

RESEARCH ARTICLE

Evidence of local adaptation in litter flammability of a widespread fire-adaptive pine

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Abstract

1. Fire is a strong ecological and evolutionary driver of plant species and terrestrial ecosystem dynamics. Numerous studies have shown that plant species vary widely in their flammability and associated traits that coincide with clear strategies of persistence in fire-prone ecosystems. Yet, intraspecific variation and phenotypic plasticity in plant flammability has received substantially less attention. Some evidence has demonstrated high plasticity in flammability among populations in species adapted to low-frequency, high severity fire regimes which suggests the capacity of local adaptation; however, intraspecific variability of species in high-frequency, low severity fire regimes has not been conducted. Given that frequent fire-adaptive species tend to produce fast-flammable litter that is associated with survival following fire, we hypothesized that these species would have highly conserved leaf traits with low variation in litter flammability.
2. We used an existing common garden study to test our hypothesis in *Pinus rigida* (pitch pine) with source populations that span most of its distribution in eastern North America. We examined both phenotypic and genotypic variation as well as phenotypic plasticity (relative distance plasticity index) in *P. rigida* leaf traits and litter flammability among populations grown in situ (population) and the same populations grown in a common garden or provenance study (provenance).
3. Phenotypic and genotypic variation in fuel traits and litter flammability differed among source locations. Phenotypic plasticity in litter flammability among source locations were associated with fuel trait plasticity and biogeographic factors. Populations located in warmer and drier climates with presumably more frequent historical fire regimes were associated with greater plasticity in physical litter traits and their resulting flammability.
4. *Synthesis*. Our study demonstrates the utility of common garden experiments to examine intraspecific variation and phenotypic plasticity in litter flammability. Our results indicate that litter flammability in *Pinus rigida* has the capacity

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for local adaptation. We hypothesize that intraspecific variation in plant flammability provides ecologically and evolutionary relevant information and that other frequent fire-adaptive species will similarly demonstrate local adaptation in plant flammability.

KEYWORDS

common garden, fire behaviour, fire ecology, fuels, intraspecific trait variation, *Pinus rigida*, plant traits, provenance

1 | INTRODUCTION

Fire has been a major ecological and evolutionary driver that has long shaped plant species and terrestrial ecosystems world-wide (Bond & Keeley, 2005; Bowman et al., 2009). Not only do plants respond to fire, but plants also serve as the primary source of fuel that directly influences the ignition and combustion of fire (Rothermel, 1983). Thus, many plant traits are interpreted to be adaptations to certain fire regimes that promote avoidance, resistance or recovery strategies following fire (Keeley et al., 2011; Keeley & Zedler, 1998). This process, referred to as 'niche construction', suggests that plants have traits selected by fire that, in turn, modify their environments and the environments of competing neighbours to promote fitness advantages (Schwilk, 2003). One such way species in fire-prone ecosystems can modify their environments is through their flammability, or a species' ability to ignite, combust and spread fire (Varner, Kane, Banwell, & Kreye, 2015).

While there has been considerable debate about the degree to which plant flammability is an evolutionary adaptation to fire, multiple lines of evidence continue to support this possibility. Early criticisms of the Mutch (1970) hypothesis, that fire was a selective force promoting ecosystem flammability, were dismissed for being 'group selectionist' (Snyder, 1984; Troumbis & Trabaud, 1989). Subsequent modelling and field experiments have demonstrated that enhanced flammability could have been selected as a suite of traits that confers fitness advantages at the individual plant level (e.g. Bond & Midgley, 1995; Kerr et al., 1999; Schwilk, 2003). Still, there is a persistent perspective that plant flammability may be environmentally determined rather than selected for by fire (Midgley, 2013). Isolating the causal mechanism of adaptation remains a challenge, but continued research examining possible evidence in support of or in refutation of existing ideas is needed to advance our understanding.

Three flammability strategies have been proposed that align with other known fire-adaptive traits and promote fitness benefits to plants in fire-prone environments (Pausas et al., 2017). In the first strategy, plant traits result in rapid low-intensity fires (i.e. 'fast flammable') often paired with thicker bark and self-pruning branches that limit fire-caused mortality and reduce competition from less fire-tolerant species. In the second strategy, species have traits that promote high-intensity, long duration fire (i.e. 'hot flammable') benefit from reduced competition and higher quality seedbed conditions that commonly occur following fire. These species tend to have

other traits such as thin bark, retained branches, serotinous cones, resprouting or heat-triggered germination. Species with traits promoting poor flammability (i.e. 'non-flammable') are likely best suited to relatively fire-naïve ecosystems (i.e. avoiders) or by impeding fire (i.e. impiders sensu Kane et al., 2008). Fitness is enhanced in these cases through increased survival either by passively avoiding fire (e.g. some individuals survive fire in unburned refugia) or by actively reducing fire spread to limit damage (e.g. fire dampening litter). In these species, we would not expect to see other adaptations to fire.

Numerous studies have examined interspecific plant flammability (e.g. Kane et al., 2021; Kreye et al., 2018; Saura-Mas et al., 2010; Scarff & Westoby, 2006; Schwilk & Ackerly, 2001) with substantially fewer investigations into intraspecific plant flammability. Studies examining intraspecific variation of plant flammability have primarily focused on 'hot-flammable' obligate seeder species (mature plants that die but reproduce from seeds stored in the canopy or soil that germinate following fire) or 'non-flammable' species (Pausas et al., 2012; Romero & Ganteaume, 2020; Schwilk, 2003). For instance, Schwilk (2003) artificially enhanced flammability by adding dead branches in the obligate seeder shrub *Ceanothus cuneatus* that resulted in higher post-fire seed germination rates, demonstrating a clear fitness benefit of higher flammability. Another study, examining flammability within the shrub *Ulex parviflorus*, indicated that plants growing in areas with more frequent fire had enhanced flammability traits compared to areas with no recent fires (Pausas et al., 2012). Thus, it is reasonable to expect that hot-flammable species would have high variation in flammability among populations due to higher fire intensity (i.e. stronger selective force) and faster turnover rates (via post-fire mortality of adult plants) that can contribute to greater incidences of local adaptation. We are unaware of any studies that have examined intraspecific variation in flammability among populations within 'fast-flammable' species. Since the primary fitness advantage of this strategy is survival during fire resulting in longer turnover rates, we might expect flammability traits in this strategy to be conserved with low intraspecific variability in flammability among populations.

Senesced leaves, or 'litter', often represent a substantial portion of the surface fuel layer and is one of the major drivers of fire behaviour in many woodland and forest ecosystems. Litter flammability varies widely among species reflecting particle and fuelbed trait differences (Burton et al., 2020; Popović et al., 2021; Varner, Kane, Kreye, & Engber, 2015). Physical traits such as long leaves and large

surface area-to-volume ratios tend to result in more flammable litter (Engber & Varner, 2012). These traits also influence fuelbed attributes, such as bulk density and packing ratio that contribute to variation in litter flammability among species (Burton et al., 2020). Litter that has a high volatile content or high cellulose-to-lignin ratio also have higher flammability (Ormeño et al., 2009). While these characteristics are known to vary among species, intraspecific variation is less well-understood.

We chose to examine intraspecific variability in litter flammability of *Pinus rigida* (pitch pine) due to its wide ecological amplitude and well-known genotypic diversity. *P. rigida* is a mostly non-serotinous conifer that spans a wide range of climatic conditions in eastern North America extending from Georgia northwards to Maine, with outlying populations slightly farther north in southern Quebec and Ontario. Prior to colonization, much of this species' range experienced relatively frequent fire (<15-year fire return interval) with highly variable intensity depending on vegetation structure and substrate (Brose & Waldrop, 2006; Guyette et al., 2012; Stambaugh et al., 2015). Generally, *P. rigida* is capable of surviving surface fires because of its thick bark and rapidly burning litter (Little & Garrett, 1990; Varner, Kane, Banwell, & Kreye, 2015). This species also has the capacity to sprout basally or epicormically following fire. Interestingly, two known coastal populations located in the Pine Plains region of New Jersey and Long Island, New York are mostly serotinous with >90% of trees having closed cones (Givnish, 1981; Jordan et al., 2003). The serotiny level of populations generally declines rapidly away from these coastal populations (Ledig & Fryer, 1972). Past research has demonstrated high genetic diversity and high variability in growth rates among trees from a wide range of source populations (Guries & Ledig, 1982; Leland et al., 2016), indicating the potential for substantial variation in flammability among populations.

The primary objective of our study was to examine the intraspecific variability and phenotypic plasticity of litter flammability and associated traits in *P. rigida* across its distribution. Our hypothesis was that litter flammability would be highly conserved, or in other words, that litter flammability and associated traits would be consistent across a broad climatic and topographic gradient and that litter flammability from different source populations but grown in a common garden experiment (i.e. provenance study) would also be similar. If this hypothesis is supported, our results would suggest that litter flammability in species adapted to low severity and high-frequency fire regimes may be highly conserved and less prone to variation due to local adaptation.

2 | MATERIALS AND METHODS

2.1 | Experimental design and litter collection

We based our experiment on an existing *P. rigida* provenance (i.e. common garden) study located within the Brendan T. Byrne State Forest (formerly the Lebanon State Forest; 39.923087 N,

−74.431403 W) in Ocean County, New Jersey, USA (Ledig et al., 1976). The site has well-drained sandy soils common in the outer coastal plain of New Jersey. The provenance study was established in 1971 and planting followed a compact family (i.e. stands) design with seed sources from 29 different geographic locations with one to three 'families' randomly assigned to each of the three blocks.

We collected intact litter from 10 source populations (one family from each geographic location) that were planted within the provenance study site (hereafter 'provenance'). Source populations ranged from Georgia to Maine, USA (Figure 1), representing a large climatic and geographic gradient within the distribution of *P. rigida* (Table 1). Then, we collected corresponding litter samples from the in situ locations of each of the 10 source populations (hereafter 'population') that were sampled within the provenance study. Population samples served as a representation of phenotypic variation of litter and flammability traits and provenance samples represented genotypic variation. Within each population and provenance, we separately collected 20–30 g of litter (surficial Oi horizon) lacking visual indications of decay from beneath nine or 10 trees, with each tree's litter collection serving as an independent sample. Litter from trees within each source population were haphazardly collected within each site that corresponded to the seed source used for the provenance study. However, the exact genotypes of the trees sampled from the source populations remain unknown. We placed litter from each tree separately into labelled paper bags, allowed them to air-dry and shipped them to the HSU Wildland Fire Lab in Arcata, California for burning.

For each source population, we gathered geographic, topographic and climatic data for subsequent analyses. Geographic and topographic variables considered included latitude, longitude, elevation (m), distance to the coast (km) and distance to the provenance site (km) using a geographic information system and relevant data layers. Climatic variables considered in our study included annual precipitation (mm); minimum, mean and maximum temperatures (°C); Palmer Drought Severity Index (Palmer, 1965); and minimum and maximum vapour pressure deficit (kPa). We used 30-year (1981 to 2010) climate data from PRISM Climate Group (2020) for each of the 10 source locations.

2.2 | Fuel traits

Leaf trait measurements were taken from 20 randomly selected needles of each population and provenance litter collection. Needle length was measured using electronic calipers to the nearest millimetre. Fuel moisture content (%; dry weight basis) was measured by taking ~5 g litter sample from each population and provenance sample. Each sample was then placed in a drying oven at 40°C for at least 24 h to estimate the moisture content under equilibrium conditions in the laboratory at the time of burning. Fuelbed depth measures are described below in the burning trials section.

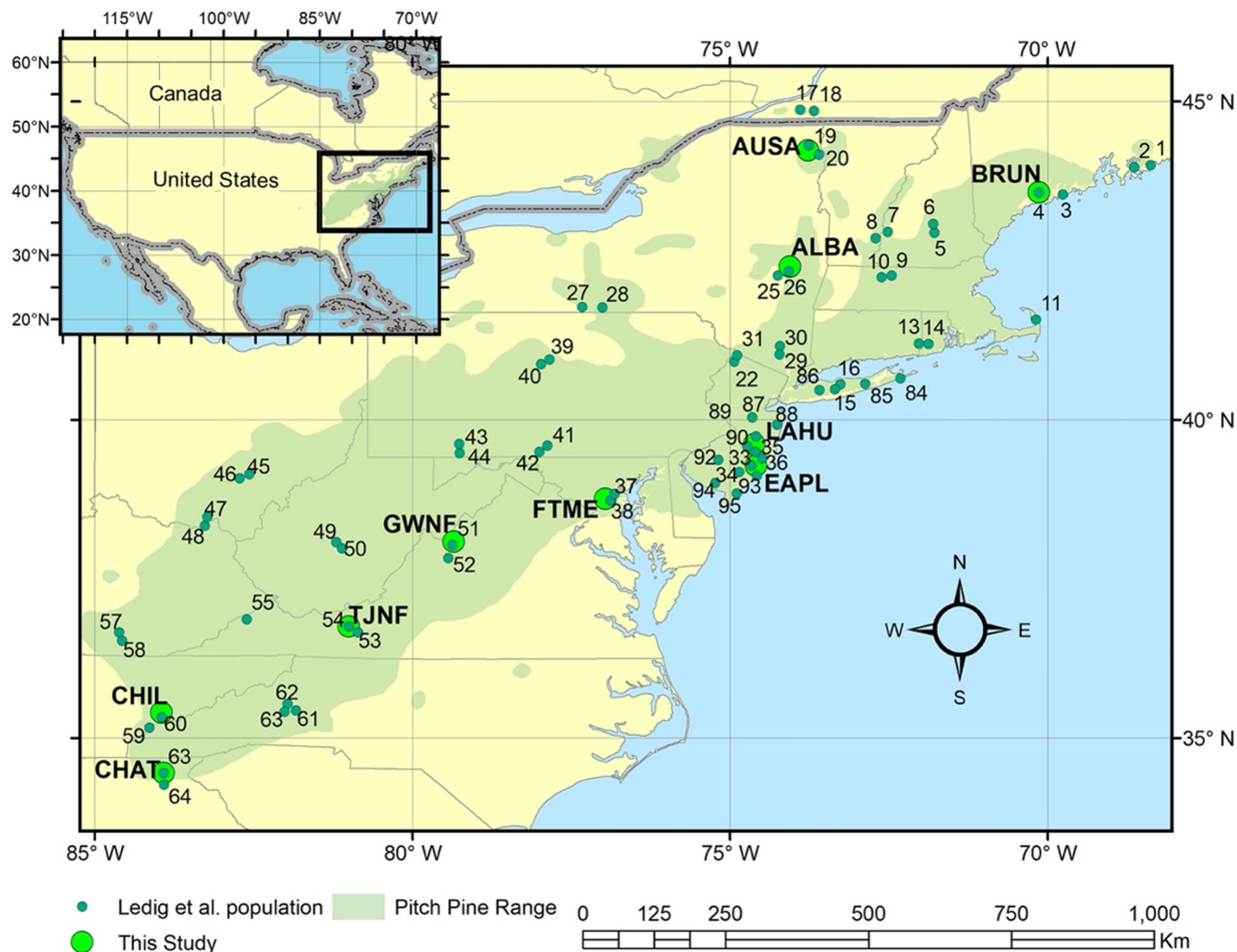


FIGURE 1 Locations of *Pinus rigida* (pitch pine) sites where litter collection occurred. Green shading denotes the current distributional range of pitch pine (Little & Garrett, 1990). The provenance site was located at the Lakehurst (LAHU), New Jersey, USA site. Location abbreviations are defined in Table 1. Numbered points refer to the original source locations and families (i.e. stands) that were used by Ledig et al. (1976) to establish the provenance study

TABLE 1 Source and collection locations and their associated climate, geography and topography information for the *Pinus rigida* (pitch pine) litter flammability study. The provenance study site was located within Lakehurst, New Jersey. NF, National Forest; NP, National Park

ID	Geographic area	Provenance	Elevation (m)	Dist. to provenance (km)	Precipitation (mm)	Mean temp. (°C)
ALBA	Albany-Schenectady Sand Plains, NY	Karner	99	314	1,015	8.8
AUSA	Champlain Valley, NY	Ausable	203	510	880	7
BRUN	Brunswick, ME	Perimeter Rd	26	576	1,229	7.6
CHAT	Chattahoochee NF, GA	Crumbly Mt	724	1,004	1,761	13.4
CHIL	Great Smokey Mtn NP, TN	Chilhowee	324	947	1,287	14.5
EAPL	Pine Plains, NJ	East Plains	44	27	1,145	12.3
FTME	Fort Meade, MD	Trainfire Road	46	224	1,101	12.9
GNWF	George Washington NF, VA	Grooms Ridge	605	444	1,022	10.7
LAHU	Lakehurst, NJ	Lakehurst	42	1	1,158	12.2
TJNF	Jefferson NF, VA	Mt Olivet	663	641	977	11.4

2.3 | Burning trials

We conducted litter flammability experiments for each source population and provenance separately using well-established methods (Fonda, 2001). Litter samples were burned at their equilibrium moisture content (Fosberg et al., 1970) to accentuate any potential differences in moisture gain or loss among samples. However, fuel moisture content of samples did not significantly differ among source location or type, that is population or provenance ($p > 0.08$). Each 15 g litter fuelbed was evenly distributed within a 35 cm × 35 cm lattice of xylene-soaked cotton strings on a stainless steel platform, with most of the litter located within the interior 20 cm × 20 cm portion. A 2.75 × 2.75 m fume hood above the platform generated a constant draw of 15 to 20 cm/s, though no airflow was detected at the fuelbed. Prior to ignition, fuelbed depth was measured to the nearest millimetre from four locations (7 cm from each corner of the fuelbed). Strings were ignited from all sides and a timer was started once litter ignited. Maximum flame height was visually estimated to the nearest centimetre using a vertical ruler placed behind the burning platform. Flaming time was measured as the duration from litter ignition to flaming extinction, and smouldering time was measured as the duration from flaming extinction to smouldering extinction (no visible smoke and no glowing combustion observed under darkened conditions). Both flaming time and smouldering time were recorded to the nearest second. Per cent litter consumption was calculated as the proportion of the initial litter mass (15 g) that was consumed, measured following the extinction of smouldering (and removing unburned string). Burn trials were repeated nine or 10 times for each population and provenance ($n = 191$ trials).

2.4 | Phenotypic plasticity

To quantify phenotypic plasticity of fuel and litter flammability traits for each location, we calculated the relative distance plasticity index (RDPI). This index represents an ecological and evolutionary relevant measure of environmentally driven trait variation that is well-correlated with most other measures of plasticity and is more amenable to statistical analyses than other measures (Valladares et al., 2006). RDPI ranges from 0 (no plasticity) to 1 (maximum plasticity) and was calculated for each location as

$$\text{RDPI} = \Sigma \left(\frac{d_{ij \rightarrow i'j'}}{(x_{i'j'} + x_{ij})} \right) \div n,$$

where $d_{ij \rightarrow i'j'}$ is defined as the absolute difference between trait values for all possible pairs of populations and provenance samples of a given source location. Each of these differences were then relativized by dividing by the corresponding sum of the two values being compared ($x_{i'j'} + x_{ij}$), representing the maximum possible plasticity between the two samples. n is the total number of distances calculated per source location.

2.5 | Data analysis

A series of two-way permutation multivariate analysis of variance (PERMANOVA) tests, assessed with the Jaccard distance measure, were conducted in the R environment (R Development Core Team, 2020) using the *adonis* function in the *VEGAN* package (Oksanen et al., 2017). Specifically, we separately examined if the multivariate fuel traits (needle length, fuel moisture and fuelbed depth) and flammability characteristics (maximum flame length, flaming time, smouldering time and consumption) differed by source type (population or provenance), source location and their interaction. We subsequently examined univariate differences for each trait using a two-way analysis of variance (ANOVA) of the same variables used in the PERMANOVA. Model selection was determined based on the lowest Akaike information criterion (AIC) value and in cases where the top models were within 2 AIC, the model with the fewest parameters was selected (Burnham & Anderson, 1998). Residuals of the top-selected model were examined for any trends suggesting violation of normality or equal variance. A post hoc test was used to compare differences among source type and locations using the *EMMEANS* package (Lenth, 2020). We used a Bonferroni correction factor to detect differences while limiting the chance for Type I errors due to the number of comparisons. We followed the same analytical approach to examine differences in RDPI values among source locations. RDPI values were log-transformed to meet statistical test assumptions.

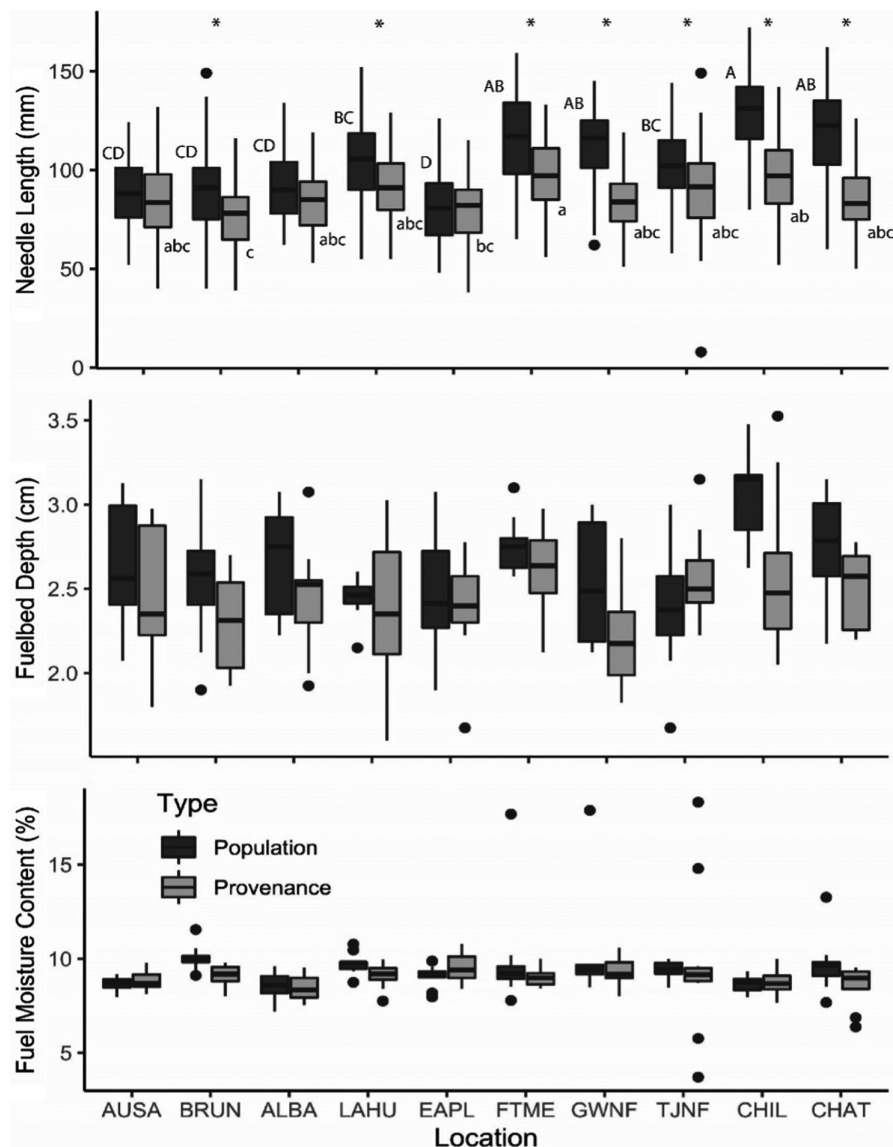
We used a principal component analysis to visualize the multivariate comparisons in RDPI among source locations using the *prcomp* function in the *VEGAN* package. Since smouldering time was not significantly different among source types in our previous analysis, we excluded this variable from consideration in our principal component analysis. The retention of components was determined using the parallel analysis in the package *PARAN* (Dinno, 2018) and we retained any factor with an eigenvalue greater than the randomly generated mean eigenvalue (Franklin et al., 1995). Correlation analysis (i.e. loadings) was conducted to examine the relationship between principal component axis scores and biogeographic factors of climate, geography, topography and fuel traits. In addition to considering observed values of biogeographic factors, we also compared RDPI values for all fuel traits. We report all biogeographic factors and fuel traits that had a significant correlation with the flammability axes scores ($\alpha = 0.05$).

3 | RESULTS

3.1 | Fuel traits

P. rigida litter traits demonstrated intraspecific variability and differences across both source types (e.g. population or provenance) and locations (Figure 2). Based on PERMANOVA, litter traits differed by source type ($F_{1,171} = 100.3$, $p = 0.001$), location ($F_{9,171} = 16.5$, $p = 0.001$) and the interaction of source type and location

FIGURE 2 *Pinus rigida* (pitch pine) litter traits by source location for population and provenance source types. Locations are arranged from north to south and the abbreviations are defined in Table 1. Capitalized letters above the boxplot denote significant differences among source locations of population samples, while lower case letters denote differences among source locations of provenance samples. An asterisk denotes significant differences between provenance and population samples within a location



($F_{9,171} = 5.7$, $p = 0.001$). Based on ANOVA results, an interactive model with source type and source location was most explanatory for needle length ($p < 0.00001$). Across all locations, population samples had 18.7% longer needles than the provenance samples. Differences in needle length between source types were significant in all locations except ALBA, AUSA and EAPL. An additive model of fuelbed depth with source type and source location was most explanatory ($p < 0.004$). On average, population samples had 7.4% deeper fuelbeds than provenance samples, but differences were primarily driven by one site (CHIL) having 15% to 17% cm deeper fuelbeds than BRUN, GWNF and LAHU. Fuel moisture content did not differ by source location or source type ($p > 0.08$).

3.2 | Litter flammability

P. rigida litter flammability differed by source type and location (Figure 3). Based on PERMANOVA, litter flammability differed by source type ($F_{1,171} = 4.78$, $p = 0.008$) and the interaction of source

type and location ($F_{9,171} = 1.92$, $p = 0.016$), but did not differ by location alone ($F_{9,171} = 1.01$, $p = 0.45$). However, when maximum flame height was examined alone using an ANOVA, only source type was significant ($F_{1,189} = 4.12$, $p = 0.044$). Population samples had slightly taller flame length estimates ($68.8 \text{ cm} \pm 0.92 \text{ SE}$) than provenance samples ($66.1 \text{ cm} \pm 0.9 \text{ SE}$). Flaming time also only differed by source type ($F_{1,189} = 6.68$, $p = 0.01$), with provenance samples ($132 \text{ s} \pm 2.36 \text{ SE}$) flaming longer than population samples ($124 \text{ s} \pm 2.32 \text{ SE}$). Smouldering time differences were not associated with source type ($F_{1,189} = 2.69$, $p = 0.1$) or location ($F_{9,181} = 0.74$, $p = 0.67$). Source type ($F_{1,171} = 41.98$, $p < 0.0001$) was informative in explaining variation in consumption, with slightly greater consumption in population samples ($88.3\% \pm 0.18 \text{ SE}$) compared to provenance samples ($86.7\% \pm 0.18 \text{ SE}$).

3.3 | Phenotypic plasticity

Phenotypic plasticity, measured as RDPI, in litter flammability differed among source locations and was associated with

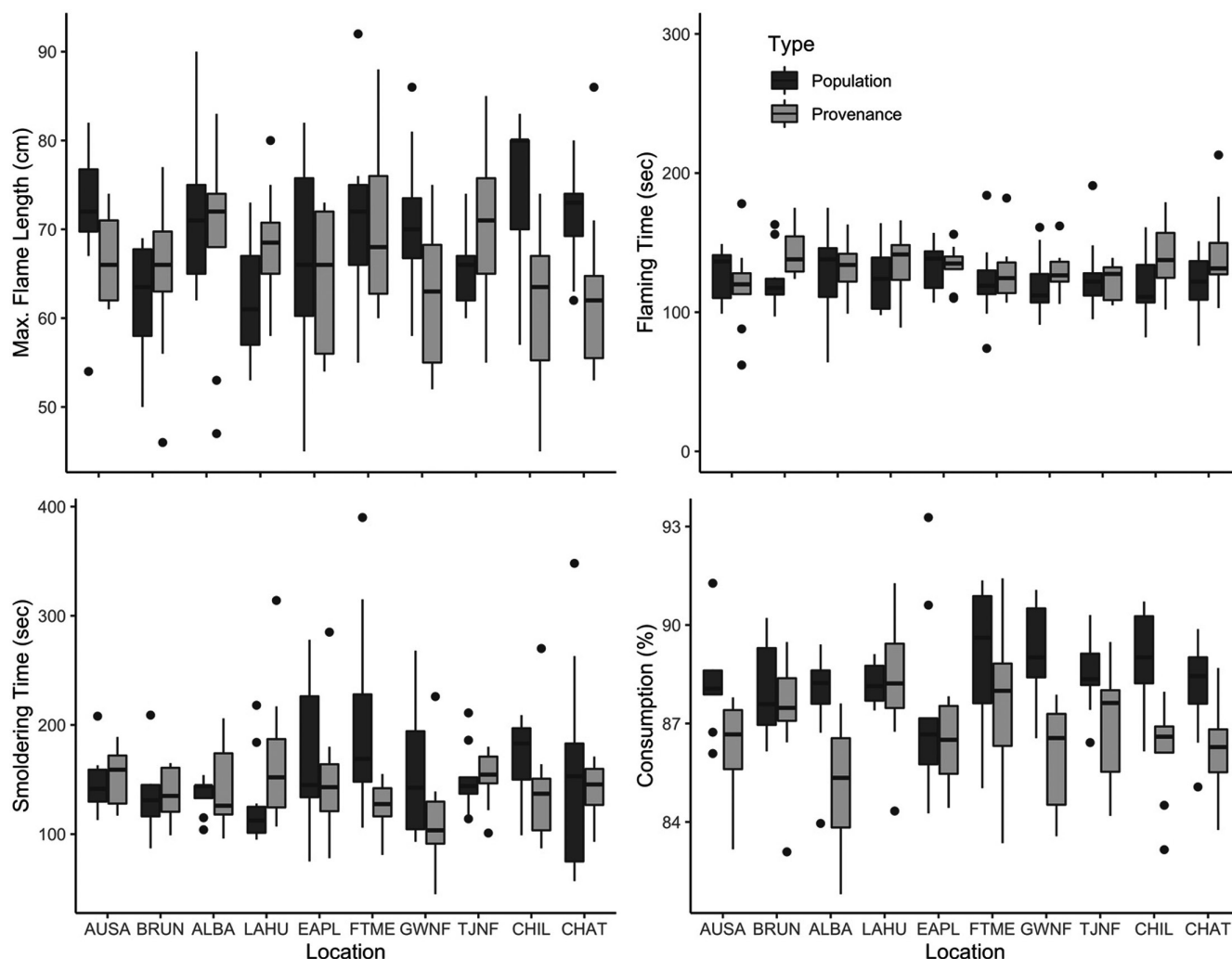


FIGURE 3 *Pinus rigida* (pitch pine) litter flammability by location for both population and provenance sources. Locations are arranged from north to south and the abbreviations are defined in Table 1. Source type was the only factor found to be significant for maximum flame length, flaming time and consumption based on the analysis of variance tests

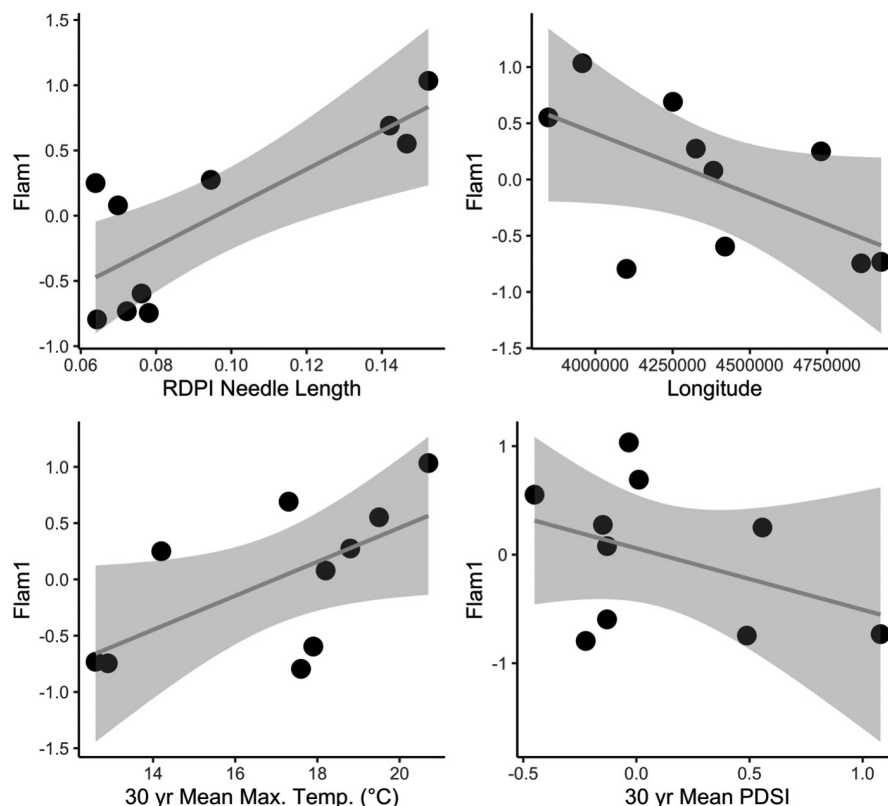
fuel trait, climate and geographic factors (Figure 4). Based on PERMANOVA, RDPI of litter flammability differed by source location ($F_{9,84} = 2.34$, $p = 0.003$). Univariate differences in plasticity among locations from ANOVA were primarily associated with RDPI of maximum flame length ($F_{9,84} = 2.56$, $p = 0.0119$), smouldering time ($F_{9,84} = 5.45$, $p = 0.000007$) and consumption ($F_{9,84} = 3.62$, $p = 0.0007$). Source locations that had the largest relative distances in litter flammability between population and provenance types were associated with warmer (maximum temperature), drier (PDSI) and more interior locations (longitude) that also had greater relative distances in needle length (Figure 4). Only the first PCA axis (Flam1) was selected based on parallel analysis, explaining 33.7% of the variation in litter flammability. Flam1 was positively associated with RDPI of maximum flame height ($r = 0.65$), smouldering time ($r = 0.46$) and consumption ($r = 0.57$). RDPI of needle length ($r = 0.96$, $p = 0.03$), longitude ($r = -0.94$; $p = 0.002$), maximum temperature ($r = 0.92$; $p = 0.002$) and PDSI ($r = -0.77$, $p = 0.02$) were associated with Flam1.

4 | DISCUSSION

We present the first study to examine distribution-wide, intraspecific variation in litter traits and litter flammability of a fire-adaptive tree species. Our hypothesis that intraspecific variation in litter flammability of *P. rigida*, a 'fast-flammable' species, would be highly conserved was not supported. Phenotypic plasticity in litter flammability among source locations differed, indicating the potential for local adaptation. We also detected a clear relationship between the biogeographic factors examined and phenotypic plasticity in litter flammability. Populations with warmer, drier and presumably more frequent fire historically were associated with more flammable litter and greater plasticity in flammability.

Variability in litter flammability across a wide range of biogeographic conditions in a fast-flammable species is somewhat surprising given the likely pleiotropic (multiple genes control variation) nature of litter flammability due to the multiple physical and chemical factors that influence flammability. This coupled with typically

FIGURE 4 Relationships between multivariate differences in relative distance plasticity index (RDPI) for the first principal component analysis axis of *Pinus rigida* (pitch pine) litter flammability among source locations. PDSI, Palmer Drought Severity Index



longer life spans of 'fast-flammable' species seemingly would have limited the heritability of differences in litter flammability. While we did not examine chemical differences (e.g. terpene content) in the litter, which is known to influence flammability among pine species (Ormeño et al., 2009), we suspect that genotypic and phenotypic variation in *P. rigida* litter chemistry may also contribute to local differences in flammability. We also acknowledge that the naturally senesced foliage focused on in this study is most useful for understanding how flammability may relate to adaptations in the context of surface fires where senesced dead pine needles comprise an important proportion of surface fuel. However, surface fires are a precursor to crown fires which involve live needles that vary phenologically in terms of chemistry and moisture in ways that could interact with surface fire conditions to either limit or promote crown fire as a component of the flammability strategy (Jolly et al., 2016).

Our findings add to the developing knowledge related to trait variation in plant flammability and the potential evolutionary implications. The presence of variation in litter flammability in *P. rigida* does not resolve whether flammability is an emergent trait based on other environmental factors (Midgley, 2013). However, our findings suggest that biogeographic factors contribute to intraspecific variation and phenotypic plasticity in litter flammability. We did find that the litter trait of needle length explained plasticity in flammability between provenance and population samples that are associated with biogeographic factors (Figure 4). Our findings are in agreement with prior research examining intraspecific variation of litter flammability in a 'hot-flammable' (*Pinus halepensis*) and a 'non-flammable' (*Pinus sylvestris*) pine species, which detected relationships of phenotypic

variation with climatic factors (Romero & Ganteaume, 2020). However, the magnitude of variation in intraspecific variation and phenotypic plasticity among different plant flammability strategies is still unknown and the relative differences may yield interesting insights. Thus, we suggest that additional studies that use a similar common garden experimental approach to examine phenotypic and genotypic variation across different plant flammability strategies are needed.

The provenance site used in our study coincidentally occurred within the centre of the known serotinous populations of *P. rigida* (Givnish, 1981). Past research suggests that serotinous pine species tend to have lower litter flammability than non-serotinous, fast-flammable pine species (Stevens et al., 2020). It is possible that the relatively low productivity soils of the provenance site promoted conditions that resulted in shorter needles and more compact fuelbeds across source locations with concomitantly lower flammability. It would have been interesting to examine if cooler and wetter populations that were grown in the warmer and drier portion of the range (e.g. CHIL, CHAT) would have demonstrated plasticity that resulted in longer needles and higher flammability. However, a provenance site of *P. rigida* in this portion of range was not available.

Phenotypic variation was greater than genotypic variation in some fuel traits and flammability measures of *P. rigida*. We suspect that this difference may in part be due to ontogenetic differences between population and provenance types, as has been found to affect flammability in other pine species (Romero & Ganteaume, 2020). All trees growing in the provenance site were the same age (46 years at the time of sampling) while population

sites were likely older with more varied age structures. However, we note that phenotypic plasticity was not consistent across locations and the degree of plasticity varied differentially along biogeographic factors that likely reflected differences in historical fire regimes. While the magnitude of difference in litter traits and flammability was statistically significant, we emphasize that this difference may not be ecologically meaningful. For example, maximum flame height observed across population samples had <2 cm taller flames than provenance samples. It is possible that this subtle difference may not have strong ecological implications and other factors such as slope or wind would have a larger influence on fire behaviour across sites.

The ecological implications of intraspecific variation in *P. rigida* flammability are not clear as phenotypic plasticity in traits can be adaptive, neutral or maladaptive (Ghalambor et al., 2007). Our results suggest that phenotypic plasticity of litter flammability in *P. rigida* is locally derived and that this species may have the capacity to adapt to potential climate change-induced alterations to fire regimes. Thus, it is possible that fast-flammable species may in part modify their environment by producing longer needles that form less compact fuelbeds that can facilitate lower intensity and shorter duration surface fires.

The topic of intraspecific trait variation in plants has received increasing attention over the past decade and the understanding of its importance to ecological and evolutionary processes is developing (Westerband et al., 2021). Our findings contribute to the advancement of this topic by demonstrating local or regional variability in litter flammability of a frequent fire-adaptive species. Taken together with previous findings (Pausas et al., 2012; Romero & Ganteaume, 2020), we propose that the degree of intraspecific variability differs among fire-adaptive strategies in consistent ways that reflect different selective mechanisms of fire.

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CONFLICT OF INTEREST

The authors do not have any conflict of interests to declare.

AUTHORS' CONTRIBUTIONS

J.M.K., J.M.V. and M.R.G. conceived the ideas and designed the methodology; M.R.G. and N.S.S. collected litter samples; J.M.K. assisted with burn trials and analysed the data. All authors contributed to the writing of the manuscript, critiqued subsequent drafts and gave final approval for publication.

PEER REVIEW

The peer review history for this article is available at <https://publons.com/publon/10.1111/1365-2745.13857>.

DATA AVAILABILITY STATEMENT

Data are available at <https://doi.org/10.6084/m9.figshare.19143083> (Kane et al., 2022).

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REFERENCES

- Bond, W., & Keeley, J. (2005). Fire as a global 'herbivore': The ecology and evolution of flammable ecosystems. *Trends in Ecology & Evolution*, 20(7), 387–394. <https://doi.org/10.1016/j.tree.2005.04.025>
- Bond, W. J., & Midgley, J. J. (1995). Kill thy neighbour: An individualistic argument for the evolution of flammability. *Oikos*, 73(1), 79. <https://doi.org/10.2307/3545728>
- Bowman, D. M. J. S., Balch, J. K., Artaxo, P., Bond, W. J., Carlson, J. M., Cochrane, M. A., D'Antonio, C. M., DeFries, R. S., Doyle, J. C., Harrison, S. P., Johnston, F. H., Keeley, J. E., Krawchuk, M. A., Kull, C. A., Marston, J. B., Moritz, M. A., Prentice, I. C., Roos, C. I., Scott, A. C., ... Pyne, S. J. (2009). Fire in the earth system. *Science*, 324(5926), 481–484. <https://doi.org/10.1126/science.1163886>
- Brose, P. H., & Waldrop, T. A. (2006). Fire and the origin of Table Mountain pine – Pitch pine communities in the southern Appalachian Mountains, USA. *Canadian Journal of Forest Research*, 36, 710–718.
- Burnham, K. P., & Anderson, D. R. (1998). *Model selection and inference: A practical information-theoretic approach*. Springer.
- Burton, J. E., Cawson, J. G., Filkov, A. I., & Penman, T. D. (2020). Leaf traits predict global patterns in the structure and flammability of forest litter beds. *Journal of Ecology*, 109(3), 1344–1355. <https://doi.org/10.1111/1365-2745.13561>
- Dinno, A. (2018). paran: Horn's test of principal components/factors. R package version 1.5.2. Retrieved from <https://CRAN.R-project.org/package=paran>
- Engber, E. A., & Varner, J. M. (2012). Patterns of flammability of the California oaks: The role of leaf traits. *Canadian Journal of Forest Research*, 42(11), 1965–1975. <https://doi.org/10.1139/x2012-138>
- Fonda, R. W. (2001). Burning characteristics of needles from eight pine species. *Forest Science*, 47(3), 390–396.
- Fosberg, M. A., Lancaster, J. W., & Schroeder, M. J. (1970). Fuel moisture response–drying relationships under standard and field conditions. *Forest Science*, 16(1), 121–128.
- Franklin, S. B., Gibson, D. J., Robertson, P. A., Pohlmann, J. T., & Fralish, J. S. (1995). Parallel analysis: A method for determining significant principal components. *Journal of Vegetation Science*, 6(1), 99–106.
- Ghalambor, C. K., McKay, J. K., Carroll, S. P., & Reznick, D. N. (2007). Adaptive versus non-adaptive phenotypic plasticity and the potential for contemporary adaptation in new environments. *Functional Ecology*, 21(3), 394–407. <https://doi.org/10.1111/j.1365-2435.2007.01283.x>
- Givnish, T. J. (1981). Serotiny, geography, and fire in the pine barrens of New Jersey. *Evolution*, 35(1), 101–123. <https://doi.org/10.2307/2407945>

- Guries, R. P., & Ledig, F. T. (1982). Genetic diversity and population structure in pitch pine (*Pinus rigida* Mill.). *Evolution*, 36(2), 387. <https://doi.org/10.2307/2408058>
- Guyette, R. P., Stambaugh, M. C., Dey, D. C., & Muzika, R. M. (2012). Predicting fire frequency with chemistry and climate. *Ecosystems*, 15(2), 322–335. <https://doi.org/10.1007/s10021-011-9512-0>
- Jolly, W. M., Hintz, J., Linn, R. L., Kropp, R. C., Conrad, E. T., Parsons, R. A., & Winterkamp, J. (2016). Seasonal variations in red pine (*Pinus resinosa*) and jack pine (*Pinus banksiana*) foliar physio-chemistry and their potential influence on stand-scale wildland fire behavior. *Forest Ecology and Management*, 373, 167–178. <https://doi.org/10.1016/j.foreco.2016.04.005>
- Jordan, M. J., Patterson, W. A., & Windisch, A. G. (2003). Conceptual ecological models for the Long Island pitch pine barrens: Implications for managing rare plant communities. *Forest Ecology and Management*, 185(1–2), 151–168. [https://doi.org/10.1016/S0378-1127\(03\)00252-4](https://doi.org/10.1016/S0378-1127(03)00252-4)
- Kane, J. M., Gallagher, M. R., Varner, J. M., & Skowronski, N. S. (2022). Pitch pine flammability data. *Figshare*, <https://doi.org/10.6084/m9.figshare.19143083>
- Kane, J. M., Kreye, J. K., Barajas-Ramirez, R., & Varner, J. M. (2021). Litter trait driven dampening of flammability following deciduous forest community shifts in eastern North America. *Forest Ecology and Management*, 489, 119100. <https://doi.org/10.1016/j.foreco.2021.119100>
- Kane, J. M., Varner, J. M., & Hiers, J. K. (2008). The burning characteristics of southeastern oaks: Discriminating fire facilitators from fire impiders. *Forest Ecology and Management*, 256(12), 2039–2045. <https://doi.org/10.1016/j.foreco.2008.07.039>
- Keeley, J. E., Pausas, J. G., Rundel, P. W., Bond, W. J., & Bradstock, R. A. (2011). Fire as an evolutionary pressure shaping plant traits. *Trends in Plant Science*, 16(8), 406–411. <https://doi.org/10.1016/j.tplants.2011.04.002>
- Keeley, J. E., & Zedler, P. H. (1998). Evolution of life histories in *Pinus*. In D. M. Richardson (Ed.), *Ecology and biogeography of Pinus* (pp. 219–249). Cambridge University Press.
- Kerr, B., Schwilk, D. W., Bergman, A., & Feldman, M. W. (1999). Rekindling an old flame: A haploid model for the evolution and impact of flammability in resprouting plants. *Evolutionary Ecology Research*, 1, 807–833.
- Kreye, J. K., Varner, J. M., Hamby, G. W., & Kane, J. M. (2018). Mesophytic litter dampens flammability in fire-excluded pyrophytic oak-hickory woodlands. *Ecosphere*, 9(1), e02078. <https://doi.org/10.1002/ecs2.2078>
- Ledig, F. T., & Fryer, J. H. (1972). A pocket of variability in *Pinus rigida*. *Evolution*, 26(2), 259–266.
- Ledig, F. T., Lambeth, C. C., & Linzer, D. I. H. (1976). Nursery evaluation of a pitch pine provenance trial. *Proceedings of the 23rd Northeastern Tree Improvement Conference*, 93–108.
- Leland, C., Hom, J., Skowronski, N., Ledig, F. T., Krusic, P. J., Cook, E. R., Martin-Benito, D., Martin-Fernandez, J., & Pederson, N. (2016). Missing rings, synchronous growth, and ecological disturbance in a 36-year pitch pine (*Pinus rigida*) provenance study. *PLoS ONE*, 11(5), e0154730. <https://doi.org/10.1371/journal.pone.0154730>
- Lenth, R. (2020). *emmeans: Estimated marginal means, aka least-squares means* (1.5.0) [R package]. Retrieved from <https://CRAN.R-project.org/package=emmeans>
- Little, S., & Garrett, P. W. (1990). *Pinus rigida* Mill. In R. M. Burns & B. H. Honkala (Eds.), *Silvics of North America. Volume 1, Conifers* (pp. 456–462). United States Department of Agriculture Handbook.
- Midgley, J. J. (2013). Flammability is not selected for, it emerges. *Australian Journal of Botany*, 61(2), 102. <https://doi.org/10.1071/BT12289>
- Mutch, R. W. (1970). Wildland fires and ecosystems – A hypothesis. *Ecology*, 51(6), 1046–1051. <https://doi.org/10.2307/1933631>
- Oksanen, J., Blanchet, G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P. R., O'Hara, R. B., Simpson, G. L., Solymos, P., Stevens, H. H., Szoecs, E., & Wagner, H. (2017). *vegan: Community ecology package* (2.4-4) [R package].
- Ormeño, E., Céspedes, B., Sánchez, I. A., Velasco-García, A., Moreno, J. M., Fernandez, C., & Baldy, V. (2009). The relationship between terpenes and flammability of leaf litter. *Forest Ecology and Management*, 257(2), 471–482. <https://doi.org/10.1016/j.foreco.2008.09.019>
- Palmer, W. C. (1965). *Meteorologic drought*. U.S. Weather Bureau Research Paper No. 45. 58 pp.
- Pausas, J. G., Alessio, G. A., Moreira, B., & Corcobado, G. (2012). Fires enhance flammability in *Ulex parviflorus*. *New Phytologist*, 193(1), 18–23.
- Pausas, J. G., Keeley, J. E., & Schwilk, D. W. (2017). Flammability as an ecological and evolutionary driver. *Journal of Ecology*, 105(2), 289–297. <https://doi.org/10.1111/1365-2745.12691>
- Popović, Z., Bojović, S., Marković, M., & Cerdà, A. (2021). Tree species flammability based on plant traits: A synthesis. *Science of The Total Environment*, 800, 149625. <https://doi.org/10.1016/j.scitotenv.2021.149625>
- PRISM Climate Group. (2020). *Prism climate group*. Retrieved from <http://www.prism.oregonstate.edu/>
- R Development Core Team. (2020). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing.
- Romero, B., & Ganteaume, A. (2020). Does recent fire activity impact fire-related traits of *Pinus halepensis* Mill. and *Pinus sylvestris* L. in the French Mediterranean area? *Annals of Forest Science*, 77(4), 106. <https://doi.org/10.1007/s13595-020-01016-1>
- Rothermel, R. C. (1983). *How to predict the spread and intensity of forest and range fires* (General Technical Report INT-143; p. 162). USDA Forest Service Intermountain Forest and Range Experiment Station.
- Saura-Mas, S., Paula, S., Pausas, J. G., & Lloret, F. (2010). Fuel loading and flammability in the Mediterranean Basin woody species with different post-fire regenerative strategies. *International Journal of Wildland Fire*, 19(6), 783. <https://doi.org/10.1071/WF09066>
- Scarff, F. R., & Westoby, M. (2006). Leaf litter flammability in some semi-arid Australian woodlands. *Functional Ecology*, 20(5), 745–752. <https://doi.org/10.1111/j.1365-2435.2006.01174.x>
- Schwilk, D. W. (2003). Flammability is a niche construction trait: Canopy architecture affects fire intensity. *The American Naturalist*, 162(6), 725–733. <https://doi.org/10.1086/379351>
- Schwilk, D. W., & Ackerly, D. D. (2001). Flammability and serotiny as strategies: Correlated evolution in pines. *Oikos*, 94(2), 326–336. <https://doi.org/10.1034/j.1600-0706.2001.940213.x>
- Stambaugh, M. C., Varner, J. M., Noss, R. F., Dey, D. C., Christensen, N. L., Baldwin, R. F., Guyette, R. P., Hanberry, B. B., Harper, C. A., Lindblom, S. G., & Waldrop, T. A. (2015). Clarifying the role of fire in the deciduous forests of eastern North America: Reply to Matlack. *Conservation Biology*, 29(3), 942–946. <https://doi.org/10.1111/cobi.12473>
- Stevens, J. T., Kling, M. M., Schwilk, D. W., Varner, J. M., & Kane, J. M. (2020). Biogeography of fire regimes in western U.S. conifer forests: A trait-based approach. *Global Ecology and Biogeography*, 29(5), 944–955. <https://doi.org/10.1111/geb.13079>
- Snyder, J. R. (1984). The role of fire: Mutch ado about nothing? *Oikos*, 43, 404–405.
- Troumbis, A. S., & Trabaud, L. (1989). Some questions about flammability in fire ecology. *Acta Oecologica - Oecologia Plantarum*, 10, 167–175.
- Valladares, F., Sanchez-Gomez, D., & Zavala, M. A. (2006). Quantitative estimation of phenotypic plasticity: Bridging the gap between the evolutionary concept and its ecological applications. *Journal of Ecology*, 94(6), 1103–1116. <https://doi.org/10.1111/j.1365-2745.2006.01176.x>
- Varner, J. M., Kane, J. M., Banwell, E. M., & Kreye, J. K. (2015). Flammability of litter from southeastern trees: A preliminary assessment. In G. A. Holley, K. F. Connor, & J. D. Haywood (Eds.), *Proceedings of the 17th Southern Silvicultural Research Conference: Vol. eGTR-SRS-203* (pp. 183–187). USDA Forest Service.

- Varner, J. M., Kane, J. M., Kreye, J. K., & Engber, E. (2015). The flammability of forest and woodland litter: A synthesis. *Current Forestry Reports*, 1(2), 91–99. <https://doi.org/10.1007/s40725-015-0012-x>
- Westerband, A. C., Funk, J. L., & Barton, K. E. (2021). Intraspecific trait variation in plants: A renewed focus on its role in ecological processes. *Annals of Botany*, 127(4), 397–410. <https://doi.org/10.1093/aob/mcab011>

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