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REVIEW

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Managing forward while looking back: reopening closed forests to open woodlands and savannas

Lauren S. Pile Knapp[1*], Daniel C. Dey[1], Michael C. Stambaugh[2], Frank R. Thompson III[1] and J. Morgan Varner[3]

Abstract

Background Ecosystem management, community restoration, and managing for climate resilience have become major priorities of land management in recent decades. For woodlands and savannas (i.e., "open forests"), this transition has meant moving fire-deprived, closed-canopy forests to structures and compositions characteristic of natural communities that are rare today: open-grown, wide-spreading trees, and endemic flora and fauna associated with frequent, low to moderate intensity fires. Open forest restoration is complex; its approach and operational prescriptions are dependent on a multitude of factors. Reopening forests to achieve ecological objectives associated with open forests is hampered by site histories, novel species compositions, and structures that resist fire.

Results Fire histories shed light on fire regimes that promote open forests, informing prescriptions at stand and landscape levels, but due to many social and environmental factors, managers are challenged to recreate those fire regimes. As fire was removed from these ecosystems, successional processes led to changes in species compositions concomitant with changes in woody structure and fuel complexes further inhibiting restoration without active management. As active management aims to transition residing fine fuels from mesophytic hardwood-shrub litter to herbaceous dominant fuels with canopy openness, fire effects, and prescriptions also change. Silvicultural prescriptions have been developed to aid in the process of transition but maintaining mature, continuous canopy open forests through the regeneration and recruitment phase of predominantly shade intolerant of oaks and pines remains speculative. Further, as a legacy of woody densification, contemporary fire practices may result in undesirable increases in sprouting woody species impacting objectives for herbaceous cover and diversity. Invasive plants and depauperate seed banks may further limit successful outcomes.

Conclusions Even with these formidable challenges, transitioning closed forests to open structures and compositions is critically important for wildlife that depend on them, especially at the size, scale, and connectivity necessary to sustain their populations. Many birds and pollinators of conservation concern require open forests and early successional forests may not serve as surrogates for mature, open forest habitat. In this review, we outline the advances, challenges, and importance for reopening closed canopied forests to open forests in the central and midsouth, USA. Further, we set the stage for new approaches and learned outcomes from the papers of the 7th Fire in Eastern Oak Forests Conference in Tyler, TX, included in this special collection of *Fire Ecology*.

Keywords Savannas, Open forests, Mesophication, Fuels, Birds, Pollinators, Ground flora, Restoration, Silviculture, Prescribed fire

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*Correspondence:
Lauren S. Pile Knapp
lauren.pile@usda.gov
Full list of author information is available at the end of the article

Resumen

Antecedentes El manejo de ecosistemas, la restauración de comunidades, y el manejo para lograr una resiliencia climática se han transformado en importantes prioridades en el manejo de tierras en décadas recientes. Para bosques abiertos y áreas de sabanas, esta transición implica el cambiar áreas en las que los fuegos fueron suprimidos –y que resultaron en bosques con doseles muy cerrados–, en estructuras y composiciones características de comunidades naturales que son raras de encontrar hoy: áreas abiertas, árboles creciendo espaciadamente, y flora y fauna endémica asociada naturalmente con fuegos frecuentes y de moderada intensidad. La restauración de áreas forestales abiertas (i.e. sabanas), es compleja: su enfoque y prescripciones operacionales son dependientes de una multitud de factores. El reabrir los bosques para alcanzar objetivos ecológicos están obstaculizadas por la historia del sitio, la composición actual de especies, y estructuras resistentes al fuego.

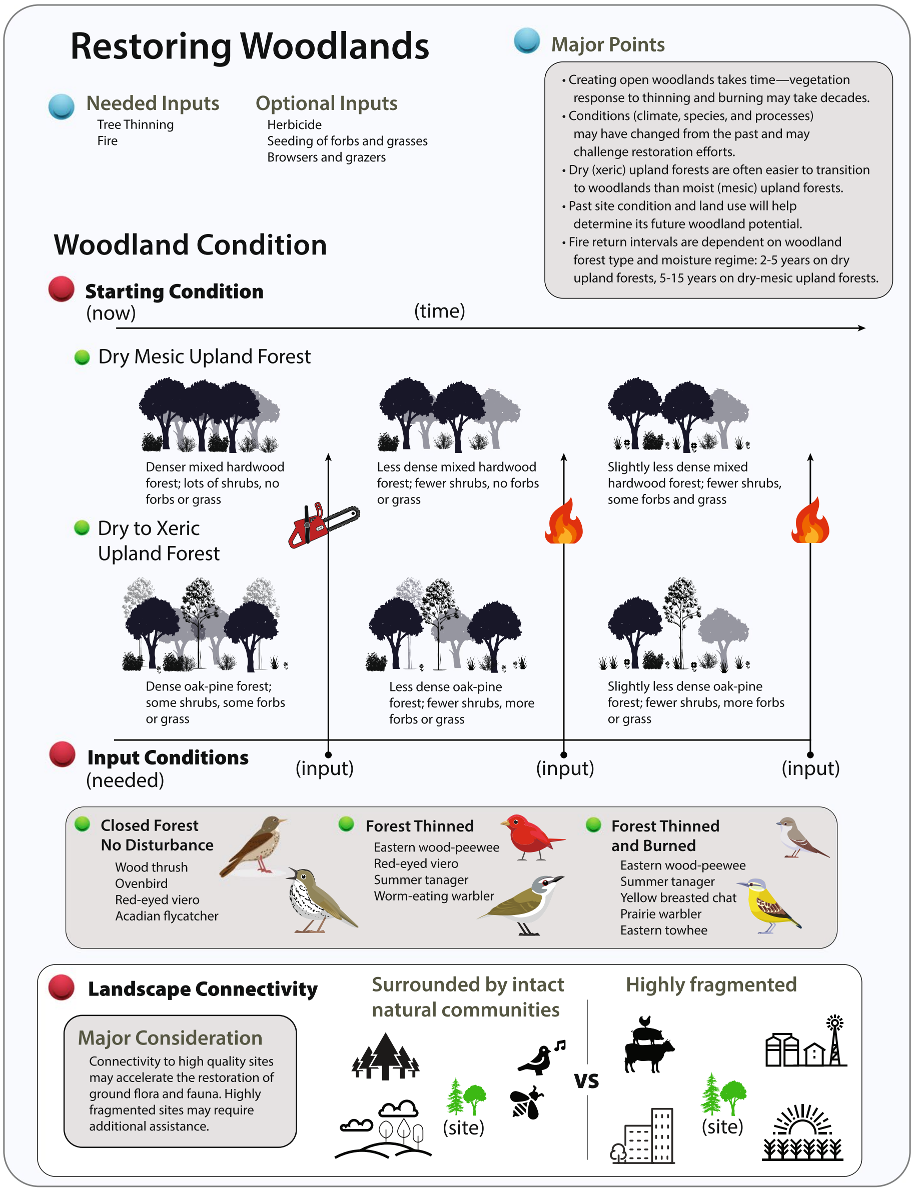
Resultados Las historias de fuego arrojan luz sobre los regímenes de incendios que promueven bosques abiertos, lo que nos ilustra sobre las prescripciones a realizarse a nivel de rodal o paisaje: desde luego y debido a muchos factores sociales y ambientales, esto representa un desafío para los manejadores de recursos para poder recrear esos regímenes de fuego. Dado que el fuego fue eliminado de esos ecosistemas, los procesos sucesionales condujeron a cambios en la composición de especies de manera concomitante con cambios en la estructura leñosa y con los complejos de combustibles, lo que inhibe la restauración si no está apoyada en un manejo activo. Dado que el manejo activo implica lograr la transición de los combustibles que se encuentran en bosques mesofíticos leñoso-arbustivos y su transformación en combustibles dominados por herbáceas en bosques con doseles abiertos, tanto los efectos del fuego como las prescripciones de quemas (para lograr esos objetivos), también deben cambiar. Las prescripciones silviculturales han sido desarrolladas para ayudar en este proceso de transición, aunque el mantenimiento de bosques maduros con doseles abiertos a través de la regeneración y la fase de reclutamiento de especies de robles y pinos intolerantes a la sombra se mantiene aún de manera especulativa. Además, como un legado de la densificación de leñosas, las prácticas actuales de quemas pueden resultar en el rebrote indeseable de especies leñosas que impacten en los objetivos de lograr la cobertura y diversidad de herbáceas deseada. Especies invasoras y un banco de semillas empobrecido pueden ser limitantes en el éxito futuro.

Conclusiones Aún con estos formidables desafíos, la transformación de bosques cerrados en estructuras forestales más abiertas es críticamente importante para la fauna que depende de esas estructuras, especialmente en lo que hace a tamaños, escalas, y conectividad necesaria para sostener esas poblaciones. Muchas aves y polinizadores de importancia requieren de bosques abiertos, y muchos bosques en estados sucesionales tempranos no pueden ser considerados como substitutos de un hábitat representado por un bosque maduro y abierto. En esta revisión, delineamos los avances, desafíos, y la importancia de reabrir los bosques con doseles cerrados en bosques abiertos en el centro y el centro-sur de los EEUU. Establecimos, además, el estado de nuevos resultados y lecciones aprendidas de los trabajos presentados en la 7ma. Conferencia sobre fuego en bosques de Roble del Este llevada a cabo en Tyler, Texas, incluidas en esta colección especial de Fire Ecology.

Introduction

Open forests (i.e., savannas and woodlands) were once common on the landscape of eastern North America (Hanberry et al. 2020a, 2020b) but are now rare due to fragmentation, land use change, and the cessation of frequent surface fires. Open forests are recognized as some of the most endangered communities in North America (Noss et al. 1995). For example, early 19th century open forests covered 13–33 million ha in the central USA but were reduced to < 1% of this extent by the late 20th century (Nuzzo 1986; Hanberry and Abrams 2018). The structure and composition of these open forests were shaped by topoedaphic features and frequent fire that influenced their openness (Grimm 1983). Recovering these ecosystems is important for enhancing and sustaining the ecological goods and services they provide such as native biodiversity conservation, wildlife habitat for species of conservation concern, pollination services, and often high-quality timber; but their restoration is often as complex as they are diverse (Abella et al. 2020) (Fig. 1).

Frequent fire historically kept open forests from converting to closed-canopied forests. Ignited by humans and lightning, frequent fires (e.g., every 1 to 10 years) dramatically affected tree structure and floristic composition. Prior to European colonization, uplands in this landscape occurring throughout the central and mid-south, USA, were predominantly open oak (*Quercus* spp.)- or pine (*Pinus* spp.)-forest ecosystems maintained by frequent, low-severity surface fires (Batek et al. 1999; Lorimer 2001; Guyette et al. 2003; Hanberry



- Creating open woodlands takes time—vegetation response to thinning and burning may take decades.
- Conditions (climate, species, and processes) may have changed from the past and may challenge restoration efforts.
- Dry (xeric) upland forests are often easier to transition to woodlands than moist (mesic) upland forests.
- Past site condition and land use will help determine its future woodland potential.
- Fire return intervals are dependent on woodland forest type and moisture regime: 2-5 years on dry upland forests, 5-15 years on dry-mesic upland forests.

Connectivity to high quality sites may accelerate the restoration of ground flora and fauna. Highly fragmented sites may require additional assistance.

Fig. 1 Graphic illustration of reopening hypothetical dry-mesic and dry-xeric upland closed woodlands in the central and midsouth, USA. While thinning may not always be necessary, reductions in tree densities resulting from mesophication may not occur with fire alone. Changes in response to thinning and burning will be dependent on the starting condition of the natural community which includes the site's inherent productivity. The process may take time and novel conditions may hamper outcomes. In addition, landscape connectivity may influence success, as accessibility to high-quality, intact natural communities may accelerate restoration of native flora and fauna. Although reopening closed forests is challenged by a diversity of issues, birds of conservation concern are reported to follow changes in forest structure and composition. Graphic illustration designed by Jeremy Siegrist, USDA Forest Service, Northern Research Station, in collaboration with manuscript authors

and Nowacki 2016; Stambaugh et al. 2016; Rooney and Stambaugh 2019). Savannas were more sparsely treed (10–30% crown cover, basal area < 7 m^2 ha^{-1}, or < 30% stocking) with ground floras dominated by grasses, whereas woodlands had more trees (30–80% crown cover, basal area ranging from 7–18 m^2 ha^{-1}, 30–75% stocking, ranging from open to closed woodland), less grass, and greater components of forbs and sedges (Ginrich 1967; Dey et al. 2017; Kabrick et al. 2022). Topography affected past fire regimes through its influence on the fire environment (fuels, temperature, moisture) and fire behavior (Stambaugh and Guyette 2008). Relatively flat prairies transitioned to savannas where waterways, north slopes, and increasing topographic roughness reduced fire frequency, intensity, and severity with increased soil moisture. Woodlands and structurally complex, multi-layered forests were common in even more dissected and topographically rough areas and where large water bodies and waterways created “fire shadows” (Harper 1911). Further, because fire was an important driver of vegetation, successional forests were historically rare on the landscape (Lorimer 2001). In stark contrast, successional forests are ubiquitous today (Shifley et al. 2014; Hanberry et al. 2020b). Site productivity driven by soil type (texture and inherent fertility) and moisture regime influenced fire regime and the extent and distribution of open forests (Jacqmain et al. 1999). With the cessation of fire due to suppression and other forms of exclusion, open forests transitioned to dense forests with complex overstory structures and understories dominated by leaf litter and shade-tolerant woody plants; species with traits that dampen fire spread and intensity shifting composition, structure, and function through processes known as mesophication and densification (Varner III et al. 2005, Nowacki and Abrams 2008; Woodbridge et al. 2022). Site conditions also interacted with the removal of fire to modify these changes. Sites with low fertility, shallow-rocky soils, high evaporative demand, and xeric moisture regimes were more resistant to the loss of open forest character (Nowacki and Abrams 2008). The loss of these open forests not only affected the structure, composition, and diversity of the plant communities, but also resulted in the large-scale loss of habitat and connectivity for imperiled open forest wildlife such as native birds and pollinators.

Guiding principles for open forest restoration and management will be most effective if they rely on our understanding of past processes and conditions but also allow for adaptation to novel conditions arising from a multitude of interacting factors (e.g., exploitative land uses, fragmentation, invasive species, and climate change), especially with the loss of fire (Fig. 1). Restoring fire regimes and altering community composition to favor “pyrophytes” (that is, fire-adapted species with fire-related or physiological traits that contribute to their persistence in fire-prone ecosystems; see Varner et al. (2016b) for discussion on oaks) may not be logistically or financially feasible nor result in the full suite of desired outcomes for open forests across sites. Although the literature provides evidence that fire in combination with tree thinning, and often herbicide, can promote and maintain open forest structure, little is known about the interactions of open forest restoration with complex of topography, variable disturbance regimes, and the influence of past land use on restoring ecosystem function. Despite these shortcomings, the importance of open forests is apparent given the declines in the cultural ecological services (e.g., high aesthetic, wildlife viewing, and hunting value) and ecological systems that depend on them (Hendee and Flint 2014; Irvine and Herrett 2018). Further, active forest management including tree thinning and prescribed burning that favors open forest conditions, such as lower stand densities and favoring drought-tolerant species compositions, will increase forest resilience in a changing climate (Vose and Elliott 2016). In this review, we discuss the transition of open oak and oak-pine forests of the central and midsouth, USA to closed forests by focusing on their developmental history, changes wrought by fire cessation, silvicultural approaches for recovering their openness, ground flora considerations, and the habitat requirements of open forest birds and pollinators. In the central region, open forests are predominantly oak, extending from western Missouri, USA to southern Ontario, Canada (Nuzzo 1986). The savannas of the Cross Timbers region occur from southeastern Kansas to central Texas and are dominated by xeric oak species, these open forest communities retain a high degree of fidelity but require restoration (Stotts et al. 2007). Open forests in the midsouth USA are predominantly oak-pine (Hanberry and Nowacki 2016; Hanberry et al. 2018, 2020b) becoming oak-juniper woodlands on the south-westernmost extension of the Ozarks. This paper helps set the stage for this Special Collection from the 7th Fire in Eastern Oak Forests conference focused on reopening closed-canopied oak and oak-pine forests to open savannas and woodlands. Many of the challenges facing the understanding of how these fire-prone ecosystems function, or might in the future, follow past calls for filling research gaps (Varner et al. 2016a).

Open forests of the past—how do they inform us today?

Recurring fires are arguably the single most important factor for open forest ecology and management in the central and midsouth, USA. Vegetation changes over nearly a century of fire exclusion provide universal evidence that decreased fire dramatically altered open forests allowing increased survival of woody species through resprouting and new colonization, ingrowth of fire-intolerant species, and overall forest densification.

Though many historical open forests closed during the past century, the historical ecology of their development and succession can be recovered (Swetnam et al. 1999). Demography and growth of relic open forest trees provide important information about their biogeography, disturbance regimes, vegetation structure and composition, and developmental pathways (i.e., regeneration, canopy ascension, survival, and longevity). Tree growth rates provide spatial and temporal information on forest succession such as cohort establishment and canopy openness (Clark et al. 2005). Growth signals from disturbances are revealed through abrupt growth changes that are independent of climate conditions (Guyette et al. 2007). Together, growth and disturbance records of relic trees provide a design for open forest developmental pathways that include inhibiting densification and mesophication, and mitigating threats such as high severity fire (Cocking et al. 2014; Stambaugh et al. 2014).

Historical open forest structure also aids in understanding the conditions and processes whereby fire-tolerant tree species can be sustained (i.e., regenerated and recruited to the overstory) while undergoing frequent and long-term burning. In regions with frequent fire regimes (e.g., < 5 years), periods with longer fire-free intervals are important for allowing for tree regeneration to recruit to the forest canopy [see Knapp et al. (2022) on frequent fire bottleneck on overstory recruitment] (Blankenship et al. 2023). Fire-free intervals can occur at small to large spatial scales and are influenced by other disturbance agents, topography, and site conditions that result in unburned islands that serve as refugia for establishment (Robertson et al. 2019). Generally, across the central and midsouth USA, historical fires were frequent (e.g., mean fire intervals of 3–12 years depending on open forest type), low to moderate severity (Fig. 1), and occurred during the dormant vegetation season or the late-growing season (Stambaugh et al. 2020, 2021; Flatley et al. 2023). Variability in these conditions did occur. For example, fire intervals can be highly variable through time, and sequences of very frequent (e.g., annual) burning were common. Based on modern fire activity and events, other fire conditions likely existed, such as fires that were high severity and occurred during the growing season.

Changing human populations and cultures through time have been strongly associated with the historical variability in fire frequency in these regions (Guyette et al. 2002; Abrams et al. 2021; Flatley et al. 2023). Removal of human ignitions has threatened open forests as humans, both Indigenous and early European, were major drivers of frequent fire regimes on large spatial scales. The spatial size of historical fires on the landscape is currently poorly understood, but fires had the potential to be very large and synchronous, especially in regions with continuous fine fuels, little topographic relief, and during dry periods (Guyette et al. 2006).

New research is needed to improve our understanding of the spatial and temporal extent to which open forests were promoted by humans and through what specific fire regime and vegetation conditions. This clarification would help to inform open forest ecology at ecosystem and landscape scales, and management systems for their restoration and sustainability. Clarification would also inform ecocultural burning practices and purposes, and to some degree, early human history and ecology that informs modern societal challenges like wildfire management (Roos et al. 2021). Culturing of open forests by humans included the promotion of herbaceous vegetation used as food, medicine, and textiles which is not present on the landscape today. Diverse herbaceous plant communities enhanced habitat for birds and mammals, especially large ungulate grazers, and insects important in fruit, seed, and nut production (e.g., insect-pollinated plants, oak associates) (Long et al. 2021). Undoubtedly, fire regimes and biota interacted with other disturbances altering forest composition and structure (McEwan et al. 2011; Abrams et al. 2021; Mueller et al. 2021). The historical importance of these factors is difficult to ascertain, but observations and experiments demonstrate that open forest conditions can arise from wind disturbance (e.g., tornadoes), severe and prolonged droughts, and herbivory (Harrington and Kathol 2009). However, repeated low-intensity disturbance, namely fire, interacts with other disturbance agents to promote ground flora diversity and abundance and maintain open forest structures which would otherwise not develop or would infill through successional processes. Also, it is important to consider that not all historical fires ignited by humans were done to promote open forests specifically. These fires resulted from a multitude of reasons including signaling, warfare, hunting, and more (Krech and Krech III 1999).

The mesophication of forests—are they now recalcitrant to change?

Even before Nowacki and Abrams' (2008) synthesis and coining of the term "mesophication," numerous publications pointed to similar directional change in community succession (Heinselman 1963), including in former oak-dominated open forests (Beilmann and Brenner 1951). The lament in the literature continues today (current authors included), with abundant contemporary research on the effects of mesophication on fuels, fire behavior, understory vegetation, forest composition and structure, hydrology, pollinators, and wildlife (see reviews in Hanberry et al. (2020a), Alexander et al. (2021), Arthur et al. (2021)). What is lacking (and arguably more relevant than tracking the decline in these ecosystems), is developing and testing the methods and results of successful treatments for recovery and maintenance of open forests across diverse ecosystems.

Reversing the changes wrought by mesophication is somewhat complex, as are many of the challenges imposed by ecosystem restoration (Suding 2011). The changes in forest structure and composition are straightforward, to a degree. Removing mesophytes via harvesting is also deceivingly simple (remove mesophytes and leave pyrophytes), although harvesting costs can be high to avoid damage to residual trees (Akay et al. 2006; Kizha et al. 2021) and the fact that the majority of the mesophytes lack sufficient timber value, due in part to their currently smaller diameters. As with restoring overstory composition, removing small trees in the midstory and understory is often not profitable and may require repeated treatments. These financial hurdles often prohibit the adoption of open forest restoration beyond stand-level scales of localized natural area management (Löf et al. 2019). Beyond simply removing mesophyte trees, fire exclusion likely also increased the density and basal areas of pyrophytes. Perhaps slowing restoration and recovery of open forest conditions, restoration treatments rarely consider the removal of native pyrophytes likely because prescriptions are often based on uneven-aged silvicultural practices for improving growing stock rather than open forest management.

The classification of “mesophyte” v. “pyrophyte” is additionally fraught with problems that can impact restoration activities. Central and midsouth forests harbor a high diversity of tree species. These species’ functional traits related to fire tolerance, drought tolerance, and shade tolerance (Nowacki and Abrams 2008; McEwan et al. 2011; Varner et al. 2016a, b) complicate simple categorization and vary within closely-related species of the same genera (Rebbeck et al. 2011, 2012; Varner et al. 2016b; Pile et al. 2017; Kaproth et al. 2023). For example, many woody species in the region readily resprout following topkill from fire, but resprouting itself is not only an evolutionary adaption to fire (Keeley et al. 2011; Keeley and Pausas 2022). The capacity of shortleaf pine (*Pinus echinata* Mill.) to sprout from the root collar is suggested as an advantage in mixed oak-pine woods where sprouting competition is vigorous (Guldin et al. 2004; Varner et al. 2016b; Clabo and Clatterbuck 2019; Kaproth et al. 2023). The need to understand these silvical characteristics weighing fire-adapted traits is critical to restoration treatment prescriptions in existing mixed species stands as well as artificially regenerated sites.

Differences abound in presettlement tree densities (Noss 1985; Cogbill 2023) and the regional or site-specific overstory structure and broader classifications as savanna, woodland, or forest. Determining the desired density for the restoration of open forests is also complicated by these dynamic systems; communities have regenerated and sustained their overstory in any number of developmental pathways including transitional states from woodland-savanna-prairie over time. As with the categorization of species along mesophication gradients, tree density is an obvious prescription parameter for restoration treatments as well as for planting. Research that better informs this spectrum, and its variability within and across landforms, has great potential.

Harvesting that removes mesophytes, and thus their shade and litter inputs should hasten the restoration of community flammability. However, midstory removal of mesophytes may do little to improve fuel conditions if mesophytic canopy dominants remain (Cabrera et al. 2023). The effects of mesophyte litter are clear: their litter retains moisture longer and burns poorly (Kreye et al. 2013, 2018; Varner et al. 2021). The magnitude of mesophyte removals and the sequencing of harvesting, burning, and potential mechanical and chemical treatments is not fully known. Beyond the few site-specific studies, a better understanding and predictability of ecosystem responses to the suite of potential restoration prescriptions remains a major need. A fundamental aspect of the mesophication challenge (and of vegetation-fire feedbacks more broadly) is that these feedbacks are site-dependent and are particularly sensitive to site productivity. Beyond the influence of site productivity, the impacts from a diversity of land use history (e.g., past harvesting, grazing, agricultural abandonment), along with a changing climate also complicate community trajectories and the interplay between vegetation and fire (Fig. 1).

Tending the woods—can we take back the open forests?

Timely restoration of open forests where they once occurred increases the chance of successfully recovering their diverse native ground flora through natural regeneration from remnant plants or seedbanks (Hutchinson et al. 2005a, 2005b; Barefoot et al. 2019; Vander Yacht et al. 2019). Sites that retain some of their relic openness and have a high degree of connectivity with other intact communities may hasten the restoration process compared to sites that are long unburned, disjunct, or that have lasting, intensive land use histories (Fig. 1). Open forest sites can be identified by the presence of remnant open forest ground flora (Kinkead et al. 2013).

Recovery of open forests is possible through active management (Fig. 2) including cultural burning and prescribed fire, which may require the use of herbicides when burning is challenging or for the control of woody sprouts. Prescribed fires in the central and midsouth, USA are usually conducted as low-intensity burns in the dormant to early growing season (Ryan et al. 2013; Goode et al. 2024). Increasing interest in fire use that represents variants of prescribed fire include cultural burning (Lake and Christianson 2020; Lake 2021; Long et al. 2021), extending burning windows further into the growing season (Petersen and Drewa 2006; Meunier et al.

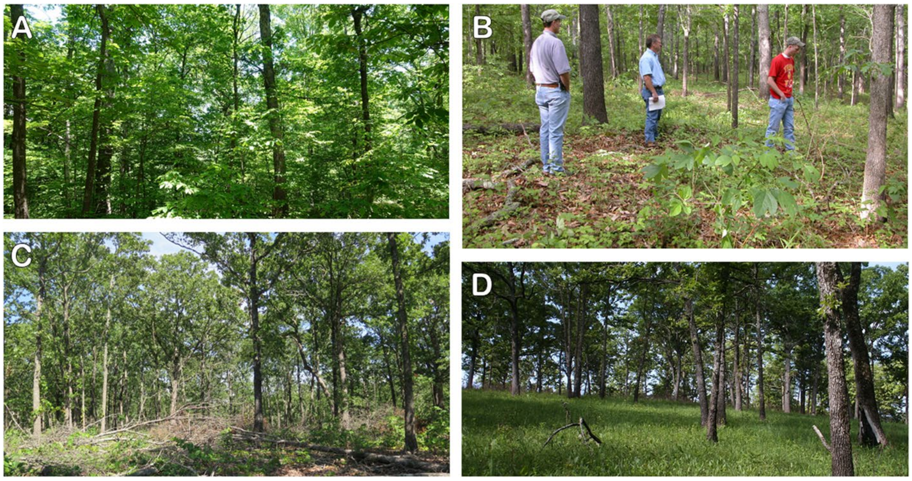


Fig. 2 **A** In the absence of fire and other management, central and midsouth hardwood forests develop a closed overstory, midstory canopy layer, and understory dominated by woody trees and shrubs, with sparse herbaceous flora dominated by shade-tolerant species in the lowly lit environs. **B** Frequent prescribed fire can reduce the density of mid and understory woody stems and canopy cover but have little influence on overstory density. In this example, changes in woody structure are shown after 4 fires in 10 years in an oak-hickory forest in the Missouri Ozarks. **C** Reducing overstory density through commercial timber harvesting and thinning is the most expedient method for achieving desired open forest structure to promote ground flora development, potentially providing revenue to support restoration, and giving managers more control over the spatial arrangement and composition of the open forest. **D** The combination of overstory thinning and prescribed burning accelerates the development of open forest plant communities

2021; Goode et al. 2024), and managing wildfires within prescription to achieve ecological goals and the needs of people.

Managed wildfire (i.e., naturally ignited wildfire that is allowed to safely burn to meet ecological goals and objectives) holds the promise, with greater use, of adding to the ways managers can use fire at large scales and in remote areas to reduce wildfire risk and severity. Managed wildfire can restore heterogeneity and diversity to ecosystems and landscapes, improve watershed health and condition, reduce widespread drought, insect and disease-related tree mortality, and improve wildlife habitat (Boisramé et al. 2017). Wildfires in the eastern US, while comparatively rare to the western USA, are increasing in size and occurrence, and although most are caused by human ignitions, climate, and vegetation status likely contribute to the shifting patterns in frequency, scale, and seasonality (Donovan et al. 2023). Additionally, in some contexts, the ability of managed wildfires to restore open forests with specific fire regime parameters and prescriptions could inform approaches to wildfire mitigation and managed wildfire prescriptions. For example, understanding details of treatments, fire behavior, and fuels consumption from prescribed fire operations increases understanding for similar fire risk and fuels reduction scenarios encountered during managed wildfires.

Prescribed fires, as practiced today, are effective in managing litter, seed bed conditions, seedbanks, understory vegetation, certain invasive plants, and smaller-diameter trees (Ryan et al. 2013; Pile Knapp et al. 2023). Low-intensity, dormant season fires are effective in topkilling trees of many species that are smaller than about 10 cm diameter at breast height (Fig. 2), and the probability of topkill decreases with an increasing diameter above that threshold (Arthur et al. 2012). Topkilled trees of many hardwood species and a few conifers [e.g., pitch pine (*Pinus rigida* Mill.) and shortleaf pine] often resprout initially, but frequent fires have differential effects on tree mortality among species over time (Dey and Hartman 2005). Modern prescribed fires usually cause minor reductions in stand basal area and stocking (Regelbrugge and Smith 1994; Hutchinson et al. 2005b, 2012; Smith and Sutherland 2006; Fan and Dey 2014; Knapp et al. 2015; Kinkead et al. 2017). Higher fire intensity and increased exposure to lethal temperatures are needed to kill trees larger than 25 cm; this may occur locally during low-intensity fires where accumulations of fuels occur near the base of individual trees (Brose and Van Lear 1999). However, after recent decades of fire exclusion, trees have grown in diameter to sizes and sufficient bark thicknesses to be resistant to low-intensity fires, even species considered to be fire sensitive (Hood et al. 2018). Low-intensity fires may cause wounds at the base of trees but seldom cause overstory (trees > 25 cm) mortality or reduce overstory density even after decades of intermittent burning (Knapp et al. 2015). Thus, in the initial stages of restoration, tree harvesting, and thinning may be required to increase canopy openness and light to the ground layer.

The timing and combination of prescribed fire with other management practices depends on a multitude of factors including management goals, current vegetation, threats from invasive plants, fuel conditions, vegetation response, and other resource concerns. Early restoration of open forests focused solely on reintroducing frequent fire (Jenkins and Jenkins 2006; Bowles et al. 2007; Holzmueller et al. 2009). Within a decade or so it became obvious that fire alone was insufficient to move novel conditions in current vegetation toward desired future conditions because the vegetation, especially larger trees, had developed high resistance to fire (Bassett et al. 2020; Vander Yacht et al. 2020). Thus, thinning and harvesting were done in conjunction with prescribed burning to accelerate the rate of open forest restoration (Fig. 2). Harvesting, if feasible, is the most effective way of managing overstory tree density and distribution, and potentially generates revenue to defray costs of restoration. However, an emerging issue is that reducing stand density early in the restoration process may release understory woody shrub and tree reproduction that prospers in the increased sunlight (Fig. 3). This rapid proliferation emphasizes the importance of also restoring a frequent fire regime to maintain control over woody competition and sustain herbaceous flora. New prescriptions are needed to initiate restoration in a way that does not promote dominance by woody vegetation or invasive plants, requiring foresight, long-term commitment, and patience. One approach is to apply treatments to reduce the density of woody plants *before* opening the overstory canopy using either repeated prescribed fire and/or herbicides. Restoration prescriptions will change through time shifting from practices needed to initiate restoration to those required to maintain desired conditions with modifications as needed to allow for the recruitment of tree sprouts into the overstory at a rate that sustains the desired structure.

Fig. 3 A common approach to open forest restoration is to thin the overstory and follow with frequent prescribed burning. An emerging problem often observed is that the woody tree and shrub understory sprouts vigorously and thrives in the more open, lighted environment, developing dense and recalcitrant understory canopies. These low woody canopies retard herbaceous development and may require more frequent burning or burning during the growing season. An alternative approach may be to use frequent fires and herbicide before overstory canopy thinning to reduce woody stem density

There are unique effects (e.g., thermal, chemical) on plants, species, and ecosystems that can only be had by using fire. Fire is the most effective and ecologically-based treatment for managing fine fuels, litter, high densities of small diameter stems, and understory environments over large and sometimes remote, inaccessible areas. For example, results from the National Fire and Fire Surrogate Study highlight the need for repeated prescribed fire to advance restoration goals, with mechanical-plus-burning treatments being more effective at opening the canopy than burning alone (Waldrop et al. 2010, 2014). After repeated treatments, changes in understory composition are small and ruderal (Oakman et al. 2021), mastication can further be used to reduce midstory densities and increase the ground cover of forbs and graminoids (Black et al. 2019). Once the initial restoration phase is completed, prescribed fire can be used to maintain open forests for decades with provisions for occasional recruitment of trees into the overstory to maintain the desired tree density (Fig. 4).

Is ground flora lost when open forests close?

An implied expectation of open forest restoration is that ground flora will increase in abundance and diversity. Research and observation clearly demonstrate that tree thinning and repeated surface fire can achieve these goals, with decreasing tree canopy cover often increasing ground flora diversity (Zenner et al. 2006; Barefoot et al. 2019). Fire modifies understory environments and promotes the establishment and development of herbaceous vegetation and tree advance reproduction. Fire can be used to favor species that have fire adaptations in certain life stages while discriminating against competing and undesirable vegetation that is vulnerable to fire. The proper use of fire requires knowledge of plant biology and community ecology to manage existing vegetation toward more desirable future conditions.

Fire is essential for reducing litter which promotes the germination and growth of herbaceous plants (Hutchinson et al. 2005b) and provides more favorable seedbeds for light-seeded species. Although the heat and smoke produced by fire may help break seed dormancy and

Fig. 4 Fire is an important tool for maintaining open forest structure and composition. After restoration activities have focused on reducing mesophytic hardwoods, frequent prescribed burning is important for maintaining the open overstory structure and increasing pyrophytic species compositions in the understory. In the black belt region in Chickasaw County, Mississippi, burning is used to maintain a post oak (*Quercus stellata*) woodland (**A** and **B**). At the Strawberry Plains Audubon Center in Holly Springs, Mississippi fire is used to maintain structure and composition following restoration activities (**C**)

initiate germination in some species, in herbaceous open forests with surface fire regimes, germination is not often directly related to fire but often the conditions resulting from fire (Pausas and Lamont 2022). Herbaceous species in fire-frequent ecosystems often rely on mechanisms to maintain their persistence through rapid regrowth and seed germination post-fire (Pausas and Lamont 2022). Surface fires release nutrients that are tied up in the litter increasing their supply and availability for plant growth (Anderson and Menges 1997; Schafer and Mack 2010; Agbeshie et al. 2022). Fire also increases soil surface temperatures accelerating microbial activity, decomposition, and nutrient release (Jr. et al. 1993; Iverson and Hutchinson 2002; Scharenbroch et al. 2012). The understory environment is improved for plant survival and growth by fire by reducing woody and herbaceous canopy cover, which increases growing space, light, and moisture availability in the short-term (Leach and Givnish 1999; Peterson et al. 2007; Ratajczak et al. 2012). Overall, low to moderate intensity fires increase herbaceous richness and coverage by modifying conditions in the understory, especially when combined with reductions in overstory density (Hutchinson et al. 2005b; Zenner et al. 2006; Waldrop et al. 2008; Kinkead et al. 2017).

The heterogeneity of the overstory representative of open forests influences the heterogeneity of the ground flora contributing to increased species richness by providing a diversity of microsite conditions (Peterson and Reich 2008). Further, fire is not the only disturbance driving plant community structure and composition. Herbivory and fire often interact to favor some species over others (Harrington and Kathol 2009), and this interaction is a noted gap in open forest research (Mason and Lashley 2021). Departures from historical fire and herbivory regimes can result in communities that deviate outside of their historical range of variation, resulting in shrub and tree densities that are resistant to burning alone and whereby burning may only increase midstory densities of resprouting species (Tester 1989; Peterson and Reich 2001; Knapp et al. 2009; Meunier et al. 2021;

Fig. 5 Research site in the Missouri Ozarks that has been twice browsed and burned within a 4-year period for oak (*Quercus* spp.) woodland restoration with the explicit objectives to reduce midstory sprouting densities and increase the abundance and diversity of native ground flora, when burning alone was not enough

Blankenship et al. 2023). These dense midstory layers directly compete with resources for ground flora and can often challenge restoration goals without additional management (Fig. 5). Fire frequency, seasonality, and time since fire and the monitoring of plant response are important (Sparks et al. 1998). For example, biennial burns may favor forbs whereas annual burning may promote the dominance of grasses (Peterson and Reich 2008). Although reconstructing past open forest structure and composition is possible with historical accounts and land surveys, little is known about the historical composition and relative abundance of ground flora. Further, a diversity of reference conditions across different site conditions are often lacking for comparison and historical records do little to inform targets for ground flora abundance, functional and species diversity, and floristic quality.

Ground flora restoration often relies on what is already available either through seed or perennial vegetative structures. However, the length of time that seeds and reproductive structures lay dormant may impact their response to restoration treatments. Seeds and reproductive structures have limited lifespans and species-specific information on seed and bud banking is limited. Further, establishment from seed in the forest understory is likely rare, relying on new shoots to arise following disturbance from the belowground bud bank (Ott et al. 2019). Sites with shorter departures from historic disturbance regimes or those that are topoedaphically resistant to change may respond to treatment more quickly. Further, the seed rain from the surrounding landscape may be beneficial when open forests are nested within a matrix of high connectivity but in a landscape of increasing fragmentation seed rain will be ruderal and often invasive (Reid et al. 2020; Lamb et al. 2022). Logging can increase resident species richness and abundance in the seedbank compared to unlogged sites (Penman et al. 2011). However, this increase in richness and abundance may come at a cost to conservative plant species, especially with repeated entry and opportunities for invasive plant establishment or the proliferation of ruderal species. Recovery of native species on former open forest sites can be done through artificial regeneration by sowing seed and planting seedlings of desired species (Kaul et al. 2023), however, this will also require prescriptions that favor germination and growth that are sustained for the long-term (Glennemeier et al. 2020; Maddox 2022) (Fig. 6).

Invasive species (flora and fauna) challenge the restoration of open forest ecosystems—through their alterations to open forests structure, composition, and function but also through the resources needed to control them. Invasive plants can alter successional trajectories, create shrublands from woodlands, change fire regimes, homogenize floristic diversity, alter resource availability, quantity, diversity, and phenology for wildlife, and change nutrient cycling (Hartman and McCarthy 2008; Rodewald et al. 2010; Poulette and Arthur 2012). Disturbance can be a driver of invasive plant establishment and population growth and disturbances for open forest restoration, like tree thinning and prescribed burning, may facilitate plant invasion (Willms et al. 2017; Meunier et al. 2021). Unfortunately, many invasive plants have become well-established across the central and midsouth USA, and silvicultural prescriptions for open forests will

Fig. 6 Restoring ground flora in open forests may require enrichment seeding. In this oak-hickory (*Quercus* spp.–*Carya* spp.) woodland, a dormant season prescribed burn (**A**) was conducted to topkill invasive bush honeysuckle (*Lonicera* spp.) and to promote native ground flora. To facilitate increases in the diversity and abundance of native forbs and grasses, following burning, residual leaf litter was removed with raking (**B**), and a seed mix was spread over bare mineral soil in canopy openings (**C**). Germination occurred several months later during spring green up (**D**)

need to include invasive plant control and containment strategies in their planning (Pile Knapp et al. 2023). Further, invasive wildlife, particularly, wild hogs can actively challenge restoration efforts by impacting enrichment plantings while also altering nutrient cycling and plant composition (Siemann et al. 2009; Barrios-Garcia and Ballari 2012).

Build it and wildlife will come

Many species of wildlife that are currently of conservation concern benefit from open forest restoration and their status as species of concern is partly related to the wide-scale reduction in the extent of open forest ecosystems from fire exclusion. Open forests may be of greater value to wildlife than other disturbance-dependent or successional communities that are often promoted, such as regenerating forests following even-aged management. This is easiest to illustrate with birds because of the existence of standardized, long-term monitoring data for much of North America's bird fauna. Further, compared to other wildlife, birds are quick to respond to newly available habitats and species stratify by preferences for vegetation structures (Fig. 1) (e.g., grassland vs. woodland vs. forest).

Analyses of long-term trends in bird abundance often group birds based on their association with plant communities to try and link declines to habitat loss. Declining most are grassland and scrub/successional birds (Brawn et al. 2001, Hunter et al. 2001, Thompson III and DeGraaf 2001, Sauer et al. 2017). These groups include species that are dependent on disturbance (e.g., fire, grazing, or timber harvest) to reset succession or prevent these communities from succeeding to more closed forest habitats of lesser value to them. The elements of these plant communities that are important to many of these birds are a diverse ground cover of grasses and forbs and varying amounts of low woody cover. Disturbance is also important because it stimulates ground cover that supports abundant insect prey.

Substantial attention has been brought to the plight of these birds and plant communities, but much of it has focused on the value of young forests or early successional communities created by timber harvest in closed-canopy forests (Thompson III and DeGraaf 2001, Hanberry and Thompson III 2019). Forests in the stand initiation stage provide habitat for many of these species but it may be short-lived because as a stand develops to the stem exclusion stage (and canopies close), it loses its value to most of these species and this usually happens within 10 years after harvest (Thompson III and DeGraaf 2001, Kendrick et al. 2015). Interestingly, there may now be more early successional forest in parts of the country than pre–Euro-American colonization. For example, in neighboring forestland of the southeastern USA, greater than 15% of forests are 1–15 years old (Hanberry and Thompson III 2019). Even-aged management or planted forests quickly move stands through the stem initiation stage, quickly losing value for disturbance-dependent wildlife. It is difficult to link declines of many of these bird species to early successional forest; rather, the great reductions in the extent of continuous open forests with high spatiotemporal fidelity seems a more likely cause. We suggest that the restoration of open forests would

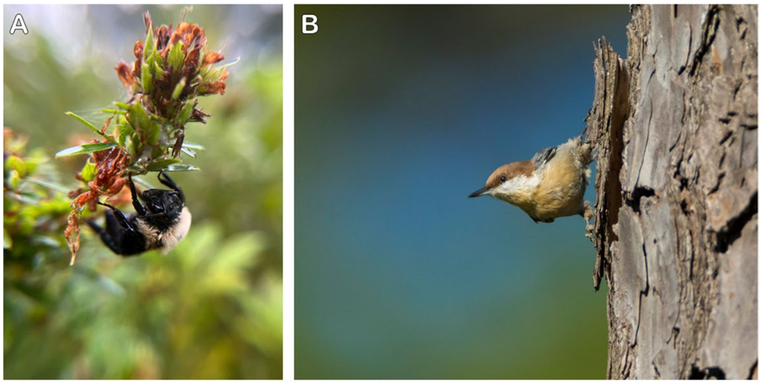


Fig. 7 Species of conservation concern that require open forest habitat respond positively to restoration. Important pollinating species, including native bees, require diverse and abundant floral and nesting resources. This native bumblebee (*Bombus* spp.) was photographed on slender lespedeza (*Lespedeza virginica*) that was seeded to promote pollinator habitat on the Hoosier National Forest in southern Indiana (**A**). Photo credit: Dacoda Maddox, USDA Forest Service. The Brown-headed Nuthatch (*Sitta pusilla*) was reintroduced to Missouri pine (*Pinus* spp.) woodlands and is once again nesting there after being absent for 100 years (**B**). The reintroduction was possible due to the successful efforts of the USDA Forest Service, Missouri Department of Conservation, and other cooperating agencies at restoring pine woodlands in the Ozark Highlands. Photo credit: Noppadol Paothong, Missouri Department of Conservation

benefit many of these bird species of concern across the central and midsouth USA.

There is now good evidence that restoring open forests can provide habitat for many species of concern (Fig. 7). Bird densities in open forests can exceed those in early succession/young forests (Hanberry and Thompson III 2019, Roach et al. 2019). These open forest species prosper even with modest overstories, which could seem surprising given their lack of response to selective cutting or thinning in closed forests (Kendrick et al. 2015). However, the combination of thinning to remove midstory trees and reduce overstory density along with periodic fire to stimulate ground cover and prevent the redevelopment of a midstory is an important distinction between open and closed forest management that is key to these species' responses. To this point, we have referred to these species as a group, but habitat needs do vary among them. The primary difference in habitat associations of these species is related to the amount of canopy cover in the overstory, midstory, and understory and the amount of herbaceous ground cover (Fig. 1) (Reidy et al. 2014; Roach et al. 2019). This diversity of habitat needs can be addressed across a landscape with staggered burn treatments and variations in thinning prescription. Landscape-scale approaches to burning can also create a natural diversity in structure as fire burns across different landforms. Strong responses by disturbance-dependent birds exist in large landscape burns (Roach et al. 2019). However, birds are mobile and do respond to stand-level treatments if imbedded in a larger landscape dominated by open and closed forest (Kendrick et al. 2015). Habitat management for birds generally focuses on vegetation structure but there are potential reasons why the composition may also be important. For example, Eastern Whip-poor-will (*Antrostomus vociferus*) and Chuck-will's-widow (*Antrostomus carolinensis*) are abundant in restored open forests (Thompson III et al. 2022). This may be because the open structure of savanna and woodland facilitates these birds' nocturnal foraging and mating displays. However, pollinators are important prey for these birds and their abundance may be linked to ground flora composition in open forests.

Open forest birds and pollinating insects intrinsically interact requiring the restoration of ecosystems that that promote a diverse and abundant ground flora. Many studies cite pesticide use, climate change, and disease to population reductions in multiple pollinating species (Goulson et al. 2015; Koh et al. 2016). However, habitat loss may be the most significant (Potts et al. 2010). Densification of open forests with concomitant reductions in insect-pollinated herbaceous flora is likely contributing to these pollinator declines (Potts et al. 2010; Hanula et al. 2015). Few studies explicitly link open forest restoration to outcomes for native pollinators and the response of bees to treatments will likely vary across site conditions (Moretti et al. 2009). Further, few restoration projects are designed and managed to meet the needs of pollinators (Tonietto and Larkin 2018). However, similar to open forest birds of conservation concern, reductions in tree densities to savanna-like conditions are associated with increased native bee abundance and diversity (Breland et al. 2018). Although burning can result in immediate reductions to native bee abundance and diversity by destroying nesting habitat, fire benefits native bee by increasing the diversity and abundance of floral resources (Potts et al. 2003; Tonietto and Larkin 2018).

Guiding principles for reopening closed canopied forests:

1. Today's trees can inform us of past forest developmental and successional processes which can guide contemporary management practices.
2. Achieving the desired objectives for openness and facilitating of ground flora diversity and abundance may require reducing the density of large, pyrophytic trees.
3. A multitude of site conditions and characteristics will influence outcomes associated with reopening forests, many of these are unknown.
4. High landscape connectivity and relict conditions may hasten the recovery of open forest conditions, these sites should be considered for priority restoration.
5. Woody and invasive plant competition can be an impediment to reopening forests, challenging status quo management.
6. Herbaceous response may not meet management objectives without active intervention.
7. Early successional wildlife species of conservation concern benefit from reopening closed canopied forests, but the importance of the habitat provided is not simply attributed to the structure and composition of trees, but the diversity and abundance of the herbaceous and insect communities that are facilitated by frequent fire.

Conclusions and next steps

Reopening forests is of increasing interest and necessitates new ecological understanding, management capacity, and long-term commitment, particularly to maintaining fire regimes. Fire regimes associated with open forests are characteristically frequent and low to moderate intensity, however restoring historical fire regimes may not fully result in their historical character. In addition to frequent burning, other treatments are often needed for open forest restoration and management, especially when faced with challenges of forest mesophication and densification.

Additional research is needed to direct management across a complexity of site conditions and land use legacies. For example, how can we better control hardwood sprouting in stands actively being restored, because controlling stem densities can require high effort costs (e.g., herbicides and/or mastication) and can become too dense for the species of concern in as little as 5 years without fire? How can we maintain a mature multi-aged, open forest long-term, because current fire prescriptions may maintain ground flora but a pause in burning frequency for overstory tree recruitment may erase gains in the diversity and abundance of ground flora, especially in plants of high floristic quality? The response of ground flora and wildlife to restoration of open forests is encouraging, however, several important questions and considerations remain. For instance, how important are the characteristics of the ground flora community, because it conceivably affects higher trophic levels including insect communities that are important pollinators and prey for some species a conservation concern? As the importance of reopening forests for the conservation of ecological goods and services continues to grow, so too will the need for research and applications that acknowledge their history while adapting for their future.

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Authors' contributions

LPK made substantial contributions to the conception, design, and writing of the manuscript. DD made substantial contributions to the conception, design, and manuscript writing. MS made substantial contributions to the conception, design, and manuscript writing. FT made substantial contributions to the conception, design, and manuscript writing. JMV made substantial contributions to the conception, design, and manuscript writing. All authors have read and approved the manuscript.

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Availability of data and materials

The datasets used and/or analyzed during the current study are available from the corresponding author on reasonable request.

Declarations

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Not applicable.

Consent for publication

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Competing interests

The authors declare that they have no competing interests.

Author details

[1]Northern Research Station, USDA Forest Service, 202 Anheuser-Busch Natural Resources Building, Columbia, MO 65211, USA. [2]School of Natural Resources, University of Missouri, 203 Natural Resources Building, Columbia, MO 65211, USA. [3]Tall Timbers Research Station, 13093 Henry Beadel Drive, Tallahassee, FL 32312, USA.

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