Vegetation’s influence on fire behavior goes beyond just being fuel

E. Louise Loudermilk1*, Joseph J. O’Brien1, Scott L. Goodrick1, Rodman R. Linn2, Nicholas S. Skowronski3 and J. Kevin Hiers4

Abstract

Background: The structure and function of fire-prone ecosystems are influenced by many interacting processes that develop over varying time scales. Fire creates both instantaneous and long-term changes in vegetation (defined as live, dead, and decomposing plant material) through combustion, heat transfer to living tissues, and subsequent patterns of recovery. While fuel available for combustion may be relative to the amount of vegetation, it is equally instructive to evaluate how the physical structure and other characteristics of vegetation influence fire dynamics, and how these interactions change between fire events. This paper presents a conceptual framework for how vegetation not only embodies the legacy of previous fires but creates the physical environment that drives fire behavior beyond its combustion as a fuel source.

Results: While many environmental factors affect both the post-fire vegetation trajectory and fire dynamics themselves, we present a conceptual framework describing how vegetation’s structural characteristics control the local microclimate and fluid dynamics of fire-induced flows, and how that is influenced by ecosystem and atmospheric processes. Shifting our focus from fuels to vegetation allows us to integrate spatial and temporal feedbacks between fire, vegetation, soil, and the atmosphere across scales. This approach synthesizes the combustion and flammability science, the physical influence on fire behavior, and the ecosystem dynamics and processes that occur between fires and within a fire regime.

Conclusions: We conclude that fire behavior, including its prediction and ecological effects, should be broadened to include the dynamic processes that interact with vegetation, beyond its role as fuel. Our conceptual framework illustrates the crucial feedbacks across scales that link the finer details of vegetation and fire behavior processes that occur within a fire and have additive effects that feedback into the coarser scale processes and functions within an ecosystem. Shifting the fuels paradigm to integrate the combustion, physical, and ecological roles of vegetation as complex drivers of fire behavior and outcomes will broaden discovery within wildland fire science and ecology.

Keywords: Ecology of Fuels, Wildland fire, Microenvironment, Fire effects, Feedbacks, Fire behavior

*Correspondence: eva.l.loudermilk@usda.gov

1 Center for Forest Disturbance Science, Southern Research Station, USDA Forest Service, 320 Green St, Athens, GA 30602, USA

© The Author(s) 2022. Open Access This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit http://creativecommons.org/licenses/by/4.0/.
**Introduction**

Many ecosystems depend on the complex interactions between fire and vegetation (Bond and Keeley 2005) where variation in vegetation—defined as live, dead, and decomposing plant material—drives wildland fire behavior across scales (Lentile et al. 2006; Mitchell et al. 2009), and multiple fires create legacy effects on ecosystems (Franklin et al. 2007). These interactions create a tight feedback loop: fire is a keystone biophysical process driving the structure, composition, and function of vegetation, while vegetation determines the distribution of combustible material, air movement, and moisture balances for the next fire. Finally, post-fire vegetation responses influence ecosystem trajectories between fires (Fig. 1). These feedbacks are complex because of the strong influences of local and nonlocal drivers of both fire and vegetation dynamics, as well as interactions between the immediate conditions (Pickering et al. 2021; Kreye et al. 2020) and historical legacies of fire (Bond and Keeley 2005). A deeper understanding of the evolution and function of fire-influenced ecosystems and identifying the causal links among feedback components requires a holistic approach in considering these complex interactions in space and time. In this paper, we review the role of vegetation beyond its function as a fuel or a short-term post-fire response, where we consider the mechanisms responsible for the entire cycle of fire-vegetation-atmosphere feedbacks as an approach for a more comprehensive view of fire ecology.

Many fire ecology studies are focused on fire effects on vegetation as framed by a particular ecosystem’s fire regime. This creates an often-circular logic, since the term “fire regime” is defined by the broad-scale and long-term effects of fire frequency and intensity on overall ecosystem response, post-fire recovery, and successional patterns (Archibald et al. 2013). However, fire effects research can be improved by focusing on quantifying heat energy transfer as a driver of plant tissue damage and examining plant responses both individually and as a cumulative ecosystem effect (O’Brien et al. 2018; Smith et al. 2016). Legacies of fires and contemporary influences (weather, ignition characteristics, seasonal phenology, etc.) are rarely explicitly captured and incorporated into ecological studies (Bonner et al. 2021), yet these factors set the stage for observed effects, including changes in species composition and interactions with other disturbances and processes (Zhang et al. 2021; Smith 2018; Hohnert et al. 2019). Much attention is focused on large high-severity fires that have dramatic

---

**Resumen**

**Antecedentes:** La estructura y función de ecosistemas propensos al fuego están influenciados por muchos procesos interactivos que se desarrollan sobre escalas espaciales variables. El fuego crea cambios instantáneos y de largo plazo en la vegetación (definida como viva, muerta y material vegetal en descomposición) a través de la combustión, la transferencia de calor a tejidos vivos y los subsecuentes patrones de recuperación. Aunque el combustible disponible para quemarse puede relacionarse con el total de la vegetación, es igualmente instructivo evaluar cómo la estructura física y otras características de la vegetación influencian la dinámica del fuego, y cómo esas interacciones cambian entre eventos de fuego. Este trabajo presenta un marco conceptual de cómo la vegetación no sólo incorpora el legado de previos fuegos, sino que también crea el ambiente físico que tracciona el comportamiento del fuego más allá de su combustión como fuente de combustible.

**Resultados:** Aunque muchos factores ambientales afectan tanto la trayectoria de la vegetación post fuego como la dinámica del fuego, presentamos un marco conceptual que describe cómo las características estructurales de la vegetación controlan el microclima y la dinámica de fluidos de los flujos inducidos por el fuego, y cómo éste es influenciado por procesos atmosféricos y del ecosistema. Desviando nuestro foco desde los combustibles a la vegetación nos permite integrar la retroalimentación espacial y temporal entre fuegos, vegetación, suelos y atmósfera a través de diferentes escalas. Este enfoque sintetiza la ciencia de la combustión y la inflamabilidad, la influencia de factores físicos en el comportamiento del fuego y la dinámica y procesos de los ecosistemas que ocurren entre fuegos dentro de un régimen de fuego.

**Conclusiones:** Concluimos que el comportamiento del fuego, incluido su predicción y efectos ecológicos deben ser ampliados para incluir los procesos dinámicos que interactúan con la vegetación, más allá de su rol como combustible. Nuestro marco conceptual ilustra las retroalimentaciones cruciales a través de escalas que ligan los detalles finos de la vegetación y los procesos de comportamiento del fuego que ocurren dentro de un fuego y que tienen efectos aditivos que retroalimentan a una escala más grande de procesos y funciones dentro de un ecosistema. Modificando el paradigma de los combustibles para integrar la combustión, y los roles físicos y ecológicos de la vegetación como conductores complejos del comportamiento y sus resultados, podría ampliar los descubrimientos dentro de la ciencia del fuego y su ecología.
effects as well as contrasting the ecological outcomes in burned-vs-unburned areas (Keeley 2009). Within the burned area of one large fire, there is much heterogeneity in the fire environment resulting in diverse fire intensities, plant responses, and long-term ecosystem effects (Owen et al. 2017; Kolden et al. 2012). Researchers working in mixed-severity fires are questioning this simplified view of fire and fire effects, recognizing that structural and biological heterogeneity is the defining legacy of burns (Duff et al. 2017, Castro Rego et al. 2021, Kane et al. 2015).

Because vegetation is often seen as influencing fire behavior primarily through its consumable mass, i.e. fuel, it detracts from the complete fire-vegetation-atmosphere feedbacks. Here, vegetation structure varies in three dimensions, which influences air flow, fire behavior, and changes at both short- and long-term time scales (Banerjee 2020). Vegetation and fire are continually interacting with each other and responding to many environmental factors within a given fire, while vegetation response and change among fires contribute to ecological function (Clarke and Lawes 2013, Glitzenstein et al. 2003). Attention has shifted from evolutionary adaptations to surviving fire (Gill 1975) to focused work on functional traits such as flammability (Stevens et al. 2020). Vegetation's role in fire science is only partially captured by the term fuels because the term fuels does not account for vegetation's trajectory as it responds to climate, the physical environment, prior fire, and other disturbances. As the vegetation progresses along this trajectory, it shapes the environment for the next fire.

The overemphasis on vegetation as consumed fuel and fire effects on vegetation only as a reaction to combustion can be characterized as “post-fire ecology.” Here, pre-fire weather conditions, vegetation variations, and frequently the fire itself are often not measured or accounted for. As such, the full extent of fire-vegetation-atmosphere feedbacks is currently poorly conceived. Our objective was to create a conceptual framework (Fig. 1) illustrating how vegetation not only embodies the legacy of previous fires but creates the physical environment that drives fire behavior beyond acting as a fuel source. We review vegetation's structural characteristics that influence the local microclimate and dynamics of fire, and how those characteristics are themselves influenced by ecosystem and atmospheric processes. Although we recognize other factors, including ambient weather, soil, and topography, are critical contributors to vegetation conditions and the fire environment, we focus on the fire-vegetation feedbacks and their interactions with the microclimate.

**Ecology of Fuels**

The concept of the “Ecology of Fuels," or using vegetation as the link between fire and ecological processes, was presented over a decade ago by Mitchell et al. (2009). The term “ecology" is used to represent the dynamism of the
system in contrast to the often-static term “fuels.” Here, vegetation is static combustible materials and biological organisms that change in response to environmental conditions, phenology, and complex life cycles. Plant communities create dynamic moisture and mass characteristics, as well as spacing and distribution of vegetative components, including live and dead plant material and organic soil formation (Carpenter et al. 2021, Hiers et al. 2007, Kauf et al. 2018). These determine if or when vegetation hinders or contributes to fire activity. Fuels are thus as spatially heterogeneous and dynamic as the vegetation. Fuels can even change during a fire, but the ecology defines the wide range of vegetation characteristics between fires. Utilizing this concept, fuels are a momentary state at which the vegetation comprising the ecological system can burn.

The Ecology of Fuels concept also recognizes the importance of fire-vegetation feedbacks that determine ecosystem trajectories and ultimately future fire behavior. While the regular occurrence of fires can enhance long-term ecosystem balances, such as supporting biodiversity hotspots, the absence of fire or lengthening fire return intervals can cause ecological instability (Beckage and Ellingwood 2008; Clarke and Lawes 2013) and modify how vegetation influences a future fire—the efficiency with which it serves as fuel, retains moisture, or modifies winds surrounding a fire.

Effects of vegetation structure on fire

Fuels, defined as a combustion source and a positive impact on fire intensity and spread, are typically characterized into types (Ottmar et al. 2007) or models (Anderson 1982; Scott and Burgan 2005). The development of these fuel models is tied to the legacy of early semi-empirical fire-spread models such as those developed by Rothermel (1972). These fire spread models simplified complex fire-atmosphere dynamics into empirical equations, driven by the need for computational efficiency. As such, fuels were simplified into fuel models that were tied to a vegetation's combustion and flammability characteristics. However, current advancements in modeling coupled fire-atmosphere dynamics (Hoffman et al. 2018) require a more detailed representation of three-dimensional vegetation structure that more closely approximates ecological reality.

These aforementioned fuel models provide details on stand- to landscape-level estimates of mass or ‘loading’ of fuel types, such as trees, shrubs, and grasses as well as detritus characterized by their time-lag of drying potential (Gisborne 1936; Keane and Dickinson 2007). Furthermore, these fuel models categorize vegetation into broad groups that coarsely represent some canopy structural components (canopy base height, etc.), but they are assumed to be homogeneous (averaged) across a species, stand, or ecosystem type. As such, they do not account for complex three-dimensional variation in vegetation structure, defined here as aboveground vertical and horizontal distribution of live and dead plants and plant material, that defines the dynamic physiognomy of an ecosystem. This structure continuously interacts with ecosystem processes and disturbances. During a fire, each structural component and arrangement of components can represent the resistance to ignition and potential energy of combustion, and the heat exposure of surrounding vegetation, through fluid drag and convective cooling (Banerjee et al. 2020; Linn et al. 2002). The structure determines how parts of biological organisms within a given fire heat up, cool down, lose moisture, combust, or obstruct or redirect winds and fire movement, including spotting and fireline interactions (Hoffman et al. 2018).

Structure also influences vegetation moisture content before and during a fire event. Canopy morphology or structure determines the shading of under-canopy vegetation and shielding from the winds that contribute to drying. An ecosystem's water balance is influenced by vegetation structure, by either storing or dissipating water in plant material or its immediate environment. In closed-canopy systems, such as moist tropical forests, moisture retention and high productivity are conducive to low combustion potential (Cochrane 2009). In more open canopied ecosystems, diurnal solar radiation penetrates through canopy gaps and between each tree's leaves and branches at different times of the day as the sun moves overhead (Kreye et al. 2018). Subcanopy vegetation can quickly lose moisture content from the sun but gain moisture with nocturnal dew accumulation (Bigelow and North 2012). These spatial and diurnal changes in moisture conditions determine how well any given low-intensity surface fire ignites and spreads (Kreye et al. 2020).

Vegetation dynamics between fires that influence the next fire

While the long-term landscape legacy of fire dictates the fire regime and associated ecosystem trends, the shorter-term localized legacy of fire determines the fine-scale compositional and structural variability in a given ecosystem that influences the behavior and effects of the next fire. Between fires, vegetation is constantly changing as a result of dynamic drivers, such as succession, responses to climate, and legacy effects of previous fires (Fig. 1). At any given moment, vegetation is either growing, dying, decomposing, or actively transitioning between these processes. Transition rates vary with their characteristics.
that avail the vegetation to a combustible state, their influence on the fire environment, and resulting fire effects. Including interactions with weather, a vegetation’s state is never identical for each fire, and as such defines the heterogeneity between fires and within a fire regime. Vegetation dynamics between fires are mainly associated with how a particular ecosystem produces and processes vegetative material, including plant productivity, mortality, phenology, and decomposition. The importance of which vegetative components influence fire is dependent on the ecosystem type, regional climate, ignition properties, local weather, and microclimate (Duff et al. 2017).

Phenology is critical to understanding vegetation effects on fire. For example, the status of leaf senescence of deciduous trees has a significant impact on the ecosystem’s physiognomy and microclimate. This structural change creates a more permeable surface from the atmosphere that increases both canopy windflow and solar transmittance. In fully deciduous forests, this opening of the canopy during leaf-off can be profound (Hutchison and Matt 1977). This phenomenon can also be found in frequently burned pinelands (Fig. 2), where the deciduous component can dominate the understory and midstory (Addington et al. 2015). Here, leaf senescence and abscission create a fuelbed and wind environment conducive to surface fire ignition and spread. In the southeastern USA, peak fire intensity and spread rates often occur when ambient air temperatures and forest floor insulation rapidly increase in the late winter, just prior to leaf emergence. This phenomenon, known locally as the “March bump (Fig. 2a),” is the result of less atmospheric drag and drier available surface fuels (including dead vegetative material) than what would be found with shorter day lengths or after canopies leaf-out (Fig. 2b).

For evergreen trees, the influence of phenology governed leaf litter production is different, as the aerodynamics of the canopy does not undergo such a steep structural change, resulting in less dramatic changes to wind flow and moisture content. Instead of the “March bump,” the “Spring dip” describes the accumulation of combustible carbohydrates just before leaf-out, resulting in an effectively lower leaf moisture level in pines (Jolly et al. 2014).

---

**Fig. 2** Phenological influences on vegetation structure and moisture characteristics can influence microclimate, winds and fluid drag during a low-intensity surface fire. Pictures are from a frequently burned woodland at the Hitchiti Experimental Forest in the Piedmont region of Georgia, USA, with an overstory of loblolly pine (*Pinus taeda*) and understory of deciduous hardwoods (*Quercus, Acer, Liquidambar* spp.) during leaf-off (a) and leaf-on (b). Leaf-off (a) illustrates less obstruction to fluid flow (less drag causing more wind entrainment and aeration), lower vegetation moisture (more solar penetration and heating), and lower live:dead fuels (more available dead fuels), than leaf-on (b). All of these can increase fire intensity and spread in a, even though surface vegetative biomass may be higher in b.
and when combined results in a more flammable state during canopy fires (Thomas et al. 2014).

Dead vegetative material, particularly leaf litter is an important driver of wildland fires. Accumulation of leaf litter (i.e., “litter” here) on the forest floor is based on the previous fire's consumption patterns affecting residual litter, as well as post-fire ecosystem processes that drive forest canopy dynamics. Spatially, litter mass and structure are variable and correlated with overstory stem locations, but this relationship can be confounded by wind as litter is also blown around and collected by shrubs, other trees, or downhill (Orndorff and Lang 1981). Furthermore, the structural characteristics and moisture of leaf litter are dynamic through time, which influence their flammability (Varner et al. 2015). Regional climate patterns have long-term impacts on tree productivity and phenology, while seasonal and daily precipitation or snow is important for changes in litter moisture content and compaction. The mass of litter changes with the addition of new litter through leaf senescence and litterfall. The decomposition processes throughout the year reduce the mass, but at a variable rate across ecosystems (Olson 1963). The bulk density (mass per unit volume) of the litter is also variable because of these same processes. Bulk density can decrease with the addition of fresh litterfall, creating “fluffy” aerated fuels, then increase as this litter decomposes or is physically compressed by precipitation, snow, or animal traffic (Kauf et al. 2018). Moisture dynamics of litter can also be affected by the interception of precipitation (wetting) and solar radiation (drying) through gaps in overstory trees and shrubs (Kreye et al. 2018; Pickering et al. 2021), as well as physical positioning of leaf litter as it falls on and intermixes with understory herbaceous and woody plants. For example, perched pine needles draped over grasses lose moisture faster than litter deposited on the ground (Nelson and Hiers 2008). Coarse woody debris (e.g., snags, downed trees, and branches) can be an important driver of fire behavior; its availability for combustion and intermixing with other vegetation (leaf litter, grasses) is dependent on regional climate and weather patterns that drive its temporal moisture content and decomposition. For instance, in western US dry conifer forests, coarse woody debris is often an available fuel source because of the consistently low moisture content and slow decomposition rates compared to more temperate-subtropical systems of the southeastern USA, where dead vegetative material retains moisture longer and decomposes quicker (Harmon et al. 1986; Van Lear 1996).

Vegetation productivity also drives leaf litter, and other organic inputs to the detrital pool. Organic soil layer (or “duff”) formation is variable within and across ecosystems and dependent on climate, biogeochemical cycles, and soil environment, and more locally by plant composition, morphology, and phenology (Olson 1963). Duff is defined as the Oa and Oe soil horizon, which is the partially decomposed organic matter that is neither identifiable detritus, nor mineral soil, and is driven by leaf litter quality (Olson 1963). Duff, characteristically nestled around tree boles, creates an environment favorable to the ingrowth of fine tree roots and when dry enough, promotes high-intensity smoldering fires (Varner III et al. 2005). Combustion of the duff, even in surface fires can cause significant fine-root death and mortality of large overstory trees (Miyanishi 2001). Although, this is dependent on the degree of root colonization in the duff layer, which varies across ecosystems (Miyanishi 2001, O’Brien et al. 2010). Frequent fire, however, consumes the litter layer before significant duff forms, maintaining resilience in many fire-dependent ecosystems (Hood 2010).

The groundcover plant community is an important component of the physiognomy of many frequently-burned ecosystems. Between fires, the overstory dictates the above- and below-ground resources required by the understory (Palik et al. 1997; Pecot et al. 2007) and drives competitive and facilitative dynamics driven by fire (Hiers et al. 2007; Loudermilk et al. 2016). This includes the balance of an ideal light, soil, and moisture environment for plant production and regeneration. Fires restart the competitive process in the understory community, often creating a diverse plant community (Loudermilk et al. 2019; Glitzenstein et al. 2003). The variation in groundcover community and interaction with leaf and woody debris create distinct fine-scale vegetation structure characteristics that interact to drive heterogeneity in fire spread and consumption (Loudermilk et al. 2012; Hiers et al. 2021). Non-native invasive grass understories can also influence fire spread, driving novel vegetation recovery trajectories post-fire (Franklin et al. 2006; Strand et al. 2019).

**Structure of space**

It is important to note that the absence of vegetation in three-dimensional space is of equal importance as its presence. The forest canopy can be viewed as a porous medium separating the atmosphere and sub-canopy environment (Bohrer et al. 2009). Shifts in canopy composition and structure will alter the permeability of the canopy layer and thus change the light, temperature, moisture, and airflow dynamics of the sub-canopy environment (Banerjee 2020; Banerjee et al. 2020). For instance, an increase in the deciduous component of the canopy will introduce a seasonal variability to the canopy’s permeability, creating local variations in a site's microclimate. During a winter burn, when leaves are off, there is less aerodynamic drag through the canopy and less optical obstruction from the canopy than during leaf-on periods. This allows for easier penetration of
wind and solar radiation through the canopy. First, this causes higher momentum air to be entrained into the flaming front. With reduced canopy obstruction, thermal radiation disperses more broadly, which can preheat, dry, and contribute to the ignition of nearby vegetation. On the other hand, the combination of more dispersed (less concentrated) radiation and increased wind entrainment during leaf-off conditions can result in increased convective cooling. This can inhibit fire spread in flanking or backing fire scenarios, yet may cause increased fire intensity when resulting flanking firelines converge, all of which can occur at multiple spatial scales (Linn et al. 2005; Parsons et al. 2017).

Understanding the structure of space is critical because counterintuitive effects on fire behavior can occur (Banerjee 2020, Banerjee et al. 2020), whether it be fire-enhancements from vegetation removal or fire-dampening effects from vegetation growth or redistribution. Vegetation removal, such as forest thinning, mastication, or herbicide treatments, ideally followed by prescribed fire, is used to reduce available fuels, enhance forest resilience to fire, and kickstart restoration (Agee and Skinner 2005; Barros et al. 2019; Barnett et al. 2016). If removal is large and complete enough, it can slow or even stop fire spread in the short term. However, the efficacy of vegetation removal is dependent on the pace, scale, and arrangement patterns of these ‘fuel treatments,’ timing of the next fire, ecosystem response, and moisture conditions during a given fire (Schmidt et al. 2008; Loudermilk et al. 2014; Barnett et al. 2016). Furthermore, there are instances when removing small to moderate portions of vegetation can do the opposite of its intention; opening the canopy and midstory space can increase the penetration of solar radiation and entrain more winds, including heavy wind gusts. Both can promote moisture loss within and beneath the canopy, including drying of groundcover plants and the litter layer, creating a more favorable combustion environment for fire ignition and spread (Banerjee 2020; Banerjee et al. 2020; Russell et al. 2018; Marshall et al. 2020; Matthews et al. 2012).

On the other hand, vegetative ingrowth or changes to an alternative stable ecosystem state can dampen the potential for fire due to increased moisture retention and changes to species composition which impede fire spread and intensity (Kane et al. 2008, Pickering et al. 2021). Without fire, canopies can increase cover fraction, which decreases solar penetration, increases moisture retention, and reduces surface winds and entrainment, making it more difficult to sustain low-intensity fire in marginal weather conditions. In the end, vegetation removal becomes a balancing act of reducing available fuels versus creating an ideal microclimate, and understanding complex counteracting effects (Graham et al. 1999, Banerjee 2020, Banerjee et al. 2020, Marshall et al. 2020, Kalies et al. 2016). These tradeoffs of removing vegetation can be moot in some instances, where extreme fire weather (high temperatures, high winds, low relative humidity) coupled with extensive drought (little to no precipitation causing tree stress or death and excessively low fuel moisture) are conducive to high fire intensity and spread. Here, fuel treatment efforts or changes in ecosystem state could have less impact on fire behavior compared to less extreme conditions (Collins et al. 2019).

Implications and conclusions
Recognizing the importance of and making use of these vegetation-fire-atmosphere feedbacks can advance wildland fire science, support National prescribed fire initiatives, increase the pace and scale of vegetation manipulation to support wildfire suppression and human safety efforts, and enhance ecosystem resilience (Hiers et al. 2020; North et al. 2015). A focus on vegetation beyond just fuels incorporates the combustion and flammability portion, the physical influence on fire behavior, and the ecosystem dynamics and processes that occur between fires and within a fire regime (Fig. 1). The recognition that these components cannot be investigated in isolation is what we are proposing as critical for breakthroughs in our understanding of not just current fire behavior, but for projecting future fire behavior and effects. Understanding that vegetation is a combustion source, has ecological properties, and acts as a structural influence on microclimate and fluid drag (Fig. 1) suggests that long-term fire management is more about vegetation and ecosystem management than fuels management, yet encompasses both. This is particularly vital given that changing vegetation structure through management can alter fire spread and intensity positively or negatively (Fig. 2). Many fire practitioners, including prescribed fire managers, and those that monitor fire behavior during wildfires, intuitively understand these concepts. This is especially relevant to those in prescribed fire programs where finer-scale processes matter (Hiers et al. 2020). Here, practitioners can actively moderate wind entrainment by the canopy’s effect on fluid drag, monitor diurnal moisture changes, and control fire-wind dynamics by altering ignition patterns.

Fire has been a functioning process in our terrestrial ecosystems for millennia, where its role in ecology is as dynamic and cyclic as any other natural process (Archibald et al. 2018). Linking fire with ecological and atmospheric processes provides the opportunity to focus on mechanistic fire effects research, which captures the heterogeneity driving fire-ecosystem dynamics important for novel within-fire and multi-fire interactions. Furthermore, while there has been considerable advancement
in fluid dynamics-based models of fire behavior that consider the three-dimensional structure of vegetation (Hoffman et al. 2018), these models lack any ties to the ecological dynamics that create the burning vegetation or how fire energy transfer will influence post-fire vegetation development. The recognition that vegetation as more than just fuels is imperative for advancing the field of fire ecology because the term “fuels” is limiting and counterintuitive. Furthermore, current legacy fuel models oversimplify forest structural attributes and limit the role of vegetation heterogeneity, including dynamic and interactive live, dead, and decomposing material in driving complex fire behavior, especially in low to moderate intensity fires. Assessing these feedbacks across scales (Fig. 1) considers the finer details of vegetation and fire processes that typically occur within a fire and have additive effects that feedback into the coarser scale processes and functions within the system. Shifting the fuels paradigm to integrate the combustion, physical, and ecological roles of vegetation as complex drivers of fire behavior and outcomes will enhance discovery in wildland fire science.

Acknowledgments
We acknowledge the endless conversations with managers and researchers, particularly Ben Hornsby, Brett Williams, James Furman, and the late scientist, Bob Mitchell, in the field and out. We acknowledge the support by the USDA Forest Service Southern Research Station and USDA Forest Service Northern Research Station. We thank Leslie Boby and the Southern Regional Exchange Forestry, and the graphic design skills of Jessica Shaklee. The findings and conclusions in this publication are those of the authors and should not be construed to represent any official USDA or US Government determination or policy.

Authors’ contributions
ELL, JJO’B, NSS, SLG, RRL, and JKH contributed to the ideas, perspectives, and figure design. ELL lead the writing of the manuscript. JJO’B, NSS, SLG, RRL, and JKH provided critical feedback and significant writing for the manuscript. The authors read and approved the final manuscript.

Authors’ information
ELL, JJO’B, NSS, SLG, RRL, and JKH have 20+ years of experience in wildland fire science and ecology. ELL, JJO’B, NSS, and JKH have 20+ years of experience in wildland fire management, including operations of prescribed burns and fire suppression. ELL, JJO’B, NSS, and JKH have 20+ years of working with land managers to engage in linking fire science to management. SLG and RRL have 20+ experience simulating coupled fire-atmosphere dynamics, where RRL is the creator of the FIRETEC/HIGRAD model and RRL and SLG are creators of the QUIC-Fire model.

Funding
Funding was provided in part by the Department of Defense through the Strategic Environmental Research and Development Program (RC19-1119, RC20-1346, RC-2643) and the Environmental Security Technology Certification Program (RC-201303), the USDA Forest Service Research and Development branch, the Los Alamos National Laboratory LDRO program, and Tall Timbers Research Station.

Availability of data and materials
Not applicable.

Declarations
Ethics approval and consent to participate
Not applicable.

Consent for publication
Not applicable.

Competing interests
The authors declare that they have no competing interests.

Author details
1 Center for Forest Disturbance Science, Southern Research Station, USDA Forest Service, 320 Green St, Athens, GA 30602, USA. 2 Earth and Earth Sciences Division, Los Alamos National Laboratory, Los Alamos, NM 87545, USA. 3 Climate, Fire, and Carbon Cycle Sciences, Northern Research Station, USDA Forest Service, 180 Canfield St, Morgantown, WV 26505, USA. 4 Tall Timbers Research Station, 13093 Henry Beadle Drive, Tallahassee, FL 32312, USA.

Received: 1 March 2022 Accepted: 9 May 2022 Published online: 10 June 2022

References
Addington, Robert N., Benjamin O. Knapp, Geoffrey G. Sorrell, Michele L. Elmore, G. Geoff Wang, and Joan L. Walker. 2015. Factors affecting broad-leaf woody vegetation in upland pine forests managed for longleaf pine restoration. Forest Ecology and Management 354: 130–138.
Agee, J.K., and C.N. Skinner. 2005. Basic principles of forest fuel reduction treatments. Forest Ecology and Management 211 (1–2): 83–96.
Anderson, H.E. 1982. Aids to determining fuel models for estimating fire behavior Grass, shrub, timber, and slash, photographic examples, danger ratings. In USDA Forest Service general technical report INT-Intermountain Forest and Range Experiment Station, 122. Ogden: USDA Forest Service.
Archibald, Sally, Caroline E.R. Lehmann, Claire M. Belcher, William J. Bond, Ross A. Bradstock, Anne-Laure Daniau, Kyle G. Dexter, Elisabeth J. Forrestel, Michelle Greve, and Tianhua He. 2018. Biological and geophysical feedbacks with fire in the Earth system. Environmental Research Letters 13 (3): 033003.
Archibald, Sally, Caroline E.R. Lehmann, Jose L. Gómez-Dans, and Ross A. Bradstock. 2013. Defining pyromes and global syndromes of fire regimes. Proceedings of the National Academy of Sciences 110 (16): 6442–6447.
Banerjee, Tirtha. 2020. Impacts of forest thinning on wildland fire behavior. Forests 11 (9): 918.
Banerjee, Tirtha, Warren Hellman, J. Scott Goodrick, Kevin Hiers, and Rod Linn. 2020. Effects of canopy midstory management and fuel moisture on wildfire behavior. Scientific Reports 10 (1): 1–14.
Barnett, Kevin, Sean A. Parks, Carol Miller, and Helen T. Naughton. 2016. Beyond fuel treatment effectiveness: characterizing interactions between fire and treatments in the U.S. Forests 7 (10): 237.
Barros, Ana M., A.A. Agier, M.A. Day, and P. Palaiologou. 2019. Improving long-term fuel treatment effectiveness in the National Forest System through quantitative prioritization. Forest Ecology and Management 453: 514–527. https://doi.org/10.1016/j.foreco.2018.10.041.
Beckage, Brian, and Chris Ellingswood. 2008. Fire feedbacks with vegetation and alternative stable states. Complex Systems 18 (1): 159.
Bigelow, Seth W., and Malcolm P. North. 2012. Microclimate effects of fuels-reduction and group-selection silviculture: Implications for fire behavior in Sierran mixed-conifer forests. Forest Ecology and Management 264: 51–59. https://doi.org/10.1016/j.foreco.2011.09.031.
Bohner, G., Daniel G. Katul, Robert L. Walko, and Roni Avissar. 2009. Exploring the effects of microscale structural heterogeneity of forest canopies using large-eddy simulations. Boundary-layer Meteorology 132 (3): 351–382.
Bond, William J., and Jon E. Keeley. 2005. Fire as a global ‘herbivore’: the ecology and evolution of flammable ecosystems. Trends in Ecology & Evolution 20 (7): 387–394.
Bonner, Sophie R., Chad M. Hoffman, Jeffrey M. Kane, J. Morgan Varner, J. Kevin Hiers, Joseph J. O’Brien, Heather D. Rickard, Wade T. Tinkham, Rodman R. Linn, and Nicholas Skowronski. 2021. Invigorating Prescribed Fire Science Through Improved Reporting Practices. Frontiers in Forests and Global Change: 163.
Carpenter, Dana O., Melanie K. Taylor, Mac A. Callaham, Kevin J. Hiers, Louise E. Loudermilk, Joseph J. O’Brien, and Nina Wurzburger. 2021. Benefit or liability? The ectomycorrhizal association may undermine tree adaptations to fire after long-term fire exclusion. Ecosystems 24 (5): 1–16.
O’Brien, J.J., J.K. Hiers, J.M. Varner, C.M. Hoffman, M.B. Dickinson, S.T. Michaletz, E.L. Loudermilk, and B.W. Butler. 2018. Advances in mechanistic approaches to quantifying biophysical fire effects. Current Forestry Reports 4 (4): 161–177.

O’Brien, J.J., J.K. Hiers, R.J. Mitchell, J.M. Varner, and K. Mordecai. 2010. Acute physiological stress and mortality following fire in a long-unburned longleaf pine ecosystem. Fire Ecology 6 (2): 1–12.

Olson, Jerry S. 1963. Energy storage and the balance of producers and decomposers in ecological systems. Ecology 44 (2): 322–331.

Omdorff, Kenneth A. and Gerald E. Lang. 1981. Leaf litter redistribution in a West Virginia hardwood forest. The Journal of Ecology 69: 225–235.

Otto, Roger D., David V. Sandberg, Cynthia L. Riccardi, and Susan J. Pritchard. 2007. An overview of the Fuel Characteristic Classification System—Quantifying, classifying, and creating fuelbeds for resource planning. Canadian Journal of Forest Research 37 (12): 2383–2393.

Owen, Suzanne M., Carolyn H. Sieg, Andrew J. Sánchez, Peter Z. Meador, José M. Fulé, L. Scott Iniguez, Paula J. Baggett, and Fornwall, and Michael A. Battaglia. 2017. Spatial patterns of ponderosa pine regeneration in high-severity burn patches. Forest Ecology and Management 405: 134–149.

Palik, Brian J., Robert J. Mitchell, Greg Houseal, and Neil Pederson. 1997. Effects of canopy structure on resource availability and seedling responses in a longleaf pine ecosystem. Canadian Journal of Forest Research 27: 1458–1464.

Parsons, Russell A., Rodman R. Linn, Francois Pimont, Chad Hoffman, Jeremy Sauer, Judith Winterkamp, Carolyn H. Sieg, W. Matt, and Jolly. 2017. Numerical investigation of aggregated fuel spatial pattern impacts on fire behavior. Land 6 (2): 43.

Pecot, Stephen D., Robert J. Mitchell, Brian J. Palik, E Barry Moser, and J.A. Kevin Hiers. 2007. Competitive responses of seedlings and understory plants in longleaf pine woodlands: Separating canopy influences above and below ground. Canadian Journal of Forest Research 37 (3): 634–648.

Pickering, Bianca J., Thomas J. Duff, Craig Baillie, and Jane G. Cawson. 2021. Darker, cooler, wetter: forest understories influence surface fuel moisture. Agricultural and Forest Meteorology 300: 108311.

Rego, Castro, Penelope Morgan Francisco, Paulo Fernandes, and Chad Hoffman. 2021. Fuel and Fire Behavior Description. In Fire Science: From Chemistry to Landscape Management, ed. Francisco Castro Rego, Penelope Morgan, Paulo Fernandes, and Chad Hoffman, 101–114. Cham: Springer International Publishing.

Rothermel, Richard C. 1972. A mathematical model for predicting fire spread in wildland fuels. Intermountain Forest and Range Experiment Station. Ogden: USDA Forest Service.

Russell, Eric S., Heeping Liu, Harold Thistle, Brian Strom, Mike Greer, and Brian Lamb. 2018. Effects of thinning a forest stand on sub-canopy turbulence. Agricultural and Forest Meteorology 248: 295–305.

Schmidt, David A., Carl N. Skinner, and Alan H. Taylor. 2008. The influence of fuels treatment and landscape arrangement on simulated fire behavior, Southern Cascade range, California. Forest Ecology and Management 255 (8-9): 5170–5184. https://doi.org/10.1016/j.foreco.2008.01.023.

Scott, Joe H., and Robert E. Burgan. 2005. Standard fire behavior fuel models: a comprehensive set for use with Rothermel's surface fire spread model. Fort Collins: USDA Forest Service, Rocky Mountain Research Station.

Smith, Alistar M.S., Aaron M. Sparks, Crystal A. Kolden, John T. Abatzoglou, Alan F. Talhelm, Daniel M. Johnson, Luigi Boschetti, James A. Lutz, Kent G. Apostol, Kara M. Yedinak, Wade T. Tinkham, and Robert J. Kremens. 2016. Towards a new paradigm in fire severity research using dose–response experiments. International Journal of Wildland Fire 25 (2): 158–166. https://doi.org/10.1071/WF15130.

Smith, Annabel L. 2018. Successional changes in trophic interactions support a mechanistic model of post-fire population dynamics. Oecologia 186 (1): 129–139.

Stevens, Jens T., Matthew M. Kling, Dylan W. Schwillik, J. Morgan Varner, and Jeffrey M. Kane. 2020. Biogeography of fire regimes in western US conifer forests: a trait-based approach. Global Ecology and Biogeography 29 (5): 944–955.

Strand, Eva K., Kevin L. Satterberg, Andrew T. Hudak, John Byrne, Azad Henareh Khaliyan, and Alistair Smith. 2019. Does burn severity affect plant community diversity and composition in mixed conifer forests of the United States Intermountain West one decade post fire? Fire Ecology 15 (1): 1–22.

Thomas, Janc, Albert Simeoni, Michael Gallagher, and Nicholas Skowronsks. 2014. An experimental study evaluating the burning dynamics of pitch pine needle beds using the FPA. Fire Safety Science 11: 1406–1419.

Van Lear, David H. 1996. Dynamics of coarse woody debris in southern forest ecosystems. In Biodiversity and coarse woody debris in southern forests. USDA Forest Service General Technical Report SE–94, ed. James W. McMinn and D.A. Crossley, Jr, 10–17. Asheville: USDA Forest Service.

Varner, J. Morgan, III, Doria R. Gordon, Francis E. Putz, and J Kevin Hiers. 2005. Restoring Fire to Long-Unburned (Pinus palustris) Ecosystems: Novel Fire Effects and Consequences for Long-Unburned Ecosystems. Restoration Ecology 13 (3): 536–544.

Varner, J. Morgan, Jeffrey M. Kane, Jesse K. Kreye, and Eamon Engber. 2015. The flammability of forest and woodland litter: a synthesis. Current Forestry Reports 1 (2): 91–99.

Zhang, Yao, Jocelyn M. Lavallee, Andy D. Robertson, Rebecca Even, Stephen M. Ogle, Keith Paustian, M. Francesca, and Cotrufo. 2021. Simulating measurable ecosystem carbon and nitrogen dynamics with the mechanistically defined MEMS 2.0 model. Biogeosciences 18 (10): 3147–3171.

Publisher's Note
Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.