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Dearth under earth: Understudied plant-soil-fire feedback as drivers of forest mesophication and oak regeneration failures

Eva O.L. Legge [a,b,*], Akihiro Koyama [c], Christopher W. Fernandez [b], Katherine E.A. Wood [d], Narda J. Triviño Silva [c], Lars A. Brudvig [e], Andrew L. Vander Yacht [a]

[a] Department of Sustainable Resources Management, SUNY College of Environmental Science and Forestry (SUNY ESF), 1 Forestry Drive, Syracuse, NY 13210, USA
[b] Department of Biology, Syracuse University, 107 College Place, Syracuse, NY 13210, USA
[c] Department of Forestry, Michigan State University, 480 Wilson Road, East Lansing, MI 48825, USA
[d] USDA Forest Service Pacific Southwest Research Station, 800 Buchanan Street, Albany, CA 94710, USA
[e] Department of Plant Biology and Program in Ecology, Evolution and Behavior, Michigan State University, 612 Wilson Road, East Lansing, MI 48824, USA

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A B S T R A C T

Regeneration of drought-tolerant and fire-adapted (pyrophytic) trees like oaks (*Quercus* spp.) is broadly limited by mesophication – a positive feedback where darker, wetter, and cooler microsites promoted by fire suppression favor drought-intolerant and fire-sensitive (pyrophobic) trees like maples (*Acer* spp.). Given projected increases in fire and drought, mesophication could reduce forest resilience to future stressors. Although the issue is widely recognized, corrective management has almost exclusively focused on aboveground drivers (*i.e.*, fire suppression effects on fuel and microclimatic properties). We propose a complex feedback framework involving mature and immature trees, fire, and abiotic and biotic soil properties (*i.e.*, "plant-soil-fire feedback") that may provide a more complete understanding of mesophication. Focusing on the eastern US, we: 1) review the current mechanistic understanding of mesophication, 2) identify overlooked belowground drivers (*i.e.*, plant-soil-fire feedback), 3) explore future research needs, and 4) derive forest management implications. We argue that fire suppression directly and indirectly increases soil moisture and nutrient availability and alters soil microbial communities in ways that favor pyrophobic tree species. Such trees then outcompete pyrophytic trees by further promoting such belowground conditions that reinforce their dominance and further exclude fire. We conclude that mesophication cannot be fully understood – or reversed – without considering plant-soil-fire feedback. Such perspective can inform forest management that ensures resilience by promoting drought-tolerant and pyrophytic trees like oaks.

1. Background

Present structure and composition of forests throughout the eastern United States differs substantially from pre-European settlement conditions (Hanberry et al., 2020). Homogenous closed canopies of drought-intolerant, shade-tolerant, and fire-sensitive tree species like maples (*Acer* spp.) – hereafter, pyrophobic species – are replacing forests characterized by more open canopies and the dominance of drought-tolerant, shade-intolerant, and fire-adapted tree species like oaks (*Quercus spp.*) and pines (*Pinus spp.*) – hereafter, pyrophytic species (Hanberry et al., 2018; Hanberry and Abrams, 2018). Such shifts have been driven by mesophication: a self-reinforcing process whereby fire exclusion leads to forest densification and increasingly wetter, cooler, and darker microclimates that favor correspondingly adapted (*i.e.*, pyrophobic) tree species that further promote such conditions and outcompete disturbance-adapted and fire-reinforcing pyrophytic tree species (Nowacki and Abrams, 2008). Among other important factors like ungulate browsing (Parker et al., 2020) and invasive species (Ward et al., 2018), mesophication explains widespread declines in the very disturbance-dependent biodiversity that forecasted climatic change is predicted to favor (Iverson et al., 2008; Vose and Elliott, 2016). Evidence of pyrophobic tree expansion and the decline of pyrophytic forest

* Corresponding author at: Department of Biology, Syracuse University, 107 College Place, Syracuse, NY 13210, USA.
E-mail addresses: elegge@syr.edu (E.O.L. Legge), koyamaak@msu.edu (A. Koyama), cferna10@syr.edu (C.W. Fernandez), keawood93@gmail.com (K.E.A. Wood), trivinon@msu.edu (N.J. Triviño Silva), brudvig@msu.edu (L.A. Brudvig), avandery@esf.edu (A.L. Vander Yacht).

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ecosystems exists around the world (Choung et al., 2020; Drobyshev et al., 2021; Spînu et al., 2020), so globally ensuring future forest resilience will likely require implementing management that effectively reverses mesophication.

However, the success of such management has been mixed (Arthur et al., 2012; Bowles et al., 2007; Carter et al., 2015; Hutchinson et al., 2024; Oakman et al., 2019; Scharenbroch et al., 2012; Vander Yacht et al., 2019; Waldrop et al., 2016) – which may be the result of an incomplete mechanistic understanding of mesophication. Aboveground drivers of mesophication have been thoroughly documented (Alexander et al., 2021; Alexander and Arthur, 2014, 2010; Babl et al., 2020; Kreye et al., 2018a, 2018b; McDaniel et al., 2021) and involve shifts towards wetter, cooler, and darker forest microclimates via the more robust canopies (Babl et al., 2020; Kreye et al., 2018a) and reduced leaf litter flammability (Alexander et al., 2021; Kreye et al., 2018b; McDaniel et al., 2021) of pyrophobic relative to pyrophytic tree species. However, deviations from long-term patterns of fire frequency, intensity, severity, seasonality, and spatial extent over many repeated fires through time have likely affected abiotic and biotic soil properties – including alterations to hydrology, nutrients, and microbial communities (Agbeshie et al., 2022) – and such effects may also be mechanistic drivers of mesophication (Beals et al., 2022). Fire can alter the abiotic and biotic properties of soils to enhance pyrophytic tree success (Beals et al., 2022; Hopkins et al., 2023). Moreover, fire can induce changes in mature plant composition that further alters soil properties, future fire behavior and fire effects, and immature plant performance via plant-soil-fire feedback – a concept we join others in promoting (Hewitt et al., 2023; Kardol et al., 2023; Senior et al., 2018) as an extension of plant-soil feedback (Bever et al., 1997). However, plant-soil-fire feedback has not yet been explicitly named – and only rarely even hinted at (Alexander et al., 2021) – as a driver of mesophication.

To address this dearth under earth, we begin by reviewing the history, current mechanistic understanding, and future implications of mesophication and then conceptually explain evidence for overlooked belowground drivers. Such insights build towards our description of the potential interactions among these above- and belowground drivers, subsequent plant response, and fire (*i.e.*, plant-soil-fire feedback) and the role such interactions may play in driving mesophication. We conclude by exploring research needs and integrative management approaches that may better address mesophication by explicitly considering plant-soil-fire feedback. Our overall goal is to provide a more complete understanding of mesophication to facilitate development of management strategies that can address the threat it poses to forest resilience across the globe.

1.1. *Mesophication's history, modern effects, and future implications*

Fire has influenced the structure, composition, distribution, and function of terrestrial plant communities for nearly 500 million years (Pausas and Keeley, 2009). As recent as two hundred years ago, the forests of the eastern United States existed as a complex mosaic of forested community types that ranged from open savannas to closed-canopy forests (Nowacki and Abrams, 2008). Interior dry-mesic oak forests of the northeastern and north-central United States included at least five distinct successional classes that spanned grassland prairies, open savannas and closed forests dominated by oaks, and mixed mesic forests dominated by maples, yellow poplar (*Liriodendron tulipifera*), and American beech (*Fagus grandifolia*; Slaughter et al., 2020). Much of this diversity within forests was created and maintained by agents of disturbance, including wind, insects, disease, gap dynamics, indigenous land-clearing, and lightning- and anthropogenic- ignited fire (Abrams, 1992; Guyette et al., 2012). Declines and displacement of indigenous populations, associated cultural practices, and mid-20th century fire suppression policies have largely removed fire's ecological influence from the current landscapes of the eastern United States (Pyne, 2015).

Fire's prolonged absence has altered the structure and composition of forests in eastern North America (hereafter, "eastern forests") and beyond, leading to an overall decline in tree species diversity (Frelich et al., 2021; Rudolph et al., 2024; Vander Yacht et al., 2024), the loss of more open woodland and savanna forest structure (Nuzzo, 1986), and declines in disturbance-dependent wildlife (Cox et al., 2016; McShea et al., 2007; Rodewald and Abrams, 2002; Vander Yacht et al., 2016). Ninety-six percent of birds and mammals in hardwood ecosystems are known to consume acorns (McShea et al., 2007); as such, oak decline will undoubtedly and negatively affect important wildlife species (McDonald and Fuller, 2005). For example, white-footed mice (*Peromyscus leucopus*) density can increase 15-fold following high acorn production – reducing invasive spongy moth populations (Jones et al., 1998). Further, the complex structure of oak savannas provide high quality habitat for declining eastern whip-poor-wills (*Antrostomus vociferus;* Larkin et al., 2025), red-headed woodpeckers (*Melanerpes erythrocephalus*), eastern kingbirds (*Tyrannus tyrannus*), prairie warblers (*Setophaga discolor*), and many other regionally and continentally declining bird species (Barrioz et al., 2013; Brawn, 2006; Davis et al., 2000; Rodewald and Abrams, 2002; Vander Yacht et al., 2016). The critically endangered rusty patch bumblebee (*Bombus affinis*) is also more likely occur in oak- and pine- dominated landscapes than mesophied forests (Hepner et al., 2024), and oak savanna restoration can increase native bee abundance and species richness (Lettow et al., 2018). Finally, mesophication can dramatically reduce the groundcover and species richness of herbaceous layers (Benz et al., 2025; Stephen et al., 2024; Vander Yacht et al., 2020).

The United States Forest Service's Forest Inventory and Analysis (FIA) database shows that the current canopy composition of northeastern forests (trees >50 cm in diameter at 1.4 m in height) is often equally distributed across pyrophobic and pyrophytic tree species according to percent basal area, but smaller size classes are often exclusively dominated by pyrophobic trees (Vander Yacht et al., 2024). Such evidence indicates an imminent and concerning shift in the structure and composition of eastern forests over the coming decades (Vose and Elliott, 2016) that will have significant economic implications: not only do many harvestable game species that fund conservation prefer oak forests, but oaks are also a high-value timber resource (Dey, 2014; McShea and Healy, 2002) – especially on private land which compose the majority of eastern oak forests (McShea et al., 2007). Further, oaks and pines have been ranked as the two most valuable genera in the contiguous US, ranked at > $22B and > $25B respectively when one accounts for ecosystem services along with timber value (Cavender-Bares et al., 2022).

Declines in structural and functional diversity, and reduced representation of tree species projected to thrive in future regional climates, may render forests less resilient to climate change (Millar et al., 2007) – especially given the increasing risk of large wildfires in the eastern US (Donovan et al., 2023; Ivey et al., 2024; Kerr et al., 2018). Pine-oak vegetation communities are global in extent and increasingly recognized as a nature-based solution to climate change due to high resilience to severe fire, drought, and other disturbances (Singh and Zobel, 2025). However, mesophication is slowly eliminating these species from eastern US forests (Vander Yacht et al., 2024) which are hypothesized to eventually reach a "tipping point" where the restoration of pyrophytic tree populations to pre-colonial states becomes extremely difficult due to the lack of seed sources and shifts towards above- and belowground conditions that favor pyrophobic tree species (Abrams, 2005; Nowacki and Abrams, 2008). This creates urgency for action, but limited management success (Arthur et al., 2012; Bowles et al., 2007; Carter et al., 2015; Hutchinson et al., 2024; Oakman et al., 2019; Scharenbroch et al., 2012; Vander Yacht et al., 2019; Waldrop et al., 2016) underscores the importance of improving our understanding of mesophication's underlying mechanisms (Alexander et al., 2021).

1.2. Current mechanistic understanding of mesophication

Aboveground changes in forest microclimates and fuel characteristics that result from fire suppression and exclusion undoubtedly drive mesophication (Fig. 1A-B; Table 1; Nowacki and Abrams, 2008). Fire historically altered microclimates (Fig. 1A; Table 1) by maintaining open-canopy savanna and woodland structures that allowed sunlight to reach ground layers and created warmer and drier conditions (Kreye et al., 2018a). Even closed pyrophytic canopies (*i.e.*, certain pine-oak forests) allow more light infiltration than closed pyrophobic canopies (*i.e.*, maple-beech forests) due to differences in tree architecture and leaf surface area between the tree species groups (Vander Yacht et al., 2022). Without fire, forests slowly densify (Hanberry et al., 2020) which creates moister, cooler, and darker understories that promote the growth of pyrophobic seedlings adapted to such conditions (Fig. 1A; Babl et al., 2020) and that further alter understory environments (Woodbridge et al., 2022).

Fire suppression also alters fire-fuel feedback – the cyclical relationship among vegetation as fuel, fuel effects on fire behavior, and fire behavior effects on vegetation (Alexander et al., 2021; Kreye et al., 2018b; McDaniel et al., 2021) – to drive mesophication (Fig. 1B; Nowacki and Abrams, 2008). Pyrophytic oak leaves are decay-resistant and lobed – which makes them tent, bend, and curl upon drying – and pine litter contains volatile oils (Platt et al., 2016). In combination, these litter characteristics create a less dense, more aerated, and more flammable fuel-bed (Kreye et al., 2013; Varner et al., 2015). In contrast, pyrophobic sugar maple (*Acer saccharum*), American beech (*Fagus grandifolia*), and black cherry (*Prunus serotina*) leaves dampen flammability through greater moisture retainment, decomposition rates, and fuel-bed bulk densities (Kreye et al., 2018b, 2018a, 2013; McDaniel et al., 2021). Pyrophobic trees further reinforce moist understory conditions through higher water stemflow (Alexander et al., 2021; Alexander and Arthur, 2010; Babl et al., 2020) and create microclimates that foster greater rates of decay for woody debris (Graham and McCarthy, 2006; Kreye et al., 2013; Onega and Eickmeier, 1991). Forest densification and understory woody encroachment can also eliminate robust herbaceous layers (Bassett et al., 2020) that perch leaf litter to facilitate drying and provide a continuous, well-ventilated, and easily-ignited source of fine fuels (Maynard and Brewer, 2013; Mitchell et al., 2009). Such shifts in fuel characteristics suppresses fire activity, promotes pyrophobic trees, and propels mesophication (Alexander and Arthur, 2014; Babl et al., 2020; Vander Yacht et al., 2018).

2. Towards a deeper explanation: overlooked belowground drivers of mesophication

Additional biotic and abiotic processes occurring below, and interacting with, the litter layer may also contribute to mesophication (Fig. 1C-F; Table 1). While belowground processes have been implied as drivers of mesophication (Alexander et al., 2021; Beals et al., 2022; Hopkins et al., 2023), historical bias towards aboveground processes has been pervasively dominant in the mesophication literature (Nowacki and Abrams, 2008). Recent advances in soil science and molecular approaches have reduced the financial and logistical barriers to studying the physical, chemical, and microbial properties of forest soils (Horton and Bruns, 2001; Kubiak et al., 2024; Nilsson et al., 2019; Piccini et al., 2024; Thomas et al., 2021) – allowing relationships among fire, tree regeneration, microbial communities, and other soil properties (Fig. 1) to be more thoroughly examined. Indeed, the contribution of belowground processes to forest ecosystem function – including interactions with fire – has been the subject of recent research (Kardol et al., 2023; Karst et al., 2023) including within the context of eastern forest mesophication (Hewitt et al., 2023).

Despite these advances, research focused on directly linking plant-

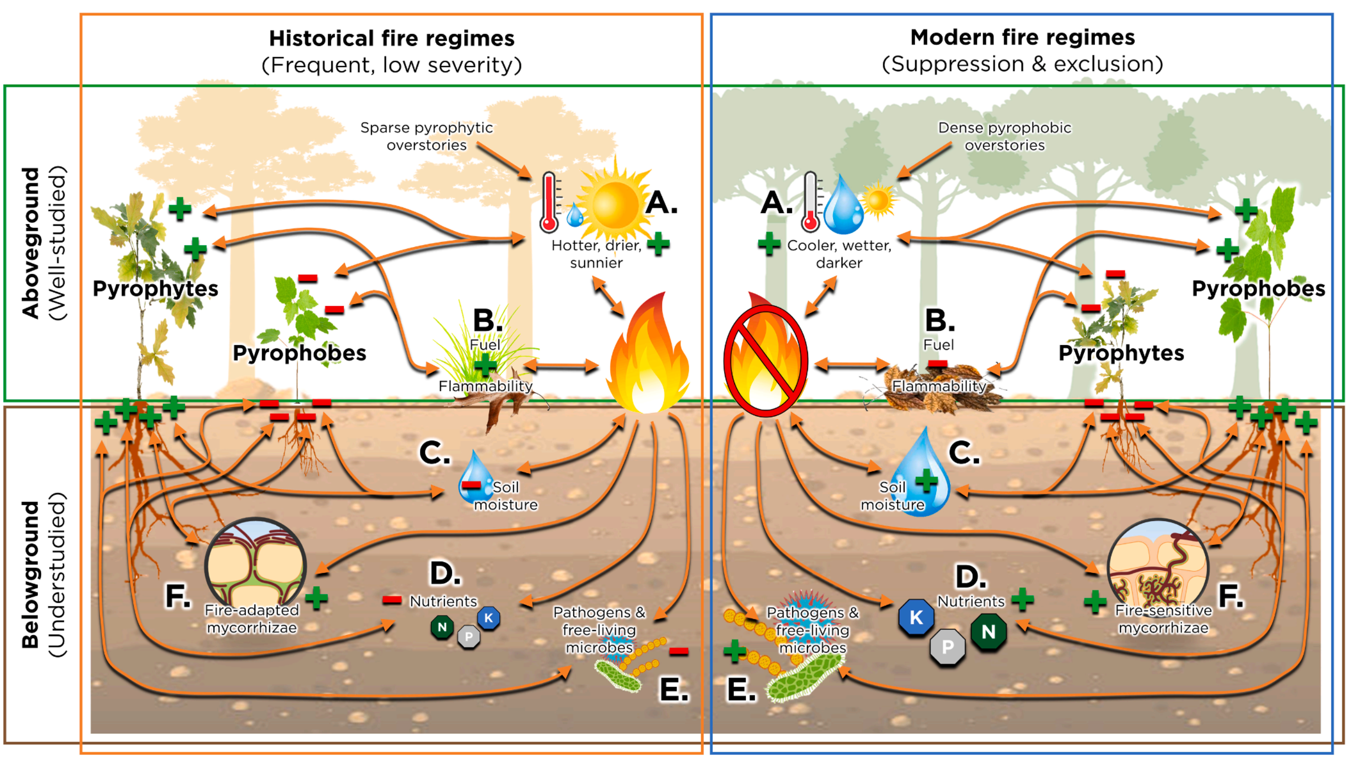

Fig. 1. Conceptual model of above- and belowground drivers of mesophication in forests, including fire effects on microclimates (A), fuel-bed flammability (B), soil moisture (C), soil nutrients (D), pathogens and free-living microbes (E), and mycorrhizal fungi (F). Left panel depicts effects of historic high-frequency, low-severity fire regimes and right panel depicts effects of fire's modern absence. Unidirectional arrows depict effects, bidirectional arrows depict feedbacks, and effects are labeled as positive (+) or negative (-) for each community property and, ultimately, the performance of pyrophytic or pyrophobic tree species. Visualizations for part F were taken from Genre et al. (2020).

Table 1
Overview of the commonly accepted (aboveground) and understudied (belowground) drivers of mesophication.

Forest strata	Factors driving mesophication	Effects of frequent, low-severity fire (historical fire regimes)	Effects of fire exclusion (modern fire regimes)	Citations[1]
Aboveground	Forest microclimates	Open canopies, reduced shade, ample air movement → warmer, dryer, and sunnier microclimates	Closed canopies, heavy shade, limited air movement → cool, moist, and dark microclimates	Nowacki and Abrams (2008); Kreye et al. (2018a); Babl et al. (2020)
	Fuel characteristics	Rough bark and decreased stemflow, curled leaves, low bulk density → drier and more flammable litter and robust herbaceous layers	Smooth bark and increased stemflow, flat leaves, high bulk density → moist and relatively inflammable litter	Kreye et al. (2013); Mitchell et al. (2009); Platt et al. (2016)
Belowground	Soil hydrology	Consumption of organic matter → increased bulk density, decreased aggregate stability, increased water infiltration rates → drier soils	Accumulation of organic matter → decreased bulk density, increased aggregate stability, and reduced water infiltration rates → moister soils	Mataix-Solera et al. (2011); DeBano et al. (1981); Alcañiz et al. (2018)
	Soil nutrients	Loss of nutrients through ash convection, volatilization, and runoff → low-nutrient soils and pyrophytic tree feedback	Accumulation of organic matter and nutrients, increased stemflow → high-nutrient soils and pyrophobic tree feedback	Neary et al. (1999); Agbeshie et al. (2022); Bodí et al. (2014); Alexander and Arthur, (2010)
	Free-living soil microbes	Reductions in N-acquiring microbial communities, and depression of decomposers, lower pathogen abundance → low nutrient availability, promotion of fire through litter accumulation, and higher pyrophytic tree survival	Increases in N-acquiring microbial communities, decomposers, and pathogens → high nutrient availability, pyrophobic tree feedback and less fuel for fire through litter decomposition	Vazquez et al. (1993); Zhou et al. (2022); Pelligrini et al. (2021); Meentemeyer et al, (2011)
	Mycorrhizal fungi	Fire promotes ectomycorrhizal associations with fire-adapted trees → pyrophytic tree dominance	Absence of fire promotes arbuscular mycorrhizal associations with fire-sensitive trees → pyrophobic tree dominance	Jo et al. (2019); Fox et al. (2022); Wurzburger et al. (2023)

[1] Note: citations for commonly accepted (aboveground) mechanisms refer to work done directly within the context of mesophication. Citations for understudied (belowground) mechanisms refer to work largely done outside the context of mesophication and/or eastern forests due to the lack of related studies.

soil-fire feedback to mesophication is virtually nonexistent. We define plant-soil-fire feedback as an extension of plant-soil feedback: the process by which plants alter the abiotic and biotic properties of the soils they grow in to influence current and subsequent plant growth (Bever et al., 1997). Plant-soil feedback is foundational to forest succession: establishing plants alter the physical, chemical, hydrological, and biological properties of soils (Ehrenfeld et al., 2005) to promote tree species better adapted to the new conditions that then amplify such changes (Eppinga et al., 2018; Kulmatiski et al., 2008) to ultimately reduce the fitness of other plants (Bever, 2003). The strength and direction of plant-soil feedback can change with forest successional stage (Kardol et al., 2013, 2006; Kulmatiski and Kardol, 2008) as canopies close, and the legacies of previous successional stages can influence later stages (Kardol et al., 2007). Since fire influences forest succession (Chapin et al., 2011), it likely influences plant-soil feedback. However, current understanding of mesophication fails to sufficiently recognize the role plant-soil feedback and its interactions with fire may play in the process. As a primary driver of forest successional trajectories, plant-soil feedback should be integrated into the mechanistic understanding of mesophication. Only then can the process be effectively reversed.

Before such integration can occur, it must be understood that fire effects on soils can be direct, indirect, and vary substantially across fire regime properties – *i.e.*, fire frequency, intensity, severity, seasonality, and spatial extent (Neary et al., 1999). Fire can affect abiotic soil properties directly via heating or indirectly via altered microclimates (Agbeshie et al., 2022; Alcañiz et al., 2018; Certini, 2005; Neary et al., 1999). Similarly, soil biota experience direct heat-induced mortality (Kipfer et al., 2010; Pingree and Kobziar, 2019; Vazquez et al., 1993) and respond indirectly to fire-induced changes in abiotic soil properties (Dove et al., 2021; Ibáñez et al., 2022; Knelman et al., 2015; Martin et al., 2022). Isolated fire events, or small fires of low intensity (*i.e.*, energy output) and/or severity (*i.e.*, removal of biomass), will generally lead to short-term and reversible shifts in soil properties (Neary et al., 1999). Conversely, repeated or expansive fires of greater intensity and/or severity can create greater and longer-lasting effects (Agbeshie et al., 2022). Fire effects on soils often dissipate with time since burn as organic layers redevelop with litter accumulation and soil texture increases in complexity (Hopkins et al., 2024; Neary et al., 1999).

Further, fire effects on soils vary with the depth of soil heating as influenced by soil moisture and organic layer thickness (Agbeshie et al., 2022; Alcañiz et al., 2018). Soil is an effective insulator, and temperatures during fires typically decrease markedly with soil depth (Neary et al., 1999; Swift Jr. et al., 1993; Trammell et al., 2004). However, the smoldering combustion of litter can transfer heat to underlying mineral soil for sustained periods (Campbell et al., 1995; Dimitrakopoulos et al., 1994; Neary et al., 2005). For example, fire in a long-unburned southeastern pine forest resulted in temperatures > 60 °C (sometimes accepted as the "lethal" temperature threshold for many soil biota if sustained for >1 min) for several hours at a soil depth of 10 cm and temperatures > 300 °C for up to 35 min at mineral soil depth (Kreye et al., 2020). Even at frequently burned sites, temperatures > 60 °C can be sustained for several minutes down to at least 5 cm (Kreye et al., 2020). As most plant-available nutrients, fine roots, and soil biota are concentrated in the top 20 cm of soil profiles (Mou et al., 1995; Yanai et al., 2008, 2006), fire-induced soil heating is likely to reach thresholds capable of altering abiotic and biotic characteristics. Nevertheless, how soil heating and its effects vary with depth and interactions with fire suppression is understudied in eastern US forests (Kreye et al., 2020).

We propose and detail four interactions between fire and belowground processes that could act as drivers of mesophication – including two abiotic properties (water and nutrients) and two biotic properties (free-living microbes and mycorrhizal fungi) of soils and associated feedback on tree regeneration (Fig. 1C-F). Such properties are readily altered by fire and underpin tree establishment, survival, and growth across the globe (Alexander et al., 2021).

2.1. *Plant-soil-fire feedback: hydrology*

In the absence of fire, plant-soil interactions may create conditions in which soil moisture accumulates, driving mesophication. Fire effects on soil bulk density, aggregate stability, and water repellency decrease soil water retention capacity, increase infiltration rates, or both to reduce the amount of water held in soils (Fig. 1C; Agbeshie et al., 2022). Therefore, fire affects soil hydrology in ways that facilitate pyrophytic species that tend to be more drought-tolerant (Fig. 2B). Conversely, fire suppression alters hydrologic soil properties to promote drought-intolerant pyrophobic species (Fig. 2A).

Although effects can be variable (Alcañiz et al., 2018), fire frequently increases soil bulk density (Granged et al., 2011; Kennard and Gholz, 2001; Phillips et al., 2000) and decreases soil porosity (Wieting et al.,

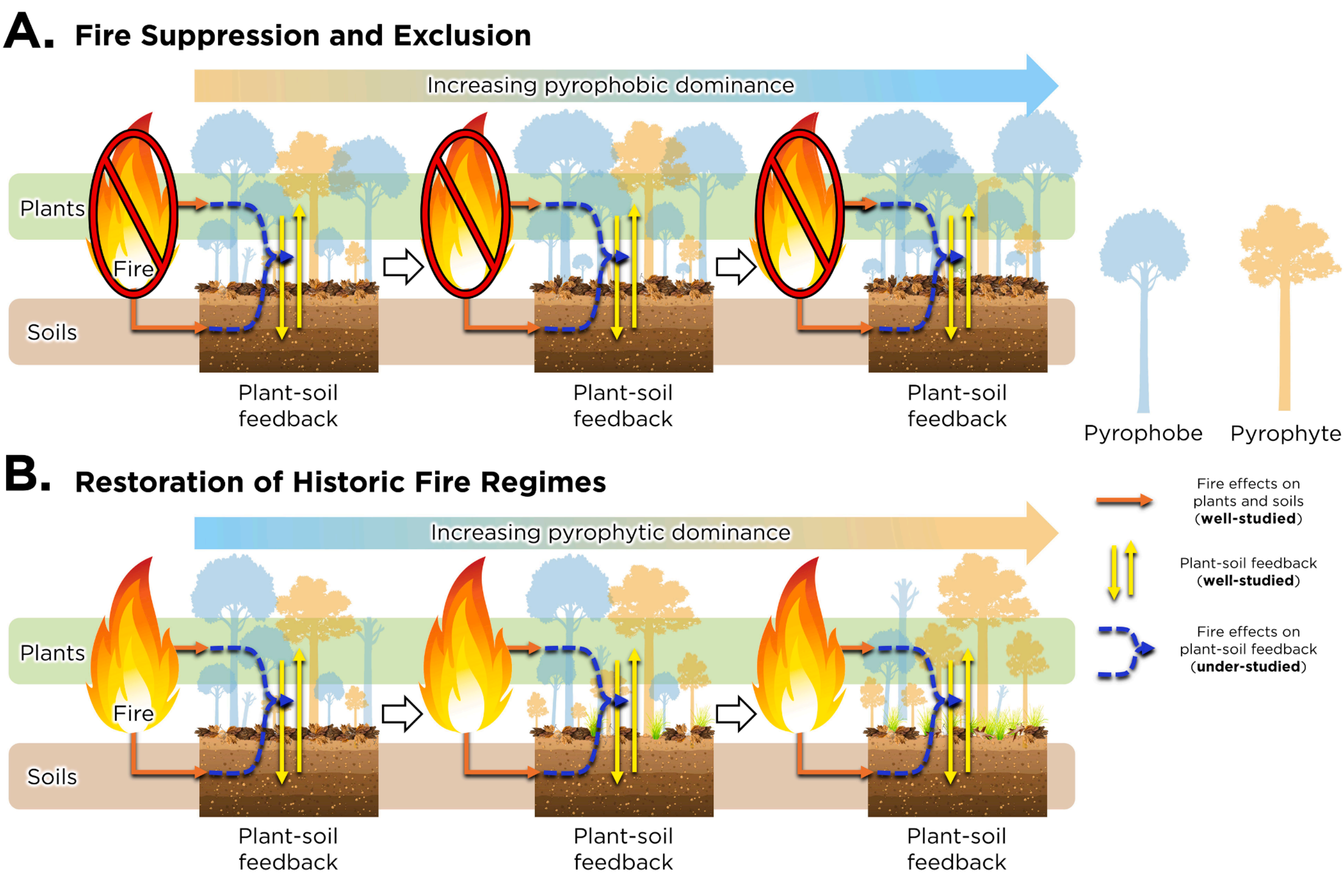

Fig. 2. Conceptual diagram depicting the well-studied effects of fire on plants and soils (orange arrows) and well-studied plant-soil feedback (yellow arrows) relative to knowledge gaps concerning fire's effects on plant-soil feedback (blue arrows) – especially in terms of how such effects change over periods of fire's absence (A) and repeated occurrence (B).

2017) to result in less space for water to occupy. Fire can destroy soil aggregates, increasing soil bulk density (Agbeshie et al., 2022), by consuming organic matter or degrading clay particles that act as cementing agents (Alcañiz et al., 2018; DeBano, 1981; Mataix-Solera et al., 2011). However, the relatively high temperature ranges necessary for clay particle degradation were unlikely during historic fire regimes of eastern forests (Heydari et al., 2017; Neary et al., 2005; Schweizer et al., 2021; Six et al., 2004) and most pyrophytic communities occur in association with sandy soils lacking clay (Corbin and Flatland, 2022; Host and Pregitzer, 1992). The latter observation also discounts the idea that moderate soil heating (30–60 ℃) may have increased aggregate stability by destroying the clay lattice structure and leading to the to the aggregation of finer particles into sand and silt (Agbeshie et al., 2022). Thus, it is more likely that fire historically reduced soil moisture by consuming organic matter – in place as a cementing agent or prior to its availability within aggradation processes. Thus, historically frequent low-intensity fire regimes of eastern forests (Guyette et al., 2012) likely reduced soil aggregates, and thus soil moisture, via organic matter consumption.

Fire can also decrease soil water by increasing water infiltration from the surface into deeper soil layers (Robichaud, 2000). The removal of litter and organic matter by fire from the surface of underlying sandy to loamy soils upon which pyrophytic oaks and pines thrive (Corbin and Flatland, 2022; Host and Pregitzer, 1992) eliminates physical barriers to water infiltration and results in greater downward movement to layers largely inaccessible to immature plants and near-surface soil biota. Although low-intensity fire can reduce infiltration by forming hydrophobic layers (Agbeshie et al., 2022; DeBano, 1981; Mataix-Solera et al., 2011), this effect has been shown to degrade within one year post-fire (MacDonald and Huffman, 2004) and hydrophobicity is often destroyed as temperatures approach 300 ℃ (Alcañiz et al., 2018; Zavala et al., 2010). It is therefore more likely that the most persistent and long-lasting effect of fire is periodic increases in water infiltration tied to the consumption of organic soil horizons over highly permeable soils.

Without fire, thick organic layers that retain soil moisture accumulate, prevent rapid infiltration, and contribute to the formation of complex organic soil aggregates that further retain soil moisture (Islam et al., 2022; Sarkar, 2018; Schweizer et al., 2021; Wiseman and Püttmann, 2006). Greater soil moisture promotes pyrophobic species that further alter the physical, chemical, and decay-rate properties of litter layers in ways that increase soil moisture (Kreye et al., 2013; Scavotto et al., 2024). The greater leaf area index of pyrophobic versus pyrophytic trees also creates cooler and darker understories that retain more moisture in the soil (Nowacki and Abrams, 2008). In addition, the relatively smooth bark of pyrophobic species increases stemflow rates relative to rough-barked oaks and pines, leading to greater water inputs (Alexander and Arthur, 2010), increases in fine-fuel moisture (Alexander et al., 2021; Qi et al., 2012), and reductions in forest flammability. Thus, fire effects on belowground moisture ultimately interact with a more well-known aboveground mechanism of mesophication – fuel feedback – to further reinforce this process.

2.2. Plant-Soil-Fire Feedback: Nutrients

Long-term, frequent, low-intensity burning can deplete soil nutrient pools (Agbeshie et al., 2022; Alcañiz et al., 2018; Neary et al., 1999; Pellegrini et al., 2018) and promote pyrophytic trees that often thrive in nutrient-poor soils (Fig. 1D; Table 1; Hauser, 2008; Rogers, 1990; Rudolph, 1990; Tirmenstein, 1991); therefore, the current lack of fire-driven nutrient loss may be facilitating mesophication. Nutrient loss during fires occurs via ash convection and nutrient volatilization, along with erosion, runoff, and leaching following mineralization (Agbeshie et al., 2022; Alcañiz et al., 2018; Neary et al., 1999). Smoke columns physically transport ash particles (Bodí et al., 2014) and volatilization converts solid nutrients into liquids and then vapors that escape into the atmosphere. Volatilization requires high temperatures for most nutrients (*e.g.*, K to >760 °C, P to >774 °C, S to >800 °C, and Ca to >1240 °C; Neary et al., 1999). However, nitrogen (N) – the limiting nutrient in most eastern forests – can volatilize at a relatively low 200 °C (Bodí et al. 2014), and such temperatures were routinely reached in historical fire regimes (Alexis et al., 2007; Carrington, 2010; Trammell et al., 2004). Long-term fire exclusion prevents a natural N loss pathway as fixation and depositional inputs continue, leading to N accumulation in eastern forests (Carpenter et al., 2020). Fire has also been shown to lead to significant decreases in soil phosphorous over long periods of time (Coates et al., 2018) – another essential plant nutrient that may be limiting in some eastern US forests.

Over shorter terms (1–5 years), fire may increase plant-available N (Prieto-Fernández et al., 2004) as it mineralizes N during the partial combustion of fuel (Neary et al., 1999). A meta-analysis of 185 datasets from 87 studies between 1995 and 1999 found that fire increased soil ammonium (NH_4^+) by 94 % and nitrate (NO_3^-) by 152 %: peaks in NH_4^+ and NO_3^- occurred immediately and one year after fire, respectively, with available N decreasing with time since fire (Wan et al., 2001). Initial spikes of available nutrients following fire can be of benefit to seedling success (Loneragan and Loneragan, 1964; Senior et al., 2018), and may be of greater benefit to pyrophytic than pyrophobic species given their ability to withstand fire and thus have more rapid post-fire recruitment than fire-damaged pyrophobic trees (Hopkins et al., 2023). Over slightly longer timescales (*i.e.*, ~10–25 years), fire can also increase soil total N and inorganic N (Liechty et al., 2005; Scharenbroch et al., 2012). Although not conclusive, a threshold at ~30 years reveals mixed results where frequent fire sometimes increases plant-available N (Taylor and Midgley, 2018) and sometimes reduces it (Vance and Henderson, 1984). This is likely due to local climate and soil characteristics, along with fire frequency. Indeed, 30 years of annual and biennial interval burning in a longleaf pine forest lowered soil total N compared to unburned conditions, but 3 and 4-year interval burning did not (Binkley et al., 1992). This suggests that it may take decades of frequent fire to effectively reverse mesophication's effects on soil nutrient properties. Further, initial spikes in nutrient availability may be offset over time as inorganic N is lost through denitrification, leaching, and overland flow (Neary et al., 1999).

Fire can also reduce N availability via the combustion of organic matter (Prieto-Fernández et al., 2004), reducing microbial biomass N (Akburak et al., 2018; Fernández-García et al., 2019b; Knelman et al., 2015), and creating condensed aromatic compounds called pyrogenic organic matter, or py-OM (Roth et al., 2023; VanderRoest et al., 2024). Py-OM's resistance to microbial degradation can decrease overall N availability (Alexis et al., 2012; Chen et al., 2022), likely favoring pyrophytic plants. Fire suppression removes this additional N loss and aromatization pathway, ultimately increasing N availability and favoring pyrophobic trees.

Pyrophobic trees can then amplify the effects of mesophication on soil nutrients by increasing inorganic N inputs through leaf litter and stemflow. Because pyrophytic oaks and pines dominate low-quality sites but are easily outcompeted by pyrophobic trees on higher-quality sites where fire is rare (Hauser, 2008; Rogers, 1990; Rudolph, 1990; Tirmenstein, 1991), the pronounced effects of mesophication are restricted to intermediate quality sites (Brose et al., 2014). On such sites, mesophication-induced invasions of *Acer spp.* contribute relatively low C:N (Finzi et al., 1998) and fast-decomposing (McClaugherty et al., 1985; Melillo et al., 1982) litter that promotes high nutrient availability in the soil (Lovett et al., 2002). Specifically, sugar maple litter has relatively high N content that drives correspondingly high levels of plant-available N like nitrate in soils associated with the species (Lovett and Mitchell, 2004; Zak et al., 1986; Zak and Pregitzer, 1990). Further, the smooth bark of pyrophobic species yields higher stemflow of water than rough-barked pyrophytes – increasing nutrient inputs 2–3 fold via transportation of dissolved nutrients and generation of localized areas of higher N mineralization (Alexander and Arthur, 2010; Siegert et al., 2019). These two processes – litter quality and stemflow – may increase site quality to further favor pyrophobic tree dominance with mesophication.

2.3. Plant-soil-fire feedback: free-living microbes

Repeated fire likely affects the composition and relative abundance of free-living microbes present in forest soils – such as bacteria, decomposers, and pathogens (Certini et al., 2021; Hardison, 1976) – in ways that reinforce the competitive dominance of pyrophytic trees (Fig. 1E; Table 1). Fire reduces pyrophytic tree pathogens directly through soil heating and/or indirectly by creating drier and hotter microclimates (Neary et al., 1999). Fire can also decrease disease transmission rates by reducing root density (Pellegrini et al., 2021). Beals et al. (2022) found that prescribed burning lowered the diversity and relative abundance of plant pathogenic fungi in soils, which correlated with enhanced oak growth. Finally, the greater fire-induced stress experienced by pyrophobic trees lacking fire-adaptive traits may render them more susceptible to the soil-borne pathogens that survive fire, yielding the competitive advantages for pyrophytes (Abella et al., 2021; Dey and Schweitzer, 2018).

Conversely, fire's absence may increase pyrophytic trees' susceptibility to soil-borne pathogens through increasing root density and pathogen loads. For example, fire exclusion in forests of Minnesota led to a 765 % increase in oak mortality from the fungal pathogen oak wilt (*Bretziella fagacearum*) – which can spread via root transmission – while the frequently burned savannas saw only minor declines (Pellegrini et al., 2021). Modern fire exclusion has also promoted dense canopies and sub-optimal growing conditions that place greater stress on pyrophytes (Nowacki and Abrams, 2008) – increasing disease susceptibility. Recent research has demonstrated how shade tolerance may involve not only photosynthetic potential in low-light conditions, but also tolerance of the soil pathogens specific to moist, dark, and cool microclimates (Wood et al., 2023) that fire exclusion promotes. Furthermore, plant pathogen abundance often increases as susceptible host density increases (Meentemeyer et al., 2011). The high conspecific density of pyrophytic trees in current forests – *i.e.*, overstocked stands as a product of mesophication – may expose pyrophytic seedlings and saplings to more species-specific pathogens (Jevon et al., 2022) accumulated during decades of fire exclusion.

Beyond pathogens, fire may promote pyrophytic regeneration by directly and indirectly depressing the abundance and activity of free-living decomposers (Fig. 1E; Table 1), which can increase litter accumulation and provide fuel for future fires. Both the relative abundance (Semenova-Nelsen et al., 2019) and the diversity (Beals et al., 2022; Semenova-Nelsen et al., 2019) of saprotrophic fungi have been shown to decrease with frequent fire, yielding higher litter (and fine fuel) accumulation. Fire can also depress the abundance and activity of decomposing invertebrates, leading to similar accumulations of organic matter and litter that can fuel future fires (Butler et al., 2019; Gibb et al., 2022; Hopkins et al., 2020). Conversely, fire suppression may promote these free-living decomposers that accelerate decomposition rates, reduce fuel loads, and suppress fire activity to reinforce pyrophobic tree dominance.

Fire effects on free-living microbial communities may also confer advantages to pyrophytic species indirectly by altering nutrient availability. For example, various N-fixing bacteria can proliferate following fire due to spikes in labile N that they further promote and that may benefit pyrophytic trees less stressed by recent fires (Klopatek et al., 1990; Neary et al., 1999). Repeated fire over extended periods may also lower available N by decreasing microbial biomass (Akburak et al., 2018; Fernández-García et al., 2019a; Knelman et al., 2015), organic matter, and resultant N-acquiring extracellular enzyme activity (Zhou et al., 2022). Decreases in N-acquiring extracellular enzyme activity following fire may yield a competitive disadvantage for pyrophobic trees that frequently rely on microbial populations to liberate N from organic sources (Frey, 2019; Tisserant et al., 2013). Further, fire can volatilize allelopathic compounds and allow nitrifying bacteria to oxidize more NH_4^+ into NO_3^- (Klopatek et al., 1990) which is then more susceptible to loss via runoff (Neary et al., 1999).

2.4. Plant-soil-fire feedback: mycorrhizal fungi

Fire effects on the relationships between plants and mycorrhizal fungi likely play a key role in maintaining pyrophytic communities (Hewitt et al., 2023). Mycorrhizal fungi form symbiotic relationships with the vast majority of vascular plants on Earth (Bonfante and Genre, 2010) in which the plant provides photosynthate to fungi in exchange for water and nutrients that can increase host drought resilience (Fan and Liu, 2011; Kakouridis et al., 2022; Lehto and Zwiazek, 2011; Plamboeck et al., 2007; Ruiz-Lozano, 2003; Wu and Xia, 2006), acquisition of scarce nutrients (Guether et al., 2009; Phillips et al., 2013), and disease resistance (Dai et al., 2023; Marx, 1972). As such, mycorrhizal fungi are essential to the growth and survival of their pyrophytic hosts growing within dry, nutrient-scarce environments; with fire suppression, the lack of suitable symbionts may be key driver of pyrophytic tree declines.

The two main types of mycorrhizal fungi associating with trees – arbuscular mycorrhizal (AM) and ectomycorrhizal (EM) fungi (Genre et al., 2020) – display an intriguing segregation across variation in the relative fire tolerance of their hosts. Nearly all pyrophytic trees disfavored by mesophication (*e.g.*, oaks, pines, hickories – *Carya* spp., chestnuts – *Castanea* spp., etc.) associate with EM fungi whereas many pyrophobic trees favored by mesophication (*e.g.*, maples, ashes – *Fraxinus* spp., cherries – *Prunus* spp., etc.) associate with AM fungi (Alexander et al., 2021; Brundrett and Tedersoo, 2020). While not yet systematically demonstrated, this pattern implies a potential unforeseen influence of mycorrhizal associations in the mesophication process.

As verification of the previous point, the broadly observable shifts in tree species composition associated with mesophication in eastern forests over the last few decades correspond with shifts away from EM and towards AM association dominance. Further, such shifts in mycorrhizal associations have been tied to fire suppression (Jo et al., 2019). The widely-demonstrated ability of mycorrhizal fungi to amplify the dominance of hosts of the same mycorrhizal type through positive feedback (Averill et al., 2022; Delavaux et al., 2023) implies the potentially pivotal role of mycorrhizal fungi in propelling mesophication. We propose that mycorrhizal fungi are involved in the plant-soil-fire feedback drivers of mesophication via three main mechanisms: 1) fire suppression's negative effects on fire-adapted EM fungi that are important to pyrophytic tree success; 2) post-fire survival of pyrophytic EM trees creating refugia for associated fungi while fiercer competition exists with fire suppression, and 3) fire indirectly promoting EM fungal symbioses by reducing nutrient availability.

First, fire suppression may prevent niche openings for fire-tolerant mycorrhizal fungi that are important to the establishment and growth of pyrophytic trees. Fire-tolerant plants tend to associate with more fire-tolerant mycorrhizal fungi (Baynes et al., 2012) and, for pyrophytic trees of the eastern US, this is EM fungi with very few arguable exceptions (Alexander et al., 2021; Brundrett and Tedersoo, 2020). Many fire-adaptive traits have been observed among EM fungi such as abundant sporulation, melanized spores, fast germination and growth rates, and survival-oriented sclerotia (Fox et al., 2022). Although some AM fungi have fire-adaptive traits (Hopkins and Bennett, 2024) such as a plastic spore pigmentation response (Hopkins et al., 2024), all such studies have occurred in grasslands. Despite an assumed generalist nature, AM fungal community composition can shift drastically depending on the functional groups of the host plants (Davison et al., 2020; Sepp et al., 2019), limiting the applicability of those results to eastern forests. Further, while some AM fungi have been shown colonize pyrophytic EM plants to facilitate post-fire recovery (Horton et al., 1998), the reverse (EM colonizing AM trees to aid in post-fire recovery) has not been observed. This may imply that fire actually shifts both AM and EM fungal communities to benefit pyrophytic plants, although more research is necessary to prove this assertion.

Second, frequent fire may increase EM fungal dominance via the greater fire tolerance of their hosts. Conversely, shifts towards fire-sensitive trees with fire suppression may favor AM fungi. Pyrophytic trees, which are largely EM associates, possess traits like hypogeal germination, effective resprouting after top-kill, emphasis on root-over-shoot growth when young, heat-insulating bark properties, and efficient wound compartmentalization that enable greater fire resilience relative to AM trees that typically lack such traits (Brose et al., 2014; Keyser et al., 2018). Pyrophytic trees are, thus, more likely to survive fire and act as refugia for EM fungi (Hughes et al., 2020) which then confer such trees competitive advantages. Further, while some EM fungi can survive in the absence of their host, AM fungi are obligatory in their associations with a living host (Bago and Bécard, 2002). Without fire, AM fungal dominance increases as forest composition shifts towards pyrophobic trees that tend to be AM associates (Alexander et al., 2021; Jo et al., 2019) and the benefits AM provide to their pyrophobic hosts (Delavaux et al., 2023) amplify such shifts. As the proportion of EM trees decreases, so does the presence of inoculum and the likelihood for positive feedback promoting EM trees (Dickie et al., 2002; Hewitt et al., 2023).

Third, nitrogen accumulation during fire suppression may be driven and reinforced by mycorrhizal associations, furthering mesophication. The lack of fire-induced nutrient loss has been implicated in driving the aforementioned and broad shifts from EM to AM tree dominance in eastern forests (Jo et al., 2019; Scharenbroch et al., 2012; Wurzburger et al., 2023). AM fungi are efficient acquirers of excess inorganic N (Jo et al., 2019) but lack the enzymatic capacity to access organic N. AM trees reinforce high N availability in soil through their low C:N, high N, and quick-degrading litter (Phillips et al., 2013). In contrast, many EM fungi proliferate in low inorganic N environments because they can produce extracellular enzymes used to access nitrogen bound in organic matter (Cheeke et al., 2017; Jörgensen et al., 2025; Mahmood et al., 2024) and some may also interact with N-fixing bacteria to aid acquisition of scarce nutrients in fire-frequent environments (Luo et al., 2023). EM trees then reinforce low N availability through producing slow-degrading, N-depleted litter (Fernandez et al., 2020; Gadgil and Gadgil, 1971; Orwin et al., 2011). Higher inorganic N stocks in fire-suppressed soils may give AM trees a competitive advantage over EM trees (Jo et al., 2019; Quinn Thomas et al., 2010) while also degrading the mutualistic potential of the EM symbiosis (Peng et al., 2022).

3. Dearth under earth: related research needs

Despite this extensive review, our current understanding of the role plant-soil-fire feedback plays in mesophication remains limited. Nearly all information presented here stems from research exploring how fire directly and indirectly affects individual soil properties (Agbeshie et al., 2022; Alcañiz et al., 2018; Certini, 2005; Dove and Hart, 2017; Fox et al., 2022; Neary et al., 1999). Research explicitly connecting all these potentially non-additive or synergistic effects within mesophication using a framework resembling plant-soil-fire feedback is nearly non-existent (Fig. 2; Beals et al., 2022). A framework integrating fire into plant-soil feedback is relatively new (Kardol et al., 2023), and extremely limited in its application to mesophication (Hopkins et al., 2023). Plant-soil-fire feedback research that experimentally parses out the mechanistic drivers of mesophication would provide vital information for managers across the world seeking to reverse the phenomenon. However, specific research gaps need to be addressed before broadly integrating plant-soil-fire feedback thinking into forest management strategies (Table 2).

First, there is a need to understand how fire affects each proposed mechanistic driver of plant-soil-fire feedback (water, nutrients, pathogens, and mycorrhizal fungi) and how they interact in a "true" feedback framework. Despite a plethora of research on how fire affects soils (Agbeshie et al., 2022; Alcañiz et al., 2018; Certini, 2005; Dove and Hart, 2017; Fox et al., 2022; Neary et al., 1999) and how changing soil properties affect forest regeneration dynamics (Cleve et al., 1990; Hansen et al., 2009; Hockman and Allen, 1996; Knoepp et al., 2019; Larson et al., 2023; Long et al., 2022; McHale et al., 1996; Warkentin, 1984; Weil and Brady, 2016), few studies have explored how both interact to dictate the relative success of pyrophytic versus pyrophobic plants (Hopkins et al., 2023), plant responses across time and environmental gradients (Dixon et al., 2022; Hewitt et al., 2023), or how fire may affect soil properties to specifically promote pyrophytic tree regeneration (Beals et al., 2022). Multi-generational field- and greenhouse-based experiments would increase mechanistic understanding of the process and lead to strategies for reversing its effects (Beals et al., 2022).

Second, one must consider how plant-soil feedback may interact with the already well-established aboveground drivers of mesophication such as changing microclimates and fire-fuel feedback (Nowacki and Abrams, 2008). For example, the loss of overstory pines can dramatically reduce the amount of more flammable, longer-burning pine fuels that increase soil heating to a greater extent than herbaceous fuels (Kreye et al., 2012; Platt et al., 2016; Wenk et al., 2011). Further, studies suggest that EM trees that are typically fire-adapted may be less resilient to fire in mesophied forests as the increasing litter with fire suppression may encourage more fine root and EM fungal growth into surface soils to access abundant nutrients – increasing risk of fine root damage with fire (Carpenter et al., 2020; O'Brien et al., 2010). Changes in microclimatic conditions with fire can also affect belowground interactions to potentially aid in reversing the mesophication process. For example, increases in light availability with fire-induced canopy opening can increase the mutualistic potential of mycorrhizal fungi (Johnson et al., 1997) since trees with more light have more exchangeable photosynthate. In the low-nutrient, open-canopy environments of fire-maintained tree communities, mycorrhizal symbioses may be particularly mutualistic – yielding climate resilience within eastern forests beyond that achieved by transitions to drought- and fire- tolerant trees alone. In sum, more research is needed to assess how fire-fuel feedback and changing microclimates potentially interact with plant-soil-fire feedback to influence the mesophication process.

In addition, more regionally specific plant-soil-fire feedback research is necessary to optimize management effectiveness within distinct ecoregions (Table 2). Most studies of fire effects on belowground properties of forests have occurred in the western United States (Dove and Hart, 2017), which is subject to different fire regimes, forest types, and management concerns (Abatzoglou and Williams, 2016; Kotrík et al., 2023). Further, most research, even in the eastern US, has taken place in systems that are already fire-adapted; particularly, pine-dominated systems (Kipfer et al., 2011; Oliver et al., 2015; Reazin et al., 2016; Semenova-Nelsen et al., 2019; Smith et al., 2005; Vazquez et al., 1993; Visser, 1995). Research in closed-canopy, actively mesophying forests – where research is likely most needed – is lacking. This dearth in prescribed fire research in eastern forests has been increasingly recognized (Hiers et al., 2020; Varner et al., 2016; Vose and Elliott, 2016) and restricts the efficacy of prescriptive management. Substantial regional differences in climate, geology, tree species composition, belowground biota, and the effects of fire exclusion likely limit the cross-applicability of such research between ecoregions (Kardol et al., 2023). Only with a thorough, regionally specific understanding of plant-soil-fire feedback's role in mesophication will managers be able to develop strategies that effectively reverse the process.

4. Conclusions and mesophication management implications of plant-soil-fire feedback

Across the eastern US and throughout the world, extreme heat and drought from climate change is leading to frequent, intense, and severe wildfires in mesic and currently fire-infrequent areas that are increasingly at the wildland-urban interface (Gao et al., 2021; Halofsky et al., 2020; Machado Nunes Romeiro et al., 2022; Taylor and MacLean, 2025). As mesophication has shifted eastern forests towards a higher proportion of pyrophobic trees, projected increases in wildfire will likely yield increasingly degraded forests (Vander Yacht et al., 2024) if active management is not taken. Alternatively, the potential to reverse mesophication yields an exciting prospect of both enhanced climate resilience and increased human health (Gilvarg et al., 2025). The evidence in this review joins an increasing accumulation of evidence underscoring the necessity of returning frequent, low-intensity fire to eastern US forests (Hutchinson et al., 2005; Nowacki and Abrams, 2008; Olson, 2011; Vander Yacht et al., 2020; Waldrop et al., 2016) due to both fire's aboveground and belowground effects.

For years, ecologists have underlined the vital role of soil in mesophication management and called for more detailed investigations on the role of belowground processes promoting oak success (Arthur et al., 2012; Beals et al., 2022; Brose et al., 2014, 2013; Taylor and Midgley, 2018). These calls are now being answered. Researchers have begun to acknowledge that fire effects on soil may be partially responsible for the success of longleaf pine savanna restoration objectives (Dixon et al., 2022). Taking it one step further, teams of scientists and managers have: 1) successfully incorporated soil-related restoration objectives (*i.e.* mineral soil N reduction) into fire management plans (Dukes et al.,

Table 2
Knowledge gaps and potential future research directions focused on the mechanistic belowground drivers of mesophication, and management aimed at reversing mesophication. (PSFF = plant-soil-fire feedback).

Research Need	Related Questions
Plant-Soil-Fire Feedback Over Generations	1. Do fire effects on plant-soil interactions persist over multiple generations? 2. How does plant-soil-fire feedback affect the competitive dynamics between pyrophytes and pyrophobes? 3. How do fire-induced changes in soil biotic and abiotic factors interact to affect forest successional dynamics?
Above-Belowground Interactions	1. How does plant-soil-fire feedback affect, and get affected by, fire-fuel feedback? 2. How do changing microclimates with mesophication affect plant-soil-fire feedback? 3. How does fire (and the lack thereof) affect the relative benefit of mycorrhizal fungi to both pyrophytic and pyrophobic host trees?
Eastern US and Regional Focus	1. How do differences in fire properties between the western and eastern US affect the magnitude and direction of PSFF? 2. Within the eastern US, how do differing fungal and tree community compositions within ecoregions affect PSFF? 3. Most related studies have focused on pyrophytic forests; how does fire affect soil hydrology, nutrients, and biota in mesophytic, AM-dominated forests?
Management Implications	1. How do fire-driven changes in soil carbon affect tree success and a forest's capacity to serve as a natural climate solution? 2. What are the biotic and abiotic "legacy effects" of pyrophobic and pyrophytic trees on soil properties and how does this influence restoration potential? 3. How does mechanical canopy disturbance *combined* with prescribed fire affect PSFF and the potential to reverse mesophication?

2020), 2) recognized that implementing low-intensity fires early in the growing season may reduce pathogen loads at the soil surface while leaving mutualists at deeper soil profiles relatively unharmed (Hardison, 1976; Hopkins et al., 2023, 2021; Katan, 2000), and 3) pinpointed conditions that reduce extensive soil heating and resultant fine-root damage of pyrophytic trees within the execution of fire management (Kreye et al., 2020; Varner et al., 2005).

Beyond simply burning, mechanical canopy disturbance – especially the selective removal of pyrophobic competitors – may help reverse mesophication (Granger et al., 2018; Jordan et al., 2003; Vander Yacht et al., 2020) by contributing to plant-soil-fire feedback. For example, Dukes et al. (2020) found that thinning combined with prescribed burns was most effective (compared with control or burn-only treatments) at reducing inorganic N and achieving restoration objectives in pine- and oak-dominated forests. Further, Rasmussen et al. (2018) found that EM fungal enzyme activity was highest in the thinned and burned areas compared to control and burn-only areas, which may be due to EM fungi foraging for scarce nutrients and giving pyrophytic trees a competitive advantage. Further, the selective removal of pyrophobic trees during mechanical thinning could help eliminate belowground barriers to pyrophytic tree success that pyrophobes reinforce.

Further, research has begun to zero in on ideal fire intervals necessary to reverse mesophication. Binkley et al. (1992) found that implementing a one- or two- year burn interval for 30 years was enough to effectively lower soil inorganic N, but longer return intervals were insufficient. Kardol et al. (2023) also notes that high fire frequency may yield a “re-direction” in plant-soil feedback towards and alternate state, while Brown et al. (2013) showed that the return interval of prescribed fire can alter mycorrhizal community assembly. This suggests a need to implement more frequent burning for at least several decades before a shift in soil properties maintaining pyrophytic tree communities is achieved. Beyond this, it may be necessary to implement more extensive mechanical treatments accompanied by large-scale plantings of pyrophytic seedlings inoculated with mycorrhizal fungi if abundance of the necessary symbionts is inadequate. If these treatments are paired with comprehensive monitoring of both above- and below ground response, and adjusted accordingly, then management may be well on its way to reversing mesophication.

Integrating a plant-soil-fire feedback lens into management is important not just for areas in which fire promotes pyrophytic trees, but also in circumstances in which it does not. One theme that has emerged from this review is that *long-term* fire is necessary to promote pyrophytic tree success through plant-soil-fire feedback. In contrast, *short-term* fire management may create plant-soil-fire feedback that hinders pyrophytic tree success (Taylor and Midgley, 2018). One to a few prescribed fires can actually increase inorganic nitrogen availability in ways that promote pyrophobic competitors (Scharenbroch et al., 2012; Taylor and Midgley, 2018), and reintroducing fire to long-unburned soil may yield increased smoldering and heat penetration which can increase fine-root mortality (Kreye et al., 2020) and ectomycorrhizal associates (Carpenter et al., 2020) of pyrophytic trees. Even after decades of frequent burning, pyrophytic tree success in terms of survival, growth, and competitive position can remain elusive (Arthur et al., 2012; Bowles et al., 2007; Carter et al., 2015; Hutchinson et al., 2024; Oakman et al., 2019; Scharenbroch et al., 2012; Vander Yacht et al., 2019; Waldrop et al., 2016). Thus, centuries of fire suppression may necessitate centuries to address – or an increased focus on correcting belowground properties hindering progress. Further, the “short-term” negative effects of fire may be abated by burning under conditions that limit fine-root mortality (Kreye et al., 2020) or using mechanical means to remove mesophytic competitors and alleviate the stress of competition during the transient periods of increased nutrient availability (Taylor and Midgley, 2018).

Such potential to revolutionize the way mesophying forests are managed validates research that integrates belowground perspectives. The mesophication problem is very likely the result of interactions between aboveground vegetation, abiotic and biotic soil properties, and fire (Kardol et al., 2023). As such, small shifts in any one of these components can yield a cascade of effects on others. While research on plant-soil-fire feedback in eastern forests is sparse, initial research linking direct fire effects on soil with pyrophytic plant success is promising (Hopkins et al., 2023). Efforts to regionally increase prescribed fire management may face opposition related to perceived fire effects on carbon pools and emissions or more general “asbestos” forest paradigms (Vander Yacht et al., 2024); however, an enhanced understanding of plant-soil-fire feedback may be the key to maintaining resilient, climate-adapted forests and thus justify an increased use of prescribed fire. Our review reveals that mesophication cannot be fully understood without considering how historical fire regimes, and prolonged fire exclusion, have affected biotic and abiotic soil properties in addition to aboveground fuel and microclimatic properties. This more holistic approach may yield management actions capable of more fully reversing the negative effects of mesophication in forests across the globe.

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CRediT authorship contribution statement

Lars A. Brudvig: Writing – review & editing, Conceptualization. **Akihiro Koyama:** Writing – review & editing, Validation, Conceptualization. **Christopher W. Fernandez:** Writing – review & editing, Validation. **Wood Katherine E.:** Writing – review & editing, Investigation, Conceptualization. **Narda J. Triviño Silva:** Writing – review & editing, Validation. **Legge Eva O. L.:** Writing – review & editing, Writing – original draft, Investigation, Conceptualization. **Andrew L. Vander Yacht:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Resources, Project administration, Methodology, Investigation, Conceptualization.

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