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Biogeography of functional traits and fire regimes in oak species (*Quercus)* across the United States

By

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This thesis has been examined and approved by the following members of the student's committee.

Advisor

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Abstract

This thesis is submitted in the form of two chapters. The first chapter encompasses background research, a literature review, important information, as well as motivation for our study. This first chapter provides insight into fire ecology, functional traits, and context about *Quercus*. The second chapter is written as a standalone paper for submission to the journal of *Global Ecology and Biogeography*, thus this second chapter can be read and understood independently of the first chapter. The study of biogeography is a discipline encompassing a species distribution across varying ecosystems in space and time. Biogeography allows for the synthesis of large-scale patterns of a species including its evolutionary history, as well as varying biotic and abiotic factors. Here, we create a framework to assess functional traits in their fire resistance using a quantitative approach, utilizing the study system *Quercus*. In our study we spatially analyzed oak species adaptation patterns to fire utilizing functional traits and large-scale forest inventory analysis (community) datasets. We employ herbarium and field-collected functional trait data (plant height, bark thickness, self-pruning, specific leaf area, leaf habit, flame height and flame duration) to map oak species fire resistance across the US. We created a community-weighted mean fire resistance score of the US oaks and were able to identify areas of mismatch between a species assigned fire resistance score (FRS) and historical fire return interval (FRI) of an area. The FRS traits were analyzed using model selection Akaike Information Criterion. The FRS and FRI were analyzed for evolutionary trends using Phylogenetic Generalized Least Squares, and Ancestral Character State Reconstruction. We provide evidence that our assigned FRS did vary depending on the fire regime group (FRG) they occurred within. Our findings indicate that oak distribution across FRGs is not uniform, with a majority of oaks existing in FRG 1. Species in our FRS index that possessed a suite of functional traits, rather than scoring very high on just one singular trait resulted in higher FRS. We provide a framework of integrating functional traits into spatial analysis with implications for future research.

Introduction

Wildfires have long been regarded as catastrophic events that cause destruction to ecosystems. However, this viewpoint has shifted, as fire is now considered a critical component in ecological functioning. Fire is also important in the evolution of plants with fire, shaping plant traits. As plants have evolved in communities with fire, fire in return has played a key role in plant community composition, structure, and distribution. (Pausas & Schwilk, 2012). Species distributions and ecosystem processes that assist in structuring species-specific niches are complex and depend on a variety of factors. Functional traits may help provide a critical link between a species distribution and their role within the environment. The field of ecology has made improvements in understanding the connections between niches and the functional traits necessary for specific ecological niches. Improvements in the knowledgebase and availability of functional trait data, along with our abilities to model and map these functional traits across a species' distribution, help to improve functional trait biogeography. Functional trait biogeography can lead to predictions about the community assemblages' plasticity to change as environmental conditions change, and this can be modeled across varying landscapes (Noble & Slatyer, 1980; Varner et al., 2016). Although functional trait databases for plant species have expanded, studies tend to focus on fine spatial scales (Valladares et al., 2000; Messier et al., 2010). Additionally, these fine scale ecological studies focus on functional trait plasticity using only a few species and as a result the general ecological understanding of how a trait may vary across temporal scales is inadequate (Messier et al., 2010). Three essential elements are needed to conduct a functional trait biogeography study, this includes a study species, traits of interest, and environmental conditions or ecosystem of interest.

The purpose of the proposed research is to conduct a biogeographical study using functional traits that relate to fire of United States oak species. The project would rank traits of fire resistance by species then mapping the overall fire resistance score of oak communities across space. The proposed study is modeled off a similar study with the model species of western conifers (Stevens et al., 2020). This question is worth investigating due to the abundance of oak and shrubs in the United States. Data from the United States Forest Service's Forest Inventory Analysis (FIA) revealed that oaks have the highest biomass and species diversity of all woody genera (Cavender-Bares, 2016; Cavender-Bares, 2019). Creating a framework of traits associated with fire resistance versus fire avoidance is valuable for understanding how the fire regimes have shaped species patterns in an area. A trait-based approach of fire resistance and biogeography patterns does not currently exist for *Quercus* on a large scale. I hypothesize that (1) Functional traits of oak species that favor fire resistance will be more dominant in areas where oaks evolved with fire; (2) Oaks across species will share a suite of similar functional traits that are related to their fire resistance.

Literature review

Quercus: diversity, range, evolutionary history, evolution with fire

Quercus is one of the most widespread, highly diverse genera within the northern hemisphere (Nixon, 1993; Valencia, 2004; Kappelle, 2006; Rodriguez-Correa et al., 2015; Hipp et al., 2018; Hipp et al., 2020). The widespread range of *Quercus* is one of the reasons it is valuable in the investigation of functional traits (Cavender-Bares, 2019). Oak species have a strong global presence, with representatives inhabiting the Americas, Asia, Europe, and Northern Africa, with various species thriving in a wide range of habitats. Most recent estimates place diversity of oaks at 435 species, with 146 of those species living in North and South America, and 92 in the United States (Kremer & Hipp, 2020; Manos & Hipp, 2021). The species range and morphology are highly diverse within the United States, as oaks can be found in wetland ecosystems such as the eastern United States, as well as in the arid mountainous regions in the southwest United

States (Denk et al., 2017; Hipp et al., 2018). As a result of this diverse species range, oaks are often regarded as a successful evolutionary species. To succeed in such varied habitats, oak species have evolved to have a range of traits that are suitable for different habitats (Cavender-Bares et al., 2004; Kaproth & Cavender-Bares, 2016). *Quercus* has been successful at diversifying into niches, allowing the species to diverge across North America. Although several factors have impacted the dominance of oak species, the presence of fire in varying degrees has been a common component for oak development. Oaks inhabit vast ecosystems in the United States, these ecosystems are located across an array of distinct historical fire regimes. A key defining aspect of fire regimes is the variance in frequency and intensity of fire, historically in those given areas. A fires frequency is defined as the number of fires over a measured time period and is largely impacted by fuel accumulation rates. Fire intensity, defined as the heat release per unit of time per unit length of fire, is critical because it determines the extent of damage to tree tissues and likelihood of spreading that could result in increased mortality with an intense fire (Keeley & Zedler, 1998). The past and present influence of fire as well as human activity have impacted the ecology of oak forest ecosystems and will continue to alter forests into the future. With continued alterations to our climate this could result in shifts in frequency and intensity making fire regimes' future patterns uncertain (Abrams, 1992).

Ecological importance of Quercus

Woody species are a vital part of ecosystems, as they provide ecological, economic, and cultural benefits. Forests are defined by the species structure and composition; they provide habitat for numerous terrestrial plants and animal species. Oaks display a wide range in the ecosystems they inhabit, but they are also keystone species within some ecosystems. A keystone species provides value to the entire ecosystem, for an oak this may mean providing a source of nutrients from the acorn fruits produced by the tree. Numerous birds, mammals and insect species seek shelter within the branches, trunks, and leaves of oaks (Dickie et al., 2007; Nguyen et al., 2016; Cheeke et al., 2017; Tallamy, 2021). These animals in return provide food for other wildlife. Oaks provide temporary shelter for migratory bird species (Greco & Airola, 2018). Oaks provide many ecosystem services on the individual level, providing habitat and resources for organisms, and on a larger scale for forest populations. Forest ecosystems are responsible for pulling carbon from the atmosphere and sequestering CO_2 into biomass contributing to climate regulation (Goodale et al., 2002). The US Forest Service estimates oaks are responsible for sequestering more carbon compared to any other woody group within the continental United States (US Department of Agriculture, Forest Service, Northern Research Station, 2015). Oaks provide coastal protection and persistence after fire and other disturbance events (Glitzenstein et al., 1995). Economically, trees provide benefit to urban areas by moderating the climate, reducing energy usage, and improving air quality. Trees in urban areas increase property values and help to mitigate runoff and flooding events (Nowak, 2017). Many people consider trees to have an aesthetic beauty and inherit value as living organisms on this planet, so much so that there is a white oak tree that lives in Athens, Georgia that legally owns itself (Mueller et al., 2011). There are also several live oaks in the southeastern US that have legal protection, this speaks to the level of cultural and historical importance that these trees possess (Cavender-Bares, 2016).

Fire ecology

Fire has an integral role across forest ecosystems and the field comes with a set of terminology (Figure 1). To better understand fire's role, fire ecology aims to examine the relationship of fire with the abiotic and biotic forest ecosystem components. Key factors to consider when studying fire, includes the origins of fire, influences of spread, frequency, and intensity. A fire’s frequency being the number of fires over a time period, which is determined by fuel accumulation and ignitions. A fire's intensity is the culmination of the following behaviors: available fuels, compositions of fuels, moisture, temperature, wind, and topography (Cissel et al., 1999). Wildfires coincide with multiple factors, understanding how these factors impact wildfires and how they relate to natural fire regimes in an ecosystem are critical for the creation and implementation of comprehensive management practices. With changes in climate and land use, fire regimes are expected to expand to new areas, subsequently resulting in changes in frequency and intensity. Various plant species, such as *Quercus,* have evolved alongside fire disturbances allowing them to acquire functional traits that aid in survival and reproduction after fire events. These protective traits present in oaks allow them to survive environmental stressors such as fire. Other functional traits present in oaks are flammability traits that alter fire behavior through effecting fuels in a fire regime (Varner et al., 2016).

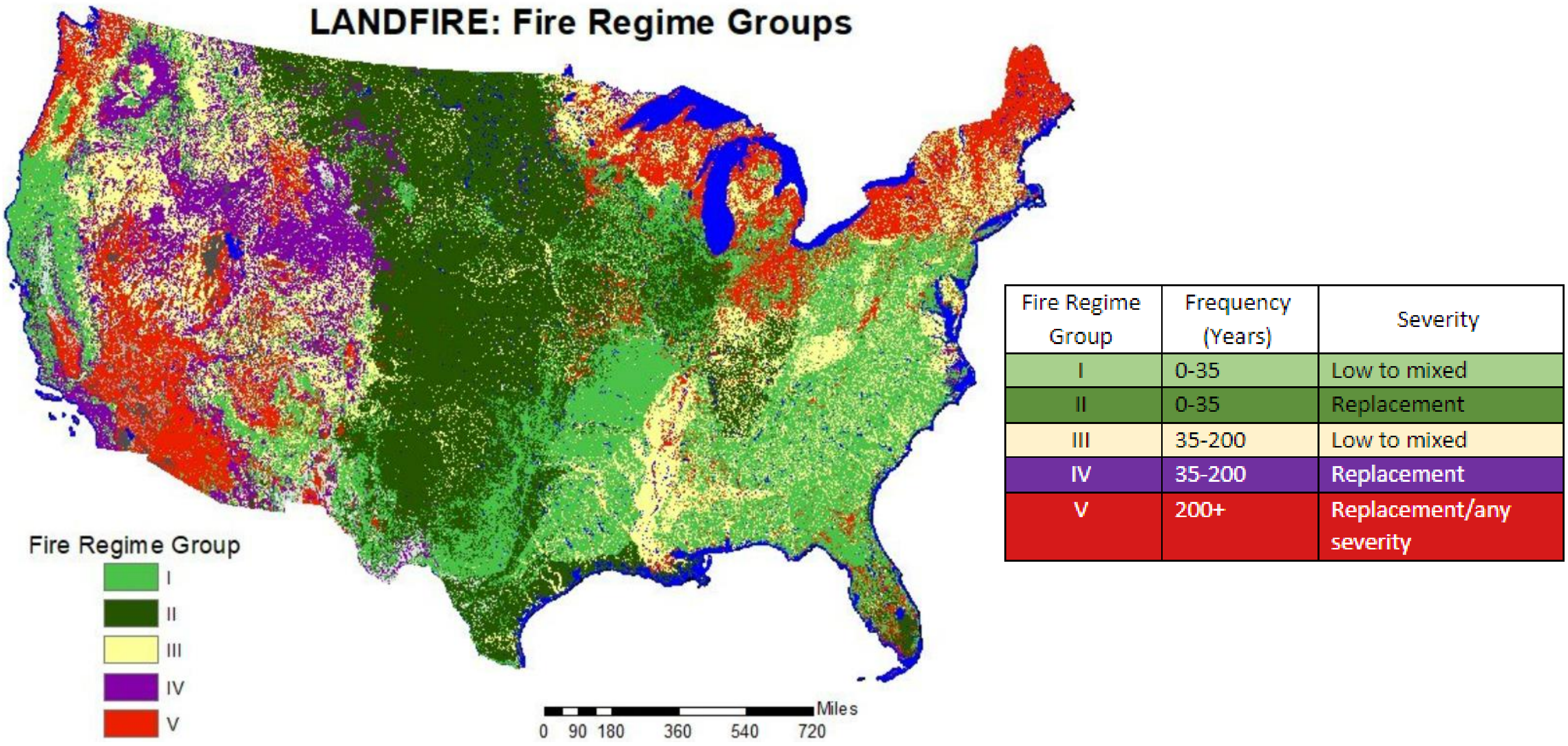
Understanding the linkages between these fire adaptive traits and how they overlap with current fire regimes is important to understanding potential mismatches or shifts to fire regimes (Varner et al., 2016; Pausas & Keeley, 2021).

Table 1. Key terminology commonly used in fire ecology, sources (Basu et al., 2016; Stevens et al., 2020; Pausas & Keeley, 2021).

Table 1. Key fire terminology
Fire Regime: The characteristic wildfire activity prevalent in a given area during a particular time. It is classified by frequency, intensity, size distribution, and types of fuels being burned. **Surface Fire:** Fire that spreads in herbaceous or litter layers, such as the forest understory, savannas, and grasslands. These fires typically are of relatively low intensity and occur at high frequencies. **Fire Resistant:** The ability of mature trees to withstand a surface fire, traits promote the survival of aboveground biomass analogous to “fire tolerant”. **Fire Avoidant:** Involving ecosystems that burn infrequently and do not select for fire adapted traits.

Historical fire regimes

Historically in the United States, fires were key drivers in developing ecosystem structure and composition and were the result of natural (lightning) or human influences. Fire-prone conditions and fire managed land promoted the regeneration capacity of oaks, such that their persistence was promoted by humans living in those ecosystems (Cavender-Bares, 2016). Many fire-dependent ecosystems across the US have historically been characterized by frequent but low intensity fires. Historical fire regimes are divided into five classes classified by years of frequency of occurrence. The classes are divided as follows; I 0–35-year frequency and low, II 0–35-year frequency and high severity, III 35-100+ year frequency and mixed severity, IV 35-100+ year frequency and high severity, V 200+ year frequency and high severity. Fire histories are based on fire behaviors before widespread settlement of European-Americans and was prior to extensive land use changes and fire suppression. Historical fire regimes have been determined using the following: fire scars, stand characteristics, charred wood, and charcoal., Fire scars are a result of heat persisting near the base of a tree for a long enough duration to damage the cambium layer, however over time the tree will grow over the scarring. When growth over fire scars occurs, collecting cross sections is necessary to determine a record of previous fires the tree has survived (Weisberg & Swanson, 2003). Stand characteristics of a forest are useful to understand past disturbance events, a range of different age classes of trees in a stand is indictive of past disturbance events, such as fire. The appearance of charred wood on the living bark of trees shows past fire events, some species, such as Douglas-fir will remain charred for centuries. Lastly charcoal can be found in sediment core samples in the soil as evidence of previous fires (Franklin et al., 2007; landfire.gov).



Fire Regime Group	Frequency (Years)	Severity
I	0-35	Low to mixed
II	0-35	Replacement
III	35-200	Low to mixed
IV	35-200	Replacement
V	200+	Replacement/any severity

FIGURE 1. LANDFIRE fire regime groups in the United States classified into the five following groups using frequency in years and the severity of fire.

Current fire regimes

Advancements in technology have increased the quality of satellite data, and mapping software that provides an aerial view of our forests. We can use historical fire regime data and apply it to spatial models. We can use these spatial models to link functional traits associated with fire resistance. The current fire regimes in the United States may experience shifts in location of where fires occur, and changes to frequency and intensity may result. The shifts in fire regime are an outcome of land use changes, management practices, community structure changes, and climate change factors. As population sizes have increased there have been ongoing changes to the natural landscape producing more fragmentation and overall loss of forested land (Pausas & Keeley, 2021). Past management practices may have promoted fire exclusion and suppression by changing stand structures in forests and fuel loads. Other management strategies of removing largest trees in a stand or reforesting altered the species composition, density, or structure. Alterations in climate resulting in changing temperature and precipitation patterns could lead to increasing or decreasing frequency and intensity within fire regimes (Varner et al., 2016).

Future fire regime shifts

There is potential the current fire regime and the future expected shifts compositions may have mismatches; using spatial models of fire regimes these mismatches could be addressed (Khwarahm, 2020; Stevens et al., 2020). Forests that are comprised of fire resistant plant species are historically abundant ecosystems that have been impacted by land use changes. Open forests such as savannas and woodlands are fire dependent and oak tree species are common in these ecosystems (Kercher & Axelrod, 1984; Hanberry, 2021). As changing fire regimes alter the current forest conditions, it is suspected that the combination of climate change, and disturbance events including wildfire will produce conditions that favor oaks (Vose & Elliott, 2016).

Functional traits

Through evolution, plant species have developed an assortment of traits in response to repeated exposure to disturbance or stress events within their environment. In theory a plant species will select for certain functional traits based on resource availability, resulting in alterations to plants functional traits across changing environmental gradients (Pellegrini et al., 2023). In the example of *Quercus* species, one could expect plasticity in plant traits thought-out a species distribution depending on the size of the species range. These adaptive traits are advantageous to the growth, reproduction, and survival of a species, as well as related to the capacity to endure disturbances (Table 2; Keeley et al., 2011). Functional trait analysis assists in uncovering the potential mechanisms in which species respond to their environment. Through analyzing functional traits, we will have a better understanding of how traits relate to fire resistance or fire avoidance. The functional traits that are important in fire survivability have been previously examined in several tree species (Kidd & Varner, 2018).

Traits of interests

Functional traits were selected using previous fire ecology literature, specifically traits important for plant fire resistance. The functional traits we selected were as follows: bark thickness, resprouting, dispersal mode, self-pruning, plant height, growth form, flame length, flame duration, and leaf size. Of the nine traits selected seven relate to tree morphology, and two relate to litter flammability. These functional traits are the traits of concern when scoring a specific species’ fire resistance score (Cornelissen et al., 2003; Stevens et al., 2020).

Bark thickness

Bark thickness is known to have associations with more fire resistant species, and particularly a trait common in species found in areas of persisting fire-prone environments. However, bark thickness by itself may not provide the best indication of fire resistance due to species differences including species-dependent growth, reproductive, and survival strategies (Jackson et al., 1999). The trait of bark thickness is classified under the category of stem and belowground traits, and in our study includes the periderm layers. Bark thickness is defined as the part of the stem that is external to the wood and is known to insulate the tree from lethally elevated temperature. The protection offered from thicker bark is dependent on the fire's intensity and duration (Cornelissen et al., 2003; Stevens et al., 2020).

Resprouting

Oaks may use resprouting to aid in their fire resistance. Smaller-stemmed trees display a well-developed root system that helps in promoting aggressive resprouting abilities after disturbance (Myers, 1990; Abrams, 1992; Jackson et al., 1999; Cavender-Bares et al., 2004b; Cavender-Bares & Reich, 2012; Schwilk et al., 2016; Vose & Elliott, 2016). The severity of wildfires has increased which has resulted in shifts from pine-oak woodland to oak shrubland in several areas in the southwestern United States. One key functional trait responsible for this shift is the resprouting ability of oaks compared to pines that have a lower regeneration rate in the aftermath of a wildfire disturbance (Poulos et al., 2020). Resprouting capacity is the ability of a species to form new shoots after a disturbance event destroys a large amount of its aboveground biomass, which is considered a regenerative trait. The trait of resprouting is a result of disturbance related events, that proves especially significant after fire events (Myers, 1990; Schwilk et al., 2013). A sprouting species tend to allocate carbohydrates to belowground organs although they typically have slower overall biomass growth in comparison to non-sprouting species (Cornelissen et al., 2003; Keeley et al., 2011; Clarke et al., 2013).

Self-pruning

Self-pruning is a trait that is associated with fire resistance and is the process of gradual decline in the number of branches on lower stem areas (Kint et al., 2010). Removal of lower limbs reduces the chance of fire spreading up the tree to the crown, thus increasing survival rates (Keeley et al., 2011).

Plant height

The height of a species is advantageous for avoiding fire; however, this trait is impacted by the age of the plant. Plant height is categorized as a vegetative trait and is measured as the shortest distance between the upper tissues on a plant and ground level. The trait is typically associated with competition, the height of a plant being impacted by disturbance events. There are tradeoffs that occur between a plant's height and the resistance or avoidance of environmental stressors. The taller a species the more likely they will be able to avoid fire disturbances (Cornelissen et al., 2003; Varner et al., 2016).

Growth form

The growth form is specific to each plant's strategies from the height of the tree to the arrangement of its leaves, typically limited by environmental factors. A plant's growth form is shaped by canopy structure and height. Growth form is a categorical trait for oak that can be sorted into one of the three groups: small tree, tall tree, and shrub. The strategies and adaptations to a plant’s growth form could be a response to predation avoidance, or resources availability such as sunlight or water (Cornelissen et al., 2003). Depending on the growth form of a tree, it can escape fire or depending on leaf size that can determine litter ignitability, smaller leaves create a compact litter-bed with less aeration and burn slowly. The growth form of an oak tree in an arid environment could result in smaller shrubs such as trees with small leaves.

Leaf size

Leaf size is a projected surface area of the leaf and is important for energy and water balance. Leaf size can be analyzed in a multitude of ways. We choose to select the trait of specific leaf area (SLA) which is a measurement of the area of one side of the leaf divided by the oven dried mass (Cornelissen et al., 2003). The variations in leaf size among varied species are connected to climate gradients, geology, altitude, or latitude. A plant’s leaf size is linked to allometric factors such as the plant’s overall size, twig size, or anatomy. The trait of leaf size is a response to both ecological and phylogenetic factors. A species SLA is a leaf morphology functional trait explaining the leaf thickness and density, providing an understanding into the investment into light capture at the expense of leaf strength (Pellegrini et al., 2023). A lower SLA value typically corresponds to high investment in leaf defense as well as a long leaf habit or lifespan, for example evergreen leaves. Leaf size is typically indicative of the ecosystem the plant inhabits, for example dry arid environments plants tend to have smaller leaves. A higher SLA value tends to correspond to environmental conditions where resources are plentiful.

Leaf habit

Leaf habit is a functional trait associated with resource acquisition and leaf economics. A plant species leaf habit is a classification of a population of leaves, not individual leaves on a plant. Specific to oak species three leaf habits can be observed: evergreen, brevideciduous, and deciduous. Although the functional trait of leaf habit is a leaf morphology trait it relates to the fuels of a forest ecosystem given the leaf litter created by deciduous species as well as chemical variation across different leaf habits. Past studies determined that traits of leaf habit and leaf margin were critical factors when determining leaf flammability, specifically in southeastern US *Quercus* species (Kane et al., 2008; Engber & Varner, 2012).

Leaf litter flammability

Flammability, also referred to as ignitability, is how easily a plant ignites and is an important trait that contributes to fire regimes. Traits associated with litter flammability include flame length and flame duration. Flammability traits are either “fast flammable” meaning they have higher flame lengths with a shorter duration of burning verses “hot flammable” traits associated with moderate flame lengths but a longer flame duration (Stevens et al., 2020). The trait of flame length is a measurement of the flame height when a leaf is ignited, while the trait of flame duration is the amount of time a leaf burns.

TABLE 2. The following are functional traits observed in *Quercus* species, and what pattern of a trait confers to either fire resistance or fire avoidance. The relationship varies based on the fire regime (frequency and severity); It is hypothesized that species that experience fire more frequently would display traits correlated to resistance verses species that experience fire less frequently would have traits that correlate with avoidance.

Functional Traits	Fire Resistance	Fire Avoidance	Citation
Plant height	Taller plant height can prevent fire from torching the crown.	Taller plant height can avoid fire from spreading into the crown.	Varner et al., 2013; Stevens et al., 2020
Resprouting	Resprouting is used in response to disturbance, as it implies the potential for repeated vegetative regeneration of underground stems. Higher resprouting rates after a fire event help to promote survival.		Clarke et al., 2013; Keeley et al., 2011
Self-pruning	Shedding branches lower to the ground creates a gap in available fuels, helping prevent fire from spreading into the crown.		Keeley et al., 2011
Bark Thickness	Thicker bark helps protect the tree from fire, species with thick and rapidly accumulating bark repair wounds rapidly. Display rapid juvenile bark accumulation.	Unknown relationship	Varner et al., 2013; Stevens et al., 2020
Growth Form	Two strategies for resisting fire, tall tree to prevent tissue loss, or shrub to regenerate quickly.		
Flame Length	Higher flame lengths spread quickly and have greater consumption of fuels but release less heat.	Non-flammable	Stevens et al., 2020
Flame Duration	The quicker the fuel burns the less heat released (less tissue damage).	Non-flammable	
Leaf Size (SLA)	Small leaves create a compact litter-bed that is less aerated and burns slowly; small leaves have a longer time to ignition.	Higher SLA is less carbon rich thus provides less fuel	Grootemaat et al., 2015; Murray et al., 2013
Leaf Habit (type)	Uncertain: evergreen species will have higher carbon content but may be less likely to ignite	Relationship depends on aridity and the accumulation of fuels	Murray et al., 2013; Varner et al., 2016

Proposed research

As fire frequency and intensity changes across the United States and around the world, improving our understanding of fire adapted traits present in *Quercus* spp. that aid in survival from fire events is increasingly important. In this study, we aim to produce a map of fire resistance within oak species across the United States using selected functional traits related to fire resistance. These functional traits will be assigned fire resistance scores (FRS) and will be ranked by species. The goal is to improve the knowledge base and ability to predict resistance to fire across oaks. With fire patterns across the US shifting, it is important to create models to understand how species will respond, and potential trait-fire shift mismatches that warrant management attention. Understanding fire regimes shifts and how they might affect the composition of our forests will result in better developed management practices for our forests (Kremer & Hipp, 2020).

Predictions

The following hypotheses I pose for my research project have predictions associated with them. For the first hypothesis I predict that there will be a correlation between certain functional traits present in oaks that are typically associated with fire resistance and will persist in areas where oaks evolved with fire historically. However, there are other opposing hypotheses, questioning if these traits are a response to evolving from fire or a result of other environmental responses (Bradshaw et al., 2011). With this prediction we would expect to see trends in the data, oak species with higher FRS near one would likely have a distribution in areas that evolved with frequent FRI's. If this prediction is not shown in the data, this could be a result of mismatches in the fire regime groups. It could mean that the functional traits selected for the research correlate to other adaptations and not specifically fire adaptation traits.

The second prediction is that there will be a shared suite of similar traits in relation to a species' fire resistance. It is predicted that oak species that have similar overall FRS will share an overlap in the functional trait associated with fire resistance. If a species shows several of the known fire resistant traits it can be assumed this species is fire adapted. It is suggested that species use a suite of traits, not just one single trait to persist in fire prone environments (Varner et al., 2016). If this prediction is not shown it may mean that functional traits selected for fire adaptation are less correlated in the combination of functional traits present in a species, but trait selection is more related to the environment each species inhabits.

The evolutionary history of oaks is critical for understanding how environmental disturbances can impact community assemblage ecology. Using a model clade such as *Quercus* provides the ability to integrate ecology and evolution, and the importance of resilience of key functional traits (Cavender-Bares, 2019). Oak species in North America diverged into two major lineages the white oaks (section *Quercus*) and the red oaks (section *Lobatae)* and live in similar ecosystems at times co-occurring (Cavender-Bares et al., 2018; Hipp et al., 2018). These different abiotic factors present in ecosystems assist in shaping species traits. This is important because if ecosystems experience changes in the intensity and severity of fire, shifting fire regimes, then species will need to adapt survive in these new conditions. One may expect that if fire regimes experience alterations because of changes in our climate that oak species that are highly plastic and could adapt to shifts in their environment will be more successful surviving and reproducing given changing climate conditions. An increased understanding of how the evolutionary history and process of a species connects to the ecology the species inhabits is the first step in understanding how a species may adapt to change.

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Chapter 2 - Biogeography of Functional Traits and Fire Regimes

Introduction

Plant communities have evolved with fire as a key disturbance event; fire is responsible for shaping many forest and plant ecosystems across the globe (Abrams, 1992; Kane et al., 2008; Keeley et al., 2011; McLauchlan et al., 2020; Greenberg et al., 2021; Pausas & Keeley, 2021). Fire events can occur with varying degrees of severity (low, moderate, or high) impacting the biomass consumed (Abrams, 1992; Engber & Varner, 2012; Hollingsworth et al., 2013). A previous study about United States (US) forest communities found that species richness and total proportional biomass had the highest amounts comprised of the genus *Quercus* with *Pinus* coming in second in both measurements (Cavender-Bares, 2016; Cavender-Bares, 2019). Regardless of the degree of fire severity, all oak ecosystems which experience fire share in the commonality that fire has served a role in the development of oak dominated forests in the United States (Abrams, 1992). Oaks are a dominant species occurring across the US existing across a range of varying fire severity, and thus are an important species to explore in their relation to fire.

Fire regimes have shaped the plant communities within that certain ecosystem and climate change resulting in alterations to temperatures, drought, and various other factors will result in shifts to fire regimes (Kelly et al., 2013; Abatzoglou & Williams, 2016; Balch et al., 2018; Walker et al., 2018; Miller et al., 2019; McLauchlan et al., 2020; Liang & Hurteau, 2023).

Fire regimes vary in the frequency and intensity of fire within a given area and thus may result in the selection of different plant functional traits, species are not necessarily adapted for fire but rather for the fire regime in which they inhabit (Cavender-Bares et al., 2004; Keeley et al., 2011). One can suspect oak species functional traits are likely dependent upon the fire regime which they inhabit, changes to fire regimes can thus threaten the survival of a species (Keeley et al., 2011). It is predicted that oaks may play an increased role of importance in mixed conifer-hardwood forest ecosystems specifically in the northeastern US because of a changing warming climate (Overpeck et al., 1991). Our research focuses on the five fire regime classes created by the shared government program LANDFIRE LF 2014 (landfire.gov) which includes the U.S. Department of Agriculture, Forest Service, and U.S. Department of the Interior's wildland fire management bureaus with direction from the Wildland Fire Leadership Council. LANDFIRE (LF) describes their Fire Regime Groups (FRG) layer as the presumed historical fire regimes within landscapes based on interactions between vegetation dynamics, fire spread, fire effects, and spatial context. LANDFIRE in collaboration with these agencies creates spatial layers and databases for the US and territories. Thus, when referring to the historical fire frequency and severity this is a representation of the fire regimes prior to European colonization, the fire patterns of an area over a long period. So, although areas may be existing within a certain fire regime group (FRG) that historically has experienced frequent fire, the early Europeans relationship to fire has often been expressed through suppression and until recently our understanding of the highly important relationship fire serves in these fire-dependent ecosystems has begun to shift (Spetich & He, 2008; Pausas & Keeley, 2021; Bataineh et al., 2022).

A plant's adaptive functional traits serve a purpose of increased fitness advantages within an ecosystem, specifically within the fire regime it inhabits. These traits may have a high degree of variation with more than one way to be successful in surviving and thriving through reproduction and productivity (Keeley et al., 2011). Critical to our study is the use of oak functional traits and a species biogeography specifically related to the fire patterns of an area. Together this link between a species' distribution across space and the functional traits they possess we can better understand their role within an ecosystem and its functioning (Violle et al., 2023).

A community's assemblage of functional traits could serve as a beneficial tool to understand how a plant community's functional traits influence function and specific to our study fire resistance. Advancements in data sharing have resulted in an expansion of availability of plant functional trait data, which can be utilized to explore traits of a community of plants (Kattge et al., 2011). Although many studies using functional trait data tend to center around small spatial scales, due to challenges of scaling up to larger spatial studies (Messier et al., 2010; Kattge et al., 2011). One approach that assists with scaling up is the use of remote sensing. Improvements in remote sensing technologies allow for the ability to incorporate a species overall abundance and functional traits possessed to utilize a functional trait biogeography approach. We aimed to explore how ecosystems oak functional traits lend to the overall fire resistance at a larger scale spatially. We employed a functional trait biogeography process to detail the trait variations and adaptations across different FRG of US oaks. We based our study on a previous study conducted using western conifer species (Stevens et al., 2020).

Wildfire is an important ecosystem function that assists in shaping plant communities, as numerous plant species have acquired robust traits that assist in survival within recurrent fire dependent ecosystems (Keeley et al., 2011). Fire regime classifications portray historical burning characteristics, such as severity, frequency, and fire patterns (Morgan et al., 2001). Fire regimes vary across ecosystems, these changes being heavily dependent on the productivity of an area (Keeley & Zedler, 1998). Fire regime characteristics such as severity and frequency of fire often and fire return intervals serve as useful modeling parameters. It is thus understood that across landscapes fire patterns will vary resulting in the plant species that comprise those ecosystems that have differing functional traits. Thus, how a plant species responds to fire varies heavily on the traits they have. However, how some traits promote the survival post-fire is better understood, such as bark thickness (Hood et al., 2018). In the past, many plant species have been assessed on their fire resistance through ranking them on a spectrum of ability to survive fire, this process relying on a qualitative consideration of the plant's natural history. Improvements to fire mortality modeling have included the use of functional traits to account for a species particular fire resistant trait (Cansler et al., 2020). While our study employs a quantitative approach of US oak species' functional traits in relation to fire resistance.

To provide context of common terms used in fire ecology a glossary was created (Table 1). Plant traits can typically be classified into the following groups based on their adaptation to fire: fire resistant, fire embracing and fire avoidant. Our study focuses on fire resistance of oak species' functional traits. Fire resistance is defined as the ability of aboveground biomass to survive surface fire (Keeley, 2012) (Table 1). Our study utilizes fire resistant functional traits opposed to "fire embracing" traits which have an emphasis on post-fire regeneration of tissues through resprouting at the expense of losing aboveground biomass during a fire event, verses survival of aboveground tissue displayed in fire resistant species. These fire embracing strategies such as resprouting can typically be observed in fire regimes that experience less frequent fire but when fire occurs the intensity is severe (Pausas et al., 2017). Lastly "fire avoiding" strategies typically concern ecosystems whose fire regime consists of infrequent burns and thus are not selecting for fire-adaptive traits.

TABLE 1. Key fire terminology to classify the different categories of how a species trait may interact with fire, in our study we focus on traits in relation to fire resistance (Basu et al., 2016; Stevens et al., 2020; Pausas & Keeley, 2021).

TABLE 1. Key terminology

Fire avoiders: Includes species found in environments where fire is highly infrequent thus species contain few traits described as fire adaptive. However, traits may be conflated with fire resistance. Traits may be a result of long fire return intervals that are able to select for "fire resistant" traits due to resource rich environments. These typically occur in alpine or desert environments with leaves adapted for conditions of extreme heat, cold, or drought. The leaves of fire avoiders having short burn durations traits that help to suppress fire spread.

Fire embracer: Associated with the loss of aboveground biomass with an emphasis on post-fire regeneration through resprouting; may be adaptive under less frequent, higher-intensity fire regimes. Fire embracers also intensify fire spread through functional traits such as limited self-pruning of dead branches, thus increasing fuels that promote crown fires. Leaves of fire embracers promote longer burn duration and increased spread of fire.

Fire resistant: A selection of traits which allow for aboveground survival when surface fire occurs. Species classified as fire resistant i.e., "fire tolerant", exist in areas that experience low intensity but high frequency fires. Species trait typically exhibit tree form (taller height), thick bark, and self-pruning of lower branches.

Functional traits and fire resistance

A species' fire resistance in relation to the functional traits it possesses should not be viewed as a one-dimensional metric but rather as a grouping of traits and how they together interact with the environment during a fire event (Pausas et al., 2012; Simpson et al., 2016, Pausas et al., 2017). The functional traits used in our study were informed through literature reviews as well as traits used in Stevens et al. (2020) conducted with conifers. The following traits were selected for our study plant height, self-pruning, bark thickness, specific leaf area (SLA), leaf habit, and leaf litter flammability traits of maximum flame height and flame duration.

Study system

When conducting an analysis that incorporates both functional trait ecology and evolution, utilization of a model clade such as the genus *Quercus* is beneficial for several reasons. *Quercus'* ecological dominance is remarkably high across the US as well as globally (Nixon, 1993; Valencia, 2004; Kappelle, 2006; Rodriguez-Correa et al., 2015; Cavender-Bares et al., 2018; Hipp et al., 2018; Hipp et al., 2020). The US contains 91 oak species of the nearly 400 species in the genus globally (Nixon, 1997; Hipp et al., 2014). Data from the United States Forest Service's (USFS) Forest Inventory Analysis (FIA) revealed that oaks have the highest biomass and species diversity of all woody genera (Cavender-Bares, 2016; Cavender-Bares, 2019). The genus *Quercus* possesses high functional trait plasticity and diversity, and thus individuals exist in a wide range of environments (Kirsch & Kaproth, 2022). Species of oaks reside in environments on opposite ends of the spectrum, with species thriving in drought prone areas to highly mesic conditions. Oaks also tolerate environments with varying minimum and maximum temperatures (Cavender-Bares, 2016; Hipp et al., 2018; McCormack et al., 2020). Oaks inhabit a wide range of FRG that differ in the frequency of fire occurrence and the severity of fire (Trejo, 2008; Schwilk et al., 2013). Through the process of environmental filtering disturbance events such as fire occur and select for species with traits that aid in survival and regeneration (Hollingsworth et al., 2013). If a species exists in an area that has frequent fire occurring within its lifespan this can thus support selection of traits related to fire resistance enhancing likelihood of survival during a wildfire event. It should also be noted that fire regimes can vary at small spatial scales impacting the plant coverage and flammability of an area (Clarke, 2002). Given the variation in environmental conditions oaks inhabit it is not surprising the widespread diversity and speciation of the genus, having members from five continents; North and South America, Europe, Africa, and Asia (Cavender-Bares et al., 2018). Lastly, an increase in *Quercus* genus resources of phylogenetic, genomic, and ecological data resources lends to the genus being an advantageous study system with the availability to explore many ecosystems (Cavender-Bares, 2019). Oaks possess an expansive evolutionary history with varying ecological pathways to be utilized in shaping the genus over millions of years (Abrams, 1992).

The global dominance of oaks results in the genus being an alluring study system. Having a model clade that possesses a wide range of functional traits and evolutionarily is expansive allows for understanding of how these traits relate to fire within an ecosystem. These trait tradeoffs shown in *Quercus* allow the genus to successfully inhabit a range of fire regimes in the US, with varying levels of frequency and severity, important to our study (Myers, 1990; Schwilk et al., 2013).

Our research aims to evaluate fire resistance in US oaks through the analysis of functional traits they possess that are understood to relate to a plant's ability to survive fire. The oaks functional traits will thus be analyzed and standardized to assign each US oak species a fire resistance score (FRS) and thus rank them using their fire resistance traits. Using the assigned FRS to spatially map the oak communities fire resistance, Forest Inventory Analysis (FIA) data. We propose the following hypotheses: the first hypothesis is there will be higher FRS in oaks that primarily persist in areas where these species evolved with historical frequent fire (FRG 1 and 2). However, opposing views exist questioning if these traits are a response to evolving in areas of fire disturbance or from other environmental stressors enacting functional traits that assist certain environmental factors (Bradshaw et al., 2011). With this prediction we would expect that oak species with higher FRS would likely have a distribution in areas that evolved with frequent fire return intervals (FRI). If this prediction is not shown in the data, this could be a result of mismatches in the historical FRG of an area suppressing fire. This could mean the functional traits selected for our study, originally conducted using conifers (Stevens et al., 2020), are a result of other adaptations to a species environment not specifically fire resistance traits. The second hypothesis being there will be a shared suite of similar traits in relation to a species fire resistance. It is predicted that oak species that have similar overall FRS will share in similar functional traits associated with fire resistance. If a species possesses several of the assumed traits that aid in fire resistance, this species is adapted to survive fire events. It is suggested that species use a suite of traits to prevail in frequent fire ecosystems, not only one single trait (Varner et al., 2016). If this prediction is not shown it may mean that functional traits selected for fire adaptation are less correlated in the combination of functional traits present in a species, but trait selection is more related to the environment each species inhabits.

Methods

Selection and quantification of functional traits

We selected seven functional traits understood to assist with fire resistance in US oak species (Cornelissen et al., 2003; Keeley et al., 2011; Clarke et al., 2013; Murray et al., 2013; Grootemaat et al., 2015; Varner et al., 2016; Stevens et al., 2020). A functional trait dataset was assembled using collections from herbaria, agency literature, and field collections on 81 US *Quercus* species. Our functional trait database consisted of seven traits, three related to tree morphology (plant height, bark thickness, and self-pruning), two related to leaf morphology traits SLA (ratio of leaf area to dry mass) and leaf habit (deciduous, brevideciduous and evergreen), and two traits related to leaf litter flammability (flame height and flame duration) (Figure 1).

The maximum plant height of oak specimens was collected through field observations and cross-referenced using literature. Plant height measurements from the field were gathered using a Haglöf EC II-D Inclination/Height/Distance Calculator. Maximum plant height from Manos & Hipp (2021) was also utilized.

The bark thickness data was collected from specimens in the field using a Haglöf Barktax Bark Gauge. To estimate the bark thickness for each species consistently, measurements were taken at diameter at breast height (d.b.h) and a linear equation assuming a linear rate of bark accumulation was utilized as modeled by Lutes & Keane (2017). This assumes that bark accumulation occurs in a linear relation as (d.b.h) increases, although this can be an oversimplification for many species, it is a widely used model that captures the variation in bark thickness shown across species. This linear model technique was implemented to adjust for the differences between observed specimens in the field with varying (d.b.h). To estimate bark thickness in our linear model species were separated by their growth forms either tree or shrub, then were analyzed using an average (d.b.h). Trees were analyzed using a mean (d.b.h) of 59.9 cm, shrubs were analyzed using a mean (d.b.h) of 13.1 cm.

The degree of self-pruning for each species was assigned using an ordinal scale from 1 to 10, using methods outlined by Keeley & Zedler (1998) and Schwilk & Ackerly (2001). An ordinal score of 1 represents a low degree of self-pruning of branches, a score of 10 represents a high degree of self-pruning. To further analyze *Quercus'* self-pruning abilities, we utilized data collected in the field of lowest limb to the ground and mature plant height, we calculated the ratio, then assigned an ordinal score for each species.

Functional traits related to leaf morphology (SLA and leaf habit) were derived from herbarium samples from Kaproth et al. (2020). A low SLA was interpreted as having a higher score of fire resistance, previous studies showed that a high SLA resulted in a quicker time to ignition compared to low SLA

(Murray et al., 2013; Grootemaat et al., 2015). Leaves with a low SLA ignite slowly and spread fire at slower rates, exhibiting more resistance to fire spread (Babl et al., 2020). The trait of leaf habit for each species was analyzed as follows. Deciduous leaf habit was classified as a short-lived leaf capable of capturing resources during a narrow time to then senescence (Kaproth et al., 2023). Previous studies in varying oak leaf habits found that deciduous species were more flammable than evergreen (Engber & Varner, 2012). Brevideciduous leaf habit experience a brief time within a year where old leaves are senescing whilst new leaves emerge (Kikuzawa & Lechowicz, 2011). Evergreen leaf habit stays on the plant year-round (Kaproth et al., 2023). Thus, the leaf habits used in our study: evergreen, brevideciduous and deciduous were assigned the following FRS values 1.0 (high), 0.5 (moderate) and 0 (low) in relation to their fire resistance. Our leaf morphology traits of SLA and leaf habit were averaged together into one value for the final FRS model to avoid overrepresentation of leaf morphology in the overall model. We wanted to account for leaf habit traits only having FRS values of 1.0, 0.5 and 0 whereas our other traits were standardized existing on a larger range of continuous values ranging from 0-1. For example, a higher FRS would be a species exhibiting a low SLA and evergreen leaf habit (Figure 1).

Flammability trait data of maximum flame height and flame duration for 31 oak species was obtained from the following: Kane et al. (2008; n = 8), Engber & Varner (2012; n = 15), Varner et al. (2021; n = 8). Flammability trait data was also collected through our own leaf litter burn trials (n = 34). All the flammability data included in our study was conducted using the same methodology described by Fonda (2001). The flammability traits of flame height and flame duration were closely negatively correlated (Pearson's r = -0.84). To avoid overrepresentation of the traits in the overall fire resistance score a principal component analysis was conducted using the two flammability traits. The first principal component (PC1) analysis axis explained 91.8% of the variance and was selected to account for flammability traits of maximum flame height and flame duration concurrently (Figure 1).

Once all the functional trait data was compiled for US *Quercus* species for the following seven traits; tree morphology (plant height, bark thickness, and self-pruning), leaf morphology (SLA, and leaf habit averaged into one trait), and leaf litter flammability (flame height and flame duration as one PC score). The traits were standardized then averaged to assign one single FRS: ranging from zero to one. The scoring was following a protocol detailed from Stevens et al. (2020). Specifically, for every species a percentile value was assigned according to where the trait fell within the range of observed trait values. The most fire resistance trait was thus assigned a percentile value of one, and the least fire resistance trait was assigned a percentile of zero. We defined traits being highly fire resistant (score of 1) as the following: tallest maximum plant height, thickest bark, greatest degree of self-pruning, lowest SLA, and evergreen leaf habit (two leaf morphology traits averaged together as a nominal and ordinal score), longest flame height and shortest flame duration joined as one trait using a principal component analysis PC1 detailed above. The FRS of each *Quercus* species was then calculated using the average of the five percentile scores comprised of the seven functional traits.

Model selection

To determine which functional traits, add to the overall model, we utilized stepwise model selection Akaike Information Criterion (AIC) with seven traits added to the model in relation to the overall FRS. Through this process it was determined that resprouting in *Quercus* was not an important trait to include in our model, likely because it is the rule that oaks will respond with resprouting after a disturbance event like fire, not the exception (Schwilk et al., 2016; Ackerly et al., 2019). The other seven traits were found to all to add to the overall model and thus were included in the final FRS. We also analyzed the functional trait values for our 81 oak species (Table 2) in JMP Pro 14 (version 14.2.0) using a multivariate correlation matrix to determine what traits were strongly correlated to each other (Appendix Figure A).

TABLE 2. Functional trait data and the assigned fire resistance scores for US oaks used in analysis.

	Trait values[1]							Percentile ranking (standardized)					
Scientific name	**Plant height**	**Specific leaf area (SLA)**	**Leaf habit**	**Self-pruning**	**Bark thickness**	**Flame duration[2]**	**Flame height[2]**	**Plant height**	**Average FRS of SLA and lh[3]**	**Self-pruning**	**Bark thickness**	**PC1 of fd and fh[3]**	**FRS**
Quercus bicolor	30	12.01	0	10	4.97	30.6	67.1	0.75	0.16	1.00	1.00	0.83	0.75
Quercus laurifolia	40	9.50	0.5	7	2.14	53.8	55.9	1.00	0.50	0.70	0.42	0.67	0.66
Quercus shumardii	35	9.13	0	6	2.83	42.9	70.2	0.87	0.27	0.60	0.56	0.81	0.62
Quercus macrocarpa	30	9.10	0	5	3.72	29.8	64.8	0.75	0.27	0.50	0.74	0.82	0.62
Quercus imbricaria	20	7.07	0	5	3.61	34.7	79.2	0.49	0.35	0.50	0.72	0.90	0.59
Quercus virginiana	35	5.78	0.5	6	2.14	84.5	33.6	0.87	0.65	0.60	0.42	0.41	0.59
Quercus velutina	25	8.84	0	5	2.67	29.1	92.3	0.62	0.28	0.50	0.53	1.00	0.58
Quercus falcata	30	11.03	0	9	2.14			0.75	0.20	0.90	0.42		0.56
Quercus nigra	30	9.43	0	8	2.14	77.1	57.3	0.75	0.26	0.80	0.42	0.59	0.56
Quercus coccinea	30	9.30	0	5	2.14	32.1	73.3	0.75	0.26	0.50	0.42	0.87	0.56
Quercus hemisphaerica	35	10.80	0.5	6	2.14	91.4	40.4	0.87	0.45	0.60	0.42	0.43	0.55
Quercus stellata	20	9.62	0	5	3.65	52.0	68.4	0.49	0.25	0.50	0.73	0.76	0.55
Quercus texana	25	8.55	0	4	2.14	23.9	88.9	0.62	0.29	0.40	0.42	1.00	0.55
Quercus palustris	25	12.09	0	6	2.36	30.4	75.2	0.62	0.16	0.60	0.46	0.89	0.54
Quercus fusiformis	25	6.03	0.5	5	2.14			0.62	0.64	0.50	0.42		0.54
Quercus alba	25	12.00	0	5	3.27	54.0	72.0	0.62	0.16	0.50	0.65	0.77	0.54
Quercus wislizeni	22	6.48	1	4	2.14	88.9	39.9	0.54	0.87	0.40	0.42	0.43	0.53
Quercus geminata	25	4.30	0.5	5	2.14	91.0	39.0	0.62	0.70	0.50	0.42	0.42	0.53
Quercus muehlenbergii	30	10.49	0	4	2.24	32.8	71.9	0.75	0.22	0.40	0.44	0.86	0.53
Quercus michauxii	20	10.31	0	6	2.63	43.7	72.3	0.49	0.22	0.60	0.52	0.82	0.53
Quercus montana*	30	14.70	0	5	3.39	46.6	49.7	0.75	0.06	0.50	0.68	0.66	0.53
Quercus pagoda	40	11.22	0	5	2.14			1.00	0.19	0.50	0.42		0.53
Quercus laevis	20	9.53	0	6	2.14	50.4	81.4	0.49	0.25	0.60	0.42	0.85	0.52
Quercus tomentella	20	5.31	1	3	2.14	75.5	35.5	0.49	0.92	0.30	0.42	0.46	0.52
Quercus phellos	30	12.33	0	6	2.14	66.7	59.0	0.75	0.15	0.60	0.42	0.64	0.51

	Trait values[1]							Percentile ranking (standardized)					
Scientific name	**Plant height**	**Specific leaf area (SLA)**	**Leaf habit**	**Self-pruning**	**Bark thickness**	**Flame duration[2]**	**Flame height[2]**	**Plant height**	**Average FRS of SLA and lh[3]**	**Self-pruning**	**Bark thickness**	**PC1 of fd and fh[3]**	**FRS**
Quercus similis	25	8.85	0	7	2.14			0.62	0.28	0.70	0.42		0.50
Quercus chrysolepis	25	5.79	1	5	0.91	110.6	37.9	0.62	0.90	0.50	0.17	0.34	0.50
Quercus rugosa	16	5.51	1	3	2.14			0.39	0.91	0.30	0.42		0.50
Quercus arizonica	18	6.22	0.5	4	2.14	54.1	49.2	0.44	0.63	0.40	0.42	0.63	0.50
Quercus kelloggii	25	15.25	0	5	2.14	34.1	83.0	0.62	0.03	0.50	0.42	0.92	0.50
Quercus garryana	20	10.52	0	5	2.14	41.1	76.0	0.49	0.22	0.50	0.42	0.85	0.49
Quercus rubra	30	12.73	0	5	1.98	44.6	55.3	0.75	0.13	0.50	0.39	0.70	0.49
Quercus polymorpha	20	8.27	0.5	5	2.14			0.49	0.55	0.50	0.42		0.49
Quercus myrtifolia	12	7.29	1	4	2.14			0.29	0.84	0.40	0.42		0.49
Quercus agrifolia	25	7.22	1	4	1.26	106.5	29.8	0.62	0.84	0.40	0.24	0.30	0.48
Quercus emoryi	15	6.78	0.5	5	2.14			0.36	0.61	0.50	0.42		0.47
Quercus ellipsoidalis	20	9.31	0	4	2.07	30.7	61.0	0.49	0.26	0.40	0.40	0.79	0.47
Quercus oglethorpensis	18	11.57	0	6	2.14	76.0	76.0	0.44	0.18	0.60	0.42	0.71	0.47
Quercus acerifolia	15	7.88	0	4	2.14	45.6	73.1	0.36	0.32	0.40	0.42	0.81	0.46
Quercus oblongifolia	10	5.90	1	3	2.14			0.24	0.89	0.30	0.42		0.46
Quercus lyrata	20	11.18	0	5	2.14	48.9	55.9	0.49	0.19	0.50	0.42	0.69	0.46
Quercus marilandica	15	8.02	0	4	2.12	54.0	68.0	0.36	0.31	0.40	0.41	0.75	0.45
Quercus lobata	25	12.80	0	6	0.63	45.4	63.6	0.62	0.13	0.60	0.11	0.75	0.44
Quercus gambelii	12	8.21	0	4	1.77	31.2	71.1	0.29	0.30	0.40	0.34	0.86	0.44
Quercus austrina	25	13.86	0	4	2.14	56.4	56.4	0.62	0.09	0.40	0.42	0.67	0.44
Quercus hypoleucoides	10	3.87	1	0	2.14			0.24	0.97	0.00	0.42		0.41
Quercus margarettae	12	10.46	0	4	2.14	66.1	68.1	0.29	0.22	0.40	0.42	0.70	0.41
Quercus canbyi	10	8.74	0.5	3	2.14			0.24	0.53	0.30	0.42		0.37
Quercus arkansana	15	16.14	0	4	2.14	46.8	46.5	0.36	0.00	0.40	0.42	0.64	0.36
Quercus prinoides	10	7.85	0	0	1.27	34.4	94.0	0.24	0.32	0.00	0.24	0.99	0.36
Quercus incana	10	9.60	0	3	2.14	77.3	52.1	0.24	0.25	0.30	0.42	0.56	0.35

	Trait values[1]							Percentile ranking (standardized)					
Scientific name	Plant height	Specific leaf area (SLA)	Leaf habit	Self-pruning	Bark thickness	Flame duration[2]	Flame height[2]	Plant height	Average FRS of SLA and lh[3]	Self-pruning	Bark thickness	PC1 of fd and fh[3]	FRS
Quercus sinuata	15	10.44	0	4	2.14			0.36	0.22	0.40	0.42		0.35
Quercus buckleyi	15	9.34	0	3	2.36			0.36	0.26	0.30	0.46		0.35
Quercus sadleriana	1	7.41	1	0	0.29	47.1	64.9	0.01	0.84	0.00	0.04	0.76	0.33
Quercus douglasii	18	7.60	0	4	1.28	113.1	21.7	0.44	0.33	0.40	0.24	0.22	0.33
Quercus turbinella	4	7.07	1	0	0.45	73.6	59.2	0.08	0.85	0.00	0.07	0.62	0.32
Quercus engelmannii	10	6.69	0.5	3	1.20	117.7	23.3	0.24	0.61	0.30	0.23	0.22	0.32
Quercus pungens	6	6.53	1	2	0.29			0.13	0.87	0.20	0.04		0.31
Quercus gravesii	13	9.98	0	2	2.14			0.31	0.24	0.20	0.42		0.29
Quercus mohriana	3	9.21	1	0	0.29	74.9	43.2	0.06	0.77	0.00	0.04	0.51	0.27
Quercus parvula	3	3.11	1	0	0.17			0.06	1.00	0.00	0.01		0.27
Quercus palmeri	3	5.51	1	0	0.29	133.3	45.6	0.06	0.91	0.00	0.04	0.30	0.26
Quercus ajoensis	3	4.80	1	0	0.29			0.06	0.94	0.00	0.04		0.26
Quercus cornelius-mulleri	3	4.84	1	0	0.29			0.06	0.93	0.00	0.04		0.26
Quercus inopina	5	7.35	1	0	0.29			0.11	0.84	0.00	0.04		0.25
Quercus ilicifolia	6	9.01	0	0	0.29	43.6	67.3	0.13	0.27	0.00	0.04	0.78	0.25
Quercus grisea	10	8.52	0	0	2.14	91.8	16.5	0.24	0.29	0.00	0.42	0.27	0.24
Quercus toumeyi	5	7.14	0.5	2	0.29			0.11	0.60	0.20	0.04		0.24
Quercus vaseyana	9	6.33	0	3	0.29			0.21	0.38	0.30	0.04		0.23
Quercus berberidifolia	2	6.87	0.5	2	0.31			0.03	0.61	0.20	0.04		0.22
Quercus durata	2	7.10	1	0	0.29	113.1	13.8	0.03	0.85	0.00	0.04	0.17	0.22
Quercus pacifica	2	7.25	0.5	0	0.29	91.8	39.4	0.03	0.59	0.00	0.04	0.42	0.22
Quercus john-tuckeri	3	6.01	1	0	0.10	157.9	24.1	0.06	0.89	0.00	0.00	0.06	0.20
Quercus chapmanii	6	7.74	0.5	0	0.29			0.13	0.57	0.00	0.04		0.19
Quercus vacciniifolia	1.5	6.58	1	0	0.29	158.9	14.6	0.02	0.87	0.00	0.04	0.00	0.19
Quercus minima	0.7	5.08	0.5	0	0.29			0.00	0.67	0.00	0.04		0.18
Quercus laceyi	8	8.74	0	2	0.29			0.19	0.28	0.20	0.04		0.18

	Trait values^1							Percentile ranking (standardized)					
Scientific name	**Plant height**	**Specific leaf area (SLA)**	**Leaf habit**	**Self-pruning**	**Bark thickness**	**Flame duration^2**	**Flame height^2**	**Plant height**	**Average FRS of SLA and lh^3**	**Self-pruning**	**Bark thickness**	**PC1 of fd and fh^3**	**FRS**
Quercus dumosa	2	6.31	0.5	0	0.10	115.9	20.6	0.03	0.63	0.00	0.00	0.21	0.17
Quercus georgiana	5	11.31	0	2	0.29	122.2	35.6	0.11	0.19	0.20	0.04	0.28	0.16
Quercus havardii	2	7.02	0	0	0.29			0.03	0.35	0.00	0.04		0.11
*Quercus elliottii**	1	8.83	0	0	0.29			0.01	0.28	0.00	0.04		0.08

Note: This table is organized by the descending FRS assigned to each species. The first set of trait values are measured values and the second has been percentile ranked or standardized values. The asterisk* after a species name denotes name changes in order of occurrence *prinus and *pumila. Species in bold are Forest Inventory Analysis (FIA) used in mapping (n = 38). 1. Units of measured trait values in order are as follows m, mm^2 mg^{-1}, 0 deciduous, 0.5 brevideciduous, and 1 evergreen, ordinal scale of 1–10, cm using mean diameter at breast height (d.b.h) of 59.9 for tree growth forms, and a mean (d.b.h) of 13.1 for shrub growth forms, s, cm. Not all species had flammability data, thus the blanks. 2. Sources for flammability data are as follows: a. Fonda (2001); b. Kane, Varner, and Hiers (2008); c. Engber and Varner (2012); d. Varner, Kane, and Kreye (2021). Additional flammability data was obtained through conducting leaf litter burn trials for 34 species for our study. 3. Traits of specific leaf area (SLA) and leaf habit FRS were averaged together to form one combined trait value, flame length (fl) and flame height (fh) were closely negatively correlated (r = -0.84) and thus combined into a principal component analysis (PC1).

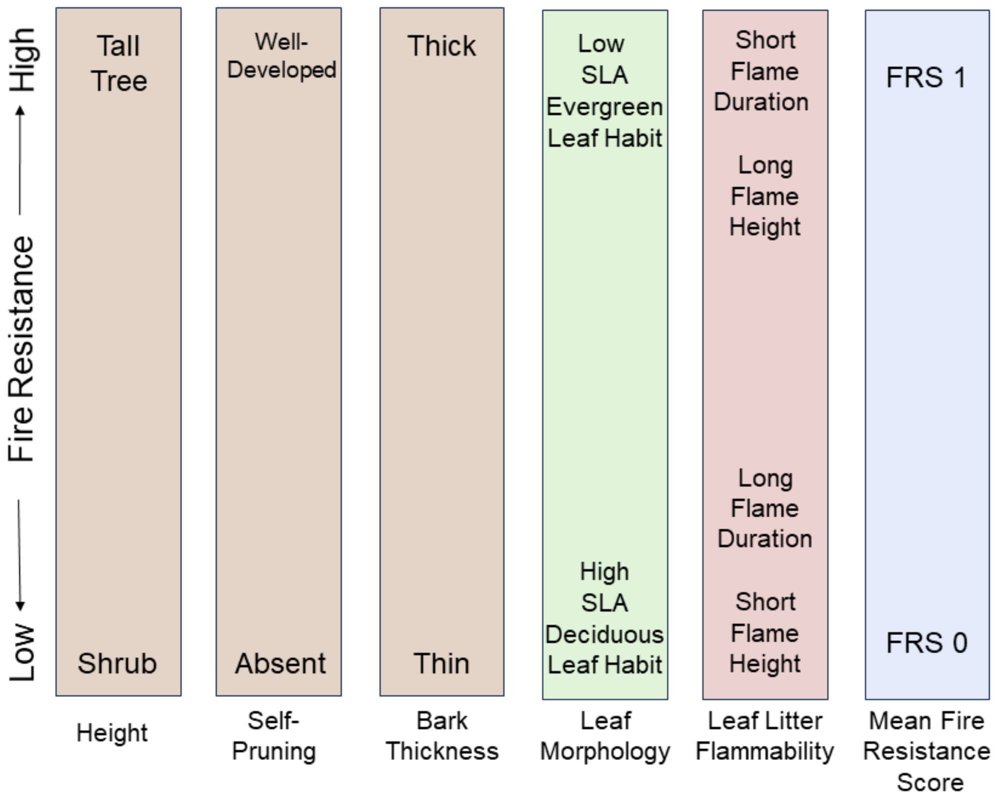

FIGURE 1. The functional traits used in our fire resistance score (FRS), FRS scoring from 1 (high fire resistance) to 0 (low fire resistance). Figure showing how fire resistance was assigned for each trait (low to high), all traits were standardized then averaged to assign one composite score. Leaf morphology trait is an average of two traits, specific leaf area (SLA), and leaf habit. Leaf litter flammability traits of flame duration and flame height were combined using a PCA (Principal Component Analysis) to assign one value for flammability traits.

Geographical methods

All maps and spatial analysis were conducted using ArcGIS Pro v3.0.2. Oak species spatial data was downloaded from USFS FIA gathered from remotely sensed satellite data layers. The validity of FIA data is moderately high, especially for more widespread species (Wilson et al., 2013). We used a 250-meter resolution geospatial raster layer of estimated basal area (m^2 $hectare^{-1}$) referred to throughout the paper as basal area. For all mapping purposes we focused on the available USFS FIA raster data allowing us to spatially analyze 38 oak species. The LANDFIRE FRG and FRI layers used were first resampled to match the spatial resolution of our FIA data of 250-meter resolution before statistical tests and comparisons were conducted. We were able to determine the primary FRG for each of our 38 FIA species by combining each individual species layer with the LANDFIRE FRG's layer using the combine spatial analyst tool. This provided a combined map with a table of pixel counts for each of the I, II, III, IV, and V FRG's to determine the primary FRG each species occurred in. We were also able to determine the total percentage breakdown for each of the five FRG's from LANDFIRE by analyzing each group's overall pixel count. The remaining *Quercus* species that did not have FIA data (n = 43) we determined primary FRG's through the comparison of species distributions maps specifically using Biota of North America Program (BONAP) and Little's maps (Kartesz, 2015; Fryer, 2018). To determine the median FRI of FIA oak species data from LANDFIRE biophysical settings (BPS) 2016 was utilized. From the BPS 2016 package the FRI_ALLFIR was used, this layer is described as "Fire Return Interval all fire" it quantifies the average period between fires under the presumed historical fire regime. These FRG and FRI LANDFIRE products utilized vegetation dynamics development tool (VDDT). Each FIA species was separately joined with the FRI layer. This produced a table that could be exported, and median FRI was identified for only the FIA species. Due to limitations within the data only FIA oak species were able to have their median FRI value identified, it should also be noted that due to low values for *Q*. *oglethorpensis* (FIA code 844) were not able to determine the median FRI for this one species so only 37 FIA species received median FRI values.

We restricted our analysis to areas comprised of one-third of our study species of oak trees/shrubs. The value of one-third was selected to include oak important communities, oaks provide numerous ecosystem services (Cavender-Bares, 2016). We also wanted to ensure we included the more sparse shrubland oak communities that otherwise would have been overlook had we increased our analysis area to a more oak dominated community of one-half (Menges & Kohfeldt, 1995; Londe et al., 2021). To determine the one-third area, we calculated the total basal area per pixel for all 38 FIA species, proportionate to total basal area of all FIA species. To acquire a community-weighted mean FRS of our FIA oaks we multiplied the assigned FRS for each individual species by its basal area per pixel, then divided by the basal area of all our oak species combined. This determined the community-weighted mean FRS for each pixel across the US. Once the community-weighted mean FRS was calculated for each pixel, we could compare it with LANDFIRE derived indices of FRG and FRI layers. The FRG and FRI layers were first resampled to match the spatial resolution as our FIA data at 250-meter resolution before statistical tests and comparisons were conducted. A random selection of 1% (n =123,132) of FRS pixel points was sampled from the one-third oak study area. The random subsample of 1% was overlaid with FRG and FRI layers to be statistically analyzed. For FRG comparisons with FRS we divided classification into five groups: FRG 1 high frequency 0-35 years with low severity, FRG 2 high frequency 0-35 years with replacement severity, FRG 3 intermediate frequency 35-200 years with low to mixed severity, FRG 4 low frequency 35-200 years with replacement severity, and FRG 5 low frequency 200+ years and replacement/high severity. For FRI, they had a wide range of values and were classified and binned into ranging classes and assigned the following median FRI (5, 15, 25, 35, 50, 100, 200 and 500 years).

To assess our community-weighted mean FRS for any mismatches between assigned scores and the FRI of an area the following analysis was conducted. Firstly, we identified one-third of our oak study area and classified the FRIs of interest: frequent (1-20 years), intermediate (41-150 years), and infrequent (151-300 years). Next, we needed to identify the assigned FRSs highest and lowest scores from our one-third oak study area. The high and low scores were found using the ArcGIS Pro data classification known as natural breaks (jenks), where we used 6 classes that are based on natural groupings inherent in the dataset and are useful with non-normal data distributions (de Smith et al., 2018). We identified the high FRS threshold of greater than or equal to 0.60 (resistant) and the low FRS threshold of less than or equal to 0.46 (sensitive). We aimed to highlight the four following groups: (a) fire-sensitive areas that have frequent historical fire (sensitive areas), (b) fire-sensitive areas that have intermediate historical fire (sensitive areas), (c) fire resistant areas that have intermediate historical fire (resistant areas), (d) fire resistant areas that have infrequent historical fire (resistant areas). It is suggested that group (a) and (b) are areas that have been colonized by species with a sensitivity to fire, this could be a response to fire suppression in an area over a long period of time. Group (c) and (d) may have been areas that experienced a certain level of historical fire allowing for the selection of fire resistant traits enough to enhance survival with fire events (Rollins 2009). We used the following classifications for our community-weighted mean FRS and FRI: (a) sensitive-frequent FRS less than or equal to 0.46 and FRI 1-20 years, (b) sensitive-intermediate FRS less than or equal to 0.46 and FRI 41-150 years, (c) resistant-intermediate FRS greater than or equal to 0.60 and FRI 41-150 years, and (d) resistant-infrequent FRS greater than or equal to 0.60 and FRI 150-300 years (Figure 7 and 8). Using our community-weighted mean FRS and FRI, we identified if these areas were either apart of fire resistant areas (resistant) or fire sensitive areas (sensitive).

Fire resistance score methods

We analyzed biogeography patterns of *Quercus* species and the FRG, the species distribution occurred in. To determine if species FRS varied by FRG, we conducted a one-way analysis of variance using all 81 species, with comparisons among FRG pairs using a Tukey-Kramer HSD via JMP Pro 14 v14.2.0.

Additionally, for the 38 *Quercus* species with FIA data, we examined if the oak community-weighted mean FRS was correlated with the fire regime it occurred in. We conducted a generalized linear model (GLM) fit on our oak study area, to analyze the community-weighted mean FRS relationship with the FRIs using a log effect test.

Leaf litter flammability methods

Leaf litter flammability methods followed previous studies (Fonda, 2001; Kane & Varner, 2008; Grootemaat et al., 2015). Leaf litter of 34 *Quercus* species was collected in the field, greenhouse specimens at Minnesota State University, Mankato, Morton Arboretum, University of California Davis Arboretum, and Denver Botanical Gardens etc (Appendix Table A). Leaf litter was collected from the one individual, in some instances collected from more than one individual but had to be occurring within the same area. Leaf litter was either gathered from recently fallen specimens prior to decomposition or removed directly from specimens. Litter flammability trials were conducted in a stabilized chamber (L 1.20m x W 0.95m x H 1.35m) with a chimney to allow for the ventilation of smoke. A Kestrel 3000 Weather Meter was used to document the weather conditions of the burn day to ensure no airflow was present at the fuel bed. Each burn trial consisted of 15g of dried leaves; oven dried at 50-60 ◦C for a minimum of 24 hours. Burns were replicated five times with dried leaf litter placed on a 35cm^2 stainless-steel platform with a grid of six xylene-soaked cotton strings. The xylene-soaked cotton strings were ignited from all sides and a timer was started once the litter became ignited.

Burning characteristics measured included maximum flame height (cm), flaming duration (s), smoldering duration (s), residual weight (g), mass loss rate (mg s^{-1}), and leaf litter bed depths (cm) measured prior to burns being conducted. Maximum flame height was measured using a ruler mounted on a stand and situated immediately behind the fuel bed. Flaming and smoldering were measured using two stop watches, simultaneously started once flames initiated within the litter bed. The first timer was stopped once flaming combustion finished and the second timer when smoldering/glowing combustion ended, representing full burning time. The end of smoldering combustion was determined to occur when the last ember was extinct. Subtraction of the flaming time from the burning time resulted in smoldering duration for each trial. Each burn trial residual weight was weighted after burns were conducted minus any unburned string pieces. Percent consumption was measured by weighing the residual litter mass and dividing this weight by the initial litter bed weight (15g). Mean mass loss rate was computed by dividing the weight consumed in mg by the entire burning time. The flammability trait data was averaged for each species, to get an average of the five burn trials. Then traits were analyzed using linear regressions to determine if there were any patterns between flammability traits recorded as well as with leaf morphology traits. All analysis was conducted in JMP Pro 14 (version 14.2.0) using an analysis of variance test.

Phylogenetic tree methods

To investigate evolutionary patterns of fire resistance within this large clade, we examined *Quercus* species FRS with LANDFIRE LF BPS 2016 FRI (median fire return intervals). To analyze if our calculated species FRS were dependent on their median FRI, we conducted a phylogenetic generalized least square (PGLS) PGLS accounts for potential phylogenetic signal in the model response, with simultaneous estimation of Pagel's λ (as the scaling parameter on the covariance matrix). A total of 81 *Quercus* species were mapped using the Hipp et al. (2020) phylogeny. We investigated if unexpected phylogenetic shifts occurred within the clade in terms of FRS adaptation. To explore relationships between *Quercus* species and their assigned FRS an ancestral character state reconstruction was conducted. Our analysis aimed to detect if any notable unexpected evolutionary shifts occurred in relation to fire resistance traits. All phylogenetic methods mentioned were analyzed using R v4.3.1. The PGLS was conducted with the following packages PHYTOOLS v.0.6-44 (Revell, 2012), APE v.5.7-1 (Paradis & Schliep, 2018), NLME v.3.1-153 (Pinheiro et al., 2020), and MAGRITTR v.2.0.1 (Bache & Wickham, 2014). The ancestral character state reconstruction was conducted with the same packages stated above PHYTOOLS, APE, NLME, MAGRITTR, in addition to TIDYVERSE v2.0.0 (Wickham et al., 2019) and PHYLOGENTICEM v1.6.0 (Bastide et al., 2017).

Results

Fire resistance score results all 81 oak species

The FRS of all 81 oak species were divided into four groups based on their growth forms, fire resistant trees (FRS 0.75-0.51), fire-associated short trees (FRS 0.50-0.41), fire-sensitive short trees and shrubs (FRS 0.37-0.26), and subalpine arid barrens shrubs (FRS 0.25-0.08) (Figure 2). Within our highest FRS group (fire resistant trees), 20 out of 25 species existed in an FRG that experienced fire at a frequency interval of 0-35 years, being FRGs 1 and 2. The fire-associated short tree species had 16 of the 22 species occurring in FRGs 1 and 2. The fire-sensitive short trees and shrubs had 12 of the 17 species in FRGs 1 and 2. Lastly species existing in the subalpine, arid and barrens regions are exclusively exhibiting the growth form of shrub, had 11 of the 17 species in FRGs 1 and 2. This group occupies the shrubland areas where historically fires are not frequently occurring. It should be noted the breakdown of FRS into the following four categories is slightly subjective especially the transitions from one to the other, these groupings are helpful visualizations of oak species fire resistance (Figure 2).

The community-weighted mean FRS were diversely spread across the US. It should be noted that our community-weighted mean FRS used in mapping consists of the 38 oak FIA species, thus the community FRS is limited in analysis compared to the full capacity of our 81 oak FRS. This limitation exists within the spatial analysis of oak FRS as well as FRG and FRI. Our FIA oaks had the highest FRS from *Q. bicolor* (swamp white oak) at 0.75 and the lowest FRS score from *Q. minima* (dwarf live oak) at 0.18. The average FRS for FIA oaks were 0.49, the median was 0.52, slightly higher compared to the 81 oak species FRS. Using our FIA oaks, we were able to compile a community-weighted mean FRS for *Quercus*. This representation of a community's fire resistance is informative, but due to the data limitations of available FIA data, the community FRS could be slightly altered (Figure 3).

The relationships of several functional traits used in our FRS (Figure 1; Table 2), traits such as plant height and self-pruning, height and bark thickness, self-pruning and bark thickness, and flame duration and flame height showed a high degree of correlation (Appendix Figure A). The FRS of all 81 oaks ranged, the highest score of 0.75 from *Q. bicolor* (swamp white oak) to the lowest score of 0.08 from *Q*. *elliottii* (runner oak) (Table 2). The average FRS for the 81 oaks was 0.41 and the median 0.46. Group 3 FRG had the highest mean FRS of 0.50 ± 0.05, following was group 1 at 0.42 ± 0.02, group 5 at 0.39 ± 0.06, group 2 at 0.35 ± 0.06, and group 4 at 0.26 ± 0.05. An analysis of variance test resulted in an F = 3.45 and P = 0.0121* (Figure 4). We predicted that species experiencing frequent fires (groups 1 and 2) would have higher FRS. The differences in FRS occurred between FRG 1 and 4 with a P = 0.02 (1 was 64% higher FRS compared to 4) and FRG 3 and 4 with a P = 0.0099 (3 having a 91% higher FRS compared to 4) (Figure 4).

The FRGs percentage breakdown for the coverage of each group was calculated using the entirety of the LF products across the US (Table 3). It is worth noting the five FRGs are not equally distributed across the US, with group 1 (26.4%), 2 (27.9%) and 3 (20.8) comprising over 2/3 the area. We also calculated the percentage for the 38 FIA oaks primary FRG, resulting in most oaks found to be predominantly occurring within FRG 1 (68%) and 3 (26%) (Table 3).

Fire resistance score results 38 FIA oak species

The 38 FIA species community-weighted mean FRS were compared to the FRG they occurred within, resulting in a X^2 = 11311.04 and P <0.0001*. All FRGs were found to be significantly different from each other using a Wald-based method all comparisons had a P <0.0001 (Figure 5). We also analyzed the community-weighted mean FRS for 38 FIA species and the FRIs they occurred within. This resulted in a X^2 = 2315.39 and P <0.0001*, the GLM showed an overall negative relationship between community-weighted FRS over an increasing FRI (Figure 6).

Mismatches between FRS and FRI results

We used the 38 FIA species community-weighted mean FRS and historical FRI to guide the four classifications of FRS and FRI mismatches (Figures 7 and 8). The following four classifications were separated by their FRS and FRI defined as: sensitive-frequent (magenta), sensitive-intermediate (orange), resistant-intermediate (green), and resistant-infrequent (light blue) (Figure 8). Within our designated FRS and FRI thresholds areas were identified as sensitive or resistant using the one-third oak study area (Table 3). Most mismatches highlighted were in areas of sensitivity (magenta and orange) at 85.8% with the remaining 14.2% identified as resistant (green and light blue) areas.

The FRGs are classified by the frequency in years that fire occurs and the severity of fire, FRIs will be limited to existing within certain FRGs. For example, the three groups of FRIs we use are frequent (1-20 years) existing within FRG 1 or 2, intermediate (41-150 years) existing within FRG 3 or 4, and infrequent (151-300 years) existing within FRG 3, 4, or 5. The results being that sensitive-frequent mismatches have 79.2% occurring within FRG 1 with the remaining occurring within FRG 2. The sensitive-intermediate mismatches are nearly equally distributed across FRGs with 53.8% occurring within FRG 3 and the remaining 46.2% occurring within FRG 4. The resistant-intermediate mismatches nearly all occur within FRG 3 at 95.9% with the remainder in FRG 4. The resistant-infrequent mismatches mostly occur in FRG 5 at 76.8% with the remainder in FRG 3, with none within FRG 4 (Table 3).

Leaf litter flammability results

We analyzed flammability data collected from our burn trials along with data gathered from previous studies, all data was collected using the same protocol outlined by Fonda, 2001. We analyzed oak species (n = 59) average flame height and average flame duration to compare how the traits correlated to each other. The $R^2 = 0.63$, $F = 98.6$ and $P < 0.0001$* (Figure 9). The three leaf habits of evergreen, brevideciduous, and deciduous were analyzed separately in their flame height and flame duration relationship and it was determined to be no significant differences in the discernable pattern when separated by leaf habit. We explored the relationship between SLA and the average litterbed depth of oak species ($n = 53$). The $R^2 = 0.17$, $F = 10.1$ and $P = 0.0025$* (Figure 10).

Phylogenetic tree results

We analyzed our median FRI of oaks ($n = 37$) along with their FRS, using a PGLS. The slope of our linear regression was $y = 0.0011x + 0.4608$. Our $P < 0.0001$ with a $T = 41.30$, and a $\lambda = -0.65$ (Figure 11). We conducted an ancestral character state reconstruction of *Quercus* phylogeny. Overall, we noticed an intermediate level of fire resistance shown within the US distribution of North American *Quercus* species. The species that deviate from the median scores around 0.50 FRS, with higher scores displayed in species *Q. bicolor*, have the growth form of tree verses species with lower fire resistance in blue being shrub species (Figure 12). We analyzed our assigned FRS values to see if any drastic phylogenetic shifts occurred across lineages of oaks regarding fire resistant traits (Figure 12). It was determined that no shifts occurred within the phylogeny that could not be explained by normally occurring random evolutionary shifts.

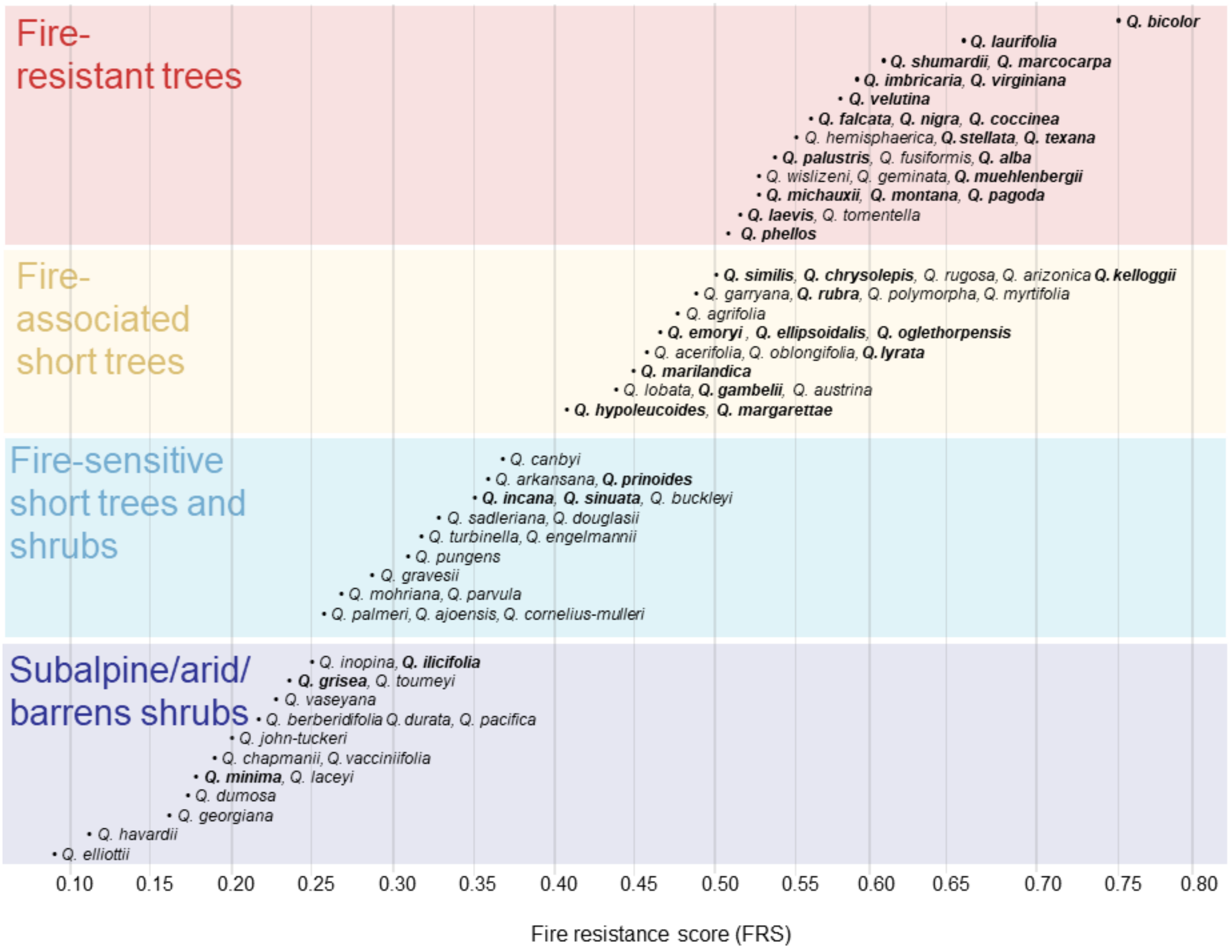

FIGURE 2. The fire ecology of 81 *Quercus* species by their fire resistance scores (FRS) delineated by their growth form and habitat; fire resistant trees (n = 25), fire-associated short trees (n = 22), fire sensitive short trees and shrubs (n =17), and subalpine arid barrens shrubs (n =17). The FRS on the x-axis is derived from seven functional traits for each species (Table 2). The species in bold (n = 38) are included in the Forest Inventory Analysis (FIA) and used for mapping purposes (Figures 3, 5-8).

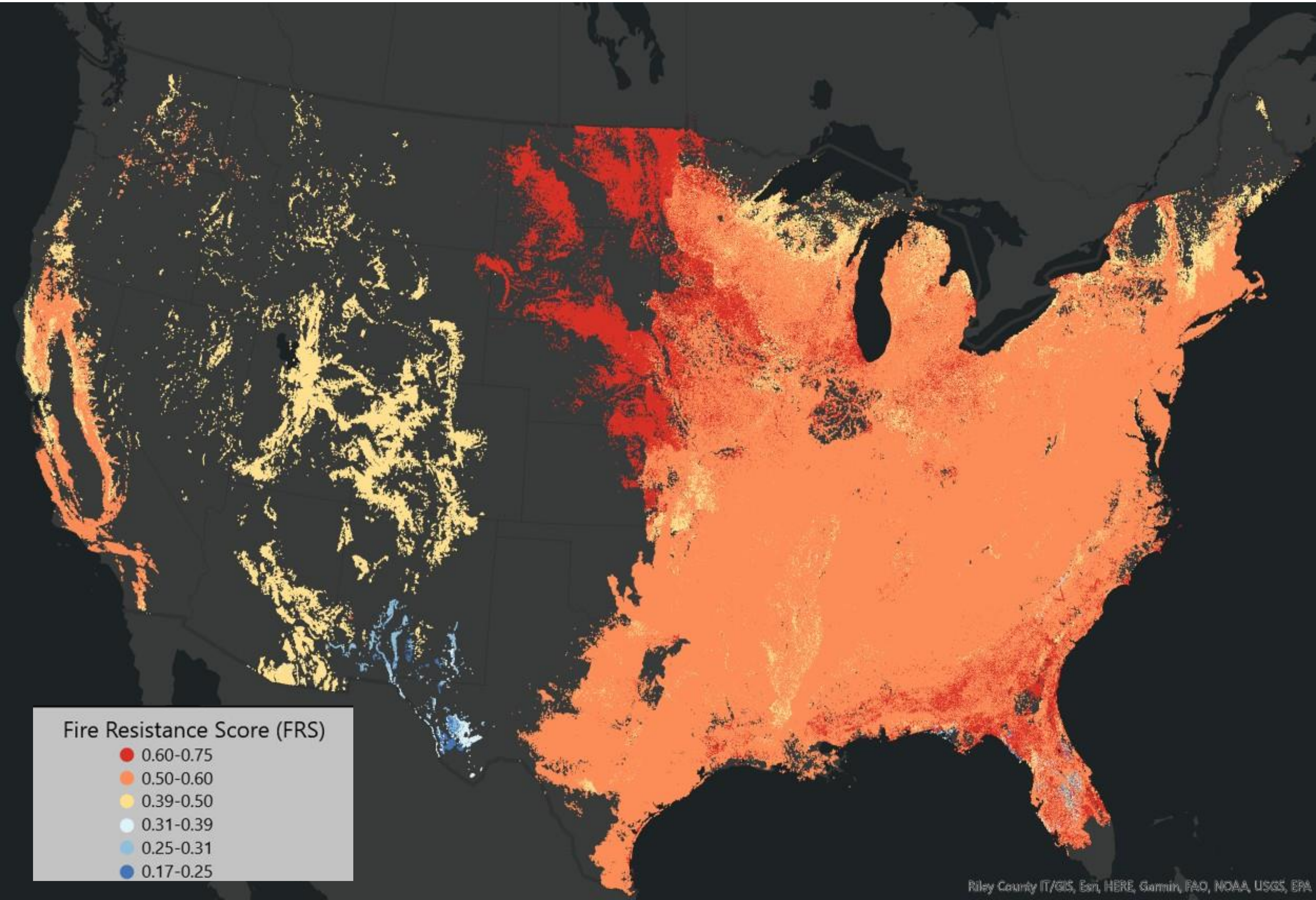

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FIGURE 3. Forest Inventory Analysis (FIA) derived community-weighted mean fire resistance scores (FRS) for 38 species of *Quercus*. This map shows areas where the overall community is comprised of at least one-third oak basal area, compared to the total FIA species (including oaks and 247 additional species).

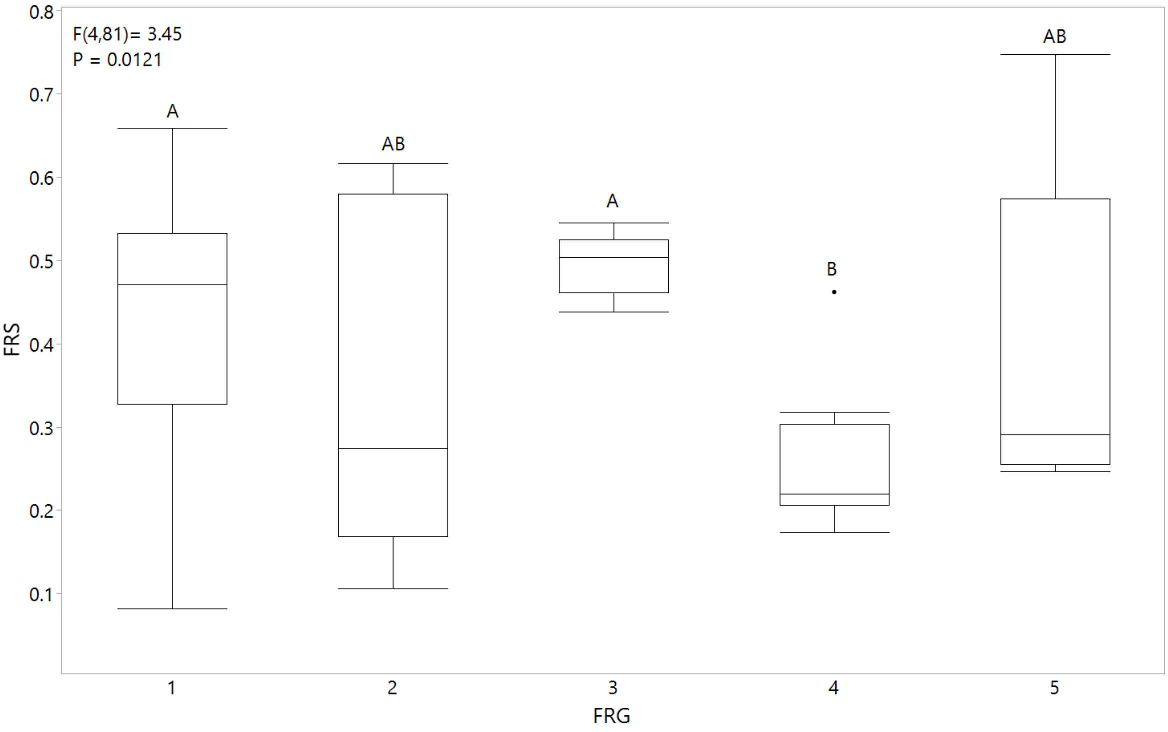

FIGURE 4. Box plot displaying quartiles and outliers for the fire resistance scores (FRS) of all 81 species of *Quercus* in comparison to their primary fire regime group (FRG). *Quercus* species FRG breakdown as follows 1 (n = 54) mean 0.42, 2 (n = 5) mean 0.35, 3 (n = 8) mean 0.50, 4 (n = 8) mean 0.26, 5 (n = 6) mean 0.39. A Tukey-Kramer HSD comparison for all pairs was conducted; significant differences denoted by varying letters.

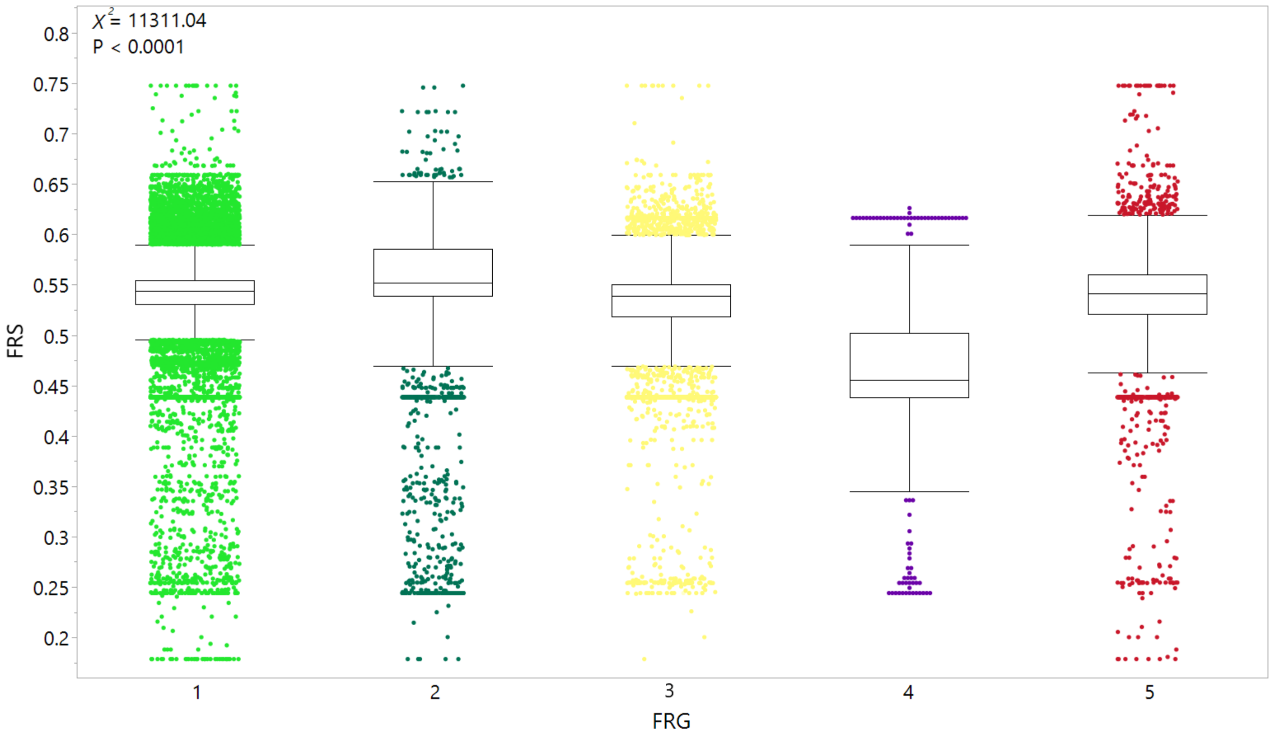

FIGURE 5. Box plot displaying quartiles and outliers for the community-weighted mean fire resistance scores for 38 *Quercus* Forest Inventory Analysis (FIA) species in comparison to the fire regime group (FRG) they occurred within. All FRGs were found to be significantly different from each other (using a Wald-based method; P < 0.0001). The FRG breakdown is as follows 1 (n = 70,588) mean 0.54, 2 (n = 16,621) mean 0.55, 3 (n = 22,089) mean 0.53, 4 (n = 2,835) mean 0.47, 5 (n = 8,664) mean 0.54. The standard error for each group is equal to or less than <0.0001. The colored points denote the five fire regime groups (FRG) numbered (1-5) reflective of the quantity of points occurring within each group.

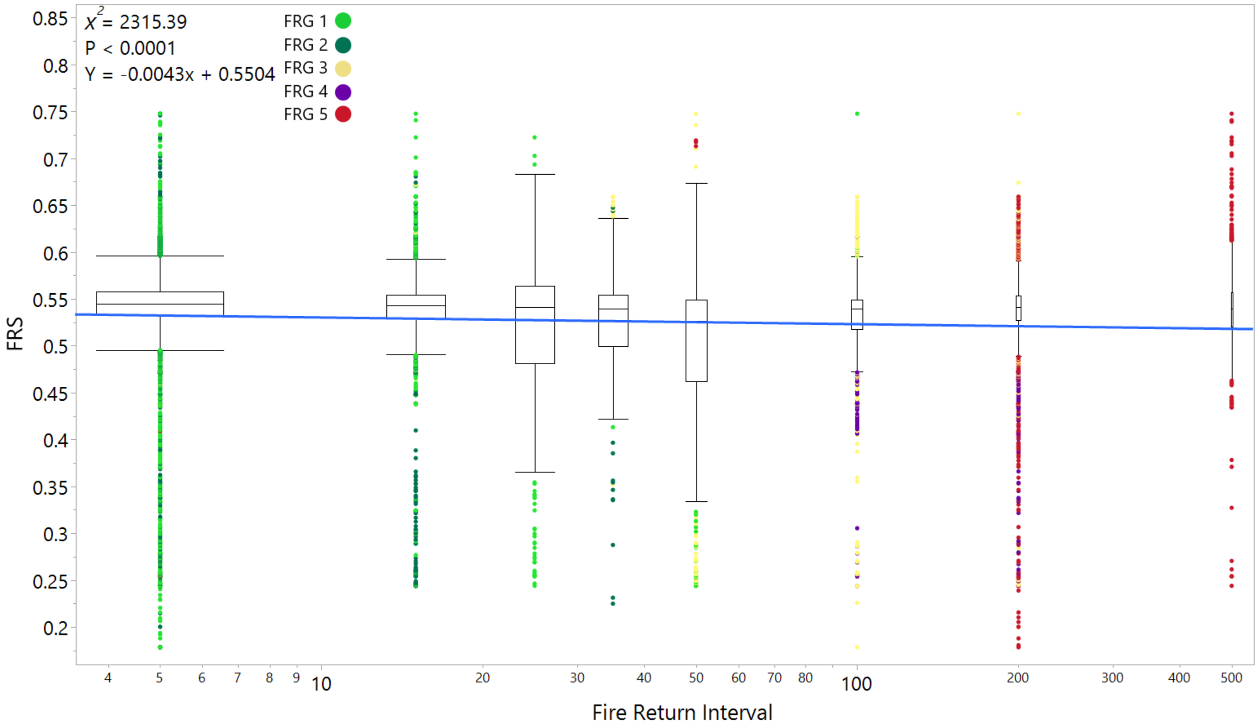

Figure 6. The community-weighted fire resistance scores (FRS) for 38 *Quercus* Forest Inventory Analysis (FIA) species, shown using a log transformation on the fire return interval (FRI) that was binned into classes and assigned the median fire return interval of the merged classes (5, 15, 25, 35, 50, 100, 200 and 500 year return intervals). The generalized linear model fit showed an overall negative relationship between community-weighted FRS over an increasing FRI. The colored points denote the five fire regime groups (FRG) numbered (1-5) with the legend of the colors displayed.

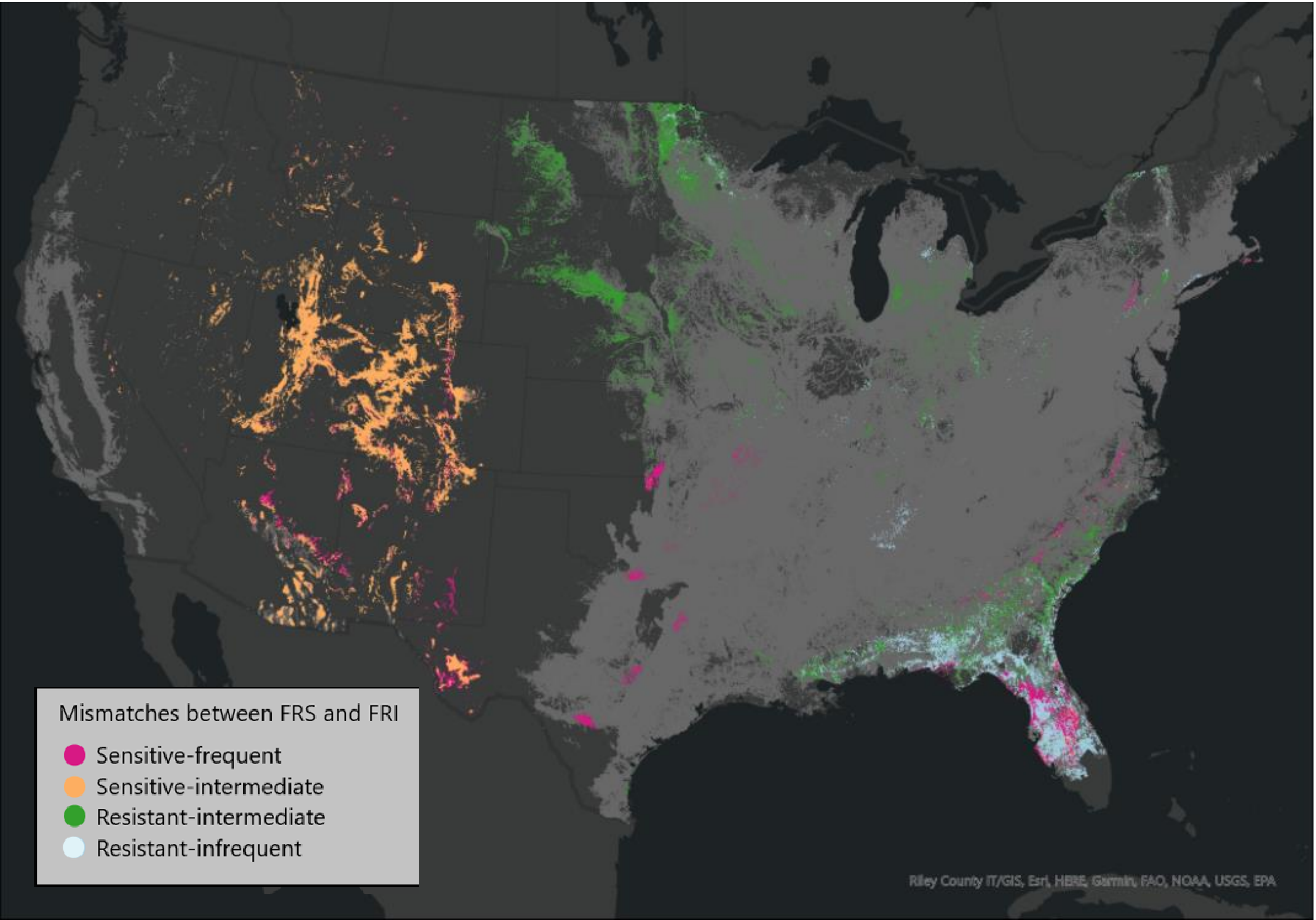

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FIGURE 7. The Forest Inventory Analysis (FIA) oak species (n = 38), potential mismatches between community-weighted mean fire resistance scores (FRS) and historical fire return intervals (FRI). Using our one-third oak study area (entirety of this area shown above in light gray), mismatches between FRS and FRI were identified. The community-weighted mean FRS was placed into 6 groups using jenks natural breaks optimization, using the first and last groupings to identify mismatches. The following four classifications were distinguished by their FRS and FRI defined as: sensitive-frequent (frequent fire 1-20 years) FRS less than or equal to 0.46 shown in magenta, sensitive-intermediate (intermediate fire 41-150 years) FRS less than or equal to 0.46 shown in orange, resistant-intermediate (intermediate fire 41-150 years) FRS greater than or equal to 0.60 shown in green, and resistant-infrequent (infrequent fire 151-300 years) FRS greater than or equal to 0.60 shown in light blue.

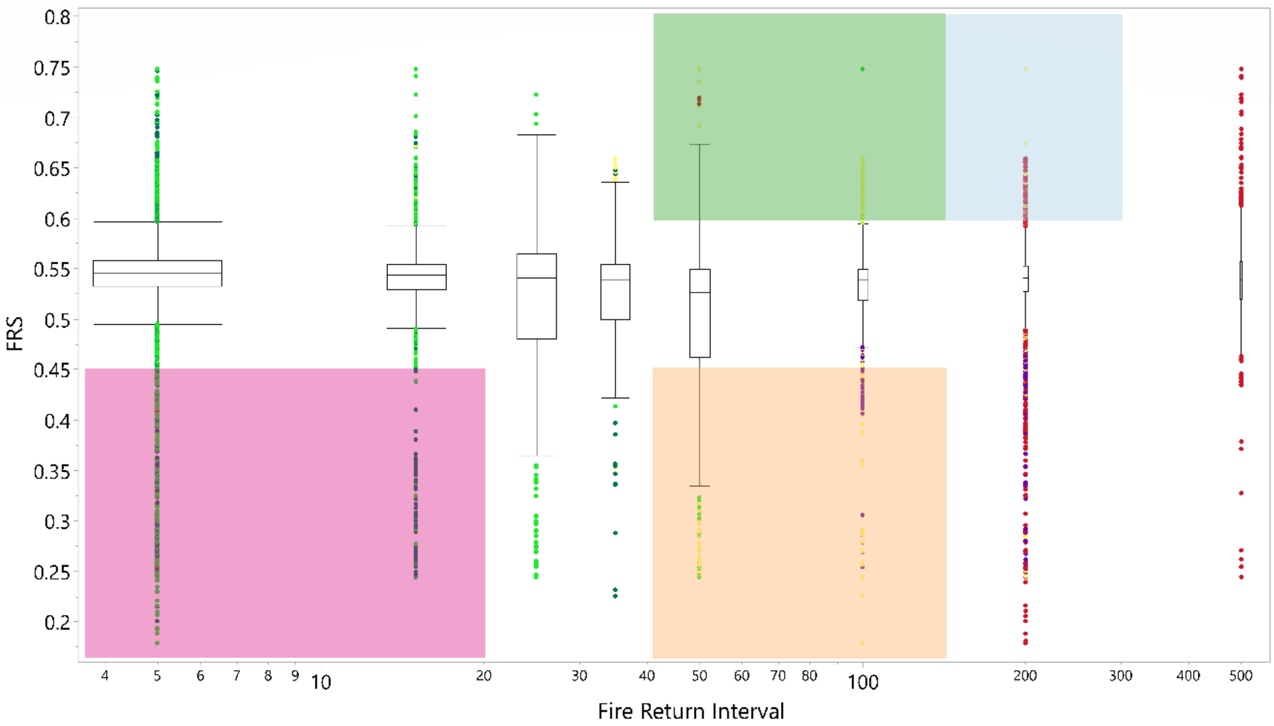

FIGURE 8. Potential mismatches of Forest Inventory Analysis (FIA) oak species (n = 38) between the fire resistance scores (FRS) and historical fire return interval (FRI). The following groups were defined as: sensitive-frequent (frequent fire 1-20 years) FRS less than or equal to 0.46 shown in magenta, sensitive-

intermediate (intermediate fire 41-150 years) FRS less than or equal to 0.46 shown in orange, resistant-intermediate (intermediate fire 41-150 years) FRS greater than or equal to 0.60 shown in green, and resistant-infrequent (infrequent fire 151-300 years) FRS greater than or equal to 0.60 shown in light blue. The colored points denote the five fire regime groups (FRG) (reference Figure 6 for more information regarding the points).

TABLE 3. The identified mismatches between community-weighted mean fire resistance score (FRS) and historical fire return intervals (FRI). Displayed values represent 0.05% (n = 564,592) of the one-third oaks points. Values are sorted into fire regime groups (FRG).

FRG	Sensitive-frequent	Sensitive-intermediate	Resistant-intermediate	Resistant-infrequent
1	138,776			
2	6,820			
3		166,284	48,642	6,832
4		142,985	2,050	-
5				22,671
Total	**175,128**	**309,269**	**50,692**	**29,503**

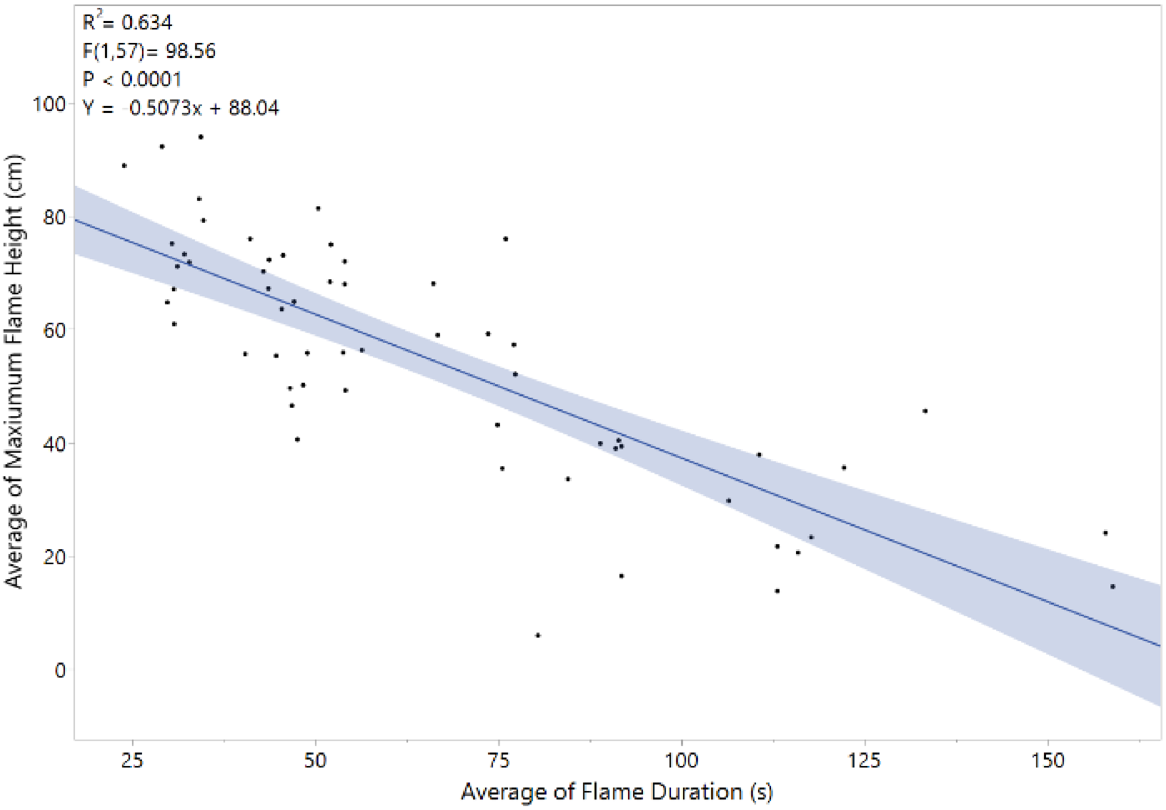

FIGURE 9. Linear regression of the average maximum flame height (cm) with average flame duration (s) for *Quercus* species (n = 59). The negative correlation value was -0.79 with an $R^2 = 0.634$, the F = 98.56 and the $P < 0.0001$, with a slope of Y = -0.5073x + 88.04. As the average maximum flame height increases the average flame duration decreases. When the leaf habit of oak species was factored into the relationship, there was no significant difference $P > 0.05$.

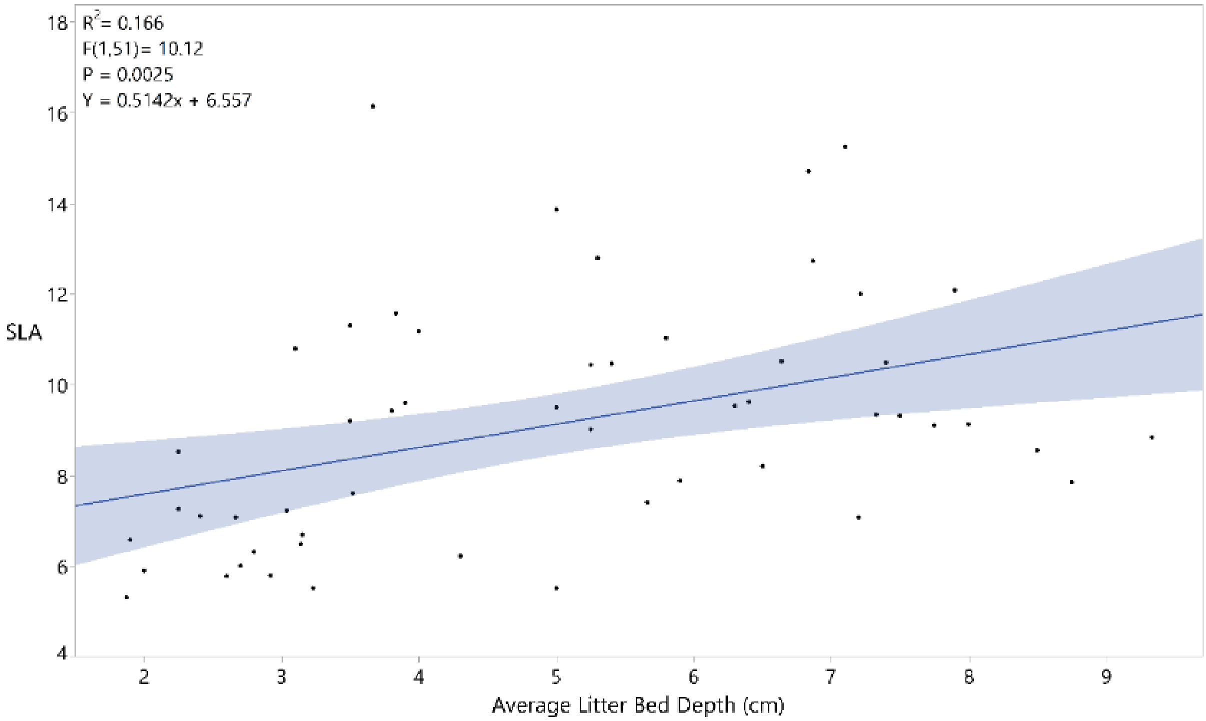

FIGURE 10. Positive bivariate linear fit of specific leaf area (SLA) (mm^2 mg^{-1}) and average litter bed depth (cm) of oak species (n = 53). The lower SLA values correspond to lower litter bed depths resulting in a significant relationship (P = 0.0025).

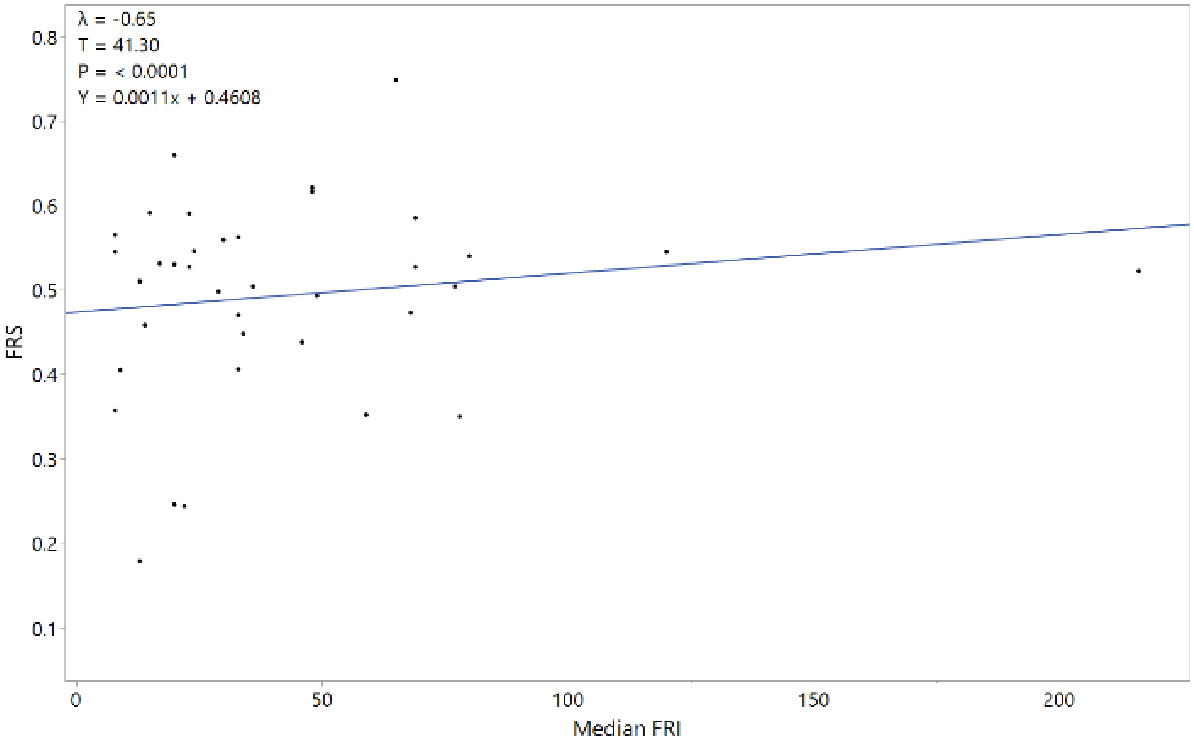

FIGURE 11. Positive relationship among mean oak species fire resistance scores (FRS) of the Forest Inventory Analysis (FIA) oaks (n = 38) with the median fire return interval (FRI). Phylogenetic Generalized Least Squares (PGLS) simultaneously estimates a negative lambda value (λ = –0.65).

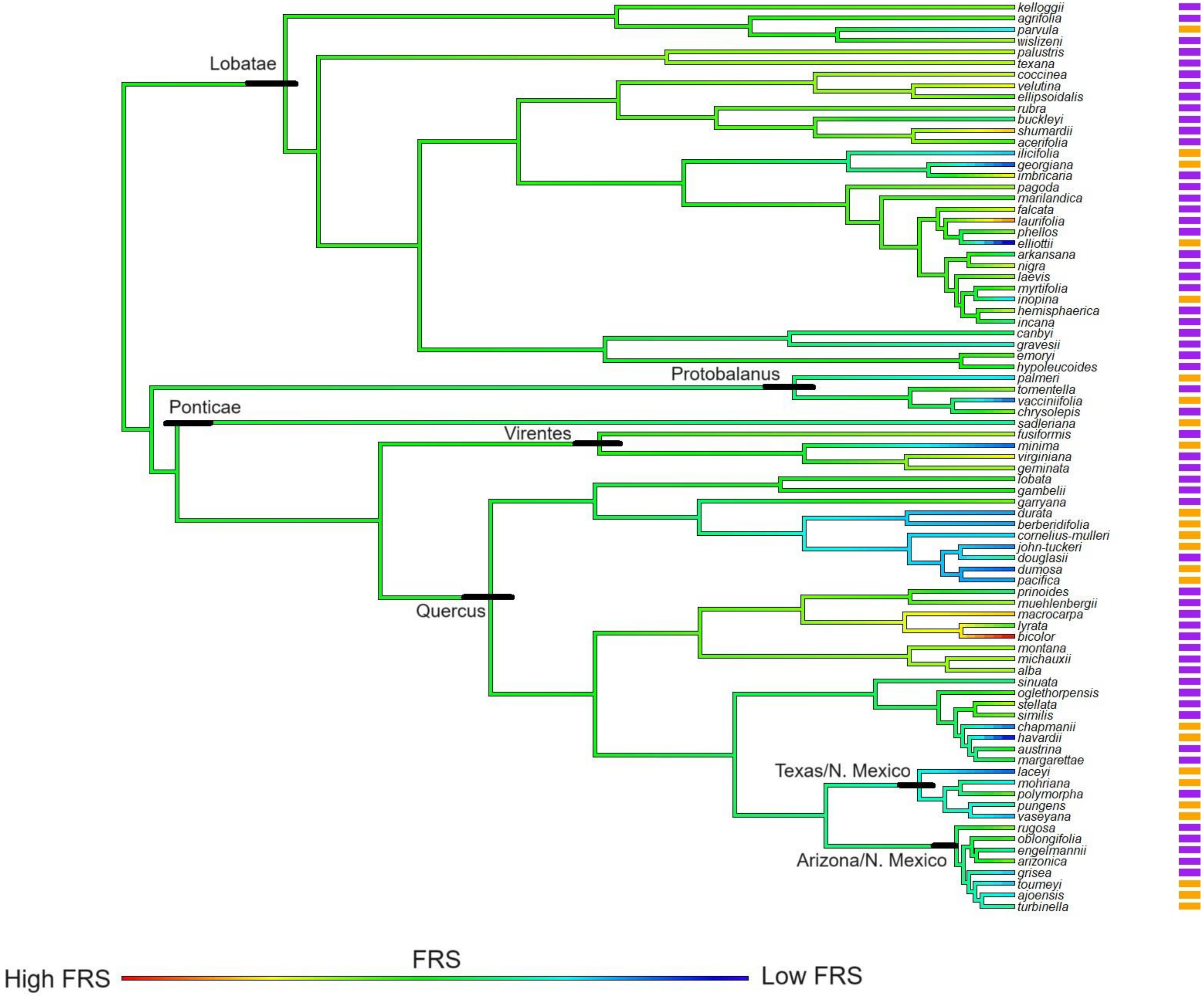
Lobatae
Protobalanus
Ponticae
Virentes
Quercus
Texas/N. Mexico
Arizona/N. Mexico
kelloggii
agrifolia
parvula
wislizeni
palustris
texana
coccinea
velutina
ellipsoidalis
rubra
buckleyi
shumardii
acerifolia
ilicifolia
georgiana
imbricaria
pagoda
marilandica
falcata
laurifolia
phellos
elliottii
arkansana
nigra
laevis
myrtifolia
inopina
hemisphaerica
incana
canbyi
gravesii
emoryi
hypoleucoides
palmeri
tomentella
vacciniifolia
chrysolepis
sadleriana
fusiformis
minima
virginiana
geminata
lobata
gambelii
garryana
durata
berberidifolia
cornelius-mulleri
john-tuckeri
douglasii
dumosa
pacifica
prinoides
muehlenbergii
macrocarpa
lyrata
bicolor
montana
michauxii
alba
sinuata
oglethorpensis
stellata
similis
chapmanii
havardii
austrina
margarettae
laceyi
mohriana
polymorpha
pungens
vaseyana
rugosa
oblongifolia
engelmannii
arizonica
grisea
toumeyi
ajoensis
turbinella
FRS
High FRS
Low FRS

FIGURE 12. *Quercus* phylogeny shows the calculated fire resistance scores (FRS) for each species (n = 81) and ancestral states. Tip values are color-coded; higher FRS are denoted in red and lower FRS are denoted in blue. The colored bars (right) indicate species growth form; tree (purple) or shrub (orange). Ancestral character state reconstruction phylogeny conducted detected no unexpected shifts. *Quercus* species were mapped using the Hipp et al. (2020) phylogeny.

TABLE 4. The LANDFIRE (LF) fire regime groups (FRG) percentage breakdown of coverage for all LF, with the primary FRG from the Forest Inventory Analysis (FIA) (n = 38) oak species. Additional columns display summary statistics of the FIA oak species.

FRG	All LAND FIRE	All Oak FIA	Sample Points	Median FRI	Mean FRI	FRI SE
1	26.4%	68%	70,588	6	9.9	±0.04
2	27.9%	3%	16,621	4	5.1	±0.04
3	20.8%	26%	22,089	53	66.3	±0.33
4	9.6%	0%	2,835	74	77.0	±0.68
5	15.3%	3%	8,664	467	676.3	±6.2
Total			**120,797**	**8**	**68.7**	**±0.66**

Discussion

We find broad evidence that *Quercus* is a moderate to high fire-adapted clade, supporting fire ecology studies which have examined portions of the oak species (Abrams, 1992; Cavender-Bares, 2016; Varner et al., 2016). Using a large spatial scale to examine trait and biogeography patterns in the dominant woody genus in the US allowed for insights that were previously missing in fire ecology. Our work leverages an innovative approach (Stevens et al., 2020) of linking relativized functional traits to assess oak community assembly and adaptation patterns in relation to fire. In the following paragraphs, we expand on these fire ecology patterns. Specifically, we present oaks fire resistance mapped across the US, using FRGs we determine what FRG oak species are primarily residing within. We examine FRS within their FRI showing that as FRS decrease the time between FRIs increases. We highlight potentially at-risk areas where communities appear relatively mismatched to their FRIs (Figures 7 and 8). We provide fundamental insights into the flammability of oak leaf litter (Figure 9) as well as relationships between flammability traits (litter bed depth) and leaf morphology (SLA) (Figure 10). We investigate evolutionary questions about *Quercus* and its relationship with fire and adaptation of fire resistant traits within the genus (Figures 11 and 12). We conclude with future research questions and provide insight into our findings along with limitations of our study.

We provide insight into central research questions on FRS and FRGs, as well as questions about functional traits of species that resulted in higher FRS (Table 2). Our community-weighted FRS vary depending on the FRG they occurred within; with each group significantly different, the highest assigned FRS occurring in FRG 2 (Figure 5). Our findings indicate that oak distribution across FRGs is not uniform, with the majority of oak existing in the frequent-fire FRG 1 (Table 4). Oak species utilize a suite of functional traits to resist fire rather than scoring very high on just one singular trait resulted in higher overall FRS. This suite of traits is reflected by thick bark, tall crowns, a high degree of self-pruning and flammable litter.

FRS and FRG biogeography

Understanding the functional traits that comprise a community we better understand how a species' traits are adapted to their environment. Through spatially mapping these oak functional traits in the context of their FRGs, we better understand how factors impacting FRGs such as fire frequency and intensity, we begin to piece together how a species traits have been informed by their FRG (Figure 3). We determined that our FIA oaks had the highest community-weighted FRS in FRG 1, 2, and 5 (Figure 5). It is likely that FRG 5 received a higher mean because *Q. bicolor* (highest FRS 0.75) exists primarily in this group. It is difficult at times to distinguish if traits are adaptations as a fire response or a response to other factors, given FRG 5 experiences fire very infrequently advantageous traits *Q. bicolor* possesses may be a result of other environmental factors (Keeley et al., 2011).

Eastern oak forests have a long history of dominance, their presence concurrent with frequent fire (Abrams, 1992) and is supported by our analysis of FIA data that a majority of oak-important communities occur in FRG 1 (Table 4). Southeastern oak species display variation in functional traits that aid in their fire adaptiveness, fire resistant traits such as high rates of bark accumulation lending to thicker bark, and fast flammable litter characteristics. Traits that contribute to fire embracing strategies can also be observed such as response to stem injury through resprouting post fire (Varner et al., 2016). Identifying that not one singular functional trait we analyzed was indicative for predicting a high FRS but rather a suite of advantageous fire resistance traits together that yield a high score.

Central to our study was creating a framework to better understand ecosystem fire processes, and how these may be altered due to climate change and result in increased fire frequency or rather conditions that promote fire frequency or intensity such as increased ignition sources, fuel loads, and drought (Pausas & Keeley, 2021). Increases in fire frequency and increased fuel loads result in a higher severity of fire that plant communities dominant within an area may not possess the functional traits to withstand fire if the shift occurs too rapidly. Functional traits that aid in a species fire resistance have the potential to be malleable given time (Cavender-Bares, 2016). However, plants are adapted to their specific fire regime that has been prevalent for a long time period and rapid shifts may not result in adaptation for future fire regime conditions (Keeley et al., 2011). The integration of functional traits across a biogeographical area within our study serves as a link between the adaptive process of traits given the historical frequency in which fire occurs. The use of functional trait analysis can help form a better understanding of such ecosystem processes (Funk et al., 2017).

We modeled our research project from a previous study conducted by Stevens et al. (2020), using western conifer species that all exhibited tree growth forms. While we applied a similar strategy of ranking and standardizing functional traits to assign each species a FRS, it is worth noting that we included shrub growth forms (n = 24) in our study (Figure 2). This resulted in shrub species having lower FRS scores compared to oaks with a tree growth form given the traits we selected for our study (Figure 1). Although it should be noted that alterative scoring systems were explored to analyze shrub growth form separately from tree growth form, resulting in low FRS for shrubs regardless; meaning more than one trait leads to low/high fire resistance. Separate from fire resistance, shrub species typically have aboveground tissues consumed by fires, but have the propensity to recover from these fires through vigorous resprouting (Keeley, 2006).

The ecosystems that shrub species occur in are FRGs with infrequent (35-200+ years) and high severity (replacement stand) fires (FRG 4 and 5) and thus this FRG environment is selecting for traits that aid in survival that may look different compared to FRG 1. These dry shrubland ecosystems may be selecting for traits suited for conservative nutrient and water use efficiency (Kaproth et al., 2023). One tradeoff of being a shrub species is the lack of investment in bark, which increases aboveground survival during fire events, especially for juveniles. However, shrubs place their resource investment in belowground carbohydrate storage and the ability to resprout resulting in recovery after highly severe fire events (Myers, 1990; Schwilk et al., 2013). The mechanism of survival for a shrub is not to avoid fire but rather to recover after fire with root and rhizome resprouts (Guerin, 1993; Greenberg & Simons, 1999; Romero et al., 2009). Thus, shrubs may be best analyzed using the framework of “fire embracer” species (Table 1). We focused on the traits important for fire resistance (crown survival) in *Quercus* species, compared to fire embracing trait strategies (post-fire regeneration). This is partly because trait strategies of resprouting are shown in the literature to be common for most oak species. Species that utilize fire embracing traits typically exist in narrow ranges or isolated stands and are associated with shrublands (Menges & Kohfeldt, 1995). Thus, for these reasons, it would be appropriate to not measure shrub species in the context of fire resistance in studies moving forward but rather in terms of fire embracing traits where the use of a separate analysis could be implemented.

Mismatches between FRS and FRI

We identified fire resistant and fire-sensitive communities (Figure 8), parts of the highlighted areas were found to be compatible with predictions and understandings of historical fire regimes, with higher fire resistance existing in areas that experience a shorter FRI (Kane et al., 2008; Engber & Varner, 2012; Varner et al., 2016). However, we highlighted communities that are mismatched to the fire regimes which they inhabit. This can be informative about the functional traits within an area and provide insight into species that pose a larger concern for protection, especially if an increase in fire frequency and severity were to occur within that species FRG. It should be noted that some spatial patterns may be reflective of the area's geology and geomorphology. We identified areas where the community-weighted mean FRS was sensitive (low FRS for the short FRIs), as well as areas of resistance in the community-weighted mean FRS (high FRS for the long FRIs).

Areas of sensitivity that we see highlighted on our map (Figure 7) are shown in magenta and orange. Notable areas of sensitivity are within northwestern to central Florida, this is attributed to the following species *Q. margarettiae* and *Q. incana* previous studies confer with these species exhibiting high degrees of flammability (Varner et al., 2021). Other pockets of sensitive species near Fort Davis, TX. *Q. marilandica, Q. incana and Q. grisea,* these species are not typically thriving post fire events.

The southwest US also is experiencing sensitivity likely due to the shrubland species of oaks (that were assigned low FRS) that exist at higher elevations in arid ecosystems, species such as *Q. minima* (0.18 FRS) and *Q. grisea* (0.24 FRS). Other species that resulted in highlighted sensitivity shown in orange are *Q. hypoleucoides*, *Q. emoryi,* and *Q. gambelii.* Species like *Q. emoryi* and *Q. gambelii* have a different fire surviving strategy of “fire embracers” both species have better chances of survival with low severity fire which does not match the sensitive-intermediate orange that exists within FRG (3,4,) that experience higher severity fires (Table 3). In Arizona notable sensitive-frequent mismatches are visible in magenta this likely reflects the distinct Mogollon Rim break within the landscape.

The Piedmont Region from Louisiana stretching into the Carolinas has a scattering of fire resistant areas with higher FRS in comparison to the fire return intervals present, with the only notable exception of sensitivity shown in magenta driven predominately by *Q. marilandica* (Figure 7). Additional areas of high fire resistance (shown in green and light blue) occurring in Florida represent species such as *Q. laurifolia* and *Q. virginiana* (Figure 7). Other notable areas of high fire resistant oak communities are scattered across the eastern US with highlighted areas occurring in the Dakotas, Minnesota, Michigan, and Ohio; this is primarily driven by *Q. macrocarpa* and *Q. bicolor.* The fire resistant areas of northern Minnesota and the Dakotas may be indicative of the remnants of Lake Agassiz basin that resulted in rich soils with an interesting topography for that area. The northeast US has sensitivity shown in magenta represented by the shrub species *Q. ilicifolia,* another example of a species representative of "fire embracing" traits that will likely have aboveground biomass killed off in a top fire to emphasize regrowth through rigorous resprouting after fire.

The "sensitive-frequent" mismatches highlighted in magenta (Figure 7) were occurring in historically frequent-fire areas and could likely be areas that experienced fire exclusion, consequentially fire-intolerant species encroached into the area. These shifts to the historical frequent fire are resultant from missed fire cycles that cause excessive fuel accumulation and increase the dominance of shade tolerant species (Liang & Hurteau, 2023). The areas where our community-weighted fire resistance scores across the US were highest were at mid-elevation California montane forests, coastal plains and Piedmont lowlands, Eastern US lowland and montane forests (Figure 3) (Vankat, 1990). These areas of higher fire resistance have relationships between climate, fuels, and fire regimes. The climate (cold/mesic conditions) act as a limitation for fire spread in montane or coastal forests where fuel conditions may otherwise support fire spreading. These ecosystems consist of high fuel loads that historically experience fire at a frequency that allows for clearing of fuels. These areas of high FRS exist in FRG 1 (frequent fire with low to mixed severity levels). The least fire resistant areas with lower community FRS occupy habitats at higher elevations (Figure 3), which historically have experienced infrequent fire and thus are subject to extensive tree mortality and rapid community shifts post fire events (Yocom-Kent et al., 2015). We utilized the fire return intervals within our study, this layer specifically quantifies the average period between fires under the presumed historical fire regime, it is intended to describe one aspect of historical fire regime characteristics within the context of broader historical time period represented by the LANDFIRE biophysical settings. Thus, climatic changes that result in alterations to historical fire return intervals are worth further consideration and investigation to how this may impact the overall ecosystem.

Leaf litter flammability

Fire behavior is a highly complex amalgamation of topography, weather (drought and temperatures), and available fuels, resulting in varying flammability (Rothermel, 1972). The variation in flammability traits observed within *Quercus* is likely attributable to differences in physical and chemical components of the leaf litter. Many properties have been found to play a critical role in leaf litter flammability or ignitability in plants, properties such as leaf thickness

(Montgomery & Cheo, 1971), surface area-to-volume (Engber & Varner, 2012), lignin levels (Castro-díez et al., 1997), proportion of volatile compounds (Curt et al., 2011), and moisture content (Ray et al., 2010; Varner et al., 2015). The flammability traits of flame height and flame duration analyzed in our study could be classified as “fast flammable” or “hot flammable” evolutionary strategies (Figure 9). Fast flammable leaf litter is distinguished by a greater maximum flame height and higher percentage consumption, but also a shorter flame duration. Whereas “hot flammable” strategies typically are associated with moderate flame heights and percentage consumption but have longer flame durations thus releasing more heat (Appendix Figure B; Pausas et al., 2017). Functional traits such as thicker bark and high degrees of self-pruning exhibit leaf litter traits conducive to “fast flammable” burning characteristics (Stevens et al., 2020) With higher flame heights and shorter flame durations this may aid in tree survival due to limiting lethal temperature exposure to the cambium of the plants (Pausas, 2015; Varner et al., 2015). The two characteristics of leaf thickness and surface area-to-volume ratios may play a critical role in leaf litter burning among different *Quercus* species. The leaf habit a species possesses as well as the area to density can result in different flammability rates. For instance, oak species that have deeply lobed and relatively thin leaves with a median SLA ratio (ex. *Q. laevis*) seemingly burn better compared to species who have an evergreen leaf habit with a lower SLA ratio (ex. *Q. virginiana*) (Kane et al., 2008). Our study also observed what previous studies had in regard to oak species that typically burned poorly fell into the leaf habit classification of evergreen with the growth form of shrub (Engber & Varner, 2012). Evergreen leaf litter had low flammability and generated short flames (<65 cm), consumed little fuel (<82%), and flamed for long durations (>47 s). Previous studies observed that the leaf morphology trait of leaf size (an individual leaves area, different from SLA area and density), showed a strong link to litterbed depth, which is known to be a driver in fire behavior (Engber & Varner, 2012). However, we observed a similar finding using the leaf morphology trait of SLA and litterbed depth, lower SLA ratios corresponded to lower depths of leaf litter (Figure 10). Continued flammability research on how a communities plant assemblage burns together, and not only in isolation is needed across a wide range of ecosystems.

Phylogenetic tree

Oaks can inhabit a wide range of environmental conditions resulting in the variation shown across the genus, however despite this variation *Quercus* is known for co-occurrence of several oak lineages of within an ecosystem displaying a pattern of phylogenetic overdispersion (Cavender-Bares, 2019). We analyzed the phylogenetic patterns for US oaks, to discern any notable phylogenetic patterns. Our analysis of species calculated FRS in response to median FRI using a PGLS, showed a strong negative lambda value pointing to strong patterns of phylogenetic overdispersion (Figures 11 and 12). Thus, species of close relation are capable of occupying different niches likely because of functional trait differences. Species FRS differ within subsections, oaks indicate a high degree of selection for traits in relation to fire resistance. This aligns with previous studies that also noted phylogenetic overdispersion patterns within *Quercus* (Cavender-Bares et al., 2018). This overdispersion phylogenetic pattern shown with median FRI is likely a result of evolutionary convergence of critical traits that were shaped by the environments FRI within a given FRG (Cavender-Bares et al., 2004). In our PGLS we observed a higher FRS with a longer median FRI. The longer the median FRI the more severe a fire's intensity, this relationship is unexpected and counter to community-weighted FRS-FRI patterns (Figure 6). One potential explanation of this unexpected relationship is in a resource rich environment, species are adapted to grow rapidly it may be thus advantageous to be a tall tree for example a species such as *Q. bicolor*. These species may not have had selection for traits as a result of exposure to fire but rather exists in an environment where it does not experience limitations in resources (i.e. light, water) (Cavender-Bares et al., 2018; Kaproth et al., 2023). It may be that traits conducive to fire resistance (tall height, thick bark, and high degree of self-pruning) also are species that would occur in resource rich environments.

Future functional trait biogeography research

The continuation of developing a standardized protocol to assign plant species an FRS calls for future studies to be conducted to determine what functional traits aid in the survival of trees/shrubs post fire events. Although our study focused on the genus *Quercus* it is worth further exploration on how the growth form of shrub species may need to be analyzed on a separate continuum compared to the growth form of trees (Stevens et al., 2020). The FRS methodology could be updated and integrated using more functional traits or different functional traits dependent upon the understanding of an ecosystem's functioning. Instead of conducting a larger scaled up spatial study, future functional trait scoring could take a community structure approach to account for the fire resistance of the overall plant community, including tree species as well as woody herbs and shrubs. We selected our functional traits using the previous study conducted by Stevens et al. (2020), as well as literature on *Quercus* and fire (Pausas et al., 2017; Hood et al., 2018).

Our FRS index has notable limitations, only utilizing a small arrangement of functional traits for analysis could be a limiting factor. The trait of bark thickness had limited data and could easily be improved through increased field collections and improved models in *Quercus* species bark accumulation. Another issue being data limitations on flammability traits, due to not being able to conduct flammability burn trials on every US oak species. Our litter flammability traits used in our FRS are reflective of the “fast flammable” or “hot flammable” (Pausas et al., 2017) strategy (Appendix Figure B). The hot flammable strategy that our leaf litter flammability traits possessed is more reflective of a “fire embracing” trait, not fire resistance (Table 1). This strategy of leaf litter flammability being “fire embracing” is compatible with ecosystems that experience crown fires; however, it is worth noting that leaf litter does not serve as the dominant fuel in such ecosystems. But rather in fire embracing ecosystems, living foliage on shrubs and trees act as a fuel catalyst. Thus, the structure and community assemblage serve an important role within a fire regime, this is a limitation not attained by our functional trait methodology. Our controlled burn settings of our leaf litter are also not entirely indicative of an actual ecosystem setting where leaf litter on the forest floor is a heterogeneous combination of many varied species and growth forms.

Fires occur from a multitude of factors such as ignition sources, fuels, and drought; even irregular weather patterns can impact these factors enhancing spread and chances of fires. (Pausas & Keeley, 2021). Thus, even the traits that aid in a plant’s resistance to fire can be impacted by these fire factors. Our FRS index is not intendent to foresee plant survival rates post fire, but rather to assess traits quantitatively to identify where oak important communities are best able to resist surface fires. Our ultimate study aim is to help guide fire/forest management and planning. However due to our changing climate and land use changes, alterations to an areas FRG or FRI is likely as the ecosystems are not stationary. Our work points to *Quercus* species that possess traits indicative of fire resistance as well as species that do not possess fire resistant traits, as patterns change future work can be conducted on how these species will react to probability metrics and risk moving forward.

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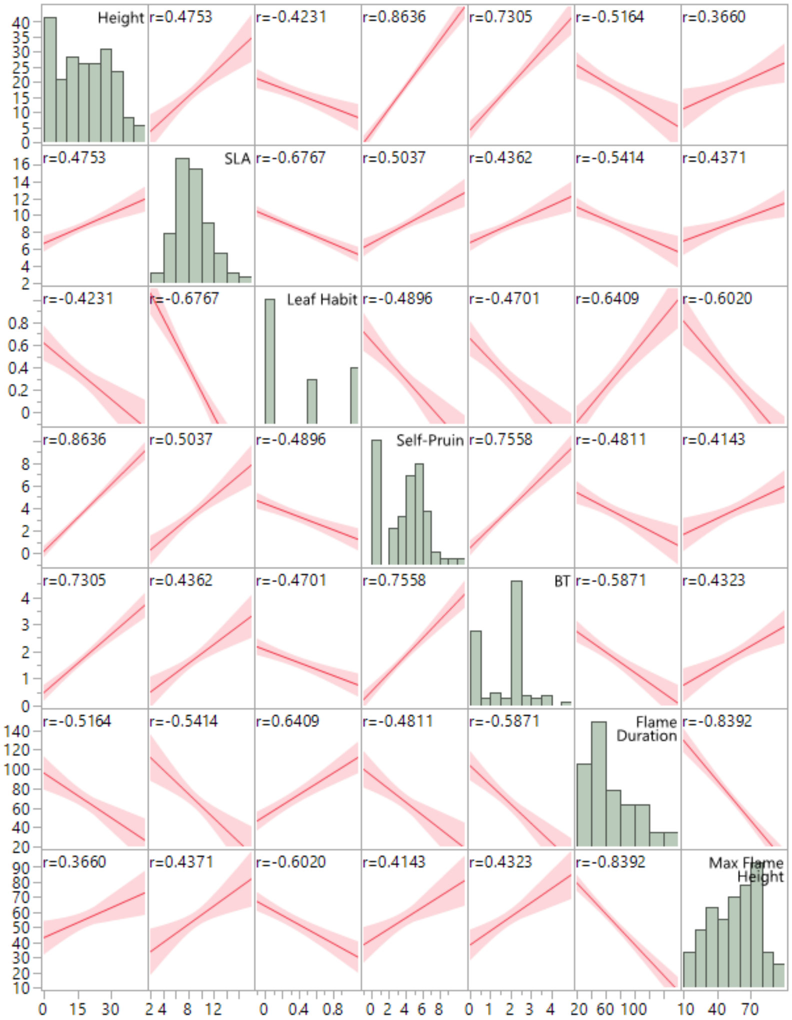
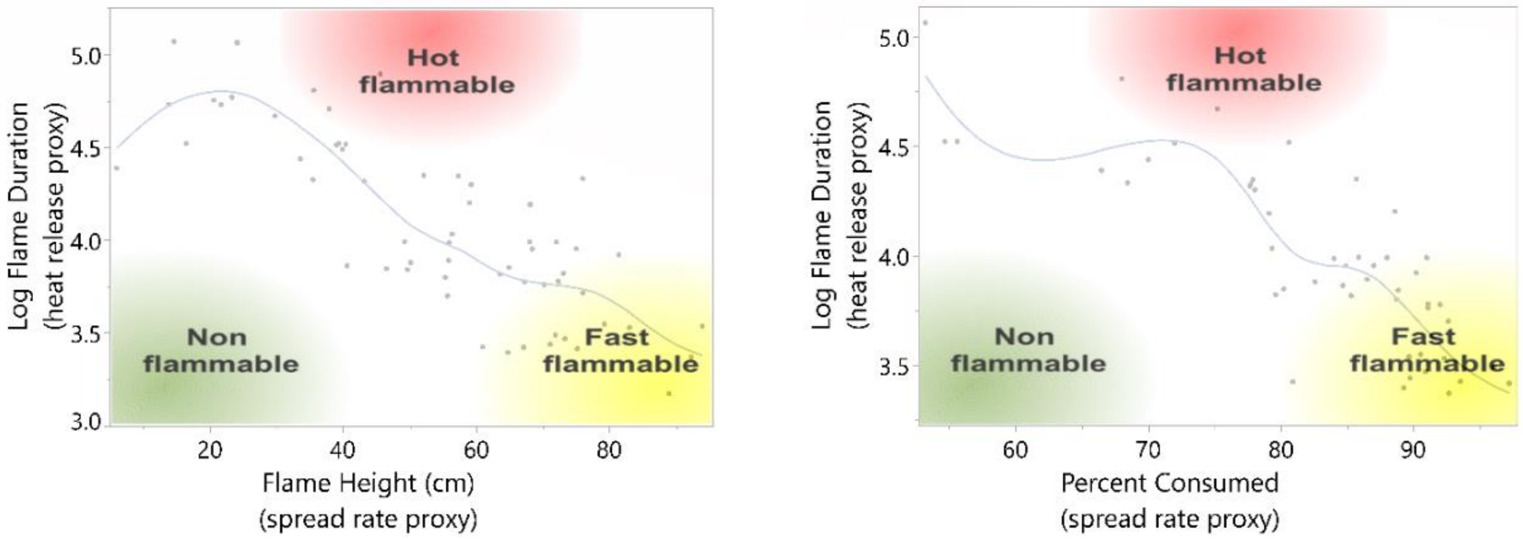
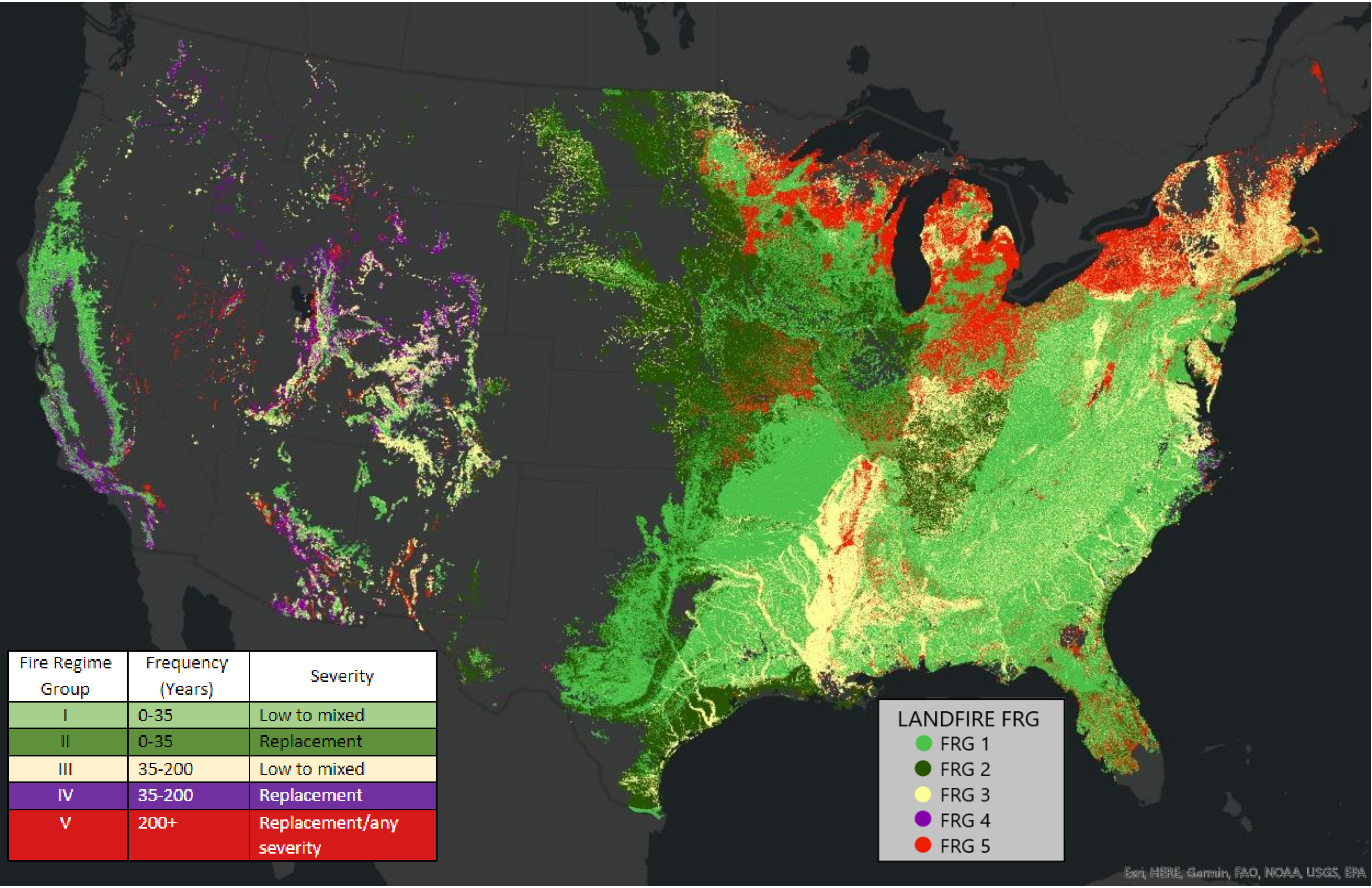
Appendix



Appendix Figure A. Our raw functional trait values are analyzed using a multivariate correlation, strength of correlations shown with the r squared value in each square. In a pairwise correlation all values were found to be significant P<0.01.



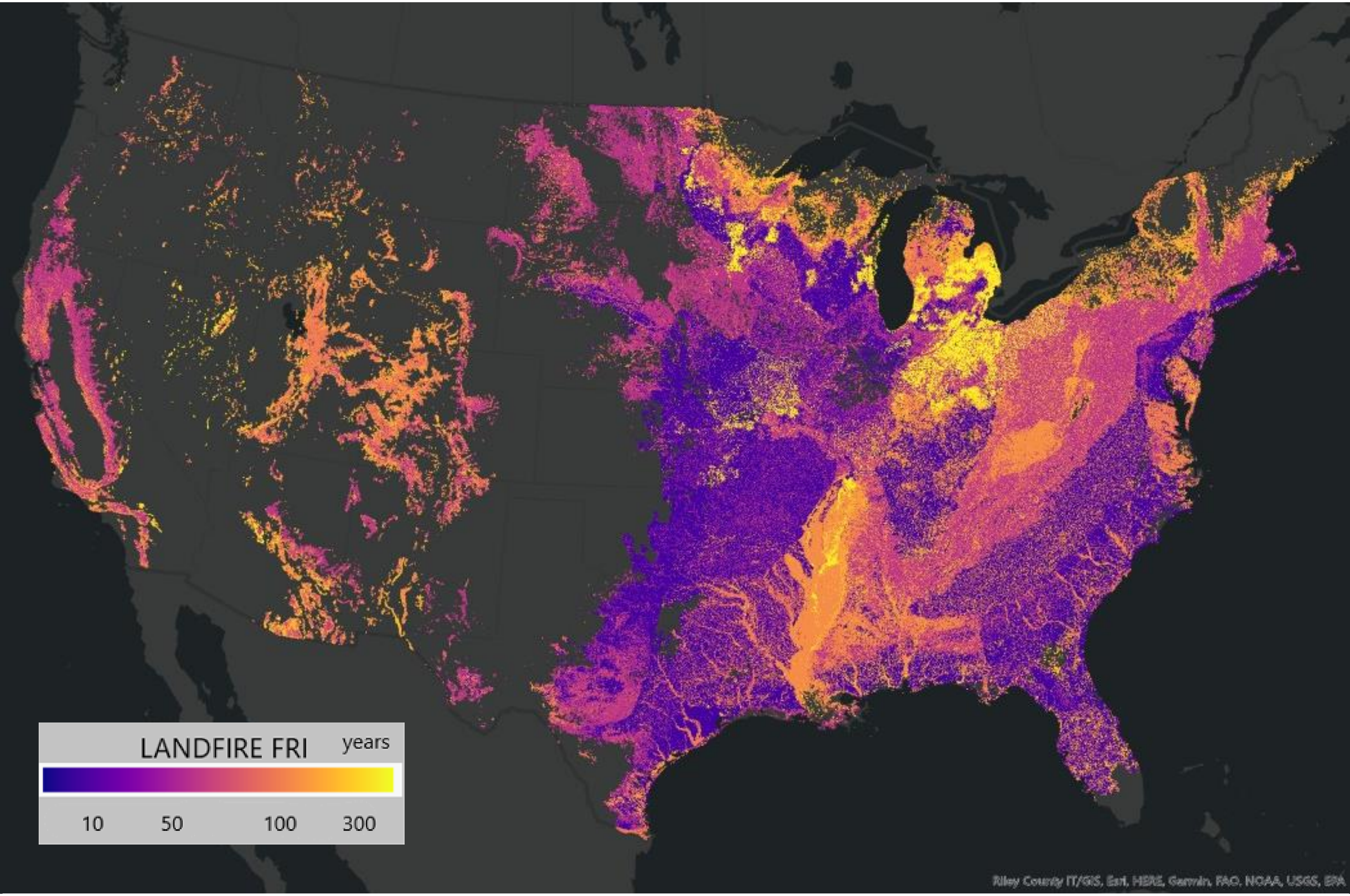
APPENDIX FIGURE B. The flammability traits are shown with log-scale flame duration (seconds) as proxy for heat release (y-axis), and flame height (a) and percent consumed (b) as proxies for spread rate (x-axis), in relation to the flammability strategies shown as modified from Pausas et al. (2017).



Fire Regime Group	Frequency (Years)	Severity
I	0-35	Low to mixed
II	0-35	Replacement
III	35-200	Low to mixed
IV	35-200	Replacement
V	200+	Replacement/any severity

Esri, HERE, Garmin, FAO, NOAA, USGS, EPA

APPENDIX FIGURE C. Our study area of one-third oak basal area shown in reference to the LANDFIRE fire regime groups (FRG).



APPENDIX FIGURE D. Our study area of one-third oak basal area shown in reference to the LANDFIRE fire return intervals (FRI).

APPENDIX TABLE A. Average leaf litter flammability trait data collected for the following *Quercus* species.

Scientific name	Litterbed Depth (cm)	Maximum Flame Height (cm)	Flame Duration (sec)	Smoldering Duration (sec)	Total Burn Time (sec)	Residual weight (g)	Consumption (%)	Mass Loss Rate mg s^{-1} (%)	Source
Quercus acerifolia	5.9	73.1	45.6	151.6	197.2	3.1	79.6	64.4	Morton Arboretum *cp
Quercus acutissima	5.5	40.6	43.6	129.0	172.6	1.0	93.2	90.5	MNSU Greenhouse *cp
Quercus agrifolia	3.0	27.4	106.3	189.7	295.9	3.7	75.2	38.4	UC Davis *cp
Quercus arizonica	4.3	49.2	54.1	279.1	333.2	2.1	85.9	39.1	Las Cruces, NM *wi
Quercus arkansana	3.7	46.5	46.8	282.3	329.1	3.0	80.2	36.6	Morton Arboretum *cp
Quercus austrina	5.0	56.4	56.4	278.2	334.6	3.1	79.3	36.6	Morton Arboretum *cp
Quercus bicolor	7.2	67.1	30.6	158.0	188.7	2.9	80.9	89.5	Mankato, MN *wi
Quercus boyntonii	3.8	36.8	68.3	267.6	335.9	4.8	68.0	30.6	Morton Arboretum *cp
Quercus buckleyi	7.3	55.7	40.4	105.3	145.7	1.1	92.6	100.3	MNSU Greenhouse *cp, Morton Arboretum *cp
Quercus cerris	7.5	45.7	55.2	57.1	112.3	1.9	87.1	116.3	MNSU Greenhouse *cp
Quercus ellipsoidalis	7.5	61.0	30.7	125.7	156.4	1.0	93.5	89.7	MNSU Greenhouse *cp
Quercus gambelii	6.5	71.1	31.2	145.7	176.8	1.5	89.7	77.5	Denver Botanical Gardens *cp
Quercus georgiana	3.5	35.6	122.2	98.3	220.5	4.8	68.0	46.3	Morton Arboretum *cp
Quercus grisea	2.3	16.5	91.8	106.3	198.1	6.7	55.6	42.4	Las Cruces, NM *wi, Morton Arboretum *cp
Quercus ilicifolia	5.3	67.3	43.6	205.3	248.9	1.2	92.0	56.4	Albany, NY *wp
Quercus imbricaria	7.2	79.2	34.7	142.9	177.6	1.4	90.5	77.8	Morton Arboretum *cp
Quercus laurifolia	5.0	55.9	53.8	223.5	277.3	2.4	84.0	45.4	Morton Arboretum *cp
Quercus lyrata	4.0	55.9	48.9	266.2	315.1	2.0	86.5	42.1	Morton Arboretum *cp
Quercus macrocarpa	7.8	64.8	29.8	67.8	97.6	1.6	89.3	137.2	MNSU Greenhouse *cp
Quercus mohriana	3.5	43.2	74.9	212.8	287.6	3.4	77.7	40.5	Morton Arboretum *cp
Quercus montana	6.8	44.9	48.4	80.6	129.0	1.7	88.4	121.3	MNSU Greenhouse *cp

Scientific name	Litterbed Depth (cm)	Maximum Flame Height (cm)	Flame Duration (sec)	Smoldering Duration (sec)	Total Burn Time (sec)	Residual weight (g)	Consumption (%)	Mass Loss Rate mg s^{-1} (%)	Source
Quercus muehlenbergii	7.4	71.9	32.8	124.5	157.3	0.6	96.1	94.2	Morton Arboretum **cp*
Quercus oblongifolia	2.0	6.0	80.4	130.1	210.5	5.0	66.5	47.4	El Paso, TX **wi*
Quercus oglethorpensis	3.8	76.0	76.0	224.7	300.7	4.7	68.4	34.8	Morton Arboretum **cp*
Quercus pacifica	2.3	39.4	91.8	315.2	407.0	6.8	54.7	20.2	Chanel islands **wi*
Quercus palustris	7.9	75.2	30.4	158.4	188.8	0.4	97.2	81.4	Morton Arboretum **cp*
Quercus prinoides	8.8	94.0	34.4	137.7	172.1	1.6	89.7	78.6	Albany, NY **wp*
Quercus rubra	6.9	51.2	44.2	114.4	158.6	1.8	87.9	83.2	MNSU Greenhouse **cp*
Quercus rugosa	5.0	50.2	48.4	152.2	200.5	2.6	82.6	62.8	UC Davis **ci*
Quercus shumardii	8.0	70.2	42.9	156.1	199.0	1.3	91.1	77.1	Denver Botanical Gardens **cp*, Morton Arboretum **cp*
Quercus sinuata	5.3	40.6	47.6	248.3	295.8	2.3	84.7	44.9	Morton Arboretum **cp*
Quercus texana	8.5	88.9	23.9	138.5	162.4	1.1	93.0	86.0	Denver Botanical Gardens **cp*
Quercus tomentella	1.4	32.4	70.8	205.3	276.1	3.3	77.7	42.5	UC Davis **ci*
Quercus turbinella	2.7	59.2	73.6	153.3	226.8	3.3	78.0	53.0	Denver Botanical Gardens **cp*, El Paso, TX **wi*
Quercus velutina	9.3	92.3	29.1	150.7	179.8	1.1	92.7	94.1	Albany, NY **wp*
Quercus agrifolia	3.22	41.4	107.4	249.4	356.8			76.6	Engber & Varner 2012
Quercus alba		72	54	249	303		91		Varner et al. 2021
Quercus chrysolepis	2.92	37.9	110.6	281.9	392.5			75.7	Engber & Varner 2012
Quercus coccinea		73.3	32.1	290.9	323		90.9		Varner et al. 2021
Quercus douglasii	3.52	21.7	113.1	296	409.1			59.6	Engber & Varner 2012
Quercus dumosa	2.8	20.6	115.9	156.2	272.1			43.9	Engber & Varner 2012
Quercus durata	2.41	13.8	113.1	96	209.1			29.3	Engber & Varner 2012
Quercus engelmannii	3.15	23.3	117.7	273.4	391.1			60.2	Engber & Varner 2012
Quercus falcata	5.8	75	52.1	399.8	451.9		87	30	Kane et al. 2008

Scientific name	Litterbed Depth (cm)	Maximum Flame Height (cm)	Flame Duration (sec)	Smoldering Duration (sec)	Total Burn Time (sec)	Residual weight (g)	Consumption (%)	Mass Loss Rate mg s^{-1} (%)	Source
Quercus garryana	6.64	76	41.1	246.7	287.8			87.9	Engber & Varner 2012
Quercus geminata		39	91	218	309		72		Varner et al. 2021
Quercus hemisphaerica	3.1	40.4	91.4	348	439.4		80.6	28.5	Kane et al. 2008
Quercus incana	3.9	52.1	77.3	341.8	419.1		85.7	31.5	Kane et al. 2008
Quercus john-tuckeri	2.7	24.1	157.9	100.4	258.3		53.2		Engber & Varner 2012
Quercus kelloggii	7.1	83	34.1	233.3	267.4		92.3		Engber & Varner 2012
Quercus laevis	6.3	81.4	50.4	350.7	401.1		90.2	35.8	Kane et al. 2008
Quercus lobata	5.3	63.6	45.4	325.1	370.5		85.3		Engber & Varner 2012
Quercus margarettae	5.4	68.1	66.1	286.5	352.6		79.1	35.4	Kane et al. 2008
Quercus marilandica		68	54	240	294		88		Varner et al. 2021
Quercus michauxii		72.3	43.7	215.9	259.6		91.1		Varner et al. 2021
Quercus montana		64	41	302.4	343.4		90.1		Varner et al. 2021
Quercus nigra	3.8	57.3	77.1	268.8	345.9		77.9	34.4	Kane et al. 2008
Quercus palmeri	3.23	45.6	133.3	189.1	322.4			76.8	Engber & Varner 2012
Quercus phellos		59	66.7	382.7	449.4		88.6		Varner et al. 2021
Quercus rubra		67.7	46.1	283	329.1		91.1		Varner et al. 2021
Quercus sadleriana	5.66	64.9	47.1	386	433.1			92.5	Engber & Varner 2012
Quercus stellata	6.4	68.4	52	216.3	268.3		84.9	50.2	Kane et al. 2008
Quercus tomentella	3.67	47.9	94.4	310	404.4			77.8	Engber & Varner 2012
Quercus vacciniifolia	1.9	14.6	158.9	79.6	238.5			34.9	Engber & Varner 2012
Quercus virginiana	2.6	33.6	84.5	230.7	146.2		70	34.4	Kane et al. 2008
Quercus wislizeni	3.14	39.9	88.9	284.6	373.5			72.1	Engber & Varner 2012

Note: The following table is comprised of leaf litter flammability trait averages. This table includes both data collected for our study and previously published data in the literature. The source column denotes species that were collected specifically for this study verses data gathered from previous studies in the literature all using protocols outlined by Fonda (2001). Specimens leaf litter collected for our study was primarily collected in the Fall (October – November) of 2022 from recently fallen leaves prior to decomposition occurring or removed directly from specimens. The following letters denote collection details *w – wild, c – cultivated* and the following letters denote specimens collected from an *i – individual, p – population*. The blanks within the table were from studies that did not collect data for that specific leaf litter flammability trait.