



# Litter Flammability of 50 Southeastern North American Tree Species: Evidence for Mesophication Gradients Across Multiple Ecosystems

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Widespread fire exclusion and land-use activities across many southeastern United States forested ecosystems have resulted in altered species composition and structure. These changes in composition and structure have been implicated in positive fire-vegetation feedbacks termed “mesophication” where fire spread and intensity are diminished. In forests and woodlands, inherent flammability of different species is the mechanistic driver of mesophication. To date, there has been limited work on documenting the high diversity of flammability among species in the region, limiting the ability to differentiate among species to restore fuels that sustain fire regimes. Here, we coalesce disparate flammability data and add missing species across the spectrum from species that facilitate fire (so called “pyrophytes”) to those that dampen fire (so called “mesophytes”). We present data on 50 important tree species from across the southeast, all burned using identical laboratory methods. We divide our results for four dominant ecosystems: Coastal Plain uplands, oak-hickory woodlands, Appalachian forests, and bottomland forests. Across ecosystems, the most flammable species were American chestnut (*Castanea dentata*), a suite of pines (*Pinus palustris*, *P. elliotii*, *P. serotina*, and *P. rigida*), several oaks (*Q. laevis*, *Q. falcata*, *Q. margaretta*, and *Q. alba*), and sourwood (*Oxydendrum arboreum*). At the mesophytic end, the least flammable species were *Tsuga canadensis*, *Acer rubrum*, and several other hardwoods previously implicated in mesophication. Each of the four ecosystems we studied contained species that spanned the pyrophytic to mesophytic gradient. These data fill in some key holes in our understanding of southeastern fire adaptations, but also provide context for restoration decisions and fire management prioritization efforts to restore and sustain fire-prone ecosystems of the region.

**Keywords:** *Acer rubrum*, fire-adapted traits, fire regimes, fuels, mesophication, *Pinus*, *Quercus*

## INTRODUCTION

Widespread fire exclusion and land-use change have resulted in dramatic impacts on species composition, structure, and ecological processes of many fire-prone terrestrial ecosystems. Many fire-adapted forested landscapes in North America, e.g., pine forests and oak woodlands, were cut over in the late 19th and early 20th century and fires were actively suppressed during recovery (MacCleery, 1993; Frost, 1998). The removal of fire from these ecosystems led to the establishment of fire-sensitive tree species into formerly fire-prone landscapes, altering species composition dramatically (Fei and Steiner, 2007; Nowacki and Abrams, 2008; Knott et al., 2019). The recruitment of fire-sensitive mesophytes coincided with increasing tree density, the formation of heavily shaded, multi-canopied forests, and development of moist forest floor conditions that resist ignition (Kreye et al., 2018a,b). This positive feedback phenomenon has been widely observed and is commonly referred to as “mesophication” (Nowacki and Abrams, 2008; Hanberry et al., 2020; Alexander et al., 2021).

Fires were very frequent across much of the southeastern United States (Stambaugh et al., 2011, 2015; Lafon et al., 2017) as reflected in the extent and diversity of fire-tolerant plant communities (Frost, 1998; Platt, 1999). In spite of the clear evidence of frequent fire and numerous species that are enhanced by fire, substantial gaps remain in the understanding of fire-related traits across tree species in the region. Protective traits such as thick bark and rapid wound closure allow fire-tolerant species to persist in fire-prone landscapes (Landers, 1991; Jackson et al., 1999; Romero et al., 2009; Varner et al., 2016). Flammability of forest litter is also a key component in fire-prone landscapes as it supports the fire regimes under which fire-tolerant or pyrophytic (hereafter simply pyrophyte) species persist (Kane et al., 2008). Recent studies have highlighted how flammable litter often corresponds with fire tolerance at the species level and may itself be a fire-adapted trait (Varner et al., 2016; Stevens et al., 2020; Varner et al., in review). Field measurements in forests, woodlands, and savannas validate the relative importance of senesced litter as the primary mechanistic driver of surface fire behavior (Wenk et al., 2011; Whelan et al., 2021).

Several studies have evaluated litter flammability of southeastern United States tree species. The majority of these studies follow standard methods as in Fonda (2001), burning single species in controlled environments (Fonda, 2001; Fonda and Varner, 2004; Kane et al., 2008, 2019, 2021; Mola et al., 2014; Varner et al., 2015a; Varner et al., in review). From these, the diverse southeastern tree flora is represented by only ca. 30 species, primarily pines and oaks. Several important tree species implicated in mesophication (e.g., *Acer rubrum*, *Nyssa sylvatica*, *Tilia americana*, and *Ostrya virginiana*) and other species thought to represent the pyrophytic end of the flammability spectrum (*Carya* spp. and other *Quercus* spp.) have yet to be evaluated. Beyond the missing species, there has been no synthetic compilation of these species.

In order to fill some of the gaps in our understanding of litter flammability of southeastern United States tree species, we conducted litter flammability experiments on a suite of

species not yet studied and compiled them with published data from species examined using the same methods. The objectives of this study were to (1) synthesize litter flammability of ca. 50 southeastern tree species and (2) examine how litter flammability differs across the mesophyte-to-pyrophyte spectrum. We hypothesized that litter of pyrophytic species would be more flammable than mesophytic species. We tested this global hypothesis for each of four ecosystems where these species are important (Coastal Plain uplands, oak-hickory woodlands, Appalachian forests, and bottomland forests; **Figure 1**). Results are expected to elucidate flammability as a potential fire-adapted trait among pyrophytic species whereas dampened flammability among mesophytic species acts as a mechanism for the hypothesized mesophication of southeastern oak and pine forests resulting from decades of fire exclusion.

## MATERIALS AND METHODS

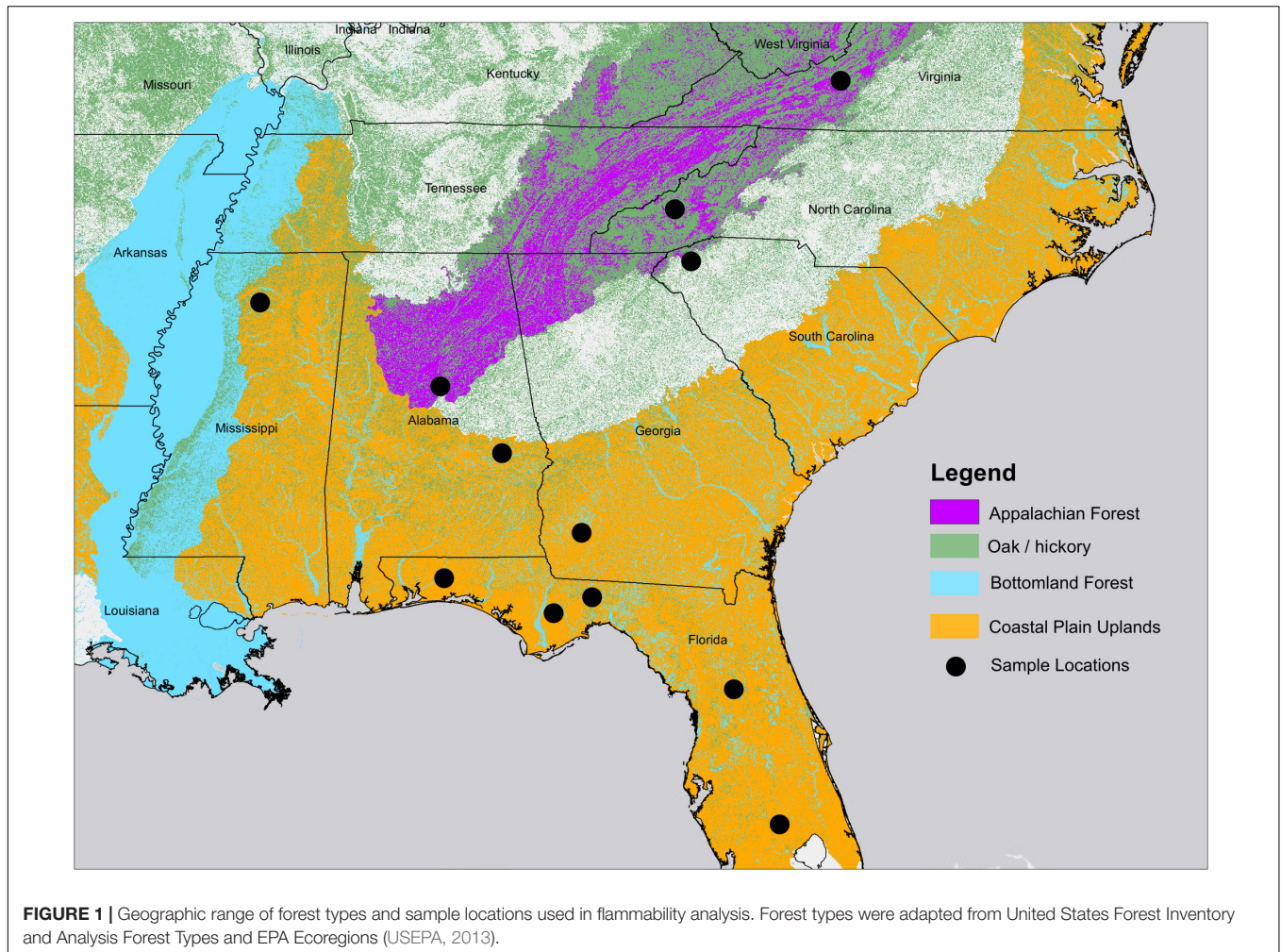
We combined published litter flammability data using the laboratory combustion methods of Fonda (2001) with new observations from recently collected litter from the region (**Table 1** and **Figure 1**). All published and new litter flammability experiments were conducted using identical methods and in the same laboratory. For all species, we collected freshly fallen litter (i.e., no signs of decomposition; Oi horizon) beneath several individual trees, with each sample serving as an independent replicate. All collected litter was shipped to the Humboldt State University Wildland Fire Laboratory for burning.

### Laboratory Burning

Litter flammability experiments, for each species separately, were conducted using established methods (Fonda, 2001). Litter samples were oven-dried at 50–60°C for at least 24 h until no further weight loss occurred. Each 15 g (dry weight) litter fuelbed was evenly distributed within a 35 cm × 35 cm lattice of xylene-soaked cotton strings on a stainless-steel platform. A 2.75 m × 2.75 m fume hood above the platform generated a constant draw of 15–20°C s<sup>-1</sup>, though no airflow was detected at the fuelbed. Burn trials were repeated five to seven times for each species. Strings were ignited from all sides and a timer was started once litter ignited. Maximum flame height was visually estimated to the nearest cm using a vertical ruler placed behind the burning platform. Flaming time was measured as the duration from litter ignition to flaming extinction, and smoldering time was measured as the duration from flaming extinction to smoldering extinction (no visible smoke and no glowing combustion observed under darkened conditions). Both flaming time and smoldering time were recorded to the nearest second. Percent litter consumption was calculated as the proportion of the initial litter mass (15 g) that was consumed, measured following extinction of smoldering (and removing unburned string). We used flame height measurements to calculate fireline intensity (Byram, 1959) using the equation:

$$I = 258 * h^{2.17} \quad (1)$$

where  $I$  is fireline intensity (kW m<sup>-1</sup>) and  $h$  is flame height (m).



## Data Analysis

Flammability metrics from all published and newly collected species were combined using Principal Components Analysis (PCA). PCA is used because flammability metrics are often highly correlated (e.g., species with rapid flaming times tend to burn with tall flames; Varner et al., 2015b). For all analyses, we first log transformed the four flammability metrics (flame height, flaming time, smoldering time, and percent consumed) to reduce the effect of outliers in the data. We standardized (mean = 0, SD = 1) four flammability metrics: flame height, flaming time, smoldering time, and percent consumed. Outliers in the transformed data were detected by calculating the maximum median absolute deviation for each species and principal component then using the departure from histogram method in the R package “bigutilsr” to identify outliers (Privé, 2021). Each PCA was re-fit after outliers were removed. Principal components that had eigenvalues greater than 1 and where cumulative variance explained was 70% were retained for further evaluation (Affifi and Clark, 1996). We then conducted a k-means cluster analysis to group species clusters of similar flammability. The number of clusters selected in the analyses was determined by plotting the within cluster sum of squares with increasing number of clusters

and identifying the “bend” in the curve at which increasing the number of clusters does not markedly decrease the within cluster sum of squares. All analyses were conducted in R version 4.0.3 (R Core Team, 2020).

Given the number of species and the diversity of ecosystems in the region, we performed PCA for each ecosystem. The four ecosystems were: Coastal Plain uplands; oak-hickory woodlands; Appalachian forests; and bottomland forests. Coastal plain uplands span a wide longitudinal and latitudinal gradient in the region, from Texas to Virginia (and beyond along the Atlantic coastal plain) and are characterized by frequent fires (Stambaugh et al., 2011, 2017; Rother et al., 2020) on the order of 1–5 years in woodlands and savannas and by longer intervals (ca. 50–100 years) in pine-oak scrub forests (Menges, 1999). Oak-hickory woodlands are widespread and often linked with the central hardwood region. Fire regimes in these ecosystems are characterized by frequent surface fires ca. 2–10 years and longer (Hart and Buchanan, 2012; Stambaugh et al., 2015). Appalachian forests span from the mountains of northern Alabama and Georgia to the northern limits of the region, have high species diversity, and diverse fire regimes dependent on landscape position (Lafon et al., 2017). Bottomland forests have high

**TABLE 1** | List of all 50 southeastern tree species burned in these experiments.

Scientific name and authority	Common name	Family	Source <sup>†</sup>
<i>Acer rubrum</i> L.	Red maple	Aceraceae	1
<i>Castanea dentata</i> (Marshall) Borkh.	American chestnut	Fagaceae	2
<i>Cornus florida</i> L.	Flowering dogwood	Cornaceae	3
<i>Carya glabra</i> (Mill.) Sweet	Pignut hickory	Juglandaceae	1
<i>Carya tomentosa</i> (Lam.) Nutt.	Mockernut hickory	Juglandaceae	1
<i>Fagus grandifolia</i> Ehrh.	American beech	Fagaceae	3
<i>Ilex opaca</i> Aiton	American holly	Aquifoliaceae	3
<i>Liquidambar styraciflua</i> L.	Sweetgum	Hammamelidaceae	3
<i>Liriodendron tulipifera</i> L.	Tuliptree	Magnoliaceae	3
<i>Magnolia grandiflora</i> L.	Southern magnolia	Magnoliaceae	3
<i>Magnolia virginiana</i> L.	Sweetbay	Magnoliaceae	1
<i>Nyssa sylvatica</i> Marshall	Blackgum	Cornaceae	1
<i>Oxydendrum arboreum</i> (L.) DC.	Sourwood	Ericaceae	1
<i>Ostrya virginiana</i> (Mill.) K. Koch	Hophornbeam	Betulaceae	3
<i>Pinus clausa</i> (Chapm. ex Englem.) Vasey ex Sarg, ssp. <i>clausa</i>	Ocala sand pine	Pinaceae	1
<i>Pinus clausa</i> (Chapm. ex Englem.) Vasey ex Sarg, ssp. <i>immuginata</i>	Sand pine	Pinaceae	1
<i>Pinus echinata</i> Mill.	Shortleaf pine	Pinaceae	1
<i>Pinus elliotii</i> Englem. var. <i>densa</i> Little & Dorman	Florida slash pine	Pinaceae	4
<i>Pinus elliotii</i> Englem.	Slash pine	Pinaceae	1
<i>Pinus glabra</i> Walter	Spruce pine	Pinaceae	3
<i>Pinus palustris</i> Mill.	Longleaf pine	Pinaceae	4
<i>Pinus pungens</i> Lamb.	Table Mountain pine	Pinaceae	1
<i>Pinus rigida</i> Mill.	Pitch pine	Pinaceae	1
<i>Pinus serotina</i> Michx.	Pond pine	Pinaceae	4
<i>Pinus strobus</i> L.	Eastern white pine	Pinaceae	1
<i>Prunus serotina</i> Ehrh.	Black cherry	Rosaceae	1
<i>Quercus alba</i> L.	White oak	Fagaceae	1
<i>Quercus coccinea</i> Münchh.	Scarlet oak	Fagaceae	1
<i>Quercus falcata</i> Michx.	Southern red oak	Fagaceae	5
<i>Quercus geminata</i> Small	Sand live oak	Fagaceae	5
<i>Quercus hemisphaerica</i> W. Bartram ex Willd.	Darlington oak	Fagaceae	5
<i>Quercus incana</i> W. Bartram	Bluejack oak	Fagaceae	5
<i>Quercus laevis</i> Walter	Turkey oak	Fagaceae	5
<i>Quercus margaretta</i> (Ashe) Small	Sand post oak	Fagaceae	5
<i>Quercus marilandica</i> Münchh.	Blackjack oak	Fagaceae	1
<i>Quercus michauxii</i> Nutt.	Swamp chestnut oak	Fagaceae	1
<i>Quercus montana</i> Willd.	Chestnut oak	Fagaceae	1
<i>Quercus nigra</i> L.	Water oak	Fagaceae	5
<i>Quercus phellos</i> L.	Willow oak	Fagaceae	1
<i>Quercus rubra</i> L.	Northern red oak	Fagaceae	1
<i>Quercus stellata</i> Wagenh.	Post oak	Fagaceae	5
<i>Quercus virginiana</i> Mill.	Live oak	Fagaceae	5
<i>Sassafras albidum</i> (Nutt.) Nees	Sassafras	Lauraceae	1
<i>Tilia americana</i> L.	American basswood	Tiliaceae	1
<i>Tsuga canadensis</i> (L.) Carrière	Eastern hemlock	Pinaceae	1
<i>Taxus floridana</i> Nutt. ex Chapm.	Florida yew	Taxaceae	3
<i>Tbireya taxifolia</i> Arn.	Florida nutmeg	Taxaceae	3
<i>Taxodium distichum</i> (L.) Rich.	Bald cypress	Cupressaceae	1

All taxonomy according to the USDA Plants database ([plants.sc.egov.usda.gov](http://plants.sc.egov.usda.gov)).

<sup>†</sup>Source refers to data source used in this analysis, where 1, collections made for this paper; 2, Kane et al. (2019); 3, Mola et al. (2014); 4, Fonda (2001); and 5, Fonda and Varner (2004).

overstory species diversity and follow major alluvial valleys and incised floodplains across the region. Fires in these ecosystems are rare, occurring perhaps on the order of 50–100 or more years between fires (Harper, 1911; Platt and Schwartz, 1990).

## RESULTS

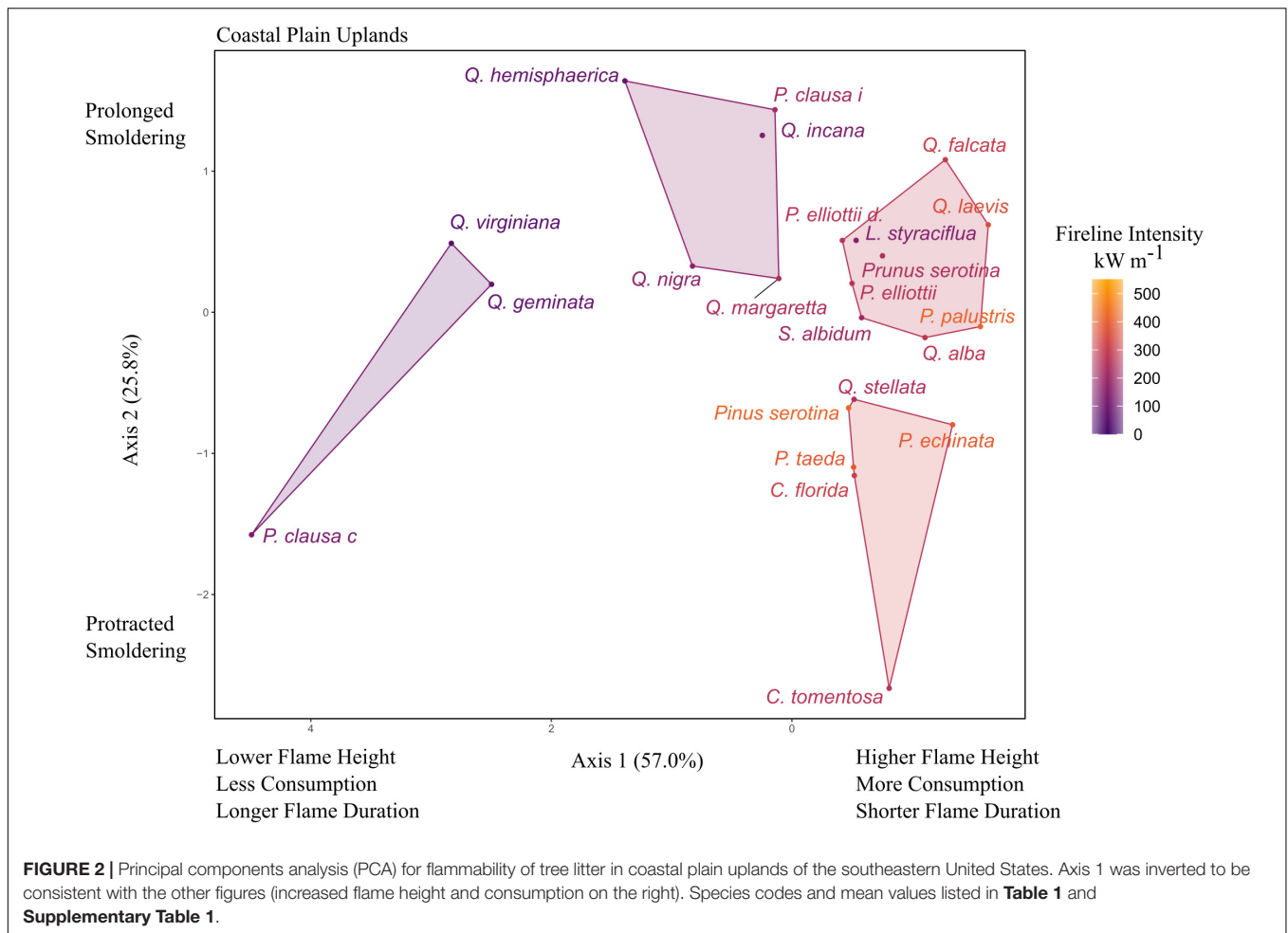
Litter from the 50 southeastern tree species varied widely in their flammability. Notable among the most flammable species were the fire-tolerant pines (*Pinus palustris*, *P. serotina*, *P. echinata*, *P. taeda*, and *P. rigida*) and several oaks (*Quercus laevis*, *Q. falcata*, and *Q. alba*), American chestnut (*Castanea dentata*), and sourwood (*Oxydendrum arboreum*). The species with the least flammable litter were two endemic conifers (*Torreya taxifolia* and *Taxus floridana*), *Tsuga canadensis*, *Pinus clausa* var. *clausa*, and two evergreen oaks (*Q. virginiana* and *Q. geminata*). The classic mesophytes *Acer rubrum*, *Tilia americana*, *Liquidambar styraciflua*, and *Nyssa sylvatica* tended to burn with low flammability. We detail community-specific flammability below and list all species and their mean flammability values in **Supplementary Table 1**.

### Coastal Plain Uplands

The 23 tree species in the coastal plain upland community spanned a wide flammability gradient (**Figure 2**). The first two principal components accounted for 82.8% of the variance, with axis 1 and 2 having eigenvalues of 2.28 and 1.03, respectively. Axis 1 was correlated with flame height (−0.53), and percent consumption (−0.63) as well as flaming time (0.53). Axis 2 was mostly correlated with smoldering time (−0.92). *P. clausa* var. *clausa* (Ocala sand pine) appeared to be an outlier with short smoldering time but was left in the analysis because it did not meet our criteria for removal. Fireline intensity ranged from 53 kW m<sup>−1</sup> (*Q. virginiana*) to 419 kW m<sup>−1</sup> (*Pinus serotina*). The k-means cluster analysis suggested four groups which explained approximately 80.3% of the variance of the ordination. A tall flaming, long smoldering group consisted of pines (*P. palustris*, *P. elliotii* var. *elliotii* and var. *densa*), oaks (*Q. alba*, *Q. laevis*, and *Q. falcata*), as well as *Liquidambar styraciflua*, *Sassafras albidum*, and *Prunus serotina*. A tall flaming, brief smoldering group also consisted of pines (*P. echinata*, *P. serotina*, and *P. taeda*), as well as *Q. stellata*, *Cornus florida*, and *Carya tomentosa*. An intermediate flaming, protracted smoldering group consisted mostly of oaks (*Q. margaretta*, *Q. incana*, *Q. nigra*, and *Q. hemisphaerica*) along with *P. clausa* var. *immuginata*. Lastly, a low fire intensity group consisted of *P. clausa* var. *clausa*, *Q. virginiana*, and *Q. geminata* (**Figure 2**).

### Oak-Hickory Woodlands

The 21 tree species in the oak-hickory community also varied widely in flammability (**Figure 3**). The first two principal components accounted for 83.3% of the variance, with axes 1 and 2 having eigenvalues of 2.33 and 1.01, respectively. Axis 1 was correlated with flame height (0.59), flame duration (−0.55), and percent consumption (0.53). Axis 2 was primarily correlated with smoldering duration (−0.89). Fireline intensity



**FIGURE 2 |** Principal components analysis (PCA) for flammability of tree litter in coastal plain uplands of the southeastern United States. Axis 1 was inverted to be consistent with the other figures (increased flame height and consumption on the right). Species codes and mean values listed in **Table 1** and **Supplementary Table 1**.

ranged from 91 kW m<sup>-1</sup> (*O. virginiana*) to 551 kW m<sup>-1</sup> for *Castanea dentata*. The k-means cluster analysis again suggested four groups which explained approximately 67.5% of the variance of the ordination. The highest flaming group consisted of only two species: *Castanea dentata* and *Oxydendrum arboreum*. A slightly lower flaming, brief smoldering group contained *P. echinata*, *L. tulipifera*, *F. grandifolia*, *Cornus florida*, and two hickories (*C. glabra* and *C. tomentosa*). A second group with similar flaming characteristics as the previous but longer smoldering was made up of mostly oaks (*Q. alba*, *Q. coccinea*, *Q. rubra*, *Q. montana*, and *Q. falcata*) as well as *Prunus serotina*. Lastly, a lower flaming group consisted of *O. virginiana*, *T. americana*, *A. rubrum*, *L. styraciflua*, *N. sylvatica*, *S. albidum*, and *Q. stellata* (**Figure 3**).

### Appalachian Forest

The 16 Appalachian forest trees had the widest range of flammability of the four ecosystems, including the least flammable *Tsuga canadensis* and the most flammable *Castanea dentata*. *Tsuga canadensis* was identified as an outlier even after the log transformation (likely due to having the lowest flame height and only 2.3% consumption) and was removed from the PCA. The first two principal components accounted for

86.6% of the variance, with axes 1 and 2 having eigenvalues of 2.19 and 1.27, respectively. Axis 1 was correlated with flame height (-0.50), flame duration (0.59) and percent consumption (-0.63). Axis 2 was again mostly correlated with smoldering time (0.84). Fireline intensity ranged from 3 kW m<sup>-1</sup> (*T. canadensis*) to 546 kW m<sup>-1</sup> (*C. dentata*). The k-means cluster analysis suggested three groups which explained 59.8% of the variance of the ordination. The highest flammability cluster contained two pines (*P. echinata* and *P. rigida*), *C. dentata*, *O. arboreum*, *Q. coccinea*, *Q. alba*, and *Cornus florida*. A lower flammability group with longer smoldering contained *Q. montana*, *Q. rubra*, *Prunus serotina*, *Pinus pungens*, *Pinus virginiana*, *Sassafras albidum*, *A. rubrum*, *N. sylvatica*, and *T. americana*. *Pinus strobus* was a singleton in a cluster with low flames and brief smoldering (**Figure 4**).

### Bottomland Forest

The diverse species of the bottomland forest ecosystem were equally diverse in their litter flammability. Fireline intensity in bottomland forest species ranged from 31 kW m<sup>-1</sup> (*T. taxifolia*) to 419 kW m<sup>-1</sup> (*Pinus serotina*). The narrow endemic conifers *Torreya taxifolia* and *Taxus floridana* were identified as outliers having the second and third lowest flame heights in the dataset



and were removed from the PCA. For the remaining 19 species, the first two principal components accounted for 75.5% of the variance, with axes 1 and 2 having eigenvalues of 2.01 and 1.01, respectively. Axis 1 was correlated with flame height (−0.61) and percent consumption (−0.60). Axis 2 was mostly correlated with smoldering time (−0.76) but was also correlated with flame time (0.54). The bottomland forest trees clustered into four groups that explained approximately 83.7% of the variance of the ordination. In this community, a high flaming, long smoldering time group was a mix of species from oaks (*Q. alba* and *Q. michauxii*), other hardwoods (*L. tulipifera*, *F. grandifolia*, and *C. florida*), and the bottomland pine, *P. glabra*. A high flame, brief smoldering group was made up of *Pinus serotina*, *P. taeda*, *M. grandiflora*, *M. virginiana*, and *I. opaca*. The intermediate flaming, long smoldering cluster contained two oaks (*Q. phellos* and *Q. nigra*), as well as *A. rubrum*, *L. styraciflua*, and *T. americana*. The lowest flammability cluster contained two species, *Q. virginiana* and *Taxodium distichum* (Figure 5).

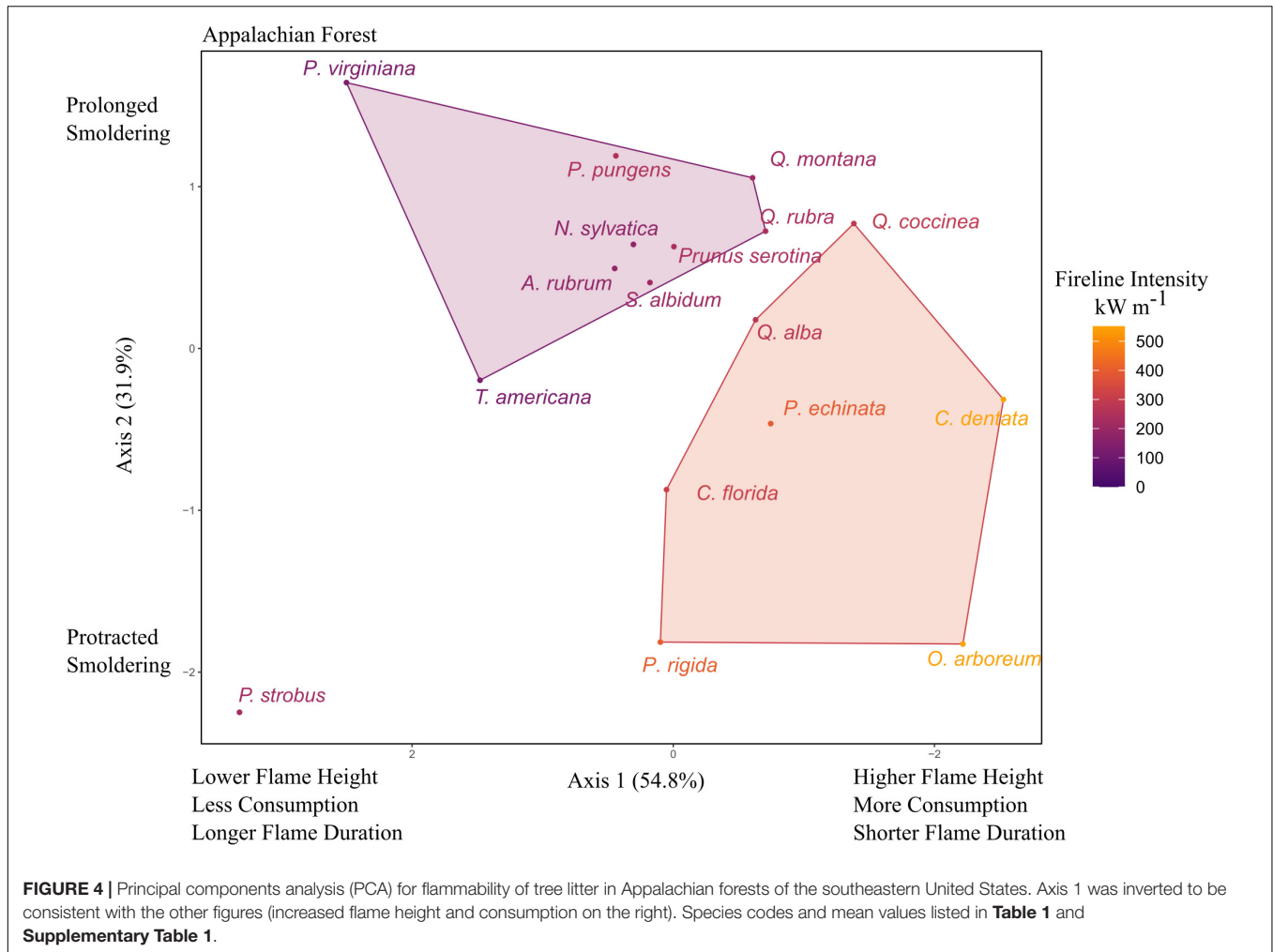
## DISCUSSION

The diverse southeastern tree species we evaluated here varied widely in their litter flammability metrics. Many of the species implicated in mesophication (e.g., *A. rubrum*, *Tilia americana*,

*Liquidambar styraciflua*, and *Nyssa sylvatica*; Nowacki and Abrams, 2008; Kreye et al., 2018b; Babl et al., 2020) had lower flammability that diminishes fire intensity and spread, enabling these species to persist in the presence of low intensity fires or continued fire exclusion. Many of the ecosystem dominants (particularly many *Pinus*, *Quercus*, *Carya*, and the formerly dominant *Castanea dentata*) occupied the pyrophytic end of the ordinations with their ability to burn with great intensity that prevents establishment or causes mortality of invading mesophytes. These patterns were emergent across the four ecosystems we evaluated.

## Flammability Across Ecosystems: Evidence for Mesophication

In the coastal plain uplands, the most flammable species were *Pinus serotina*, *P. echinata*, and *P. palustris*, with *Q. laevis* almost as flammable. All of these species are very fire tolerant and dominate frequently burned sites (Landers, 1991; Platt, 1999). *P. serotina* occurs in wetter flatwoods sites that can burn very intensely as surface fires or stand-replacing fires during dry windy periods (Frost, 1998). *P. serotina* also has serotinous cones that require intense heat to open and individual trees can persist through intense fire because of its inherent ability to basally and epicormically resprout. *P. taeda*, *Q. alba*, and *Q. falcata*

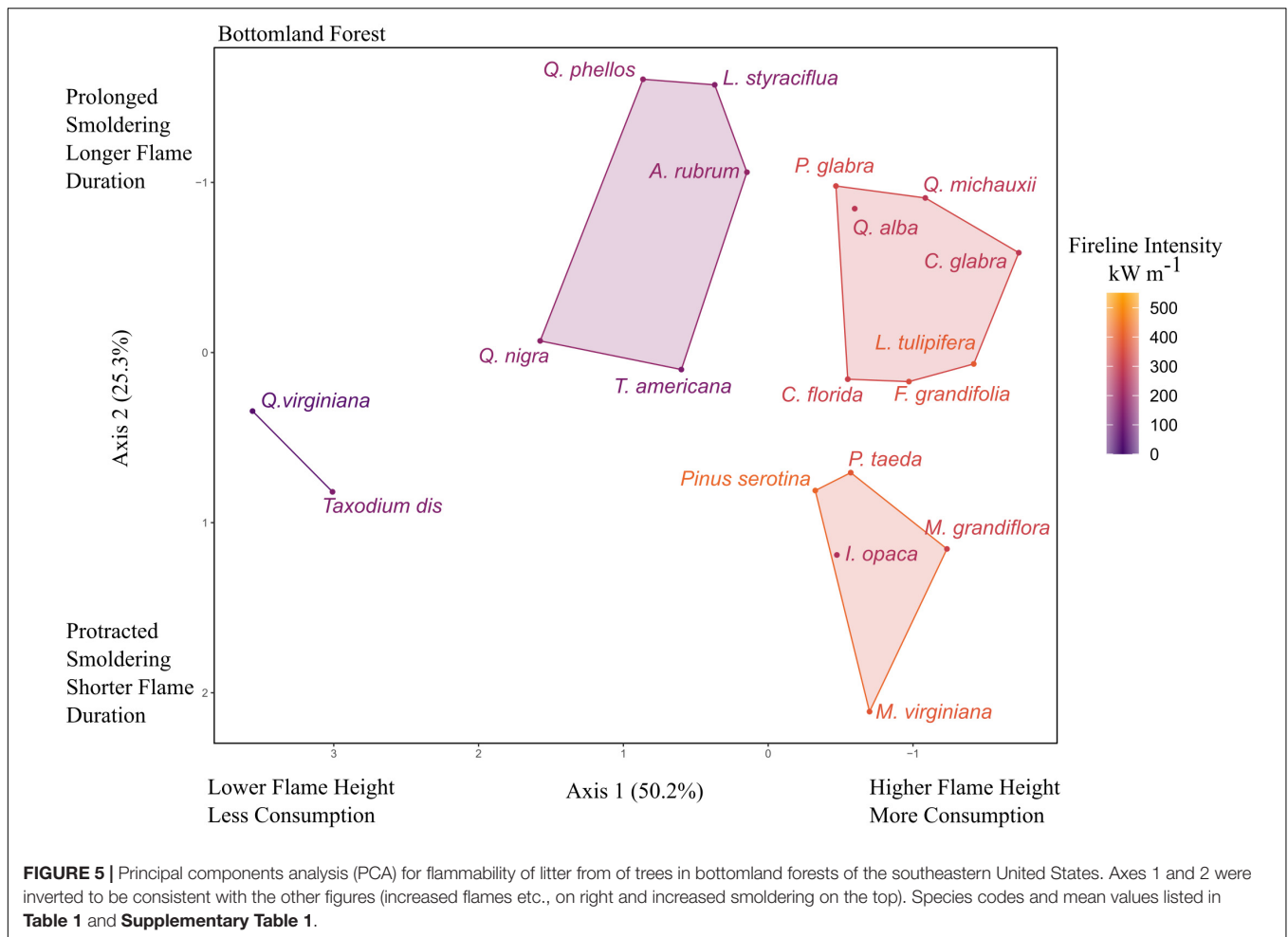


persist in sites that are burned regularly and each of these species burned with relatively high flammability. The least flammable species included three oaks known to be fire sensitive in the coastal plain, *Q. virginiana*, *Q. geminata*, and *Q. hemisphaerica*. *Q. virginiana* and *Q. geminata* are evergreen oaks with massive crowns that can extend horizontally for several meters, enabling persistence in fire-prone uplands within fire shadows that are presumably formed as a result of their heavy shading and lack of flammable fuels beneath their crowns (Varner et al., 2016). *Q. hemisphaerica* is a thin-barked (Graves et al., 2014) fire sensitive species that can invade upland pines in the absence of fire. These poorly flammable oaks highlight an important finding that all oaks are not flammable, despite the widely held belief (Nowacki and Abrams, 2008).

Flammability results for oak-hickory forests were less consistent with our expectations. Supportive of our hypothesis, the mesophytes *A. rubrum*, *L. styraciflua*, *O. virginiana*, *T. americana*, and *N. sylvatica* had the least flammability. However, a few other species unexpectedly had higher flammability, e.g., *F. grandifolia*, *Liriodendron tulipifera*, *Oxydendrum arboreum*, that are more commonly identified as mesophytes. These mismatches likely reflect the need to

incorporate differences in moisture dynamics (e.g., absorption capacity and drying rates; Kreye et al., 2013, 2018b), which we discuss in more detail below. The inclusion of these mesophytes in the high flammability cluster likely contributed to some of the more classic pyrophytes (e.g., *Q. alba*, *Q. stellata*) being included in the intermediate flammability cluster. Regardless, those species with high flammability and rapid bark accumulation (Jackson et al., 1999; Hammond et al., 2015) and/or rapid wound responses (Smith and Sutherland, 1999; Romero et al., 2009) are capable of persisting in fire-prone environments. Those species without thick bark (the thin barked mesophytes) suffer fire-caused stress and mortality in intense surface fires (Jackson et al., 1999; Hammond et al., 2015).

The litter flammability of Appalachian tree species largely conformed to expectations with a few minor exceptions. *P. echinata*, *P. rigida*, *Q. alba*, and *C. glabra* all were in the highly flammable category and are known to have relatively thick bark capable of withstanding frequent low intensity fires (Landers, 1991). American chestnut burned with high flammability as was discovered recently (Kane et al., 2019, 2020). The overstory tree species that replaced American chestnut varied widely: where flammable oaks replaced chestnut, the effects of its functional



extinction may have been minor; where mesophytic species replaced chestnut, its functional extinction may have exacerbated changes to community flammability and local fire regimes (Kane et al., 2020). The surprisingly flammable sourwood is noteworthy. Sourwood is often lumped as a mesophyte, but its thick bark as an adult and its flammable litter provoke a need to learn more about its role in these fire-prone landscapes. It may be that its litter decomposes rapidly, making its flammability contribution ephemeral or that it indeed remains and contributes to intense surface fires. This species clearly deserves more attention. Mesophytic species, such as *A. rubrum*, *N. sylvatica*, and *S. albidum*, were less flammable as expected, however, several species were grouped with them as “intermediate.” *P. pungens* was located within the intermediate flammability category as well, a result that is consistent with other species that have serotinous cones and that typically burn as a high severity crown fire (Fonda, 2001; Varner et al., in review). Although *T. canadensis* was removed from the PCA as an outlier, it is a very strong mesophyte.

The diverse bottomland forest ecosystem had species spanning a wide variety of flammability. Aside from the two rare conifer outliers noted before (Mola et al., 2014), the species in this ecosystem had four main groups: a poorly flammable pair associated with riparian and lacustrine margins (bald-cypress and

live oak); a cluster of typical mesophytes; and two clusters with moderate flammability and varying smoldering durations (pines, oaks, and a diverse suite of bottomland dominants; **Figure 4**). Many bottomlands are fire-protected due to their landscape position in riparian or lacustrine margins or because they are natural fire shadows where fire struggles to spread (Harper, 1911; Platt and Schwartz, 1990). We have observed fire spread into these ecosystems in a number of scenarios, and this likely occurred during droughts historically. At present, we have a poor understanding of the role of infrequent fire in regulating species composition in these ecosystems where the study of fire has been ignored or overlooked.

### Flammability Research: What Next?

Over the last two decades, few southeastern species have been evaluated for their flammability, despite strong suggestions that many of ecosystems are highly flammable (Platt et al., 2016) and the widespread acknowledgment that mesophication is a much more common phenomenon than previously thought (Nowacki and Abrams, 2008; Alexander et al., 2021; Kane et al., 2021). This compilation provides data for 50 tree species, which is a fraction of the high diversity of overstory dominants in the eastern United States. The discoveries of past frequent fire regimes



across eastern North America (Guyette et al., 2012; Stambaugh et al., 2015; Lafon et al., 2017; Rother et al., 2020) and the widespread interest in developing restoration and management to improve resilience and restore fire regimes begs for additional evaluation of species. Focusing research on other eastern North American species, particularly those that have debated fire regimes, should be prioritized.

Our results echo previous limitations of evaluating flammability of dry litter for species in humid environments (Varner et al., 2015b). In contrast to the western United States and many fire-prone landscapes worldwide, the southeastern United States is humid and for the most part lacks extended dry periods (Schroeder and Buck, 1970; Chen and Gerber, 1990; Stambaugh et al., 2017). Frequent rainfall and rapid overnight relative humidity recovery result in moist litter punctuated by diel drying (Kreye et al., 2018a). Flammability methods that include moisture gain and loss (as in Kreye et al., 2013; Mola et al., 2014; Kreye et al., 2020a,b) offer more potential to differentiate species that may burn well when dry, but in humid settings their water absorption capacity and slow moisture loss dampen their ignitability and diminishes their intensity once they do ignite. Understanding which leaf or fuelbed traits slow or hasten moisture loss (e.g., leaf curling or cuticle retention) may enable analyses of past flammability data to elucidate these patterns. The interaction of shading from overstory crowns or continuous canopies highlight these needs (Kreye et al., 2018a; Alexander et al., 2021). More work on including moisture retention as an interacting factor with flammability is clearly warranted (Kreye et al., 2013, 2018b).

Since we have collected litter when freshly fallen, our litter is a “best case” for a species’ flammability (i.e., before decomposition degrades litter fuel quality). Only limited research has been conducted on how decomposition may affect flammability following leaf fall (Weir and Limb, 2013). The diversity of the southeastern tree species and their differential mass loss rates and perhaps inherent fuel chemistry (Baker et al., 2001; Alexander and Arthur, 2014; Babl, 2018) should be a focus of future work. Fires in the southeastern United States can burn almost year-round, either soon after autumn litterfall or long after (months or years following senescence), affecting the fuel quality in ways that deserve attention (Weir and Limb, 2013). The humid climate and diversity of species begs for incorporating litter decomposition or time since senescence into future flammability experiments to better capture the variable contribution of litter fuels to surface fire behavior and the cascade of ecological processes these incite.

Litter is a primary fuel in woodlands and forests, but the contribution of other fuels should be better integrated. In studies of fire behavior drivers in eastern woodlands and forests, litter has been repeatedly shown to drive intensity and spread (Dickinson et al., 2016; Whelan et al., 2021). Where herbaceous fuels are proportionally more dominant, speculation exists over the importance of comparatively rare tree litter. Fill et al. (2016) measured flammability of the dominant bunchgrass *Aristida stricta* in longleaf pine savannas and woodlands and found that senesced tree litter diminished intensity and prolonged flaming and smoldering. Beyond herbaceous fuels, Emery and Hart (2020) found diverse flammability of woody, bark, and vine fuels in these ecosystems. These tree litter, herbaceous, and other fuel

interactions should be prioritized in both laboratory and field research moving forward.

## Flammability as a Fire-Adapted Trait

Litter flammability is a single fire-adapted trait, but one that is increasingly linked to other important traits that enable survival in fire-prone environments. Typical trait analyses focus on defensive traits, most classically bark thickness or the rate at which species accrue bark as juveniles (Keeley and Zedler, 1998; Jackson et al., 1999; Hammond et al., 2015). Other defensive traits include the ability to respond quickly to wounding and resist secondary effects following injury, e.g., decay (Romero et al., 2009). Other typical fire-adapted traits include pruning rates, juvenile height growth rates, resprouting or suckering capacity, and reproductive traits including fire-triggered flowering or cone serotiny (Landers, 1991; Rodríguez-Trejo and Fulé, 2003; Climent et al., 2004). Combining the multitude of fire-adapted traits including flammability into synthetic analyses that illustrate the diversity of ways that perennial woody plants persist in fire-prone environments is warranted (Schwilk and Ackerly, 2001; Varner et al., 2016; Pausas et al., 2017; Stevens et al., 2020).

## Management Implications

Restoring landscapes that historically burned regularly may be challenged by fire-sensitive mesophytic species that establish following long-term fire-exclusion (Nowacki and Abrams, 2008). The dampening effect of these species on flammability increase the difficulty of killing invading mesophytes or establishing pyrophytes (Stambaugh et al., 2015). Our results highlight how variability in flammability might explain the persistence of fire-tolerant tree species through their influence on fire behavior, but quantitative research on the relative impact of mesophytes on flammability in mixed forests deserves more attention. Mesophyte litter may have minimal effect on flammability unless it dominates the surface fuels (Kreye et al., 2018b). For example, determining the mesophication impact of different species may enable managers to prioritize removal of species in a more targeted way. These removals over time will lead to the reduction of residual mesophytic litter and the canopy shade that often facilitates the growth and expansion of mesophytes while also diminishing future fires (Alexander et al., 2021). Research should be prioritized to determine the relative effectiveness of individual mesophytic species across the region.

Our working hypothesis was that species linked to fire exclusion and the feedback phenomenon termed mesophication would burn poorly and support the mechanism for regional dampened flammability. Our results, with few exceptions, confirmed our hypothesis for the four ecosystems we investigated. These results are further evidence that the mesophication feedback is widespread, beyond the eastern United States oak forests where the phenomenon was first detailed by Nowacki and Abrams (2008). Future work across other ecosystems may show similar patterns where excluding fire leads to reduced flammability, counter to expectations in many Mediterranean and dry western North American ecosystems. Understanding how shifting species composition and structure alters ecosystem processes will be particularly necessary as

restoration efforts move forward and fire is reconsidered as a natural process in ecosystems more broadly.

## DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/**Supplementary Material**, further inquiries can be directed to the corresponding author/s.

## AUTHOR CONTRIBUTIONS

JMV, JMK, JKK, and TS conceptualized the study. TS and JMV performed the statistical analyses. JMV wrote the first version. All authors contributed to writing and editing and approved the submitted version.

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## SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/ffgc.2021.727042/full#supplementary-material>

**Supplementary Table 1** | Litter flammability metrics for 50 species in the southeastern United States.

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