poor predictors of ecosystem properties and long-term ecosystem functioning. *Nature Ecology & Evolution* 4: 1602–1611.

Van Wilgen, B. W., K. B. Higgins, and D. U. Bellstedt. 1990. The role of vegetation structure and fuel chemistry in excluding fire from forest patches in the fire-prone fynbos shrublands of South Africa. *Journal of Ecology* 78: 210-222.

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

Varner, J. M., H. G. Kuljian and J. K. Kreye. 2017. Fires without tanoak: the effects of a non-native disease on future community flammability. *Biological Invasions* 19: 2307-2317.

Varner, J. M., T. M. Shearman, J. M. Kane, E. M. Banwell, E. S. Jules, and M. C. Stambaugh. 2022. Understanding flammability and bark thickness in the genus *Pinus* using a phylogenetic approach. *Scientific Reports* 12(1): 1–10.

Viney, N. 1991. A review of fine fuel moisture modelling. *International Journal of Wildland Fire* 1: 215–234.

Walker, X. J., J. L. Baltzer, S. G. Cumming, N. J. Day, C. Ebert, S. Goetz, J. F. Johnstone, et al. 2019. Increasing wildfires threaten historic carbon sink of boreal forest soils. *Nature* 572: 520-523.

Wei, P., L. Tang, Z. Xiong, B.B. Lamont, L. Chen, W. Xue, Z. Zhao, W. Lu, J. Han, W. He, W. Yang, and Z. Yan. 2025. Non-additive effects of leaf-litter flammability on eight subtropical tree species: Implications for forest species composition and fire susceptibility. *Journal of Environmental Management* 374: 124053.

Weise, D. R., E. Koo, X. Zhou, S. Mahalingam, F. Morandini, and J.-H. Balbi. 2016. Fire spread in chaparral – a comparison of laboratory data and model predictions in burning live fuels. *International Journal of Wildland Fire* 25: 980–994.

Weise, D. R., R. H. White, F. C. Beall, and M. Etlinger. 2005. Use of the cone calorimeter to detect seasonal differences in selected combustion characteristics of ornamental vegetation. *International Journal of Wildland Fire* 14: 321–338.

White, R. H., and W. C. Zipperer. 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.

Wickramasinghe, A. M. K., M. M. Boer, C. X. Cunningham, R. H. Nolan, D. M. J. S. Bowman, and G. J. Williamson. 2024. Modeling the probability of dry lightning-induced wildfires in Tasmania:

a machine learning approach. *Geophysical Research Letters* 51: e2024GL110381.

Wood, S. W., and D. M. J. S. Bowman. 2012. Alternative stable states and the role of fire–vegetation–soil feedbacks in the temperate wilderness of southwest Tasmania. *Landscape Ecology* 27: 13–28.

Wyse, S. V., G. L. Perry, D. M. O'Connell, P. S. Holland, M. J. Wright, C. L. Hosted, S. L. Whitelock, I. J. Geary, K. J. Maurin, and T. J. Curran. 2016. A quantitative assessment of shoot flammability for 60 tree and shrub species supports rankings based on expert opinion. I*nternational Journal of Wildland Fire* 25: 466-477.

Wyse, S. V., G. L. W. Perry, and T. J. Curran. 2018. Shoot-level flammability of species mixtures is driven by the most flammable species: implications for vegetation-fire feedbacks favouring invasive species. *Ecosystems* 21: 886–900.

Xanthopoulos, G., and R. H. Wakimoto. 1993. A time to ignition–temperature–moisture relationship for branches of three western conifers. *Canadian Journal of Forest Research* 23: 253–258.

Younes, N., M. Yebra, M. M. Boer, A. Griebel, and R. H. Nolan. 2024. A review of leaf-level flammability traits in eucalypt trees. *Fire* 7: 183.

Zanzarini, V., A. N. Andersen, and A. Fidelis. 2022. Flammability in tropical savannas: Variation among growth forms and seasons in Cerrado. *Biotropica* 54: 979–987.

Zhao, L., M. Yebra, A. I. van Dijk, G. J. Cary, and D. Hughes. 2022. Controlled field experiment clarifies the influence of soil moisture on litter moisture content. *Agricultural and Forest Meteorology* 314: 108782.

Zigner, K., L. M. V. Carvalho, S. Peterson, F. Fujioka, G.-J. Duine, C. Jones, D. Roberts, and M. Moritz. 2020. Evaluating the ability of FARSITE to simulate wildfires influenced by extreme, downslope winds in Santa Barbara, California. *Fire* 3: 29.

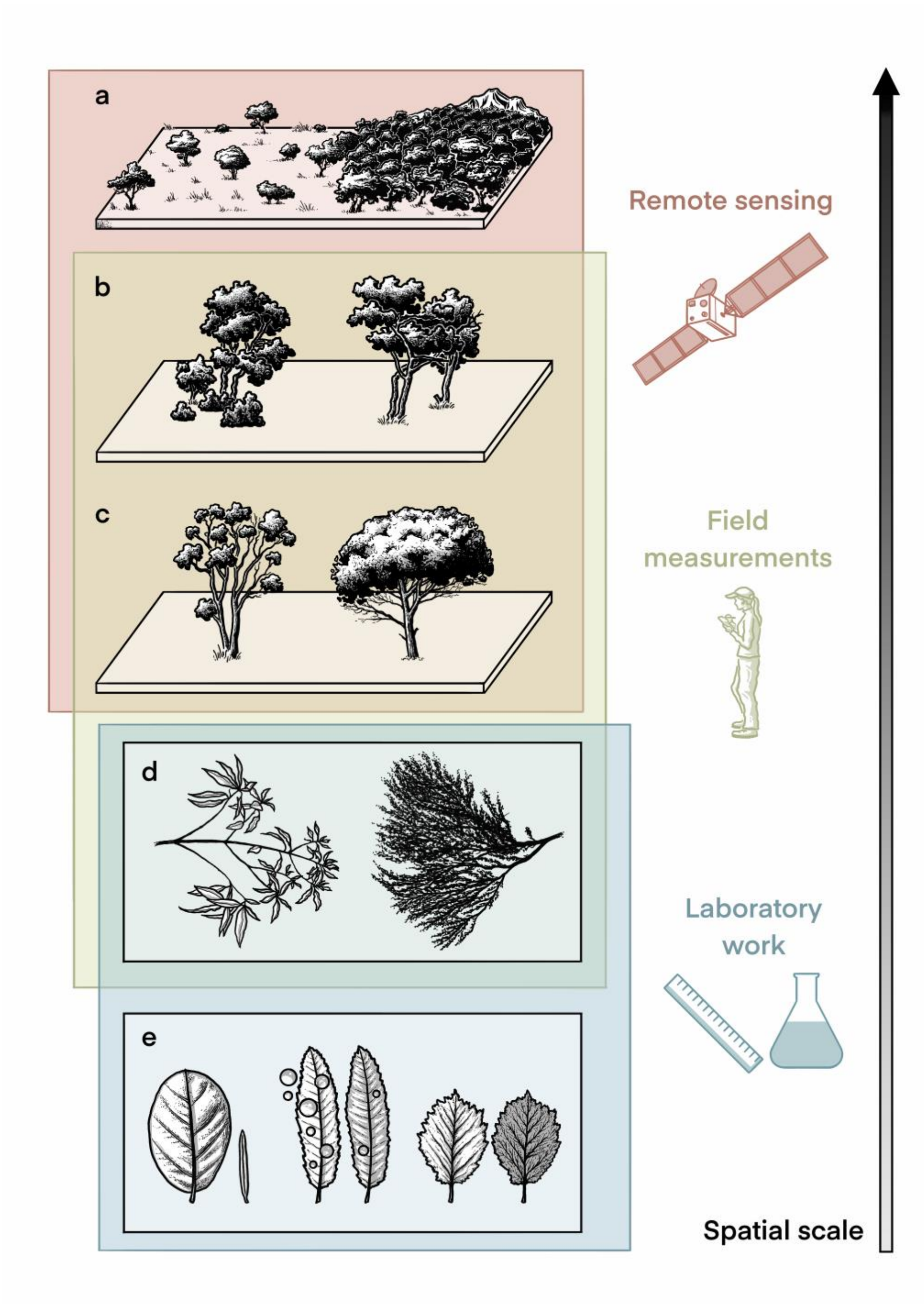
Zylstra, P., R. A. Bradstock, M. Bedward, T. D. Penman, M. D. Doherty, R. O. Weber, A. M. Gill, and G. J. Cary. 2016. Biophysical mechanistic modelling quantifies the effects of plant traits on fire severity: species, not surface fuel loads, determine flame dimensions in eucalypt forests. *PLoS One* 11: e0160715.

Box 1

Term	Definition	How is it measured?
Bottom-up approach	The assessment of species-specific flammability traits.	Laboratory trials
Combustibility	Component of flammability that accounts for the intensity of burning.	Measured variously as the highest temperature measured during burning, flame height, flame spread rate, and mass loss rate
Consumability	Component of flammability that accounts for how much of a plant is burned by fire.	Measured as the percentage of burnt biomass once combustion has finished
Fire behavior	How a fire reacts to the environment, including its spread, intensity, and how it consumes fuel.	In flammability trials: as individual components described here. In wildfire: from direct observations, remote sensing, and post-fire estimation of severity metrics.
Fire propagation	Spread of fire across a landscape	Measured as rate of spread in laboratory or field. See also measures of post-fire heterogeneity and fire perimeters
Flammability	The ability of a material to burn that includes how easy it is to ignite, the intensity at which it burns, the length of time it burns, and the percentage of material consumed by fire.	Measured in terms of combustability, consumability, ignitibility and sustainability. See these measurements in the glossary.
Fuel architecture	The size, shape, volumetric arrangement, and distribution of fuel materials that burn during wildfires	Measured in the field for the broad fuel assemblage as compaction, bulk density, and ladder fuel presence. Can also be species-specific (e.g., degree to which airflow is impeded by branches and leaves).
Fuel load	Total combustable material per unit area	Lidar/remote sensing, as well as field survey methods.
Fuel moisture	The amount of water content in plant material, affecting its likelihood of igniting and burning.	Commonly quantified in small branches for live fuels, or from litter samples
Ignitibility	Component of flammability that accounts for ease with which a plant begins to burn when exposed to an ignition source.-.	Measured as either the time to first burning from exposure or the frequency of ignition events among a set of samples
Plant traits	Measurable characteristic (e.g. architectural, morphological, phenological, physiological,	Variously. See, for example, Cornelissen et al (2003)

	chemical) to describe components of flammability	
Sustainability	Component of flammability that accounts for how long a plant continues to burn after ignition, with or without an external heat source.	Measured as as the duration of combustion and can include durations of incandescence, flaming, and smoldering
Top-down approach	Treats plants as broad vegetation types or fuel types and focuses on those plant or fuel characteristics.	Remote sensing tools often used

Figure 1. Illustration of methods used to assessed fuel characteristics (moisture, architecture, chemistry and mass) across a range of scales from individual plant organs or excised parts to communities and landscapes. Remote sensing, field measurements, and laboratory work are each suited to assessment of fuel characteristics at different but overlapping portions of this range, thereby creating opportunities to synthesize the “top-down” and “bottom-up” approaches to understanding flammability.



Figure

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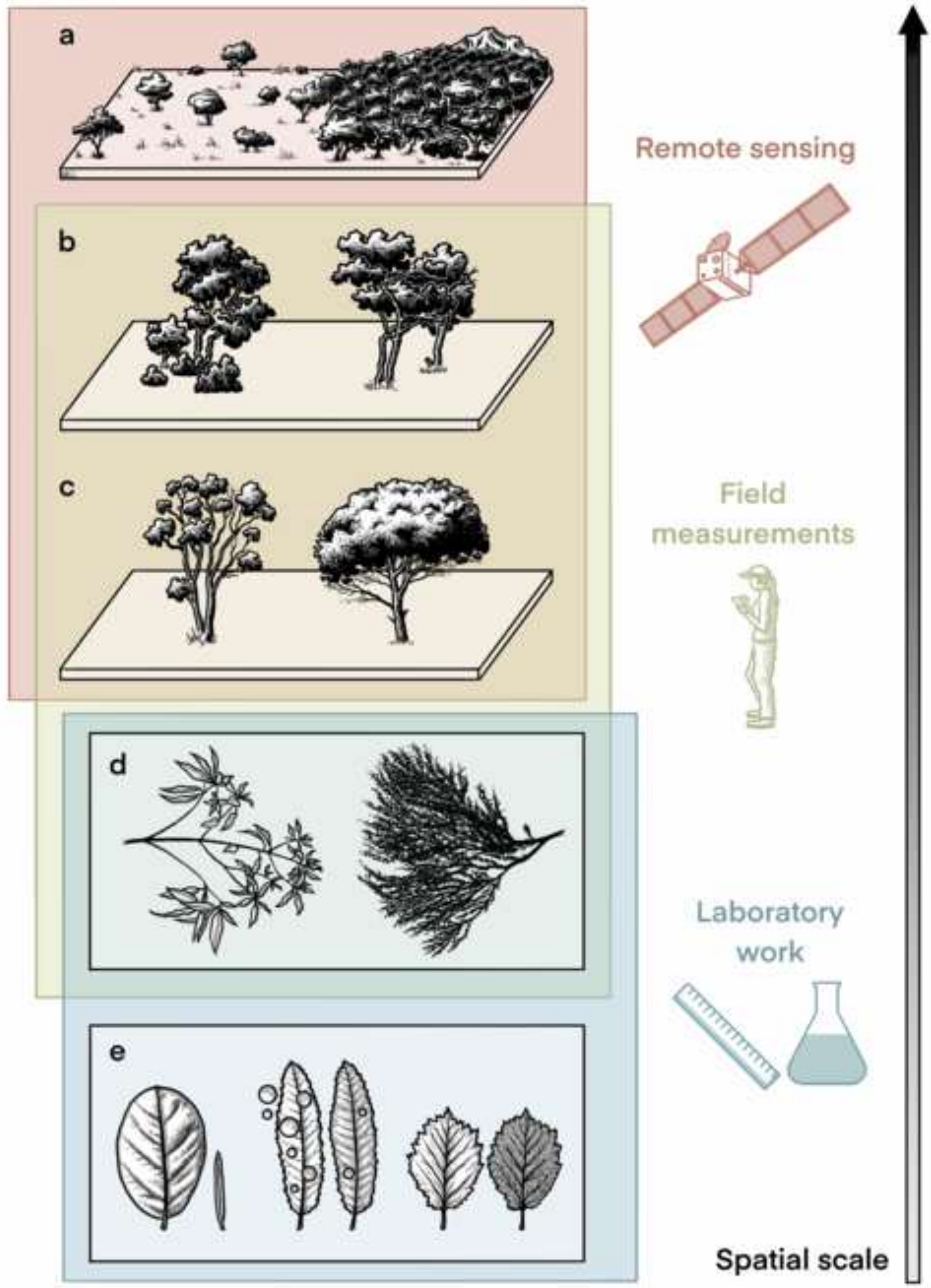

From plant traits to fire behavior: scaling issues in flammability studies

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Abstract

Despite fire being one of the oldest and most important ecological disturbance processes on Earth, many aspects of fire-vegetation feedbacks are poorly understood, limiting their accurate representation in predictive models. Translating~~Scaling from~~ plant flammability traits to fire behavior and fire effects on ecosystems has proven a challenge with different disciplines approaching the problem at widely different scales. One approach has been a top-down assessment of ecosystem-level effects of vegetation structural characteristics and plant physiology on fuel properties such as fuel moisture. This ~~approach~~ has had some success, but is often forced to collapse species-specific variation into a small number of functional types and, as a practical necessity, usually focuses on highly plastic traits (e.g. moisture content) that can be modeled across an ecosystem without the need to characterize species-specific characteristics. The other approach grew out of trait-centric comparative ecology and focused on how traits might influence individual plant flammability. However, the degree to which such lab-based flammability trials reflect real species-specific differences maintained during wildland fires has been questioned. We review the history of these approaches, discuss where each has succeeded, and identify areas of research aimed at closing the apparent gap in scale.

Background

Fire has been a key component of the Earth system for hundreds of millions of years (Glasspool et al., 2004) and may have been used by hominids as early as 1.5 MYA (Brain and Sillent, 1988). In addition to atmospheric oxygen and background ignitions, such as lightning, wildland fuels (e.g., living plants and their associated litter and debris) are a fundamental determinant of fire occurrence and behavior. Although fire regimes have an intrinsic range of natural variation, ~~we are experiencing~~ rapid changes in climate and land use ~~that~~ are leading to ~~emergence of~~ unprecedented extreme fire events (French et al., 2015; Cunningham et al., 2024). In many regions, fire seasons are lengthening~~,~~ and are associated with elevated risks of extreme fire behavior and occurrence of fire events (Jolly et al., 2015). These effects are not only amplifying fire activity in fire-prone landscapes; some ecosystems where fire has historically been extremely rare are also predicted to experience increased fire activity (e.g., Aoteaora New Zealand, Melia et al., 2022; Arctic tundra, French et al., 2015; Amazonia, Brando et al 2020). Furthermore, some ecosystems maintained by fire may experience reduced fire activity as systems move below critical biomass thresholds (Krawchuk and Moritz, 2011; McWethy et al., 2013) or experience community composition and subsequent fuel changes (e.g. "mesophication", Nowacki and Abrams, 2008). Highly flammable dead plant matter, especially leaf litter and dry graminoid cover, shaped by plant traits and phenology patterns, has been the traditional focus of fire hazard and fuel load assessments with fuel models used ~~the~~to characterize ecosystems in terms of plant functional groups and structure (Anderson, 1981). ~~(Pyne, 1984), with less attention on standing woody debris (Stenzel et al., 2019).~~ Plant characteristics, especially the characteristics of live plants, are ~~also~~ important controls of landscape flammability (Anderson, 1971), and fire behavior models have been successfully grounded in the categorization of fuel types. However,~~although~~ parametrization of ~~live fuel~~ plant flammability in terms of traits important to ecological strategies remains challenging. Consequently, critical uncertainties regarding how climate change will impact plant community composition and hence the relative flammability of fuel assemblages, limit our ability to predict future changes in fire regimes.

In an era of extreme fires, much attention has been paid to the direct effects of climate change on fire weather and fuel dryness (Ellis et al., 2022) with less consideration of the abundance of different fuel types. Living and dead fuels link fire science and plant ecology, therefore plant traits provide an important conceptual framework for fire ecology; they provide a way to predict how individual plants and their components will ignite, burn, and influence fire behavior, broadly captured by the concept of plant 'flammability' (Box 1) (Cornelissen et al. 2017; Pausas et al., 2017). For example, the quantitative description of traits such as leaf mass per area, maximum moisture content, and concentration of volatile organic compounds can inform our understanding of fine-scale fire dynamics (Murray et al., 2013; Alam et al., 2020; Burton et al., 2021; Popović et al., 2021). However, scaling from individual plants to stand-level characteristics is challenging because the interplay between plant traits and fire behavior is also shaped by environmental conditions and interactions with pathogens, herbivores, and non-fire disturbances (Younes et al., 2024; Oliveras et al., this issue). This spatio-temporal context-dependence limits the ability to scale up assessments of flammability conducted on plant components (Fernandes and Cruz, 2012; Pausas and Moreira, 2012).

The multi-scale nature of flammability (~~Fig.~~Figure 1) and the tremendous multi-scale trait diversity in plant communities resulting from variation in species composition, individual age and size, and phenotypic plasticity ~~presents~~ challenges ~~to~~ integrating functional ecology with fire science (Grootemaat et al., 2017a; Ganteaume, 2018; Tumino et al., 2019). Different vegetation types in the same climate can show different fire behaviors (van Wilgen et al., 1990; Odion et al., 2010; Archibald et al., 2018), indicating that emergent properties of living plants can shape fire. Furthermore, several biogeographical conundrums point to a possible role for lineage-specific species traits as influencing fire regimes (Rogers et al., 2015; Archibald et al., 2018; Simpson et al., 2022). Scaling from plant traits to fire behavior at landscape scales remains challenging, with fire behavior models sometimes performing ~~particularly~~ poorly when used outside of the ecosystems or climatic conditions for which they were developed (Sullivan et al., 2009a–c). Moreover, there is little overlap in traits considered between the fuel modeling of fire scientists and the functional trait measurements of ecologists.

There are two contrasting, but complementary approaches to understanding the role of plant traits in influencing fire hazard and fire behavior. One approach focuses on gross plant or fuel characteristics that are amenable to landscape-scale remote sensing or modeling from vegetation maps (Abdollahi and Yebra, 2023). We call this the "top-down" approach. The second approach is the assessment of species-specific flammability traits in laboratory trials: the "bottom-up" approach. A barrier to establishing general flammability relationships is that individual studies usually focus on a single fuel type such as surface~~ground~~ fuels measured by fire spread through artificial fuel beds, crown fire fuels measured on shoots of woody plants, or graminoid fuels with flammability measured at the whole plant scale. Different plant traits appear to affect different dimensions of flammability among these fuel types (Schwilk, 2015). The top-down and bottom-up approaches consider~~have~~ sharply contrasting spatial grains and extents~~scales~~ with limited overlap (but see exceptions e.g. Prior et al., 2017), which has inhibited the development of cross-scale integrated approaches to quantifying plant flammability. Additionally, it is important to note that this dichotomization breaks down under more extreme fire behavior and extreme fuel drying, where fuel characteristics maycease to be important because all biomass becomes available to burn (Cruz et al., 2022). For instance, extreme fires can burn tropical rainforests that are typically considered pyrophobic communities.

The top-down assessment of fuels, often using remote sensing or vegetation mapping, aims to assess ecosystem level effects of plant characteristics on stand, community, and landscape fuel properties (~~Fig.~~Figure 1). This approach is well-integrated with fire behavior models and forms the basis of tools used by fire incident teams during active fires (eg LANDFIRE, Rollins et al. 2017). These assessments~~his~~ generally require~~s~~ collapsing species-specific variation into functional types (Anderson, 1982; Scott and Burgan, 2005). The fuel model approach has underpinned fire hazard and behavior prediction particularly in the US and Europe (Cruz et al. 2025) where such fuel models combining plant traits of dominant species and ecosystem level vegetation structural characteristics are widely used. More recently, there has been increasing interest in including physiological traits in the assessment of flammability (Jolly and Johnson, 2018) and~~, as a practical necessity, usually focuses on plastic traits,~~ examining traits such as those regulating plant water use and carbon dynamics that can be modeled across an ecosystem ~~without characterizing species-specific characteristics~~ (e.g., Drucker et al., 2023). ~~The "top-down" approach shows some success for landscape-scale hazard prediction, especially under more extreme fire weather, and is better integrated with fire behavior models and forms the basis of tools used by fire incident teams during active fires~~ In ecosystems dominated by one or a few species, this approach is~~does become~~ essentially species-specific, as in chamise-dominated California chaparral where live fuel moisture content has been shown to predict fire hazard (Park et al., 2022).

The "bottom" up approach has involved laboratory experiments and has been integrated into wildland fire science for decades especially in the vast literature on measuring and modeling fuels (e.g. Anderson, 1970, Rothermel, 1986 and many others). However, such work was rarely explicitly linked with plant morphological or physiological traits.~~The~~ A trait-based "bottom-up" approach has the potential to link well-studied ecological strategies of plants with fire and vegetation feedback processes. However, it is uncertain how well individual-level measures of plant flammability predict fire behavior in wildland fires, or how these effects vary with fire weather conditions. Lab-based flammability trials of leaves, litter, and detached branches have demonstrated extensive variation in multiple~~various~~ dimensions of flammability (Varner et al., 2015; Cui et al., 2020; Popović et al., 2021). However, there is a gap between these flammability parameters usually measured at the organ or partial plant level and the emergent flammability of actual plant communities. In litter fuels, plant traits show both additive and non additive effects that extrapolate well to local fire behavior (~~-~~Schwilk and Caprio, 2011, de Magalhães and Schwilk, 2012; van Altena et al 2012; Kane et al., 2021). However, there~~There~~ is ~~also~~ debate about how trait~~such~~ variation influences wildfire relative to climate, weather, and topography, especially for crown fire. Nevertheless, there have been successful attempts to use traits in fire behavior assessment (Cardoso et al., 2018), modeling (Zylstra et al., 2016), and hazard prediction (Balaguer-Romano et al., 2022). This scaling challenge is not unique to fire ecology and is an example of a broader debate in functional ecology regarding how well plant traits predict ecosystem-level processes (van der Plas et al., 2020; Gornish et al., 2022; Hagan et al., 2023).

In this review, we examine the efficacy of trait-based bottom-up approaches and top-down landscape flammability assessment across four important fuel characteristics (fuel moisture, fuel chemistry, fuel architecture, and fuel load). This review addresses two main questions:

1. How well do traits measured at the organism-level match fuel characteristics measured at broader scales?

2. How well do species-specific traits predict fire behavior?

Finally, we identify approaches that can advance the field of plant flammability from plant to landscape scales.

Flammability is multidimensional

The dimensions of intrinsic plant flammability

Whole plant flammability is a compound functional trait (Jaureguiberry et al., 2011), and can be assessed using different variables of measurement (Pérez-Harguindeguy et al., 2013), across a range of scales of organization from plant tissues and excised parts to organs, shoots, and entire individuals (White and Zipperer, 2010; Younes et al., 2024), and for live, dry, or dead fuel (Boving et al., 2023; Melnik et al., 2024). Common to these multiple dimensions, scales, and fuel types is the measurement of intrinsic plant flammability, a multivariate concept that represents the inherent burning properties of plants as determined by their physico-chemical traits (Varner et al., 2015). Anderson (1970) established three intrinsic flammability variables that are widely used in fire ecology research: ignitibility, sustainability, and combustibility (Box 1).

Ignitibility is the ease with which a plant begins to burn when exposed to an ignition source (Gill and Moore, 1996), most frequently measured as either the time to ignition (Murray et al., 2013) or the frequency of ignition events among a set of samples exposed to an ignition source (Wyse et al., 2016). *Sustainability* is how long a plant burns after ignition, with or without an external heat source (White and Zipperer, 2010; Jaureguiberry et al., 2011). Sustainability is most frequently measured as the duration of combustion and can include durations of incandescence, flaming, and smoldering (Ormeño et al., 2009~~); Pagadala et al., 2024)~~. *Combustibility* refers to the intensity of burning, measured variously as the highest temperature measured during burning (Alam et al., 2020), flame height (de Magalhães and Schwilk, 2012), flame spread rate (Ganteaume et al., 2011b), and mass loss rate (Simpson et al., 2016). Martin et al. (1993) considered consumability as a fourth dimension of intrinsic plant flammability, representing how much of a plant is consumed by fire. *Consumability* is commonly measured as the percentage of burnt biomass once combustion has finished (Burger and Bond, 2015; Zanzarini et al., 2022).

Relationships among dimensions of flammability

Comparative flammability studies have explored inter-species relationships between the four intrinsic flammability dimensions~~variables~~ (i.e., ignitibility, sustainability, combustibility, and consumability). A key ~~practical~~ goal of such investigations has been to determine whether there are species for which all four flammability variables are aligned~~, such that there might be 'ideal' low-flammability species or high-flammability species that should be avoided\~~ (Murray et al., 2023). In this context, some evidence exists for correlations between intrinsic flammability variables. Previous work has shown that leaf ignitibility and sustainability are negatively correlated, such that species with leaves that take a long time to ignite also possess leaves that burn for a long time (Krix et al., 2019; but see Grootemaat et al., 2015). Cawson et al. (2023) showed that shoot sustainability is positively correlated with shoot combustibility. Further evidence that some flammability variables are correlated is provided by studies requiring the use of dimensionality reduction methods (e.g., principal component analysis) to consider collinearity among ignitibility, sustainability, combustibility, and consumability (Prior et al., 2017; Wyse et al., 2018).

Relationships among variables differ when measured on different fuel types. Flammability studies

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Formatted: Font: Italic, Font color: Black of surface~~ground~~ fuels (leaf and twig litter) tend to show two relatively equal and orthogonal axes of variation with one axis representing flame duration and/or total heat released and another axis associated with ignitability and spread rate (de Magalhaes and Schwilk, 2012; Engber et al., 2012; Prior et al., 2018). In well-aerated fuels such as grasses, on the other hand, flammability measures are often more strongly correlated, suggesting a single major axis of variation (Simpson et al, 2016; Gao and Schwilk, 2018; Padullés Cubino et al., 2018). In addition to differences across fuel types, another possible explanation for differing results is differences in how flammability is measured (Younes et al., 2024). There is a need to develop globally consistent methodologies of assessment and analysis of intrinsic plant flammability (Ocampo-Zuleta et al., 2024), to allow robust conclusions about the nature of inter-relationships among flammability variables.

Relationships between plant flammability variables and fire behavior descriptors

Theoretical frameworks suggest that each dimension of a plant's intrinsic flammability corresponds to a specific aspect of fire behavior and ecosystem processes (Box 1). For example, Gill and Zylstra (2005) propose that ignitability, combustibility, and sustainability at the individual plant level are linked to the rate of fire spread, flame length, and fire residence time, respectively. Conversely, Pausas et al. (2017) argue that the rate of fire spread is more closely related to combustibility. The consumability axis, ~~in turn,~~ is theoretically aligned with fire severity at the ecosystem level, often measured by the amount of above- and below-ground organic matter consumed by fire (Gill and Zylstra, 2005; Keeley, 2009). There are few empirical test theoretical models of landscape flammability, with one study from the Australian monsoon tropics ~~finding~~ supporting ~~for~~ two axes: total heat release and rate of spread (Prior et al., 2018).

Researchers have also attempted ~~not only to correlate these dimensions of intrinsic plant flammability but also~~ to connect these dimensions of flammability with flammability metrics at different scales to better predict fire behavior. For instance, Grootemaat et al. (2017b) investigated the relationship between individual leaf flammability and fuel bed flammability, finding that the time-to-ignition of individual leaves was correlated with several flammability parameters in fuel beds, including the rate of fire spread. Consequently, fire spread can be understood as a sequence of ignition events, where the ease of ignition of individual leaves accelerates the spread of fire from one leaf to another (Grootemaat et al., 2017b).

Plant traits to fuel characteristics across scales

Given the multidimensionality of flammability, predicting fire behavior at community and ecosystem scales based on bottom-up approaches is extraordinarily difficult (Loudermilk et al., 2022). To examine flammability across scales, we consider four major categories of fuel characteristics likely to be influenced by plant traits: fuel moisture, fuel architecture, fuel chemistry, and fuel load (Box 1). These are not independent, for example architecture can influence moisture dynamics and fuel load, and leaf chemistry interacts with leaf moisture. Each of these categories also encompasses mixtures of live and dead fuel components and how they interact with the fuel complex. Below we discuss how different plant traits in each category impact flammability across ecological scales and identify the challenges in bridging scales and their causes.

Fuel moisture across scales

Fuel moisture content, whether of dead or live fuels, has long been recognized to affect time to ignition (Rothermel, 1972). Water acts as a heat sink, thus, a high moisture content requires more energy to evaporate water before ignition can occur and the amount of water in the fuel impacts the effective heat of combustion as well as the rate and form of heat released (Smith et al., 2013; Campos-Ruiz et al., 2022). The relationship between fuel moisture and flammability has been extensively studied in the laboratory, and there is strong evidence that this association is negative (Bowman et al., 2014; Popović et al., 2021). Fuel moisture content is negatively correlated with ignitibility at a range of fuel scales, including leaf (Murray et al., 2013; Grootemaat et al., 2015; Simpson et al., 2016; Krix et al., 2019; Younes et al., 2024), litter (Plucinski and Anderson, 2008; Blauw et al., 2015; Burton et al., 2023), shoot (Wyse et al., 2018; Murray et al., 2023) and the whole plant (shrubs, Weise et al., 2005; grasses, Simpson et al., 2016; forbs and shrubs, Zanzarini et al., 2022). However, the relationships between moisture content and sustainability (negative, positive and neutral) and consumability (negative and neutral) are ambiguous (Popović et al., 2021; Younes et al., 2024). Associations with fuel moisture content are the best studied of all trait-flammability relationships, and the effect of moisture content may outweigh that of other traits, such as phytochemistry (Alessio et al., 2008). Moisture content can exhibit thresholds that delineate flammable and non flammable vegetation. Thresholds for dead fuels ("moisture of extinction" values) depend upon fuel type and wind speed (Matthews, 2013), but often range from 15-40% (Scott and Burgan. 2005; Smith et al., 2013). Recent research has also identified thresholds in live fuels (Sultana, 2022; Boving et al. ,2023).

Fuel moisture in dead and excised fuels

Dead fuel moisture is a strong driver of litter flammability (Varner et al., 2015; Kreye et al., 2018, de Magalhães and Schwilk, 2021). Dead fuel moisture can vary from 1% to saturated and accordingly can create fuels with low energy thresholds for ignition to levels that extinguish spreading fire and is driven by driven by relative humidity, solar radiation, wind, and microclimate conditions, as well as by plant traits that influence surface area to volume ratios, litter packing, and bulk density (Rothermel, 1986, Kreye et al., 2018, 2023).

Dead fuel moisture is represented explicitly in US fire behavior models, but this is largely in terms of atmospheric effects on wetting and drying (Rothermel, 1986; Viney, 1991; Nelson, 2000). Species-specific characteristics are included only through the fuel-type specifications. However, in systems where leaf litter drives surface fire, inter-specific differences can result in differing litter flammability where part of the species effect is realized through different moisture absorption/adsorption dynamics and drying rates (Kreye et al., 2018, 2023; Talhelm and Smith, 2018; de Magalhães and Schwilk, 2021; Kane et al., 2021). Additionally, canopy cover and soil moisture influence the litter microenvironment, affecting drying rates and flammability (Kreye et al., 2020; Zhao et al., 2022).

Fuel moisture in living plants

Moisture of live fuels is much more complex to understand than moisture in dead fuels.~~ Although variation exists, dead fuel moisture content is mainly driven by relative humidity and microclimate conditions and data for these parameters are usually available~~. Live fuel moisture~~, however,~~ depends on plant physiology and plants can transport water and nutrients across their tissues on short time scales (Nolan et al. 2022). Live fuel moisture content (LFMC) is the ratio of water mass (g) to dry mass (g) in fresh biomass and is commonly quantified in small branches. It is tightly correlated with other measures of plant water content such as leaf relative water content (proportion of water content relative to saturated condition) and can vary with plant water potential (Boving et al., 2021; Mahmud and Schwilk, this issue). In laboratory studies, the relationship between LFMC and time to ignition has been described as a linear relationship or a threshold relationship (Xanthopoulos and Wakimoto, 1993; Terrah et al., 2020). Such discrepancies potentially result from the heat flux applied or the mode of heat transfer (i.e., convective versus radiative), as radiant heating will take substantially longer to ignite small fuel pieces than similarly size~~s~~d pieces heated by convection (Cohen and Finney, 2023) and radiant heaters can produce both types of heat flux depending on sample positioning. Despite laboratory studies demonstrating a negative relationship between LFMC and flammability, the importance of LFMC in field studies is debated (Alexander and Cruz, 2013; Rossa and Fernandes, 2018). There are multiple, not mutually exclusive, potential reasons for the discrepancy between laboratory and field studies: (1) the challenges of isolating the effect of LFMC from other variables (e.g., wind speed, solar radiation, topographic slope, dead fuel moisture) in the field; (2) the higher heat fluxes in wildfires than laboratory studies may mask any effect of LFMC on time to ignition (Alexander and Cruz, 2013); (3) the relatively low variation in LFMC observed in field studies may be insufficient to induce an effect on time to ignition (Pimont et al., 2019); (4) the moister conditions of vegetation during field experiments, since~~with~~ field experiments are often conducted under mild conditions for safety reasons (Fernandes and Cruz, 2012; Alexander and Cruz, 2013; Rossa and Fernandes, 2018; Pimont et al., 2019); (5) differences in vegetation structure that may affect the relative importance of LFMC; and, (6) errors in estimates of LFMC in the field (Pimont et al., 2019). Further field-based studies are required to examine the relative importance on LFMC on fire behavior.

This ongoing debate leads to differences in how LFMC is included in fire behavior models across different systems. For example, in Australia, fire behavior models for short stature or highly horizontally connected vegetation, such as grasslands and shrublands, require inputs of LFMC or proxies for LFMC, such as plant curing (Cruz et al., 2015). In contrast, fire behavior models for taller eucalypt forests do not ~~include~~consider LFMC (Cruz et al., 2015). Live fuel moisture is not explicitly included in US fire behavior models based on the Rothermel (1972) fire behavior equations (reviewed in Sullivan 2009a–c); however, LFMC is implicitly included in such models through dead to live fuel biomass ratios or as constants in fuel type categories (known as "fuel models," Finney, 1998). It has been proposed that ~~F~~failures of the Rothermel (1972) equations to predict fire spread in shrub fuels may~~could~~ arise from how moisture effects are parameterized (Weise et al., 2016; García et al., 2020). Despite the inconsistent consideration of LFMC in models, there is growing evidence that low LFMC is associated with wildfire extent (Dennison et al., 2008; 2009; Chuvieco et al., 2009; Nolan et al., 2016; Argañaraz et al., 2018; Luo et al., 2019; Park et al., 2022, Rao et al., 2022) and increased receptivity of landscapes to lightning ignitions (Rao et al., 2023; Wickramasinghe et al., 2024).

There are multiple challenges to estimating LFMC across broad spatial scales. Top-down approaches may not characterize fine-scale spatial patterns in LFMC. Perhaps most importantly, LFMC is temporally dynamic. Remote sensing methods are used to assess hazard (e.g., Fuelcast, https://www.fuelcast.net/);~~,~~ however, such methods struggle to forecast temporal changes in fuel moisture (but see Miller et al., 2023). Ongoing efforts to link top-down with bottom-up approaches that use correlated plant traits to predict leaf flammability traits, including LFMC (Nolan et al., 2018; Balaguer-Romano et al., 2022). Recent research has attempted to predict fuel moisture and flammability from hydraulic traits such leaf saturated moisture content and leaf capacitance (Scarff et al., 2021; Nolan et al., 2022). Within and between some species, water status measured as leaf water potential predicts ignitibility (Boving et al., 2023) or integrated measures of flammability (Sultana et al. this issue), however the degree of sensitivity to water potential can vary across species and may depend not just on water content but on the rate of water loss during preheating (Mahmud and Schwilk, this issue).

Fuel architecture across scales

Fuel architecture refers to the size, shape, volumetric arrangement, and distribution of fuel materials that burn during wildfires (Box 1). Although fuel architecture is often quantified based on the volumetric arrangement of assemblages of different live and dead fuel components, with metrics such as compaction, bulk density, ladder fuel presence, among others (Kreye et al., 2014), some studies have addressed the architecture of individual plants (White and Zipperer, 2010). Fuel architecture influences flammability by affecting variables such as ignition, combustion, heat transfer, wind patterns and the airflow across fuel scales (Papió and Trabaud, 1990; Zylstra et al., 2016). ~~It~~ Architecture also influences the flammability of smaller fuel~~s~~ particles that are routinely examined in the laboratory (Alam et al., ~~in press~~2024), such as leaves, litter, and shoots, and the larger fuels and mixtures of fuels in the field, such as surface fuels (e.g., grasses, leaves, litter), ladder fuels (e.g., shrubs, small trees), and canopy fuels (e.g., tree crown).

Fuel architecture of live plants

Fuel architecture is an important determinant of flammability at larger fuel scales, such as the shoot and whole plant. For shoots, the physical arrangement of leaves in the branches likely plays a more important role in influencing flammability than leaf size and shape (Perez-Harguindeguy et al., 2016; Alam et al., 2020). However, ~~, though~~ some work has found architectural traits ~~are~~ less important in determining flammability than ~~other~~ leaf traits such as leaf dry matter content and leaf thickness

(Alam et al. 2024). Key architectural traits at the shoot-level include branch ramification, leaf and twig fraction mass and fuel bulk density, with species with more fine branches, higher leaf fraction mass, and higher bulk density being more flammable (Santacruz-García et al., 2019; Alam et al., ~~in press~~2024). At the whole-plant level, especially for trees and shrubs, the spatial arrangement and density of leaves and branches o~~i~~n the stem, the vertical and horizontal distribution of the fine fuels, and the retention of dead fuels in the crown~~anopy~~ or around the base of the plant determine flammability (Mitsopoulos and Dimitrakopoulos, 2007). For example, manipulative field experiments demonstrate that the canopy architecture of dead fuel retention in the shrub *Adenostoma fasciculatum* was more important than total fuel load in enhancing fire intensity (Schwilk, 2003). A tree crown~~anopy~~ structure with closely connected leaves and branches is more likely to carry a fire than a crown~~anopy~~ with sparse branches, due to more efficient heat transfer in the former (Saura-Mas et al., 2010; Schwilk, 2015). Also, plants with continuous vertical fuel from the ground to the ~~canopy~~crown (ladder fuels) are more likely to propagate a surface fire into the tree crown~~anopy~~, producing crown fires, which are more intense ~~crown fires~~ (Graham et al., 2004; Menning and Stephens, 2007; Mitsopoulos and Dimitrakopoulos, 2007). Likewise, dense lateral branching in the crown~~anopy~~ and well-connected aerial branching between adjacent trees ~~canopies~~ help spread and sustain a fire more than those with gaps in fuel continuity (Graham et al., 2004; Menning and Stephens, 2007; Mitsopoulos and Dimitrakopoulos, 2007). Fire ecologists have often assumed that architectural differences across herbaceous species are less important than are differences in biomass to fire behavior, supported by studies of grassland fuels indicating that flammability strongly depends on fuel load (Simpson et al., 2016; Padulles Cubino et al., 2018). ~~Crown bulk density therefore shows a positive relationship with flammability in prescribed burns (Tumino et al., 2019.~~However, there are some indications of other architectural effects on flammability in grasses related to the positioning of biomass (Gao and Schwilk, 2018; 2022).

Fuel architecture in dead and litter fuels

Extrapolating flammability across scales is challenging (Fernandes and Cruz, 2012). A striking example of the decoupling between the flammability of individual fuel elements and their corresponding fuel beds is seen in small, thin shrub leaves. These leaves ignite easily as individual plant parts or when attached to a shoot but, when organized as litter, produce low heat release rates due to poor ventilation (Scarff and Westoby, 2006). Leaf litter fuel beds possess emergent properties, such as packing ratio and bulk density, which influence airflow and can override the effects of individual leaf flammability (Grootemaat et al., 2017b). A litter layer with larger leaves and other materials facilitates ventilation and ensures more oxygen availability, resulting in fires that burn more rapidly, whereas small leaves tend to produce a compacted litter structure that can restrict airflow and so burn slowly or rarely (de Magalhaes and Schwilk, 2012; Van Altena et al., 2012; Ganteaume, 2018). Consequently, litter flammability is aeration-limited, while canopy flammability, where fuels are usually well-ventilated, is not (Schwilk, 2015; Varner et al., 2015).

Although leaf-level flammability measurements do not predict flammability of ~~ground~~surface fuels composed of leaf litter, ground fuels do provide an example where extrapolating from fine to coarser scales has succeeded: surface fire behavior in one temperate forest was predicted by the abundance-weighted leaf traits known to influence ~~ground~~ fuel aeration (Schwilk and Caprio, 2011). At the extreme of oxygen limitation, organic soils and peat bogs can exhibit extensive fuel consumption under smoldering combustion (Turetsky et al., 2015; Walker et al., 2019, Prior et al., 2024). In addition to natural fuel beds, forest management practices can lead to large areas of masticated (i.e., chipped or shredded) material as a part of fuels thinning operations, a practice that has increased over time particularly in the wildland urban interface (Reed et al., 2020). The size, shape, and chemistry of these masticated materials, as well as material depth, can affect how tightly they pack and how long they retain moisture and therefore flammability and fire spread rates. Fuel bed characteristics in this case depend upon species composition and the machinery used to create masticated material (Kreye et al., 2014).

Elevated dead fine fuels, such as fibrous and ribbon barks, are a unique, albeit important, type of wildfire fuels. Some species, particularly many eucalypts, have a comparatively high biomass of this fuel type that is often specifically measured in hazard assessments (Pickering et al., 2023). These fuels are important in generating embers and fire brands which can spread wildfires over long (> 30 km) distances through a process known as 'spotting' (Tarifa, 1965; Manzello et al., 2007) and can depend on both plant traits that facilitate brand formation (Pickett et al., 2005; Penman et al., 2017) and the receptivity of the fuel bed to ignition by lofted brands (Ganteaume et al., 2011a). Spotting is included in simulated fire spread models such as FARSITE (Fire Area Simulator, Finney, 1998, 2004), but such models struggle to predict fire perimeters accurately under conditions favorable to spotting (Zigner et al., 2022). Further work on factors influencing the likelihood that a spot fire will lead to an ignition and subsequent fire spread ~~successfully spotting~~ is needed from both top-down and bottom-up perspectives. The development of spatial vegetation flammability datasets are needed to enable utility, municipal, and land management planners to target, remove, or reduce certain vegetation types or debris identified to exhibit a higher probability of promoting spot-fire ignitions.

Fuel chemistry across scales

Plant tissues contain numerous chemical elements and compounds, many of which have been linked to plant flammability across fuel scales. The most important of these is water (see section "Fuel moisture across scales"), although plant water content is traditionally (as it is herein) considered separately from plant chemistry (Younes et al., 2024). Some of the earliest research into plant traits associated with flammability focused on chemistry, such as mineral ash content (Broido and Nelson 1964; Mutch and Philpot, 1970; Philpot 1970). Chemicals that affect flammability fall into the following main groups: essential elements, e.g., C, N, K, P, Ca, Ma, S (Salisbury and Ross, 1992); primary metabolites, which are plant-produced chemicals essential for growth, development and reproduction, e.g., carbohydrates, amino acids, fatty acids and vitamins (Schlaeppi et al., 2021); and secondary metabolites, which are plant-produced chemicals that have no direct role in this primary function but are useful in other ways, such as plant defense against herbivores (Neilson et al., 2013). While the term 'secondary metabolites' is widely used in the literature, and we have retained it here for consistency with previous work, we prefer the term 'specialized metabolites' as these are compounds derived from primary metabolism to ~~fulfil~~fulfill specific functions, essentially adaptations which enhance survival. 'Specialized metabolites' avoids the connotations of 'secondary' being a less important function.

The relationship between certain essential elements and flammability has received some attention. For instance, there is evidence for a negative relationship between P and leaf and litter flammability (Scarff and Westoby, 2008; Grootemaat et al., 2015), although this is not universal across fuel scales (Mason et al., 2016; Grootemaat et al., 2017b; Alam et al., 2020), and P may influence flammability less than traits such as moisture content and leaf morphology (Turner, 1994; Scarff et al., 2012). Nitrogen is another essential element that has been linked to flammability, although again results have been mixed across fuel scales (Grootemaat et al., 2015, 2017b; Mason et al., 2016; Gowda et al., 2022). Other essential elements, such as K, Ca, and Mg, have rarely been investigated in relation to their impact on flammability (Popović et al., 2021; Rahman et al., 2023), although Budha-Magar et al. (2024) reported negative relationships between shoot flammability and various leaf nutrients (Mg, K, S, Ca, but not P). While essential elements may be correlated with flammability, these relationships are often weaker than those between flammability and other traits (e.g. leaf moisture content, twig dry matter content and retained dead material; Budha-Magar et al. 2024).

Primary metabolites, such as carbohydrates and fatty acids, may be positively correlated with different flammability traits at leaf, litter and bark scales (Mason et al., 2016; Grootemaat et al., 2017b), likely due to their low relative molecular mass and high volatility (Page et al., 2012). Non-structural carbohydrates, such as sugars and starches~~, such as starch and lipid~~, enhanced the sustainability of living needles of *Pinus banksiana*, and foliar chemistry had a greater influence on flammability than moisture content (Campos-Ruiz et al., 2022). Further research into primary metabolite-flammability relationships should prove fruitful.

Secondary metabolites are the most extensively studied group of chemicals in relation to their influence on flammability across fuel scales, and include volatile organic compounds such as phenolics~~, lignins, ~~and terpenes, as well as lignins and tannins (Owens et al., 1998; Ormeño et al., 2009; Pausas et al., 2016; Ganteaume et al., 2021; Guerrero et al., 2022). Of these chemical groups, terpenes have received the most attention at both the leaf and litter scales for trees (Popović et al., 2021) and are considered in more detail below. The relationships between secondary metabolites and flammability are complex and can be idiosyncratic, depending on the type of fuel examined, the level at which chemical compounds are studied (e.g., at broad group, subgroup or molecular levels), and the diversity of compounds examined. As with other chemical traits, the effect of secondary compounds on flammability may be less important than that of water content (Alessio et al., 2008).

Terpenes are unsaturated hydrocarbons comprised of isoprene units (C_5) and are known to be flammable due to their high heating value and low flash point (Ormeño et al., 2009). While terpene content was by far the most frequently studied chemical trait on both live leaves and litter for trees, its relationship with flammability was inconsistent across studies (Popović et al., 2021). For instance, for combustibility, 8~~/~~ out of 10 studies reported a positive relationship with leaf terpene content, and one study each reported a neutral and a negative relationship. For ignitibility and leaf terpene the ratios were 5:3:1 for positive:neutral:negative relationships, while for sustainability five out of six studies reported a negative relationship, with the other a positive relationship (Popović et al., 2021). While general patterns between terpene content and flammability may be lacking, there is evidence to suggest that terpenes drive flammability in particular species and groups. For instance, in *Rosmarinus officinalis* high terpene content increased ignitability, and genetic differences between individuals hinted that such differences in flammability were heritable (Pausas et al. 2016). Furthermore, in the genus *Pinus*, in which flammability (He et al. 2012; Varner et al. 2022) and terpenes (Mitić et al. 2017) have been shown to be phylogenetic conserved and terpenes drive differences in the flammability of leaf litter (Ormeño et al., 2009), it has been suggested that differences in terpene content could be behind unexplained variation in litter flammability (Varner et al. 2022).

There is a paucity of research into the effect of chemistry on fire at community and landscape scales, although the widely used Rothermel fire spread equations include a mineral content damping coefficient which can be set to vary across fuel types (Rothermel, 1972). Fuel chemistry likely influences flammability at landscape scales through interactions between soil chemistry and plant traits and herbivory--induced defenses. Plants from low-fertility ecosystems tend to have traits (e.g., small sclerophyllous leaves, high leaf dry matter content) that make them more flammable (Ojeda et al., 2010; Gibson et al., 2015; Paula et al., 2024). In Australian Mediterranean-climate mallee ecosystems, soil fertility had a strong influence on the probability of fire estimated based on fire interval data, although this was dependent on vegetation type, and the effect of rainfall was stronger (Gibson et al., 2015). In a continental-wide examination of fire activity in Australia, there was a negative relationship between soil P and both area burned and fire radiative power, after controlling for climate (Prior et al., 2017). Unexpectedly, there was a weak positive relationship between soil P and flame rate of spread in grass and litter fuels, which was attributed to the influence of soil P on flammability being less than that of leaf moisture content (Scarff et al., 2012; Prior et al., 2017). In a global study of drivers of fire activity in Mediterranean-type climate regions, low-fertility soils (lower pH and higher concentration of exchangeable aluminum) were positively associated with higher fire activity, although other measures of soil fertility (P, N, C:N) were not related to fire activity (Paula et al., 2024). Intriguingly, these relationships between low soil fertility and higher fire activity may be maintained via positive feedbacks mediated by high-flammability plant species: low soil fertility selects species with traits (small leaves, high leaf dry matter content) that promote high flammability and these species burn readily, resulting in frequent fires that deplete soil nutrient pools, favoring species with traits associated with high flammability (Wood and Bowman, 2012; Hinojosa et al., 2021; Paula et al., 2024). While more work is needed to disentangle how soil chemistry influences flammability, these studies show the value of incorporating soil fertility in models predicting future fire regimes.

Fuel load across scales

Fuel load, the total combustible material, is usually defined as mass/area and is often estimated through top-down approaches. Interactions between fuel load and fuel structure across multiple scales make it difficult to isolate the effects of each driver. At the finest scales, fuel load is determined by the density of plant biomass. Leaf dry matter content (LDMC) is related to the amount of carbon in a leaf available for combustion and is calculated as the ratio of dry mass to water-saturated fresh mass (Perez-Harguindeguy et al., 2013), so is related to live fuel moisture content. At the individual leaf level, higher LDMC has shown a negative relationship with different flammability axes. For instance, Rahman (2018) reported that leaves with higher LDMC required higher ignition temperatures~~ to ignite~~. Similarly, Mason et al. (2016) reported a negative correlation between the rate of temperature increase and LDMC, indicating that higher LDMC is associated with lower combustibility. In contrast, at the shoot level, higher LDMC is associated with increased flammability, demonstrating a decoupling of flammability between leaf and shoot levels (Alam et al., 2020). Alam et al. (2020) and Potts et al. (2022) further demonstrated that LDMC significantly influenced shoot flammability measures connected to all axes of flammability (ignition percentage, burnt biomass, burn time, and maximum temperature) across growth forms and families. Ortiz et al. (2023) corroborated these findings, showing that LDMC positively influenced burn time and maximum temperature. Importantly in the context of isolating fuel load versus fuel structural effects, Alam et al. (~~in press~~2024) demonstrated that LDMC was a better predictor of shoot flammability than various architectural traits. Finally, at the global scale, patterns in LDMC have been linked to fire activity, especially among plants with postfire regeneration abilities (resprouting or reseeding), that have higher LDMC (Dai et al. 2025).

As the scale of analysis expands to include not only shoot characteristics but also individual crowns~~anopies~~, fuel density is another important predictor of flammability. At fine scales, fuel load is often measured as mass per unit volume, and at the broadest scales, as mass per unit area. As fuel density increases, fire spread rate tends to decrease while burning time increases (Grootemaat et al., 2017; Prior et al., 2017). However, an important point of distinction regarding fuel bed density (or litter-bed density) is that it may have starkly different influences on flammability/fire behavior in canopies versus litter (see section "Fuel architecture across scales"). Furthermore, herbivores and fire interact (Bond, 2005), and the flammability of vegetation on nutrient-poor soils may in part result from relatively lower herbivory pressure (Archibald and Hempson, 2015).

A central element of predicting fire behavior at broad scales is characterizing the crown size of individual trees and shrubs. In fire behavior models, crown size is often represented by canopy bulk density and canopy height (from canopy base height to top of canopy). Both are seen as essential predictors of wildland fire behavior (Affleck et al., 2012), with greater canopy sizes leading to increased fire intensity in the presence of vertical fuel continuity (Agee, 1996). Keyser and Smith (2010) demonstrated that these metrics of canopy size were insufficient without including the context of vertical structure; ~~and~~ even after accounting for vertical structure, the relationship between fuel load and fire behavior is complex and dynamic across stand-to-landscape scales. Vegetation cover affects fuel loads, thereby reducing fire spread rate, heat release, and area burned as the distance between the crowns of neighboring individuals increases. However, horizontal variability in fuel load can lead to increased spread rate, heat release, and area burned (Atchley et al., 2021). LiDAR technology facilitates efficient assessment of fuel architecture with great precision across broad scales (e.g., Price and Gordon, 2016), and methods such as structure-from-motion imaging may continue to make this possible at lower cost (Reilly et al., 2024).

Within a fuel of similar architecture such as grass fuels, biomass strongly influences fire behavior and grassland fire regimes often show effects of previous season growth conditions that influence fire season fuel loads. For example, invasive ~~cheatgrass~~*Bromus tectorum* in the Great Basin of the western US, which has altered fire regimes, exhibits multi-year effects of past precipitation on current season fire extent (Pilliod et al., 2017). ~~Bradstock (2010) proposed a biographic model of fire regimes in Australia centered on fuel load (with separate processes controlling biomass production and "availability to burn"), fire weather, and ignition. According to this model, for some ecosystems, fuel moisture inhibiting flammability limits fire occurrence while for other systems, such as grasslands, biomass production limits fire.~~ Biomass and net primary productivity have often been used as proxies for fuel density to predict landscape flammability (Bradstock et al., 2010; Pausas et al., 2017). Both these metrics can be ~~This top-down approach has powerful potential because biomass can be~~ estimated across very broad extents through remote sensing or modeling (Tsitsi, 2016), and thus biomass can be readily scaled across. Distinctions between separate categories of biomass can be important to retain even at the broadest scales; for example, Newberry et al. (2020) found grass biomass to be the primary driver of landscape flammability across savanna-forest transition zones in Brazil, although Cardoso et al. (2018) found grass species flammability to be more important than biomass in such ecosystem boundaries in Gabon.

Interactions across fuel characteristics and non-additive effects

When considering the scaling of flammability from the leaf to organism to community scale, it is important to consider how interactions between adjacent fuel components influence whether fire will propagate from one fuel element to another (Finney et al., 2010). If the first fuel element ignites, the probability of the adjacent elements also igniting will depend on intrinsic properties such as fuel moisture and chemical composition. Additionally, this probability is influenced by extrinsic properties, both inherently non-static—such as the distance between elements, which affects the degree of pre-heating and airflow (e.g., wind, air entrainment) that can supply oxygen or cool the elements through convection (Sullivan, 2009a)—and static, such as topography (Finney et al., 2010). Under non-extreme fire conditions, even in the presence of significant pre-heating, element-to-element propagation generally occurs following direct flame contact, with factors such as slope and wind increasing this degree of flame contact (Finney et al., 2010). Under extreme fire conditions (i.e., Forest Fire Danger Index (FFDI) >50), fire propagation and spread becomes independent of fuel conditions (Cruz et al., 2022), and there is evidence from a range of vegetation types (forests, shrublands) that the relevance of species-level fuel characteristics on fire behavior in the field decreases directly as a function of the Forest Fire Danger Index (Bessie and Johnson, 1995; Cruz et al., 2022). However, further work to determine thresholds where trait-based differences in fuels are relevant is warranted, especially in light of models that highlight the importance of convection for fire propagation (Cohen and Finney, 2023).

Non-additive effects challenge the extrapolation of individual plant flammability to the flammability of mixed-species communities. These effects, which arise from emergent physico-chemical properties in fuel mixtures, lead to outcomes that cannot be accurately predicted by simply considering the flammability of individual species. When plants of differing flammability burn together, they can exhibit one of two effects: an additive effect, where the flammability of the mixture reflects the average of the individual species; or a non-additive effect, where the most or least flammable species may dominate~~s~~, resulting in a net flammability higher or lower than expected (van Altena et al., 2012; de Magalhães and Schwilk, 2012; Della Rocca et al., 2018). This phenomenon of non-additivity has been documented in several studies assessing the flammability of surface~~ground~~ fuel beds (van Altena et al., 2012; de Magalhães and Schwilk, 2012; Della Rocca et al., 2018; Varner et al., 2017, Bowman et al., 2018) and shoots (Wyse et al., 2018, Wei et al., 2025). Non-additive effects are most common for fire spread and duration, which likely reflects flames propagating via the most flammable components of a fuelbed (van Altena et al. 2012). These non-additive effects indicate~~suggest~~ that it is challenging~~difficult~~ to predict the flammability of a plant community solely based on aggregating the flammability of its individual species, although attempts have been made to do this using community-weighted means of flammability (Padullés Cubino et al., 2018). Given the complexity introduced by non-additive effects, there is a pressing need to better ~~future research could focus on~~ understand~~ing~~ how these interactions occur when mixtures of species are burned, particularly using leaves, shoots or whole individuals.

Conclusions

Although some tissue and organismal scale plant traits influence flammability and hence fire behavior, their effect size remains unresolved as is how their influences vary among different vegetation types and changes with fire weather. Live fuel moisture is one fuel characteristic where scaling from leaf to landscapes has been most successfully established, with work from both approaches linking trait investigations with remotely sensed data (e.g., Scarff et al., 2021; Griebel et al., 2023). There is evidence that some plant traits (e.g., leaf traits that control ground fuel litter flammability, Schwilk and Caprio, 2011) influence patterns of local fire severity such that they drive ~~wild~~fire behavior at landscape scales. For other fuel characteristics such as architecture, there is potential to link trait measurements with newly available three-dimensional remotely sensed information, although the mechanistic connections need better study.

There has been progress in assessing which leaf-level traits matter for shoot~~-~~-level flammability, but there are still gaps in extrapolating ~~scaling~~ from shoot to individual up~~wards~~ to the community and landscape scales, despite the use of broader scale methods such as wind tunnels (e.g., Marino et al., 2014). This paucity of studies linking lab-based measurements of flammability and plant traits with wildland fire, has reinforced a conceptual disconnection between top-down and bottom-up approaches. Research that directly addresses the criticisms of trait-centric approaches (e.g., that flammability measured at low heat fluxes does not inform stand level fire, Fernandes and Cruz, 2012) is also sorely needed. To bridge this conceptual gap demands carefully designed multi-scale studies that use comparable measures of different dimensions of flammability and consistently used terminologies to describe traits, plant and community architecture. Of prime importance are experimental tests of flammability at the species-level that predict~~s~~ fire behavior at the stand and community levels. Putting aside the mechanistic understanding of how plant traits influence fire, evaluating if abundance-weighted averages of species-level shoot or individual level measurements of flammability can predict fire behavior is a key contribution. Finally, a critical applied research question is identifying how different traits affect fire weather thresholds (e.g., fire weather indices) when variation in fuel characteristics is overwhelmed by climatic factors in determining fire behavior (Cruz et al., 2022).

While in this review we have~~s~~ highlighted many areas where there are empirical and theoretical discrepancies between top-down and bottom-up approaches to predicting flammability, we remain hopeful that these can be overcome. Indeed, having researchers from both schools-of-thought working together will ~~be vital to~~ help mitigate the increasing impacts of changing fire regimes on human society (Bowman et al., 2020) and global biodiversity (Kelly et al., 2020).

Author Contributions

D.W.S. conceived the review and wrote the first outline, D.W.S., T.J.C., M.A.A., N.G., B.R.M., R.H.N., G.L.W.P., and A.M.S.S. drafted major text sections, S.O., N.G. TJ.C. an D.W.S. designed the figure, and all authors contributed text and comments to multiple drafts of the manuscript.

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References

Abdollahi, A. and M. Yebra. 2023. Forest fuel type classification: Review of remote sensing techniques, constraints and future trends. *Journal of Environmental Management 342:* 118315.

Affleck, D. L., C. R. Keyes, and J. M. Goodburn. 2012. Conifer crown fuel modeling: current limits and potential for improvement. *Western Journal of Applied Forestry* 27: 65-169.

Agee, J. K. 1996. The influence of forest structure on fire behavior. In: *Proceedings of the 17th Annual Forest Vegetation Management Conference* 52-68.

Alam, M. A. 2019. Plant functional traits associated with shoot flammability. Unpublished PhD thesis, Lincoln University, Lincoln, New Zealand.

Alam, M. A., S. V. Wyse, H. L. Buckley, G. L. W. Perry, J. J. Sullivan, N. W. H. Mason, R. Buxton, et al. 2020. Shoot flammability is decoupled from leaf flammability, but controlled by leaf functional traits. *Journal of Ecology* 108: 641–653.

Alam M. A., S. V. Wyse, H. L. Buckley, G. L. W. Perry, X. Cui, J. J. Sullivan, D. W. Schwilk, T. J. Curran. In press. Fuel architecture influences interspecific variation in shoot flammability, but not as much as leaf traits. Journal of Ecology

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

Alexander, M. E. and M. G. Cruz. 2013. Corrigendum to: Assessing the effect of foliar moisture on the spread rate of crown fires. *International Journal of Wildland Fire*, 22: 869-870.

Anderson, H. E., 1970. Forest fuel ignitibility. *Fire Technology* 6: 312-319.

Archibald, S., and G. P. Hempson. 2016. Competing consumers: contrasting the patterns and impacts of fire and mammalian herbivory in Africa. *Philosophical Transactions of the Royal Society B: Biological Sciences* 371: 20150309.

Anderson, H. E. 1982. Aids to Determining Fuel Models for Estimating Fire Behavior. USDA Forest Service General Technical Report INT-122. Intermountain Forest and Range Experiment Station, Ogden, Utah.

Archibald, Sally, et al. 2018. Biological and geophysical feedbacks with fire in the Earth system.

Environmental Research Letters 13: 033003.

Argañaraz, J. P., M. A. Landi, C. M. Scavuzzo, and L. M. Bellis. 2018. Determining fuel moisture thresholds to assess wildfire hazard: A contribution to an operational early warning system. *PloS One:* 13: e0204889.

Atchley, A. L., R. Linn, A. Jonko, C. Hoffman, J. D. Hyman, F. Pimont, C. Sieg, and R. S. Middleton. 2021. Effects of fuel spatial distribution on wildland fire behaviour. *International Journal of Wildland Fire* 30: 179-189.

Balaguer-Romano, R., R. Díaz-Sierra, M. De Cáceres, À. Cunill-Camprubí, R. H. Nolan, M. M. Boer, J. Voltas, and V. R. de Dios. 2022. A semi-mechanistic model for predicting daily variations in species-level live fuel moisture content. A*gricultural and Forest Meteorology* 323: p.109022.

Bessie, W. C. and E. A. Johnson. 1995. The relative importance of fuels and weather on fire behavior in subalpine forests. *Ecology* 76: 747-762.

Blauw, L. G., N. Wensink, L. Bakker, R. S. P. Van Logtestijn, R. Aerts, N. A. Soudzilovskaia, and J. H. C. Cornelissen. 2015. Fuel moisture content enhances nonadditive effects of plant mixtures on flammability and fire behavior. *Ecology and Evolution* 5: 3830–3841.

Bond, W. J. 2005. Large parts of the world are brown or black: A different view on the 'Green World' hypothesis. *Journal of Vegetation Science* 16: 261–266.

Boving, I., J. Celebrezze, R. Salladay, A. Ramirez, L. D. Anderegg, and M. Moritz. 2023. Live fuel moisture and water potential exhibit differing relationships with leaf-level flammability thresholds. *Functional Ecology* 37: 2770-2785.

Bowman, D. M. J. S., B. J. French, and L. D. Prior. 2014. Have plants evolved to self-immolate? *Frontiers in Plant Science* 5: 590.

Bowman, D. M., C. A. Kolden, J. T. Abatzoglou, F. H. Johnston, G. R. van der Werf, and M. Flannigan. 2020. Vegetation fires in the Anthropocene. *Nature Reviews Earth & Environment* 1: 500-515.

Bowman, D. M. J. S., C. Haverkamp, K. D. Rann, and L. D. Prior. 2018. Differential demographic filtering by surface fires: How fuel type and fuel load affect sapling mortality of an obligate seeder savanna tree. *Journal of Ecology* 106: 1010–1022.

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

Brain, C.K. and A. Sillent. 1988. Evidence from the Swartkrans cave for the earliest use of fire. *Nature* 336: 464-466

Brando, P., M. Macedo, D. Silvério, L. Rattis, L. Paolucci, A. Alencar, M. Coe, and C. Amorim. 2020. Amazon wildfires: Scenes from a foreseeable disaster. *Flora* 268: p.151609.

Broido A. and M. A. Nelson ~~M.A.~~. 1964. Ash content: its effect on combustion of corn plants. *Science* 46: 652–3.

Burger, N. and W. Bond. 2015. Flammability traits of Cape shrubland species with different post-fire recruitment strategies. *South African Journal of Botany* 101: 40–48.

Burton, J. E., J. G. Cawson, A. I. Filkov, and T. D. Penman. 2021. Leaf traits predict global patterns in the structure and flammability of forest litter beds. *Journal of Ecology* 109: 1344-1355.

Burton, J. E., T. D. Penman, A. I. Filkov, and J. G. Cawson. 2023. Multi-scale investigation of factors influencing moisture thresholds for litter bed flammability. *Agricultural and Forest Meteorology* 337: 109514.

Campos-Ruiz, R., M. A. Parisien, and M. D. Flannigan. 2022. Physicochemical characteristics controlling the flammability of live *Pinus banksiana* needles in central Alberta, Canada. *International Journal of Wildland Fire* 31: 857–870.

Cardoso, A. W., I. Oliveras, K. A. Abernethy, K. J. Jeffery, D. Lehmann, J. Edzang Ndong, I. McGregor, C. M. Belcher, W. J. Bond, and Y. S. Malhi. 2018. Grass species flammability, not biomass, drives changes in fire behavior at tropical forest-savanna transitions. *Frontiers in Forests and Global Change* 1: 14.

~~Cardoso, A. W., Oliveras, I., Abernethy, K. A., Jeffery, K. J., Lehmann, D., Edzang Ndong, J., McGregor, I., Belcher, C. M., Bond, W. J., & Malhi, Y. S. (2018). Grass species flammability, not biomass, drives changes in fire behavior at tropical forest–savanna transitions. *Frontiers in Forests and Global Change*:1 1–14.~~

Cawson, J.G., J.E. Burton, B.J. Pickering, V. Demetriou, and A.I. Filkov. 2023. Quantifying the flammability of living plants at the branch scale: which metrics to use? *International Journal of Wildland Fire* 32: 1404-1421.

Chuvieco, E., I. González, F. Verdú, I. Aguado, and M. Yebra. 2009. Prediction of fire occurrence from live fuel moisture content measurements in a Mediterranean ecosystem. *International Journal of Wildland Fire* 18: 430–441.

Cohen, J., and M. Finney. 2023. Fuel Particle Heat Transfer Part 2: Radiation and Convection during Spreading Laboratory Fires. *Combustion Science and Technology* 195: 3122-3147.

Cornelissen, J. H. C., S. Grootemaat, L. M. Verheijen, W. K. Cornwell, P. M. Van Bodegom, R. Van Der Wal, and R. Aerts. 2017. Are litter decomposition and fire linked through plant species traits? *New Phytologist* 216: 653–669.

Cornelissen, J. H., S. Lavorel, E. Garnier, S. Díaz, N. Buchmann, D. E. Gurvich, P. B. Reich, H. Ter Steege, H. D. Morgan, M. G. A. Van Der Heijden, and J. G. Pausas. 2003. A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Australian Journal of Botany:* 51 335-380.

Cruz, M. G., J. S. Gould, M. E. Alexander, A. L. Sullivan, W. L. McCaw, and S. Matthews. 2015. Empirical-based models for predicting head-fire rate of spread in Australian fuel types. *Australian Forestry:* 78: 118-158.

Cruz, M. G., C. M. Hoffman, and P. M. Fernandes. 2025. Global synthesis of quantification of fire behaviour characteristics in forests and shrublands: recent progress. *Current Forestry Reports* 11:8.

Cruz, M. G., M. E. Alexander, and P. M. Fernandes. 2022. Evidence for lack of a fuel effect on forest and shrubland fire rates of spread under elevated fire danger conditions: implications for modelling and management. *International Journal of Wildland Fire* 31: 471-479.

Cui X, A. P. Paterson, S. V. Wyse, M. A. Alam, K. Maurin, R. Pieper, J. Padullés Cubino, D. O'Connell, D. Donkers, J. Bréda, H. L. Buckley, G. L. W. Perry, and T. J. Curran. 2020. Shoot flammability of vascular plants is phylogenetically conserved and related to habitat fire-proneness and growth form. *Nature Plants* 6: 355-359

Cunningham, C. X., G. J. Williamson, R. H. Nolan, L. Teckentrup, M. M. Boer, and D. M. Bowman. 2024. Pyrogeography in flux: Reorganization of Australian fire regimes in a hotter world. *Global Change Biology 3*0: e17130.

Curran, T. J., G. L. Perry, S. V. Wyse, and M. A. Alam. 2017. Managing fire and biodiversity in the wildland-urban interface: A role for green firebreaks. *Fire*1: 3.

Dai, D., Yu, D., Gao, W., Perry, G. L. W., Paterson, A. M., You, C., Zhou, S., Xu, Z., Huang, C., Cao, D., Curran, T. J. and Cui, X. (2025), Leaf ~~D~~dry m~~M~~atter c~~C~~ontent Is p~~P~~hylogenetically c~~C~~onserved and r~~R~~elated to e~~E~~nvironmental c~~C~~onditions, e~~E~~specially ~~W~~wildfire ~~A~~activity. *Ecology Letters*, 28: e70056.

Della Rocca, G., R. Danti, C. Hernando, M. Guijarro, and J. Madrigal. 2018. Flammability of two Mediterranean mixed forests: study of the non-additive effect of fuel mixtures in laboratory. *Frontiers in Plant Science* 9: 825.

Dennison, P. E., and M. A. Moritz. 2009. Critical live fuel moisture in chaparral ecosystems: a threshold for fire activity and its relationship to antecedent precipitation. *International Journal of Wildland Fire* 18: 1021–1027.

Dennison, P. E., M. A. Moritz, and R. S. Taylor. 2008. Evaluating predictive models of critical live fuel moisture in the Santa Monica Mountains, California. *International Journal of Wildland Fire* 17: 18–27.

Drucker, J. R., A. Farguell, C. B. Clements, and A. K. Kochanski. 2023. A live fuel moisture climatology in California. *Frontiers in Forests and Global Change* 6: 1203536.

Ellis, T. M., D. M. Bowman, D. M., P. Jain, M. D. Flannigan, and G. J. Williamson. 2022. Global increase in wildfire risk due to climate-driven declines in fuel moisture. *Global Change Biology* 28: 1544-1559.

Engber, E. A. and J. M. Varner III. 2012. Patterns of flammability of the California oaks: the role of leaf traits. *Canadian Journal of Forest Research* 42: 1965-1975.

Finney, M. A. 1998. FARSITE: Fire Area Simulator - model development and evaluation. Research Paper RMRS-RP-4. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Ft. Collins, CO.

Finney, M. A., J.D. Cohen, S. S. McAllister, and W. M. ~~and~~ Jolly. 2012. On the need for a theory of wildland fire spread. *International Journal of Wildland Fire* 22: 25-36.

French, N. H. F., L. K. Jenkins, T. V. Loboda, M. Flannigan, R. Jandt, L. L. Bourgeau-Chavez, and M. Whitley. 2015. Fire in arctic tundra of Alaska: past fire activity, future fire potential, and significance for land management and ecology. *International Journal of Wildland Fire* 24: 1045–

1061.

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

Ganteaume, A., M. Guijarro, M. Jappiot, C. Hernando, C. Lampin-Maillet, P. Pérez-Gorostiaga, and J. A. Vega. 2011a. Laboratory characterization of firebrands involved in spot fires. *Annals of Forest Science* 68: 531–541.

Ganteaume, A., J. Marielle, L.-M. Corinne, C. Thomas, and B. Laurent. 2011b. Effects of vegetation type and fire regime on flammability of undisturbed litter in Southeastern France. *Forest Ecology and Management* 261: 2223–2231.

Ganteaume, A., B. Romero, C. Fernandez, E. Ormeño, and C. Lecareux. 2021. Volatile and semi-volatile terpenes impact leaf flammability: differences according to the level of terpene identification. *Chemoecology* 31: 259–275.

Gao, X., and D. W. Schwilk. 2022. Burn hot or tolerate trees: flammability decreases with shade tolerance in grasses. *Oikos* 2022: e08930.

Gao, X., and D. W. Schwilk. 2018. Grass cCanopy aArchitecture iInfluences tTemperature eExposure at sSoil sSurface. *Fire* 1: 35.

García, M., D. Riaño, M. Yebra, J. Salas, A. Cardil, S. Monedero, J. Ramirez, M.P. Martín, L. Vilar, L., J. Gajardo, and S. Ustin. 2020. A live fuel moisture content product from Landsat TM satellite time series for implementation in fire behavior models. *Remote Sensing*12: 1714.

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

Gill, A. M. and P. H. Moore.1996. *Ignitibility of Leaves of Australian Plant*s (Vol. 34). Canberra: CSIRO. 34pp.

Gill, A. M. and P. Zylstra. 2005. Flammability of Australian forests. *Australian Forestry* 68: 87-93.

Glasspool, I.J., D. Edwards, and L. Axe. 2004. Charcoal in the Silurian as evidence for the earliest wildfire. *Geology* 32: 381-383.

Gornish, E. S., C. Campbell, L. Svejcar, S.M. Munson, K. Vaughn, M.K. Spaeth, S.G. Yelenik, A.

Wolf, and R. Mitchell. 2023. Functional traits are used in restoration practice: a response to Merchant et al. (2022). *Restoration Ecology* 31: e13880.

Gowda, J. H., M. Blackhall, L. Shipley, T. Kitzberger, and F. Tiribelli. 2022. Are digestibility and flammability related? Two variables shaping landscape dynamics of Northwestern Patagonian forests. *Forest Ecology and Management* 503: 119810.

Graham, R. T., S. McCaffrey, and T. B. Jain. 2004. Science basis for changing forest structure to modify wildfire behavior and severity. General Technical Report RMRS-GTR-120, U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Ft. Collins, CO.

Griebel, A., M. M. Boer, C. Blackman, B. Choat, D. S. Ellsworth, P. Madden, B. Medlyn, V. Resco de Dios, A. Wujeska-Klause, M. Yebra, and N. Younes Cardenas. 2023. Specific leaf area and vapour pressure deficit control live fuel moisture content. *Functional Ecology* 37: 719-731.

Grootemaat, S., I. J. Wright, P. M. Van Bodegom, and J. H. C. Cornelissen. 2017a. Scaling up flammability from individual leaves to fuel beds. *Oikos* 126: 1428–1438.

Grootemaat, S., I. J. Wright, P. M. Van Bodegom, J. H. C. Cornelissen, and W. K. Cornwell. 2015. Burn or rot: leaf traits explain why flammability and decomposability are decoupled across species. *Functional Ecology* 29: 1486–1497.

Grootemaat, S., I. J. Wright, P. M. Van Bodegom, J. H. C. Cornelissen, and V. Shaw. 2017b. Bark traits, decomposition and flammability of Australian forest trees. *Australian Journal of Botany* 65: 327–338.

Guerrero, F., L. Espinoza, C. Carmona, M. Blackhall, C. Quintero, K. Ocampo-Zuleta, S. Paula, J. Madrigal, M. Guijarro, Y. Carrasco, and M. A. Bustamante-Sánchez. 2024. Unraveling the chemistry of plant flammability: Exploring the role of volatile secondary metabolites beyond terpenes. *Forest Ecology and Management* 572: 122269.

Hagan, J. G., J. J. Henn, and W. H. Osterman. 2023. Plant traits alone are good predictors of ecosystem properties when used carefully. *Nature Ecology & Evolution* 7: 332-334.

He, T., J. G. Pausas, C. M. Belcher, D. W. Schwilk, and B. B. Lamont. 2012. Fire-adapted traits of *Pinus* arose in the fiery Cretaceous. New Phytologist 194: 751–759.

Hinojosa, M. B., E. Albert-Belda, B. Gómez-Muñoz, and J. M. Moreno. 2021. High fire frequency reduces soil fertility underneath woody plant canopies of Mediterranean ecosystems. *Science of* *the Total Environment* 752, 141877.

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

Jolly, W. M., and D. M. Johnson. 2018. Pyro-Ecophysiology: Shifting the Paradigm of Live Wildland Fuel Research. *Fire* 1: 8.

Kane, J. M., J. K. Kreye, R. Barajas-Ramirez, and J. M. Varner. 2021. Litter trait driven dampening of flammability following deciduous forest community shifts in eastern North America. *Forest Ecology and Management* 489: 119100.

Keeley, J. E. 2009. Fire intensity, fire severity and burn severity: a brief review and suggested usage. *International Journal of Wildland Fire* 18: 116-126.

Kelly, L. T., K. M. Giljohann, A. Duane, N. Aquilué, S. Archibald, E. Batllori, A.F. Bennett, S. T. Buckland, Q. Canelles, M. F. Clarke, and M. J. Fortin. 2020. Fire and biodiversity in the Anthropocene. *Science* 370: eabb0355.

Keyser, T. and F. W. Smith. 2010. Influence of crown biomass estimators and distribution on canopy fuel characteristics in ponderosa pine stands of the Black Hills. *Forest Science* 56: 156-165.

Krawchuk, M. A.- and M. A. and Moritz. 2011. Constraints on global fire activity vary across a resource gradient. *Ecology* 92: 21-132.

Kreye, J. K., N. W. Brewer, P. Morgan, J. M. Varner, A. M. S. Smith, C. M. Hoffman, and R. D. Ottmar. 2014. Fire behavior in masticated fuels: A review. *Forest Ecology and Management* 314: 193–207.

Kreye, J. K., J. K. Hiers, J. M. Varner, B. Hornsby, S. Drukker, and J. J. O'Brien. 2018. Effects of solar heating on the moisture dynamics of forest floor litter in humid environments: composition, structure, and position matter. *Canadian Journal of Forest Research* 48: 1331– 1342.

Kreye, J. K., J. M. Kane, and J. M. Varner. 2023. Multivariate roles of litter traits on moisture and flammability of temperate northeastern North American tree species. *Fire Ecology* 19: 21.

Kreye, J. K., J. M. Kane, J. M. Varner, and J. K. Hiers. 2020. Radiant heating rapidly increases litter flammability through impacts on fuel moisture. *Fire Ecology* 16: 8.

Krix, D. W., M. L. Phillips, and B. R. Murray. 2019. Relationships among leaf flammability attributes and identifying low-leaf-flammability species at the wildland–urban interface. *International Journal of Wildland Fire* 28: 295–307.

Loudermilk, E. L., J. J. O'Brien, S. L. Goodrick, R. R. Linn, N. S. Skowronski, and J. K. Hiers. 2022. Vegetation's influence on fire behavior goes beyond just being fuel. *Fire Ecology* 18: 9.

Luo, K., X. Quan, B. He, and M. Yebra. 2019. Effects of live fuel moisture content on wildfire occurrence in fire-prone regions over Southwest China. *Forests* 10: 887.

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

de Magalhães, R. Q. and D. W. Schwilk. 2021. Moisture absorption and drying alter nonadditive litter flammability in a mixed conifer forest. J*ournal of Ecology* 109: 234-245.

Manzello, S. L., Maranghides, A., Mell, and W. E. 2007. Firebrand generation from burning vegetation. *International Journal of Wildland Fire* 16: 458-462.

Martin R. E., D. A. Gordon, M.E. Gutierrez, D. S. Lee, D. M. Molina, R. A. Schroeder, D. B. Sapsis, S. L. Stephens, and M. Chambers. 1993. Assessing the flammability of domestic and wildland vegetation. In *Proceedings of the 12th Conference on Fire and Forest Meteorology*. pp. 130–137. Society of American Foresters Publication 94-02: Bethesda, MD, USA

Marino, E., C. Hernando, J. Madrigal, and M. Guijarro. 2014. Short-term effect of fuel treatments on fire behaviour in a mixed heathland: a comparative assessment in an outdoor wind tunnel. *International Journal of Wildland Fire* 23: 1097–1107.

Mason, N. W. H., C. Frazao, R. P. Buxton, and S. J. Richardson. 2016. Fire form and function: evidence for exaptive flammability in the New Zealand flora. *Plant Ecology* 217: 645–659.

Matthews, S., 2013. Dead fuel moisture research: 1991–2012. *International Journal of Wildland Fire* 23: 78-92.

Melia, N., S. Dean, H. G. Pearce, L. Harrington, D. J. Frame, and T. Strand. 2022. Aotearoa New Zealand's 21st-century wildfire climate. *Earth's Future* 10: e2022EF002853.

Melnik, O. M., S. A. Paskaluk, M. Y. Ackerman, K. O. Melnik, D. K. Thompson, S. S. McAllister, and M. D. Flannigan. 2021. New in-flame flammability testing method applied to monitor seasonal changes in live fuel. *Fire* 5: 1.

McWethy, D. B., P. E. Higuera, C. Whitlock, T. T. Veblen, D. M. J. S. Bowman, G. J. Cary, S. G. Haberle, R. E. Keane, B. D. Maxwell, M. S. McGlone, and G. L. W. Perry. 2013. A conceptual framework for predicting temperate ecosystem sensitivity to human impacts on fire regimes. *Global Ecology and Biogeography* 22: 900-912.

Menning, K. M., and S. L. Stephens. 2007. Fire climbing in the forest: a semiqualitative, semiquantitative approach to assessing ladder fuel hazards. *Western Journal of Applied Forestry* 22: 88–93.

Miller, L., L. Zhu, M. Yebra, C. Rüdiger, and G. I. Webb. 2023. Projecting live fuel moisture content via deep learning. *International Journal of Wildland Fire* 32: 709-727.

Mitić, Z. S., S. Č Jovanović, B. K. Zlatković, B. M. Nikolić, G. S. Stojanović, and P. D. Marin. 2017. Needle terpenes as chemotaxonomic markers in *Pinus*: Subsections Pinus and Pinaster. *Chemistry & Biodiversity* 14: e1600453.

Mitsopoulos, I. D., and A. P. Dimitrakopoulos. 2007. Canopy fuel characteristics and potential crown fire behavior in Aleppo pine (*Pinus halepensis* Mill.) forests. *Annals of Forest Science* 64: 287–299.

Murray, B. R., L. K. Hardstaff, and M. L. Phillips. 2013. Differences in leaf flammability, leaf traits and flammability-trait relationships between native and exotic plant species of dry sclerophyll forest. *PLoS One* 8: e79205.

Murray B. R., T. Hawthorne, T. J. Curran, D. W. Krix, M. I. Wallace, K. Young, M. L. Murray, E. Morley, N. Huber-Smith, J. K. Webb. 2023. Shoot flammability patterns among plant species of the wildland-urban interface in the fire-prone Greater Blue Mountains World Heritage Area. *International Journal of Wildland Fire* 32: 1119–1134.

Mutch, R. W. and Philpot, C. W., 1970. Relation of silica content to flammability in grasses. *Forest Science* 16: 64-65.

Neilson, E. H., J. Q. D. Goodger, I. E. Woodrow, and B. L. Møller. 2013. Plant chemical defense: at what cost? *Trends in Plant Science* 18: 250–258.

Nelson Jr, R. M. 2000. Prediction of diurnal change in 10-h fuel stick moisture content. *Canadian*

Journal of Forest Research 30: 1071–1087.

Newberry, B. M., C. R. Power, R. C. Abreu, G. Durigan, D. R. Rossatto, and W. A. Hoffmann. 2020. Flammability thresholds or flammability gradients? Determinants of fire across savanna–forest transitions. *New Phytologist* 228: 910-921.

Nolan, R. H., M. M. Boer, V. Resco De Dios, G. Caccamo, and R. A. Bradstock. 2016. Large-scale, dynamic transformations in fuel moisture drive wildfire activity across southeastern Australia. *Geophysical Research Letters* 43: 4229–4238.

Nolan, R. H., B. Foster, A. Griebel, B. Choat, B. E. Medlyn, M. Yebra, N. Younes, and M. M. Boer. 2022. Drought-related leaf functional traits control spatial and temporal dynamics of live fuel moisture content. *Agricultural and Forest Meteorology* 319: 108941.

Nolan, R. H., J. Hedo, C. Arteaga, T. Sugai, and V. Resco De Dios. 2018. Physiological drought responses improve predictions of live fuel moisture dynamics in a Mediterranean forest. *Agricultural and Forest Meteorology* 263: 417–427.

Nowacki, G. J. and M. D. Abrams,. 2008. The demise of fire and "mesophication" of forests in the eastern United States. *BioScience* 58: 123-138.

Ocampo-Zuleta, K., J. G. Pausas, and S. Paula. 2024. FLAMITS: A global database of plant flammability traits. *Global Ecology and Biogeography* 33: 412-425.

Odion, D. C., M. A. Moritz, and D. A. DellaSala. 2010. Alternative community states maintained by fire in the Klamath Mountains, USA. *Journal of Ecology* 98: 96-105.

Ojeda, F., J. G. Pausas, and M. Verdú. 2010. Soil shapes community structure through fire. *Oecologia* 163: 729–735.

Ormeño, E., J. Ruffault, C. Gutigny, J. Madrigal, M. Guijarro, C. Hernando, and C. Ballini. 2020. Increasing cuticular wax concentrations in a drier climate promote litter flammability. *Forest Ecology and Management* 473: 118242.

Owens, M. K., C. D. Lin, C. A. Taylor, and S. G. Whisenant. 1998. Seasonal patterns of plant flammability and monoterpenoid content in *Juniperus ashei*. *Journal of Chemical Ecology* 24: 2115-2129.

Padullés Cubino, J., H. L. Buckley, N. J. Day, R. Pieper, and T. J. Curran. 2018. Community-level flammability declines over 25 years of plant invasion in grasslands. *Journal of Ecology* 106:

1582–1594.

Pagadala, T., M. A. Alam, T. M. Maxwell, and T. J. Curran. 2024. Measuring flammability of crops, pastures, fruit trees, and weeds: A novel tool to fight wildfires in agricultural landscapes. *Science of the Total Environment* 906: 167489.

Page, W. G., M. J. Jenkins, and J. B. Runyon. 2012. Mountain pine beetle attack alters the chemistry and flammability of lodgepole pine foliage. *Canadian Journal of Forest Research* 42: 1631–1647.

Papió, C., and L. Trabaud. 1990. Structural characteristics of fuel components of five Meditarranean shrubs. *Forest Ecology and Management* 35: 249–259.

Park, I., K. Fauss, and M.A. Moritz. 2022. Forecasting live fuel moisture of *Adenostema fasciculatum* and its relationship to regional wildfire dynamics across Southern California shrublands. *Fire* 5: 110.

Paula, S., D. P. Ramírez, S. Estay, and J. G. Pausas. 2024. Soil fertility shapes fire activity across Mediterranean-type climate regions. *Global Ecology and Biogeography* 33: 400–411.

Pausas, J. G., G. A. Alessio, B. Moreira, and J. G. Segarra-Moragues. 2016. Secondary compounds enhance flammability in a Mediterranean plant. *Oecologia* 180: 103–110.

Pausas, J. G., J. E. Keeley, and D. W. Schwilk. 2017. Flammability as an ecological and evolutionary driver. *Journal of Ecology* 105: 289-297.

Pausas, J. G. ~~B.~~ and B. Moreira. 2012. Flammability as a biological concept. *New Phytologist* 194: 610-613.

Penman, T. E., J. G. Cawson, S. Murphy, and T. J. Duff. 2017. Messmate stringybark: bark ignitability and burning sustainability in relation to fragment dimensions, hazard score and time since fire. *International Journal of Wildland Fire* 26: 866–876.

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

Philpot C. W. ~~(~~ 1970~~)~~. Influence of mineral content on the pyrolysis of plant materials. *Forest~~.~~ Science*. 16: 461–71.

Pickett, B. M., Smith, S. G., Fletcher, T. H. and D. R. Weise~~, D.R.,~~ 2005, October. Burning characteristics of live California chaparral and Utah leaf samples. In Sixth Symposium on Fire and Forest Meteorolo, J. L. Welty, and R. S. Arkle. 2017. Refining the cheatgrass–fire cycle in the Great Basin: Precipitation timing and fine fuel composition predict wildfire trends. *Ecology and Evolution* 7: 8126–8151.

Pickering, B. J., L. T. Bennett, and J. G. Cawson. 2023. Extending methods for assessing fuel hazard in temperate Australia to enhance data quality and consistency. *International Journal of Wildland Fire* 32: 1422-1437.

Pilliod, D. S., ~~J.L.~~ J. L. Welty, and R.S. ~~and~~ Arkle. 2017. Refining the cheatgrass–fire cycle in the Great Basin: Precipitation timing and fine fuel composition predict wildfire trends. *Ecology and Evolution* 7: 8126-8151.

Pimont, F., J. Ruffault, N. K. Martin-StPaul, and J. L. Dupuy. 2019. Why is the effect of live fuel moisture content on fire rate of spread underestimated in field experiments in shrublands?. *International Journal of Wildland Fire* 28: 127-137.

Plucinski, M. P., and W. R. Anderson. 2008. Laboratory determination of factors influencing successful point ignition in the litter layer of shrubland vegetation. *International Journal of Wildland Fire* 17: 628–637.

Popović, Z., S. Bojović, M. Marković, and A. Cerdà. 2021. Tree species flammability based on plant traits: A synthesis. *Science of The Total Environment* 800: 149625.

Potts, E., D. Tng, D., D. Apgaua, T. J. Curran, J. Engert, and S. G. Laurance. 2022. Growth form and functional traits influence the shoot flammability of tropical rainforest species. *Forest Ecology and Management* 522: 120485.

Price, O. F., and C. E. Gordon. 2016. The potential for LiDAR technology to map fire fuel hazard over large areas of Australian forest. *Journal of Environmental Management* 181: 663–673.

Prior, L. D., B. P. Murphy, and D. M. Bowman. 2018. Conceptualizing ecological flammability: An experimental test of three frameworks using various types and loads of surface fuels. *Fire* 1:14.

Prior, L. D., B. P. Murphy, G. J. Williamson, M. A. Cochrane, W. M. Jolly, and D. M. J. S. Bowman. 2017. Does inherent flammability of grass and litter fuels contribute to continental patterns of landscape fire activity? *Journal of Biogeography* 44: 1225–1238.

Prior, L. D., K. Storey, G. J. Williamson, and D. M. J. S. Bowman. 2024. When soil becomes fuel:

identifying a safe window for prescribed burning of Tasmanian vegetation growing on organic soils. *International Journal of Wildland Fire* 33: WF24061.

Pyne, S. J. Introduction to Wildland Fire: Fire Management in the United States. John Wiley & Sons: New York, NY, USA, 1984.

Rahman, N. E. B., S. W. Smith, W. N. Lam, K. Y. Chong, M. S. E. Chua, P. Y. Teo, D. W. J. Lee, et al. 2023. Leaf decomposition and flammability are largely decoupled across species in a tropical swamp forest despite sharing some predictive leaf functional traits. *New Phytologist* 238: 598–611.

Rao, K., Williams, A. P., Diffenbaugh, N. S., Yebra, M. and Konings, A.G., 2022. Plant-water sensitivity regulates wildfire vulnerability. *Nature Ecology & Evolution* 6: 332-339.

Rao, K., A.P. Williams, ~~A.P.,~~N. S. Diffenbaugh, ~~N.S.,~~M. Yebra, ~~M.,~~C. Bryant, ~~C.~~ and A. G. Konings~~, A.G.,~~. 2023. Dry live fuels increase the likelihood of lightning-caused fires. *Geophysical Research Letters* 50: p.e2022GL100975.

Rossa, C. G. and P. M. Fernandes. 2018. Live fuel moisture content: The ‘pea under the mattress’ of fire spread rate modeling? *Fire* 1: 43.

Reed, W. P., J. M. Varner, E. E. Knapp, and J. K. Kreye. 2020. Long-term changes in masticated woody fuelbeds in northern California and southern Oregon, USA. *International Journal of Wildland Fire* 29: 807-819.

Reilly, S., M. L. Clark, L. Loechler, J. Spillane, M. Kozanitas, P. Krause, D. Ackerly, et al. 2024. Unoccupied aerial system (UAS) Structure-from-Motion canopy fuel parameters: Multisite area-based modelling across forests in California, USA. *Remote Sensing of Environment* 312: 114310.

Rogers, B. M., A. J. Soja, M. L. Goulden, and J. T. Randerson. 2015. Influence of tree species on continental differences in boreal fires and climate feedbacks. *Nature Geoscience* 8: 228–234.

Rollins, M. G., C. Rodriguez-Franco, T. Haan, and S. Conard. 2017. Research and development wildland fire and fuels accomplishments and outcomes. U.S.D.A. Forest Service report FS-1086. Washington, DC.

Rothermel, R. C. 1972. A mathematical model for predicting fire spread in wildland fuels. USDA Forest Service, Intermountain Forest and Range Experiment Station, Research Paper RP-INT-15.

Ogden, UT)

Rothermel, R. C., R. A. Wilson, G. A. Morris, and S. S. Sackett. 1986. Modeling moisture content of fine dead wildland fuels: input to the BEHAVE fire prediction system. USDA Forest Service, Intermountain Forest and Range Experiment Station, Research Paper RP-INT-359. Ogden, UT.

Salisbury, F. B., and C.W. Ross. 1992. Plant physiology. Fourth edition. Wadsworth, California.

Santacruz-García, A. C., S. Bravo, F. del Corro, F. and Ojeda. 2019. A comparative assessment of plant flammability through a functional approach: The case of woody species from Argentine Chaco region. *Austral Ecology* 44: 1416-1429.

Saura-Mas, S., S. Paula, J. G. Pausas, and F. Lloret. 2010. Fuel loading and flammability in the Mediterranean Basin woody species with different post-fire regenerative strategies. *International Journal of Wildland Fire* 19: 783–794.

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

Scarff, F. R., T. Lenz, A. E. Richards, A. E. Zanne, I. J. Wright, and M. Westoby. 2021. Effects of plant hydraulic traits on the flammability of live fine canopy fuels. *Functional Ecology* 35: 835–846.

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

Scarff, F. R., and M. Westoby. 2008. The influence of tissue phosphate on plant flammability: A kinetic study. *Polymer Degradation and Stability* 93: 1930–1934.

Schlaeppi, K., J. J. Gross, S. Hapfelmeier, and M. Erb. 2021. Plant chemistry and food web health. *New Phytologist* 231: 957–962.

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

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

Schwilk, D. W. and A. C. Caprio. 2011. Scaling from leaf traits to fire behaviour: community composition predicts fire severity in a temperate forest. J*ournal of Ecology* 99: 970-980.

Scott, J. H. and R. E. Burgan. 2005. Standard fire behavior fuel models: a comprehensive set for use with Rothermel's surface fire spread model. General Technical Report RMRS-GTR-153. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fort Collins, CO.

Simpson, K. J., S. Archibald, and C. P. Osborne. 2022. Savanna fire regimes depend on grass trait diversity. *Trends in Ecology & Evolution* 37: 749–758.

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

Smith, A. M. S., W. T. Tinkham, D. P. Roy, L. Boschetti, R. L. Kremens, S. S. Kumar, A. M. Sparks, and M. J. Falkowski. 2013. Quantification of fuel moisture effects on biomass consumed derived from fire radiative energy retrievals. *Geophysical Research Letters* 40: 6298–6302.

Stenzel. J. E., K. J. Bartowitz, M. D. Hartman, J. A. Lutz, A. M. S. Smith, C. A. Kolden, B. E. Law, M. E. Swanson, A. J. Larson, W. J. Parton. and T. W. Hudiburg. 2019. Fixing a snag in estimating carbon emissions from wildfires. *Global Change Biology* 25: 3985-3994.

Sullivan, A. L. 2009a. Wildland surface fire spread modelling, 1990 - 2007. 1: Physical and quasi-physical models. *International Journal of Wildland Fire* 18: 349–368.

Sullivan, A. L. 2009b. Wildland surface fire spread modelling, 1990 - 2007. 2: Empirical and quasi-empirical models. *International Journal of Wildland Fire* 18: 369–386.

Sullivan, A. L. 2009c. Wildland surface fire spread modelling, 1990 - 2007. 3: Simulation and mathematical analogue models. *International Journal of Wildland Fire* 18: 387–403.

Terrah, S. M., F. Z. Sabi, O. Mosbah, A. Dilem, N. Hamamousse, A. Sahila, O. Harrouz, H. Boutchiche, F. Chaib, N. Zekri, and A. Kaiss. 2020. Nonexistence of critical fuel moisture content for flammability. *Fire Safety Journal* 111: 102928.

Talhelm, A. F., and A. M. S. Smith. 2018. Litter moisture adsorption is tied to tissue structure, chemistry, and energy concentration. *Ecosphere* 9: e02198.

Tarifa, C. S., P. P. Del Notario, and F. G. Moreno. 1965. On the flight paths and lifetimes of burning particles of wood. In: *Symposium (International) on Combustion* 10,1:1021-1037. https://doi.org/10.1016/S0082-0784(65)80244-2

Tumino, B. J., T. J. Duff, J. Q. D. Goodger, and J. G. Cawson. 2019. Plant traits linked to field-scale flammability metrics in prescribed burns in Eucalyptus forest. *PLoS One* 14: e0221403.

Turetsky, M. R., B. Benscoter, S. Page, G. Rein, G. R. Van Der Werf, and A. Watts. 2015. Global vulnerability of peatlands to fire and carbon loss. *Nature Geoscience* 8: 11–14.

Turner, I. M. 1994. Sclerophylly: Primarily Protective? *Functional Ecology* 8: 669–675.

Van Altena C., R. S. van Logtestijn, W. K. Cornwell, and J. H. Cornelissen. 2012. Species composition and fire: non-additive mixture effects on ground fuel flammability. *Frontiers in Plant Science* 3: 63.

Van Der Plas, F., T. Schröder-Georgi, A. Weigelt, K. Barry, S. Meyer, A. Alzate, R. L. Barnard, et al. 2020. Plant traits alone are poor predictors of ecosystem properties and long-term ecosystem functioning. *Nature Ecology & Evolution* 4: 1602–1611.

Van Wilgen, B. W., K. B. Higgins, and D. U. ~~and~~ Bellstedt. 1990. The role of vegetation structure and fuel chemistry in excluding fire from forest patches in the fire-prone fynbos shrublands of South Africa. *Journal of Ecology* 78: 210-222.

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

Varner, J. M., H. G. Kuljian and J. K. Kreye. 2017. Fires without tanoak: the effects of a non-native disease on future community flammability. *Biological Invasions* 19: 2307-2317.

Varner, J. M., T. M. Shearman, J. M. Kane, E. M. Banwell, E. S. Jules, and M. C. Stambaugh. 2022. Understanding flammability and bark thickness in the genus *Pinus* using a phylogenetic approach. *Scientific Reports* 12(1): 1–10.

Viney, N. 1991. A review of fine fuel moisture modelling. *International Journal of Wildland Fire* 1: 215–234.

Walker, X. J., J. L. Baltzer, S. G. Cumming, N. J. Day, C. Ebert, S. Goetz, J. F. Johnstone, et al. 2019. Increasing wildfires threaten historic carbon sink of boreal forest soils. *Nature* 572: 520-523.

Wei, P., L. Tang, Z. Xiong, B.B. Lamont, L. Chen, W. Xue, Z. Zhao, W. Lu, J. Han, W. He, W. Yang, and Z. Yan. 2025. Non-additive effects of leaf-litter flammability on eight subtropical tree species: Implications for forest species composition and fire susceptibility. *Journal of Environmental Management* 374: 124053.

Weise, D. R., E. Koo, X. Zhou, S. Mahalingam, F. Morandini, and J.-H. Balbi. 2016. Fire spread in chaparral – a comparison of laboratory data and model predictions in burning live fuels. *International Journal of Wildland Fire* 25: 980–994.

Weise, D. R., R. H. White, F. C. Beall, and M. Etlinger. 2005. Use of the cone calorimeter to detect seasonal differences in selected combustion characteristics of ornamental vegetation. *International Journal of Wildland Fire* 14: 321–338.

White, R. H., and W. C. Zipperer. 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.

Wickramasinghe, A. M. K., M. M. Boer, C. X. Cunningham, R. H. Nolan, D. M. J. S. Bowman, and G. J. Williamson. 2024. Modeling the probability of dry lightning-induced wildfires in Tasmania: a machine learning approach. *Geophysical Research Letters* 51: e2024GL110381.

Wood, S. W., and D. M. J. S. Bowman. 2012. Alternative stable states and the role of fire–vegetation–soil feedbacks in the temperate wilderness of southwest Tasmania. *Landscape Ecology* 27: 13–28.

Wyse, S. V., G. L. Perry, D. M. O'Connell, P. S. Holland, M. J. Wright, C. L. Hosted, S. L. Whitelock, I. J. Geary, K. J. Maurin, and T. J. Curran. 2016. A quantitative assessment of shoot flammability for 60 tree and shrub species supports rankings based on expert opinion. I*nternational Journal of Wildland Fire* 25: 466-477.

Wyse, S. V., G. L. W. Perry, and T. J. Curran. 2018. Shoot-level flammability of species mixtures is driven by the most flammable species: implications for vegetation-fire feedbacks favouring invasive species. *Ecosystems* 21: 886–900.

Xanthopoulos, G., and R. H. Wakimoto. 1993. A time to ignition–temperature–moisture relationship for branches of three western conifers. *Canadian Journal of Forest Research* 23: 253–258.

Younes, N., M. Yebra, M. M. Boer, A. Griebel, and R. H. Nolan. 2024. A review of leaf-level flammability traits in eucalypt trees. *Fire* 7: 183.

Zanzarini, V., A. N. Andersen, and A. Fidelis. 2022. Flammability in tropical savannas: Variation among growth forms and seasons in Cerrado. *Biotropica* 54: 979–987.

Zhao, L., M. Yebra, A. I. van Dijk, G. J. Cary, and D. Hughes. 2022. Controlled field experiment clarifies the influence of soil moisture on litter moisture content. *Agricultural and Forest*

Meteorology 314: 108782.

Zigner, K., L. M. V. Carvalho, S. Peterson, F. Fujioka, G.-J. Duine, C. Jones, D. Roberts, and M. Moritz. 2020. Evaluating the ability of FARSITE to simulate wildfires influenced by extreme, downslope winds in Santa Barbara, California. *Fire* 3: 29.

Zylstra, P., R. A. Bradstock, M. Bedward, T. D. Penman, M. D. Doherty, R. O. Weber, A. M. Gill, and G. J. Cary. 2016. Biophysical mechanistic modelling quantifies the effects of plant traits on fire severity: species, not surface fuel loads, determine flame dimensions in eucalypt forests. *PLoS One* 11: e0160715.

Box 1

Term	Definition	How is it measured?
Bottom-up approach	The assessment of species-specific flammability traits.	Laboratory trials
Combustibility	Component of flammability that accounts for the intensity of burning.	Measured variously as the highest temperature measured during burning, flame height, flame spread rate, and mass loss rate
Consumability	Component of flammability that accounts for how much of a plant is burned by fire.	Measured as the percentage of burnt biomass once combustion has finished
Fire behavior	How a fire reacts to the environment, including its spread, intensity, and how it consumes fuel.	In flammability trials: as individual components described here. In wildfire: from direct observations, remote sensing, and post-fire estimation of severity metrics.
Fire propagation	Spread of fire across a landscape	Measured as rate of spread in laboratory or field. See also measures of post-fire heterogeneity and fire perimeters
Flammability	The ability of a material to burn that includes how easy it is to ignite, the intensity at which it burns, the length of time it burns, and the percentage of material consumed by fire.	Measured in terms of combustability, consumability, ignitibility and sustainability. See these measurements in the glossary.
Fuel architecture	The size, shape, volumetric arrangement, and distribution of fuel materials that burn during wildfires	Measured in the field for the broad fuel assemblage as compaction, bulk density, and ladder fuel presence. Can also be species-specific (e.g., degree to which airflow is impeded by branches and leaves).
Fuel load	Total combustable material per unit area	Lidar/remote sensing, as well as field survey methods.
Fuel moisture	The amount of water content in plant material, affecting its likelihood of igniting and burning.	Commonly quantified in small branches for live fuels, or from litter samples
Ignitibility	Component of flammability that accounts for ease with which a plant begins to burn when exposed to an ignition source.-.	Measured as either the time to first burning from exposure or the frequency of ignition events among a set of samples
Plant traits	Measurable characteristic (e.g. architectural, morphological, phenological, physiological,	Variously. See, for example, Cornelissen et al (2003)

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	chemical) to describe components of flammability	
Sustainability	Component of flammability that accounts for how long a plant continues to burn after ignition, with or without an external heat source.	Measured as as the duration of combustion and can include durations of incandescence, flaming, and smoldering
Top-down approach	Treats plants as broad vegetation types or fuel types and focuses on those plant or fuel characteristics.	Remote sensing tools often used

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~~Figure 1~~

Figure 1. Illustration of methods used to assessed fuel characteristics (moisture, architecture, chemistry and mass) across a range of scales from individual plant organs or excised parts to communities and landscapes. Remote sensing, field measurements, and laboratory work are each suited to assessment of fuel characteristics at different but overlapping portions of this range, thereby creating opportunities to synthesize the "top-down" and "bottom-up" approaches to understanding flammability.