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Can restoration of fire-dependent ecosystems reduce ticks and tick-borne disease prevalence in the eastern United States?

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Abstract

Over the past century, fire suppression has facilitated broad ecological changes in the composition, structure, and function of fire-dependent landscapes throughout the eastern US, which are in decline. These changes have likely contributed mechanistically to the enhancement of habitat conditions that favor pathogen-carrying tick species, key wildlife hosts of ticks, and interactions that have fostered pathogen transmission among them and to humans. While the long-running paradigm for limiting human exposure to tick-borne diseases focuses responsibility on individual prevention, the continued expansion of medically important tick populations, increased incidence of tick-borne disease in humans, and emergence of novel tick-borne diseases highlights the need for additional approaches to stem this public health challenge. Another approach that has the potential to be a cost-effective and widely applied but that remains largely overlooked is the use of prescribed fire to ecologically restore degraded landscapes that favor ticks and pathogen transmission. We examine the ecological role of fire and its effects on ticks within the eastern United States, especially examining the life cycles of forest-dwelling ticks, shifts in regional-scale fire use over the past century, and the concept that frequent fire may have helped moderate tick populations and pathogen transmission prior to the so-called fire-suppression era that has characterized the past century. We explore mechanisms of how fire and ecological restoration can reduce ticks, the potential for incorporating the mechanisms into the broader strategy for managing ticks, and the challenges, limitations, and research needs of prescribed burning for tick reduction.

KEYWORDS
disturbances, forest structure, mesophication, microclimate, prescribed fire, ticks

INTRODUCTION

Over the past century, long-term fire exclusion in eastern US forests has led to structural changes and cascading effects on forest conditions and processes (Nowacki & Abrams, 2008). In the absence of fire, microclimatic and compositional feedbacks have favored the dominance of fire-sensitive mesic forest species at the expense of fire-tolerant forest species (and their ecological functions) that make up fire-dependent landscapes that were historically prevalent throughout much of the eastern United States (Alexander et al., 2021; Nowacki & Abrams, 2008). These feedbacks, known as the mesophication process, have been widely observed across the eastern United States (Alexander et al., 2021; Nowacki & Abrams, 2008). Fire-dependent landscapes or their remnants overlap substantially with current ranges of many tick species, and the degradation of these landscapes through long-term fire suppression and mesophication has likely contributed overlooked mechanisms toward the increases of tick populations and transmission of their diseases to humans, which can be reversed through landscape restoration with prescribed fire.

Shifts in relative abundance from xeric to mesic forest assemblages relate directly to the dampening and cooling of forest microclimates and reduction in forest disturbance processes (Alexander et al., 2021; Nowacki & Abrams, 2008; Vander Yacht et al., 2019). This dampening and cooling occurs over time in the absence of fire, which otherwise promotes a fast drying environment that is favored by fire-tolerant species whose litter absorbs and retains less moisture than that of fire-intolerant species (Kreye et al., 2013; Kreye, Varner, et al., 2018). Vertical and horizontal gaps in forest structure created by frequent fire also promote drying through increased air flow and solar heating at the forest floor. Conversely, mesophication in the absence of fire increasingly promotes stabilization of moderate forest temperatures and humid microclimate conditions (Nowacki & Abrams, 2008) as well as greater moisture retention in forest litter (Kreye, Hiers, et al., 2018; Kreye, Varner, et al., 2018) that effectively reduces environmental stress on ticks and optimizes questing conditions. Collectively, these changes have increased key conditions in the eastern United States known to drive tick abundance, tick–wildlife host interactions, and the geographic range expansion of ticks (Sonenshine, 2018).

Prescribed (planned) fire is a primary tool for reversing mesophication and maintaining restored fire-dependent ecosystems via restoring the fundamental disturbance process that maintains composition (Dems et al., 2021), structure (Skowronski et al., 2020; Warner et al., 2020), and function of fire-dependent ecosystems (Clark et al., 2018). Benefits of prescribed fire are often cited as wildfire hazard mitigation, invasive species control, and wildlife population restoration (Hiers et al., 2020; Varner III et al., 2005); however, prescribed fire can also create and maintain reductions in tick populations (Davidson et al., 1994; Gleim et al., 2014, 2019). Prescribed fire differs markedly from wildfire in that it is planned and applied in a controlled manner for specific purposes, with a research-based knowledge of fire behavior and effects, but can serve as a surrogate for natural wildfires (Hiers et al., 2020). While prescribed burning is often viewed as an exclusively rural activity, it is also conducted in suburban and urban areas where humans are most likely to encounter ticks. Every state in the continental United States has at least one form of a prescribed fire program that collectively treats about 3–4 M ha per year, or about twice the area annually burned in wildfires (Melvin, 2018, 2020), representing a strong existing capacity and legislative foundation to conduct and increase prescribed fire. Despite this general capacity, the potential for prescribed burning remains unmet in most regions owing to operational, legal, or social impediments that include insufficient funding and staffing, liability, narrow burn windows, and laws and regulations (Kobziar et al., 2015; Melvin, 2018; Quinn-Davidson & Varner, 2012).

The mechanistic contributions of long-term fire suppression to the continued expansion of medically important tick species in landscapes of the eastern United States remain poorly articulated in the literature, as does the potential for landscape restoration as a component of the solution to this problem. In this review, we explore the potential to reduce medically important ticks and tick-borne pathogen transmission through the restoration of xeric, fire-dependent forest ecosystems with prescribed fire. We provide a context of historic environmental and cultural shifts, including the dramatic reduction in either natural or anthropogenic fire and corresponding shifts in forest conditions in the eastern United States, that have fostered increased tick abundance and pathogen transmission. We then describe the need to revise the current tick mitigation strategy that focuses responsibility on individual tick prevention with the incorporation of ecologically holistic strategies. We then provide supporting evidence for the use of prescribed fire as a mechanistically sound and culturally viable approach to reducing pathogen transmission rates while restoring ecosystem health. We highlight the feasibility of prescribed fire as a management tool for controlling tick habitat and populations on the grounds that prescribed fire is a broadly acceptable management tool presently used to manage an average of 2.6 M ha annually in the eastern United States. Finally, we outline research needs and limitations of prescribed burning as a restoration tool to better inform the application of prescribed fire to reduce tick populations.

TICK AND TICK-BORNE DISEASE EXPANSION

Tick-borne diseases presently account for over 75% of vector-borne disease cases in the United States, with reported cases numbering 40,000–60,000 per year (Rosenberg et al., 2018). Conditions enabling this have resulted from climate change (Eisen et al., 2016; Linske et al., 2019), growth of specific wildlife populations (Ostfeld et al., 2006), and land-use change (e.g., the conversion of agricultural lands [Barbour & Fish, 1993]), and presumably forest change due to the decline of fire frequency and the conversion of burned xeric forests to fire-excluded mesic forests (Alexander et al., 2021). Collectively, these changes have increased the quality and quantity of habitat that favors ticks, their hosts, and tick–host pathogen transmission.

Basic ecology of medically important ticks of eastern United States

To fully understand the expansion of ticks and their pathogens in the eastern United States, as well as potential solutions to this problem, it is necessary to understand aspects of tick life cycles that drive interactions with their environments and other organisms. Forest-dwelling ticks that are most associated with humans and animals in the eastern United States follow a multistage, 2-year life cycle, including egg, larva, nymph, and adult stages. Each life stage requires a bloodmeal from a vertebrate host to complete metamorphosis and for egg development (Anderson & Magnarelli, 2008; Sonenshine & Roe, 2013). These ticks have asynchronous phenology among species and geographic regions, with lags between peak adult, nymphal, and larval periods, resulting in seasonal variation in tick interactions with wildlife and humans, as well as susceptibility to environmental stressors and mitigation approaches (Anderson & Magnarelli, 2008; Ogden et al., 2004; Sonenshine & Roe, 2013; Stromdahl et al., 2014). Species, life stage, and environmental conditions like air temperature, soil temperature, humidity, and time of day influence tick behavior and vertical positioning in the vegetation profile. When seeking hosts for feeding, or "questing," ticks climb from moisture-rich soil or leaf litter that protects them from desiccation to increase odds of encountering a host (Anderson & Magnarelli, 2008; Sonenshine & Roe, 2013). Desiccation is a major cause of mortality among ticks and higher ambient humidity, and moderate temperatures thus support longer questing periods (Anderson & Magnarelli, 2008; Sonenshine & Roe, 2013). Tick susceptibility to desiccation varies with species; but in general larvae are most vulnerable, with nymphs and adults becoming increasingly tolerant of dryness. Insufficient temperature and moisture can also be detrimental to molting success (Burtis et al., 2019; Ogden et al., 2004).

The most common, medically important ticks of the eastern United States are *Ixodes scapularis* (blacklegged tick), *Amblyomma americanum* (lone star tick), and *Dermacentor variabilis* (dog tick). As the carrier of *Borrelia burgdorferi*, the causal agent of Lyme disease, *I. scapularis* is the most notorious tick of the eastern United States (Burgdorfer et al., 1982). *I. scapularis* can also transmit pathogens to humans that cause babesiosis, anaplasmosis, Borrelia miyamotoi disease, ehrlichiosis, Powassan virus disease, and deer-tick virus. *A. americanum* can transmit the pathogens that can cause tularemia, and is presumed to be to be responsible for alpha-gal syndrome and the transmission of the highly fatal Heartland virus and Bourbon virus diseases. Another tick, *D. variabilis*, transmits Rocky Mountain spotted fever and tularemia. Other prominent ticks that transmit pathogens of human diseases in the region include *A. maculatum* (Gulf Coast tick) and *Ornithodoros turicata* (relapsing fever tick). *Haemaphysalis longicornis*, an invasive tick discovered in New Jersey in 2017 that has spread throughout much of the eastern United States, causes additional concern because it can carry *Theileria orientalis*, a pathogen fatal to livestock with no approved treatment in the United States (Egizi et al., 2020).

Wildlife hosts are critical in the cycles of ticks and tick-borne diseases because ticks acquire pathogens when feeding on a pathogen-carrying host (also known as a reservoir species or competent host). Except in rare cases of maternal pathogen transmission to larvae, only nymph and adult ticks tend to transmit diseases among hosts. Mice in the genus *Peromyscus*, primarily *Peromyscus leucopus noveboracensis* (white-footed mouse), are important wildlife hosts of ticks in the eastern United States, especially *I. scapularis*, and serve as key reservoir species for the pathogens that cause Lyme disease, anaplasmosis, babesiosis, Borrelia miyamotoi disease, Powassan encephalitis virus/deer tick virus, and presumably one form of Ehrlichiosis (Tsao et al., 2021). *Tamias striatus* (eastern chipmunk), *Sorex cinereus* (masked shrew), and *Blarina brevicauda* (short-tailed shrew) are also important hosts of *I. scapularis* and are also reservoirs for the pathogens that cause Lyme disease, anaplasmosis, and babesiosis (Ostfeld et al., 2018). While not an important reservoir species, *Odocoileus virginianus* (white-tailed deer) amplifies *I. scapularis* and *A. americanum* populations (Kilpatrick et al., 2014; Paddock & Yabsley, 2007). *Meleagris gallopavo* (wild turkey) and *Procyon lotor* (racoon) are also not considered reservoir species but can amplify *A. americanum* (Kollars Jr et al., 2000).

Numerous other mammals and birds also serve as lesser important amplification hosts or competent hosts (Tsao et al., 2021).

Landscape changes as drivers of tick populations

Landscape change and multiple associated effects have likely been drivers of changing tick abundance and pathogen transmission over time in the eastern United States. Since European settlement, the landscapes of the eastern United States have experienced multiple, broad-scale vegetation changes because of anthropogenic activities that have had marked impacts on key habitat conditions that ticks, their hosts, and tick–host interactions depend upon. Prior to European settlement, open forested landscapes of pine, oak, and chestnut were frequent throughout the eastern United States and favored xeric (dry) forest conditions with frequent low to moderate intensity fire (Hanberry et al., 2018, 2019). Forest litter composition, open forest structure, and the presence of frequent fire on the order of approximately 1–50 years either by anthropogenic or natural ignitions would have favored dry microclimatic conditions and diminished litter layers (Alexander et al., 2021; Hanberry et al., 2018, 2019) that would have reduced the frequency of suitable moisture and temperature conditions for ticks, limiting their activity, interaction with reservoir hosts, and overall population success prior to European settlement.

Following European settlement, intensive deforestation in the form of agricultural land clearing and timber extraction further reduced the favorability of eastern landscapes for ticks by enhancing the open, xeric conditions across landscapes (Houghton & Hackler, 2000). This pattern of deforestation was perpetuated through the mid-late 1800s and was often supplemented by frequent intentional or unintentional anthropogenic burning (Larsen, 1955; Stambaugh et al., 2018) at rates that can reduce ticks (Gleim et al., 2019). By the early 20th century, habitat destruction and overhunting caused the decimation or local extinctions of key competent and amplification hosts of ticks in the eastern United States, particularly of *O. virginianus* and *M. gallopavo* (Earl et al., 1990; Vercauteren et al., 2018). The detrimental impacts of chestnut blight in the early 1900s on *Castanea dentata* (American chestnut) mast production further contributed to the reduction in key tick hosts by nearly halving *P. leuocopus* and *T. striatus* populations (Dalgleish & Swihart, 2012). Although direct data of tick pathogen transmission rates prior to the mid-late 1900s are unavailable, these regional-scale changes in tick habitat quality and host populations would likely have severely reduced tick populations and the transmission of their pathogens through the early 1900s until favorable conditions rebounded.

Beginning in the late 1800s and early 1900s, major land-use changes and cultural interest wildlife conservation catalyzed a long-term rebound of tick habitat and host conditions in the eastern United States that has continued through the present day. Major shifts from wood fuel and to coal and other fuels and to the extraction of timber from other parts of the country diminished the need of timber in the degraded eastern forests and spawned the reversal of long-term deforestation activities through passive afforestation (Houghton & Hackler, 2000). Decades later, agricultural abandonment following the Second World War contributed an important second wave of passive afforestation throughout region (Houghton & Hackler, 2000). At the same time, improved organization and mechanization of wildfire suppression and a new cultural rejection of controlled burning catalyzed the *fire-suppression era* that has continued to limit fire on most eastern landscapes, despite its critical ecological importance (Houghton & Hackler, 2000; Nowacki & Abrams, 2008). Collectively, these changes have also catalyzed a rebound or amplification in habitat for ticks and competent hosts, which have rebounded prolifically (Barbour & Fish, 1993; Cronan et al., 2015; Earl et al., 1990; Tsao et al., 2021). Conversely, multiple top predators of these species from near or complete extirpation prior to the 1900s, further enabling key wildlife hosts of ticks to proliferate and support the tick cycle (Glick, 2014; Rose, 2015).

In the past 50 years, additional land-use change in the form of residential and commercial development has resulted in forest fragmentation that has further enhanced favorable conditions for the expansion of tick-borne diseases. Fragmentation has led to an abundance of forest edge habitat and small forest patch size, which strongly favors the concentration of *P. leuocopus* and *I. scapularis* populations, as well as high infection rates of *B. burgdorferi* among hosts (Allan et al., 2003; Brownstein et al., 2005). Fragmentation has also enabled the proliferation of large host populations that amplify tick populations by limiting the potential for the recovery of predators that require large unbroken tracts of land, such as eastern bobcats (Litvaitis et al., 2015) and cougars (Glick, 2014). It has also been theorized that fragmentation reduces host diversity and preselects for rodent hosts known to amplify tick-borne pathogens in the environment (Ostfeld & Keesing, 2012), although this concept remains debated (Linske et al., 2018).

FIRE SUPPRESSION AND MESOPHICATION AS DRIVERS OF THE RISE OF TICKS

Frequent fire has had a prolific role in North American cultures and forests for many millennia; despite this, recent regional-scale fire suppression and mesophication trends over the past century have remained overlooked as important factors in the rise in ticks. Early evidence of intentional, broad-scale burning in the Americas dates to ca. 5000 years ago (Delcourt et al., 1993; Delcourt & Delcourt, 1997) and was fairly continuous in the eastern United States, with a few exceptions, until around the past century when the fire suppression era began (Nowacki & Abrams, 2008). Fire scars in tree ring samples obtained from throughout much of the region chronicle the frequent yet low- to moderate-intensity fire in eastern landscapes during the centuries leading up to the fire-suppression era and highlight the role that both indigenous and colonial populations played in maintaining frequent fire in many eastern landscapes (Guyette et al., 2006; Lafon et al., 2017; Stambaugh et al., 2018). Tick control as a benefit of frequent burning was noted in historical accounts as early as the mid-1700s from the Delaware Bayshore area of the eastern United States (Larsen, 1955) and as late as the early 1900s in the southeastern United States immediately prior to the fire-suppression era (Shea, 1940; Stoddard, 1969). Since the fire-suppression era, however, fire has been reduced by at least 90% across the northeast (Brose, 2014; Fahey & Reiners, 1981; Forman & Boerner, 1981), with fires now occurring less than once every 50 years where they had commonly occurred at intervals of 1–25 years (Stambaugh et al., 2013, 2018).

As the fire suppression era has progressed, mesophication has gradually contributed to changes in forest composition, structure, and microclimate throughout landscapes of the eastern United States (Alexander et al., 2021; Nowacki & Abrams, 2008). Intensive fire suppression as a policy formed as a response to a singular perspective that wildfires and controlled burning alike reduced timber production rates and value (Fowler & Konopik, 2007). Prior to this, frequent low- to moderate-intensity fire was a dominant, long-term driver of open-canopy xeric forests, which we suggest were less favorable to ticks. Although these forests have sharply decreased in abundance as a result of fire suppression and mesophication (Alexander et al., 2021; Hanberry & Abrams, 2018), growing social acceptance of the numerous benefits of fire and fire-dependent ecosystems of the eastern United States offers the opportunity to reduce tick populations while restoring and maintaining fire-dependent ecosystems with prescribed fire (Kobziar et al., 2015; Quinn-Davidson & Varner, 2012).

Mechanistically, mesophication produces an excellent environment for ticks by driving shifts in forest structure and density that stabilize forest moisture and temperature regimes that gradually feedback with forest regeneration processes to perpetuate those conditions (Kreye et al., 2013; Kreye, Varner, et al., 2018). Without the consumptive effects of fire, deep litter layers and woody debris accumulate over time (Clark et al., 2015; Nowacki & Abrams, 2008), and tall, woody understory vegetation grows dense and outcompetes grasses and forbs (Lacki et al., 2016; Skowronski et al., 2020). These changes drive understory moisture retention and stabilization as well as temperature stabilization (Iverson & Hutchinson, 2002) within the ideal range for tick survival and questing (Schulze et al., 2002). Accumulation of litter through time also increases soil moisture retention and moderation of soil temperature conditions (Iverson & Hutchinson, 2002) because shifting species of the leaves that compose the litter gradually play an increasing role: mesic species' leaf litter retains more moisture and for longer (Kreye, Varner, et al., 2018). Over time, these moisture conditions feed back with shifts in overstory tree composition that enhance cool and moist understory conditions and compositional shifts that resist reversion to previous xeric conditions (Nowacki & Abrams, 2008).

Specific habitat changes resulting from mesophication that favor tick survival, activity, and pathogen transmission with hosts can be profound. Litter of forests that have experienced partial or full mesophication have approximately twice the moisture holding capacity and moisture retention time as litter from xeric forests, even when mixed with xeric litter (Kreye et al., 2013; Kreye, Varner, et al., 2018), and thus can play an important role in buffering ticks from droughty conditions that restrict questing and incur mortality (Berger et al., 2014). Similarly, increased evapotranspiration, shading, and the physical structure of dense forest vegetation within the lower levels of the forest inhabited by ticks also drives moist conditions in the questing environment. This is of key importance because even short-term periods of low moisture availability can have large consequences on tick populations (Berger et al., 2014).

Suboptimal temperatures limit periods of tick activity and can pose a significant risk of mortality. Denser vegetation and increased soil organic matter that result from mesophication moderates consistent understory and soil temperatures (Nowacki & Abrams, 2008) needed by tick eggs and molting ticks to survive when they are most vulnerable (Burtis et al., 2019). Temperature is also an important limitation for winter questing activity of ticks and can cause mortality through freezing or by incurring energy usage (Burtis et al., 2019; Linske et al., 2019); however, dense forest vegetation insulates the forest understory and soil and promotes longer duration of snow cover, which provides additional insulation to the soil.

Beyond moderating microclimate, the dense forest structure of mesophied forests facilitates other aspects of the tick pathogen cycle. Strong positive correlations have been observed between tick abundances (*I. scapularis* and *A. Americanum*) and forest canopy cover, presumably due to the stabilization of moisture availability in the tick environment (Ginsberg et al., 2020) but also due to the creation of abundant opportunities for ticks to vertically position themselves with the body heights of mammal hosts (Goddard, 1992; Mejlon & Jaenson, 1997; Tsunoda & Tatsuzawa, 2004). This is complemented by *O. virginianus* preferential use of dense understory vegetation for concealment (Kroeger et al., 2020) and thermoregulation (Wiemers et al., 2014).

A NEED TO REFORM TICK MANAGEMENT AND THE OPPORTUNITY OF PRESCRIBED FIRE

It is unlikely that current strategies will succeed in stemming increased rates of tick-borne pathogen transmission to humans, and therefore, a re-evaluation of integrated tick management approaches and tick management responsibility is required (Eisen & Stafford, 2020). Current and developing tick management approaches focus on managing wildlife hosts with mechanical, viral, and gene-editing approaches or by managing ticks through spraying habitat-wide acaracides and fungal pathogens of ticks. Although successful in certain situations, broad-scale application and success of these approaches tend to be limited by the diversity of physical and behavioral traits of tick vectors, variable (and sometimes questionable) efficacy or treatments, or the insufficient application of these approaches. Public receptions, cost, and other scientific and societal constraints have also been important limitations for broad-scale tick management approaches (de la Fuente, 2018; Esteve-Gassent et al., 2016). For instance, at this time, the only environmentally based, broad-scale methods capable of reducing the three most dangerous ticks, *I. scapularis*, *A. maculatum*, and *D. variabilis*, is the broadcast use of acaricides or fungi to kill ticks; however, acaricides are environmentally unsustainable for repeated use and can have limited efficacy in reducing human exposure (Eisen & Stafford, 2020).

The current paradigm for tick-borne disease control essentially divides tick-borne disease control into two prongs, tick bite prevention and tick management, but is problematic in its current form. This paradigm has continuously placed nearly all the burden of controlling tick-borne pathogen exposure on the individual through tick bite prevention, while the responsibility of broader-scale tick management by professionals has remained nebulous, weakly organized, and poorly applied at scales broad enough to stem increases in tick-borne pathogen transmission, despite the fact that this is a public concern (Eisen & Stafford, 2020). Actions of individuals, like homeowners, are extremely unlikely to have a significant effect on this complex regional-scale problem; however, at the same time, there is a lack of vector control agencies to accept responsibility for organizing and implementing broad-scale tick control management, so broad-scale tick control measures are almost nonexistent (Eisen & Stafford, 2020). This comes in stark contrast to the long-existing paradigm for mosquito control, in which management responsibility is placed on the community to apply broad-scale control measures (Piesman & Eisen, 2008).

A successful revision of the current paradigm can maintain the multipronged approach but will require organization and responsibility beyond the individual to conduct broad-scale, environmentally sustainable, and culturally acceptable integrated pest management approaches (Eisen & Stafford, 2020). Employing the US Centers for Disease Control and Prevention's One Health approach to the tick problem, a holistic approach would be multidisciplinary and multifaceted, with a consideration of the ecology, physiology, and behavior of ticks and their hosts in their environments (Esteve-Gassent et al., 2016; Reaser et al., 2021). Such an approach favors ecological restoration and maintenance as a means of vector control for the benefit of public health (Reaser et al., 2021).

Noting that, (1) there is currently no broadly applicable tick reduction approach available, (2) there is a need for approaches that can be readily applied by professionals and management organizations, and that (3) successful tick management should be environmentally sustainable and holistic in form, we point the reader to the role of wildland fire on eastern landscapes that has long been overlooked in the rise and fall of tick populations. We highlight that the opportunity to reduce ticks through ecological restoration of fire-dependent landscapes can integrate as a component of a multipronged strategy for tick management by leveraging (1) cultural and ecological mechanisms by which fire has historically moderated forest conditions directly related to tick habitat, (2) the standing need for restoration of ecological function in eastern forests, (3) the standing legislative and organizational capacity to conduct prescribed burning, and (4) research that supports how fire reduces ticks through multiple mechanisms.

RESTORATION OF FIRE-DEPENDENT ECOSYSTEMS WITH PRESCRIBED FIRE

Prescribed fire is the primary tool for reversing mesophication and restoring and maintaining fire-dependent ecosystems through the restoration of balance in function, community composition, and structure (Vander Yacht et al., 2019). In restoring the keystone ecological process (fire) necessary for maintaining fire-dependent landscapes, prescribed fire mimics wildfire yet differs markedly in that it is planned and intentionally implemented under predetermined conditions to achieve specific management objectives (Hiers et al., 2020). Regarding management objectives, prescribed fire leverages control of fire behavior, size, frequency, season, and intensity to achieve a diversity of ecological effects.

Scientific acknowledgment of prescribed fire as a critical tool for restoring and maintaining fire-dependent ecosystems dates to the 1920s–1940s in the eastern United States (Little & Moore, 1949; Stoddard, 1936). This approach has been successfully used to rehabilitate forest overstory structure and composition (Varner III et al., 2005), understory composition and diversity (Vander Yacht et al., 2020; White et al., 1991), and threatened and endangered wildlife habitat (Gruchy & Harper, 2014; Lacki et al., 2016), which can have profound impacts on the habitats of ticks and their hosts. The effects of prescribed fire can also improve groundwater quality and recharge (Hahn et al., 2019), mitigate fuel conditions that can prime for catastrophic fire conditions (Fulé et al., 2000), and increase landscape resilience to insect outbreaks and disturbances (McNichol et al., 2019).

Mechanistically, fire and fire feedbacks provide many direct functions in forest ecosystems by consuming vegetation, thereby modifying the layers of vegetation and detritus structurally, compositionally, or chemically. The primary effects of fire include cycling nutrients (Quigley et al., 2020), altering vegetation structure (Knapp et al., 2015; Warner et al., 2020), stimulating seed production or release (Lamont et al., 2020), and preparing substrates for germination for certain species (Sharpe et al., 2017). Fires can also damage and kill vegetation, depending on a variety of factors, and impact competitive advantages. By consuming and killing vegetation, fire can efficiently reduce woody vegetation density and enhance vertical and horizontal gaps and structural diversity at the landscape scale (Skowronski et al., 2020; Vander Yacht et al., 2020; Warner et al., 2020). Secondary effects of these changes include shifts in microclimate, improved habitat space and food sources for certain wildlife (Patterson & Knapp, 2018; Stephens et al., 2019), and diversification of understory native woody species, herbs, and graminoids that require more open-canopy conditions and become excluded by fire exclusion and mesophication (White et al., 1991; Vander Yacht et al., 2020). Collectively, these effects of fire tend to eliminate mesic overstory competitors while stimulating recruitment of native fire-tolerant oaks and pines and drive open, dry, and warm conditions as forest, woodland, and savanna communities (Nowacki & Abrams, 2008; Vander Yacht et al., 2019).

The *ecology of fuels* concept ties together the mechanistic importance of fire in restoring and maintaining fire-dependent eastern landscapes in its emphasis of the connections between fuel (e.g., vegetation) properties and fire properties and the feedbacks between them (Mitchell et al., 2009). Fuels not consumed in one fire serve as a resultant fuel structure, whereas other fire effects drive changes in microclimate, composition, and patterns of fuel redevelopment, ultimately influencing the character of the next fire. Though this feedback tends to enhance forest floor flammability through detrital composition and moisture balance (Kreye, Varner, et al., 2018; Mitchell et al., 2009; Quigley et al., 2021; Vander Yacht et al., 2019), at the same time it diminishes the potential for high-intensity or uncontrollable fire by reducing canopy density and the vertical fuel continuity between surface and canopy fuel layers of the forest (Clark et al., 2020; Warner et al., 2020).

Although the fire suppression era persists in many parts of the United States, fire has been successfully reintroduced as prescribed fire to a growing of number fire-suppressed landscapes in recent decades. Prescribed burning has been most successfully adopted and culturally accepted in the southeastern United States, which presently conducts approximately 50,000 prescribed fires annually across 2.8 M ha (2017–2019 average) (Melvin, 2018, 2020). Although the northeast treats substantially less area (138,402 ha on average, 2017–2019) (Melvin, 2018, 2020), surveys (Smithwick et al., 2020) and legislation on increasing prescribed burning (Pennsylvania Prescribed Burning Practices Act 2009, Prescribed Burn Act of New Jersey 2018) reflect shifting public and policymaker perspectives in the region in favor of prescribed fire. This reflects a growing desire to restore fire-dependent landscapes with prescribed fire for multiple objectives whose effects could include or be directed at reducing ticks and tick-borne disease.

PRESCRIBED FIRE AS A CONTROL FOR TICK POPULATIONS

Various studies have found that prescribed fire has been successful at reducing ticks of the eastern United States, including *I. scapularis* (Gleim et al., 2014, 2019; Hodo et al., 2020; Stafford et al., 1998; Wilson, 1986), *A. americanum* (Davidson et al., 1994; Gilliam et al., 2018; Gleim et al., 2013, 2014, 2019; Hodo et al., 2020; Willis et al., 2012), *A. maculatum* (Scifres et al., 1988), and *D. variabilis* (Gleim et al., 2014). This response is the result of direct and indirect impacts of fire that reduce ticks or alter local community dynamics of other organisms that ticks interact with (Figure 1). Here we cover those effects in detail.

Direct effects of fire on ticks: Mortality via heating

Heat exposure from the combustion of forest detritus and vegetation serves as the direct, initial mechanism of mortality to ticks from prescribed fires. Combustion of forest fuels (e.g., the detritus and vegetation that compose tick habitat) occurs in two forms, as either flaming or intermittent flaming and smoldering combustion, which are dictated largely by moisture content (Kreye, Varner, et al., 2018; Thomas et al., 2014), fuel structure and loading properties that affect oxygen availability proximal to combustion (Mueller et al., 2018; Thomas et al., 2014), and species (Kreye, Varner, et al., 2018). These forms of combustion are important because they often determine which layers of the forest environment will be impacted and, thus, the balance of impacts on questing and refuge portions of tick habitat. Flaming combustion occurs at and above the surface of the detrital layer and releases energy as a combination of convective and radiative heat transfer, primarily impacting the aboveground portions of vegetation and the upper portion of the soil organic layer. This affects questing ticks and their habitat, but not necessarily nonquesting ticks. Alternatively, intermittent flaming and smoldering combustion occurs primarily within detrital and soil organic materials where oxygen is limited and heat transfers primarily as radiative energy deeper into the soil (Kreye et al., 2020). These forms of combustion are driven largely by vegetation characteristics that also relate to the quality of tick habitat, including forest vegetation, such as moisture content, phenology, and physical structure, and ambient conditions, which can be planned for in prescribed burning (Hiers et al., 2020; Skowronski et al., 2020).

Temperature and residence time drive tick mortality from direct heating. In a study designed to determine the potential for killing *I. scapularis* by laundering garments, 94% were shown to survive water temperatures in a range of 15–54°C, yet under exposure to drier temperatures of 54–85°C, 100% mortality was achieved within 4 min (Nelson et al., 2016). Similarly, laboratory experimentation has shown that *A. americanum* and *D. variabilis* nymphs can withstand temperatures of 46°C for at least

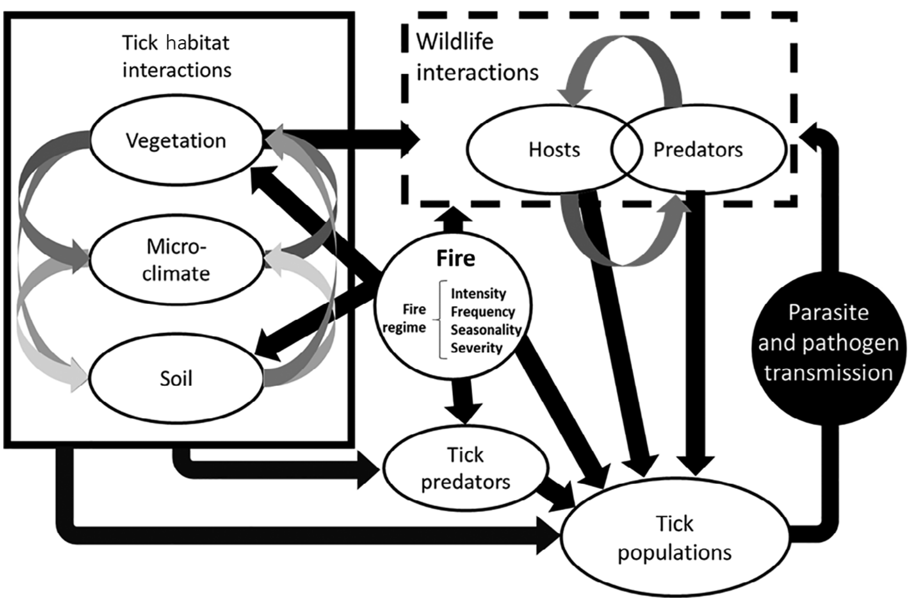

FIGURE 1 Conceptual model of fire's direct and indirect effects on tick populations. Each factor varies spatially and temporally across landscapes and regions.

1 h without detrimental effects, but temperatures above 48°C are detrimental to successful molting, and temperatures of at least 52°C for 1 h may cause complete mortality (Yoder et al., 2014). Field evidence of temperature-related mortality on ticks is more limited; however, one study found that >75% of *A. maculatum* were killed in the field in a fire where maximum fire-front temperatures reached ≥330°C (Scifres et al., 1988). This same study found that 100% mortality was achieved in the laboratory when ticks were exposed to 150–165°C for 15 s in laboratory settings.

During prescribed fires, temperatures within understory vegetation can easily peak at or above these mortality thresholds for residence times adequate to incur high levels of mortality of ticks within vegetation and detritus. For instance, during prescribed fire experiments in the New Jersey Pinelands, temperatures in understory vegetation have been shown to peak within the range of ~200–1100°C for ≥2 min in understory vegetation (Mueller et al., 2018), while elsewhere temperatures in the soil organic layer have been recorded at ≥60°C for at least 30 min in frequently burned fuels (Kreye et al., 2020) and for 1 to ≥12 h in deep accumulations of organic matter when conditions for smoldering combustion are present (Kreye et al., 2020).

Indirect effects of fire on ticks: Reduction in availability of shelter and questing space

Combustion of leaf litter and vegetation reduces shelter and questing structure in tick habitat. Reduction of detritus and understory vegetation is generally 25%–75% of understory biomass in eastern US pine and oak forests (Arthur et al., 2017; Clark et al., 2020; Mejlon & Jaenson, 1997; Prichard et al., 2017), depending on flammability (Kreye, Hiers, et al., 2018), weather (Hiers et al., 2020), ignition characteristics of unique burns (Clark et al., 2020; Skowronski et al., 2020), and other local characteristics of sites (Cronan et al., 2015). Litter cover and depth correlate positively with the abundance of *A. americanum* (Gilliam et al., 2018; Gleim et al., 2014) and *I. scapularis*, and multiple studies have linked reduction in *A. americanum* with reduction of litter from prescribed burning (Gilliam et al., 2018; Gleim et al., 2013, 2014; Willis et al., 2012), whereas mechanical litter reduction has been demonstrated to produce >70% reductions among both species (Davidson et al., 1994; Schulze et al., 1995). One exception to this in these studies, however, was *A. maculatum*, which in some instances appeared to be favored by prescribed burning and reduced litter conditions; however, the basis for this remains unclear.

Indirect effects of fire on ticks: Microclimate modification

Prescribed fire shifts forest microclimate toward a greater frequency of temperature and humidity conditions known to limit tick success and survival. Mechanistically, reductions in canopy and understory density and the creation of gap space from prescribed burning increase solar exposure (Stevens, 2017), reduce evapotranspiration (Clark et al., 2012), and increase understory wind speed (Ma et al., 2010), promoting hotter and drier understory conditions during the daytime (Iverson & Hutchinson, 2002; Refsland & Fraterrigo, 2018) and colder temperatures at night. This enhances diurnal temperature fluctuations and enables a higher frequency of moisture and temperature extremes relative to tick tolerances for behavior, development time, molting success, and overall survival (Schulze et al., 2001; Vail & Smith, 1998). Postfire remote sensing has highlighted the broad spatial scale of increased surface temperatures in burned areas, similar to a heat island effect, with spatial variability predictable by shifts in vegetation reflectance (Quintano et al., 2015). Leaf litter exposed to solar radiation in *P. palustris* forests treated with prescribed burning can peak at temperatures at least as high as 50°C and rapidly lose moisture due to large vapor pressure deficits at the litter surface, even in humid environments (Kreye, Hiers, et al., 2018). This is above the threshold at which temperature reduces *A. americanum* and *D. variabilis* nymphal molting success (48°C) and approaches the temperature (~52°C) at which 100% nymphal mortality is likely (Yoder et al., 2014). This is also well past the temperature (28°C) at which egg molting declines for *I. scapularis* and the temperature (32°C) at which *I. scapularis* larvae and nymphs fail to molt (Ogden et al., 2004). Similarly, temperatures of 32°C have been shown to cause *I. scapularis* females to produce misshapen eggs that do not hatch (Ogden et al., 2004). Other research in *P. palustris* forests indicates that average spring and summer temperatures in prescribed burned forests are frequently in excess the range of ~28–45°C and can peak as high as 55°C, well within the range of detriment to ticks at multiple life stages (Roe et al., 2017). Although limited information is available on lethal temperature thresholds for *A. americanum* and *D. variabilis* larvae, they are presumably more sensitive to environmental stress than nymphs and thus would be likely to be reduced by postfire temperature extremes. Warmer surface temperatures have been shown to persist for the entire postfire growing season or longer in burned xeric forests, though for much shorter periods in burned mesic forests (Iverson & Hutchinson, 2002; Roe et al., 2017).

In addition to amplifying temperature within tick habitat, fire impacts on vegetation and detritus can reduce temperatures in overwintering habitat past mortality thresholds. Ticks overwinter in soils that in unburned environments are buffered from freezing temperatures by the insulation of leaf litter (Linske et al., 2019). Decreased leaf litter, however, can lead to lower winter soil temperatures and may lower winter survivability for overwintering ticks (Refsland & Fraterrigo, 2018; Weise et al., 2019). Burks et al. (1996) found that temperatures of −11°C and −13°C for 2 h can result in approximately 50% mortality in a laboratory setting among *A. americanum* and *D. variabilis*, respectively. Although infrequent in forests of the eastern United States, these temperatures do occur in the northeast (Cantlon, 1953; Decker et al., 2003) and may be more frequent than in burned areas than realized. For instance, removing leaf litter during a manipulation study in Connecticut and Maine resulted in decreased winter minimum soil temperatures, which, in the absence of snow cover, resulted in periodic soil temperatures of between −10°C and −14°C (Linske et al., 2019). This reduced nymphal *I. scapularis* survivorship by an average of 25% across the 3-year study (Linske et al., 2019) and, according to Burks et al. (1996), is within the range necessary to incur substantial mortality among *A. americanum* and *D. variabilis*. Although fire was not used as the mechanism of litter removal in this instance, mechanistically it would provide a similar function and reduce soil temperatures during winter months. However, tick depth in detritus and soils in response to fire would need to be evaluated. The relevance of such effects on winter soils would obviously be limited to locations with cold enough winter conditions to impact ticks (likely at the northern margins of ticks' current ranges), and snow also insulates soil from cold winter temperatures (Linske et al., 2019). However, as the frequency of days with snow cover continue to decrease at historic rates within the eastern United States (Demaria et al., 2016), the insulating role of leaf litter on winter soils where ticks overwinter is becoming more important, especially at the northern limits of tick ranges, where they are predicted to expand.

Reductions in moisture availability, caused indirectly by fire, create an additional reduction in tick habitat quality. Tick desiccation from increased frequencies of even moderately dry periods is likely to have noticeable impacts on tick populations. Berger et al. (2014) highlighted the consistent correlation between frequency of tick-adverse moisture events (TAMEs) (e.g., >8 h at <82% relative humidity in leaf litter) and tick mortality, over 14 years in Rhode Island. Although there are limited field data specifically on the frequency of TAMEs following prescribed fire, increased vapor pressure deficits in burned areas correspond to reduced humidity and can trend for one or more growing seasons following fire (Refsland & Fraterrigo, 2018), contributing mechanistically to extended reduction in ticks following fire. Similarly, soils and litter in areas treated with prescribed fire can be notably drier than those of unburned stands (Kreye et al., 2020; Quigley et al., 2021).

Indirect effects: Increase in tick predators and reduction of host availability

Prescribed fire can promote predators of ticks and produce behavioral shifts in tick hosts. *Solenopsis invicta* (red imported fire ants) thrive in recently burned forests and prey on *A. americanum* and *A. maculatum*, thereby reducing their abundances (Gleim et al., 2013). *Solenopsis invicta* are especially quick to attack engorged *A. maculatum* nymphs but will also feed on other life stages of *A. americanum* and *A. maculatum* (Kjeldgaard et al., 2019). In response, *A. americanum* and *A. maculatum* drastically reduce their activity in the presence of *S. invicta* in an effort to go undetected, thereby reducing their time spent questing (Kjeldgaard et al., 2019). Interestingly, the presence of *S. invicta* can also reduce the behavior of rodents that ticks feed on, which serve as pathogen reservoirs, ultimately causing a reduction in tick parasitism and transmission of pathogens (Castellanos et al., 2016; Orrock & Danielson, 2004). In North America, *S. invicta* is presently limited to the southeastern United States and isolated areas of the southwest but will probably expand as far north as the Mid-Atlantic region over the next two to three decades (Korzukhin et al., 2001; Morrison et al., 2005).

Another predator of ticks, *Colinus virginianus* (the bobwhite quail), also thrives in recently burned open forests. In a multiyear regional study of counties in the southeastern United States, incidence of Lyme disease, spotted fever group rickettsia, and *Ehrlichia chaffeensis* were found to be negatively correlated with *C. virginianus* abundance, presumably due to *C. virginianus* feeding pressure on ticks (Patterson & Knapp, 2018). Although the populations of *C. virginianus* decreased substantially due to habitat degradation throughout the fire-suppression era, prescribed fire has been recognized as a critical disturbance for bobwhite quail habitat in the scientific literature for nearly 100 years (1936) and has been central in ongoing forest restoration efforts to increase populations (Gruchy & Harper, 2014; Terhune et al., 2017).

Reduced overstory and understory vegetation density and increased forest and gaps can also lead to changes in behavior and abundance of wildlife hosts as they balance tradeoffs of foraging and concealment for protection from predators. *O. virginianus* abundances have been noted to increase in recently burned areas because recovering vegetation often provides higher-quality forage than unburned areas (Main & Richardson, 2002), although females and fawns can be expected to prioritize unburned areas to improve concealment from predators (Cherry et al., 2017; Lashley et al., 2015). While it may be possible that increased *O. virginianus* usage of burned areas may bring new ticks into burned areas, multiple studies support decline in tick abundance immediately following fires (Davidson et al., 1994; Mather et al., 1993). We highlight that ticks that drop off deer into burned areas would have a reduced probability of survival, given the environmental factors described previously in this section, and hypothesize that the import and aggregation of ticks by deer in burned areas could thus actually be beneficial in decreasing the landscape-scale abundance of ticks.

Alternatively, prescribed fire can decrease abundances of some small mammal hosts of ticks. *S. cinereus*, the masked shrew, is believed to be one of the most important tick hosts in facilitating transmission of multiple tick-borne pathogens and can be reduced by prescribed fire (Ford et al., 1999; Levi et al., 2016), as can other eastern shrew species, including *B. brevicauda* (northern short-tailed shrews), *S. fumeus* (smokey shrews), *S. hoyi* (pigmy shrews), and *S. longirostris* (southeastern shrews), when fuel reductions are significant and canopy cover is reduced (Greenberg et al., 2007). Prescribed fire also reduces *Sigmodon hispidus*, the cotton rat (Morris et al., 2011), which is a reservoir host and potential pathogen amplifier of *B. burgdorferi* (Buchholz et al., 2018) and *R. parkeri* in the southeast and Mid-Atlantic (Cumbie et al., 2020). Direct mechanisms of mammal host reduction from prescribed burning remains understudied (Harper et al., 2016), including dispersal away from burns and reintroduction periods post burn. However, fire-related host reduction is likely linked to increased activity of predation, particularly from *Canis lantrans*, the coyote (Cherry et al., 2017; Jorge et al., 2020), and reduced woody plant density and downed woody debris that serve as important cover (McCay & Komoroski, 2004).

FIRE REGIME: LEVERAGING PATTERN AND PROCESS IN THE CONTEXT OF TICKS AND RESTORATION

Fire regime describes the set of characteristics and patterns of fire in an area over time, inclusive of the interactions between humans and their environments (Whitlock et al., 2010). Fire intensity, severity, seasonality, frequency, and the patterning of fire effects are characterisitcs of a fire regime and in multiple direct and indirect ways can influence habitat quality and use by ticks and their hosts in forest environments. Fire intensity specifically describes the energetic properties of heat transfer processes during the combustion of forest materials and is the primary mechanism of direct fire effects on ticks and the environment, such as injury, necrosis, or consumption. Conversely, fire severity describes the alteration of forest biomass often as loss or structure change (Keeley, 2009). Fire seasonality relates to the seasonal weather and plant phenological state during burning, which can have important interactions with floristic growth and reproductive cycles that drive direct and indirect fire effects. Fire frequency relates to the periodicity of fire occurrence, which can be considered relative to the time it takes for different species to recover or be modified from burning treatments.

Restoration of fire-dependent forest communities is a process rather than a single event and can be thought of in the context of two phases, restoration and maintenance, with differing fire regime requirements. In the restoration phase, fire regime characteristics are leveraged specifically to reduce fire-intolerant species, reduce vegetation density, reduce detritus, increase solar radiation in lower levels of the forest, increase soil exposure, and regenerate fire-adapted species. Meeting restoration objectives can require dramatic change in forest conditions that directly drive direct negative changes in tick habitat as described in previous sections. However, once restoration has been achieved, the maintenance phase of restoration differs and aims to resist encroachment of fire-intolerant invader species, regenerate fire-dependent species, maintain an open forest structure and microclimate, maintain soil and solar exposure in the understory, and maintain wildlife habitat. In accomplishing this second set of goals, prescribed fire's role is more subtle than that of the restoration phase but sustains changes in tick habitat, as well as host and predator conditions, in addition to direct tick reduction during prescribed fire events.

The silvicultural value of fire regimes driving forest composition has been a prominent focus in eastern fire ecology literature and is beyond the scope of this review. We focus instead on how fire regime characteristics can be considered in the planning, implementation, and evaluation of prescribed burning for tick management in the context of forest restoration and maintenance.

Fire intensity and severity

Fire intensity and severity are common descriptors of fire regime that are each informative but often confused in meaning, which has led to poor characterizations of fires and interpretations of their effects (Keeley, 2009). Fire intensity, particularly heat flux, describes the quantity of energy transmitted via combustion to the soil, vegetation, and the ambient environment. Fire severity refers to the physical effect fire has on vegetation and soil given interactions between fire intensity, plant characteristics and phenological state, and environmental factors (Keeley, 2009). Fire intensity is largely dependent on fuel loading (i.e., the mass of forest fuels), fuel condition (e.g., porosity, structure, chemistry, and moisture), weather, and ignition pattern, and thus frequent burning typically reduces the possible range of intensity for subsequent fires (Clark et al., 2020; Linn et al., 2020). However, the increased moisture and reduced flammability properties of litter in mesophied forests of the eastern United States can challenge efforts to achieve sufficient fire intensity to create necessary fire effects (Alexander et al., 2021; Kreye, Varner, et al., 2018). Thus, where achieving desired fire intensity is challenged by mesophitic fuel conditions, fire managers may need to utilize complex ignition patterns to achieve greater intensity or, alternatively, may find greater opportunity by focusing on seasonally dependent weather conditions and plant phenological states that maximize damage to targeted species (Knapp et al., 2009; Linn et al., 2020).

Fire frequency

Fire frequency, the rate at which fire recurs at a location, is critical for restoring and maintaining fire-dependent forests as well as reducing ticks. Davidson et al. (1994), Gleim et al. (2014), and Gleim et al. (2019) show that repeated burning can have significant effects on tick populations lasting for at least 2 years, despite several other studies that suggest ticks recover within 1–2 years (Mather et al., 1993; Willis et al., 2012; Wilson, 1986). As Gleim et al. (2014) pointed out, these studies that fail to identify a reduction in ticks did not represent real-world management conditions, using single burns in unrealistically small areas (<1–15 ha) that were previously unburned. In contrast, the majority of area burned in the eastern United States is treated at scales of dozens to thousands of hectares at a time (Gleim et al., 2014; Nowell et al., 2018; Skowronski et al., 2020) with the knowledge that the cumulative effects of repeated burning are critical to modifying and maintaining structure and composition (Dems et al., 2021; Warner et al., 2020). These cumulative effects of prescribed burning are important for forest restoration and maintenance, as well as tick control, because they gradually reduce vigor among sprouting species, reduce woody vegetation density, and shift the competitive advantage toward fire-dependent species (Hutchinson et al., 2012). This iteratively reduces the moisture retention of soil and litter (Burton et al., 2011; Clark et al., 2015; Quigley et al., 2021) and promotes the warmer and drier conditions that limit ticks and favor fire-adapted species (Knapp et al., 2015; Peterson & Reich, 2001; White et al., 1991).

Though frequent burning can be critical for reducing forest structure and eliminating competition, too much burning can impede desirable regeneration (Hutchinson et al., 2012; Reilly et al., 2017). We suggest that adjustments of fire return intervals within a range of 1–20 years may be appropriate for different restoration and maintenance phase objectives. This is based on recommended return intervals to maintain open forest structure, reduced vegetation density, and regeneration of fire-tolerant eastern oaks and pines (≥3–16 years) (Peterson & Reich, 2001; Warner et al., 2020); reduced litter and shrubs that provide refuge and questing structure for ticks (1–14 years) (Clark et al., 2015); diverse and dispersed understory flora (1–4 years) (White et al., 1991; Burton et al., 2011); and hazard reduction (1–10 years) (Kobziar et al., 2015). These are within the range of historic fire frequencies common to the region prior to fire suppression (~1–18 years depending on location, see Figure 2) (Guyette et al., 2006; Stambaugh et al., 2018). However, low-impact fires that produce little change in vegetation density, soil, and microclimate conditions are unlikely to achieve restoration or maintenance objectives, even when repeated (Hutchinson et al., 2005).

Fire seasonality

Seasonality of fire describes the phenological conditions of burning that mechanistically drive fire effects on flora, fauna, and their environment and will affect the balance of direct and indirect effects on ticks. Seasonal variation in weather conditions drives heterogeneity in fire intensity and plant susceptibility, resulting in diverse ecological effects on vegetation. Similarly, the phenology of tick activity dictates tick location within the environment and susceptibility to direct mortality from fire but is typically asynchronous between species and regions. Dormant and growing seasons are the coarsest descriptors of fire seasonality, although this does not preclude more nuanced definitions of burning seasons. The majority of prescribed fires have typically occurred in the dormant season in this region when cool air temperatures and cold damp soil reduce the potential for plant injury and stored carbohydrates in roots are ready to aid in recovery from burning while helping to protect from above- and belowground injury to plants (Guyette et al., 2006; Reilly et al., 2017).

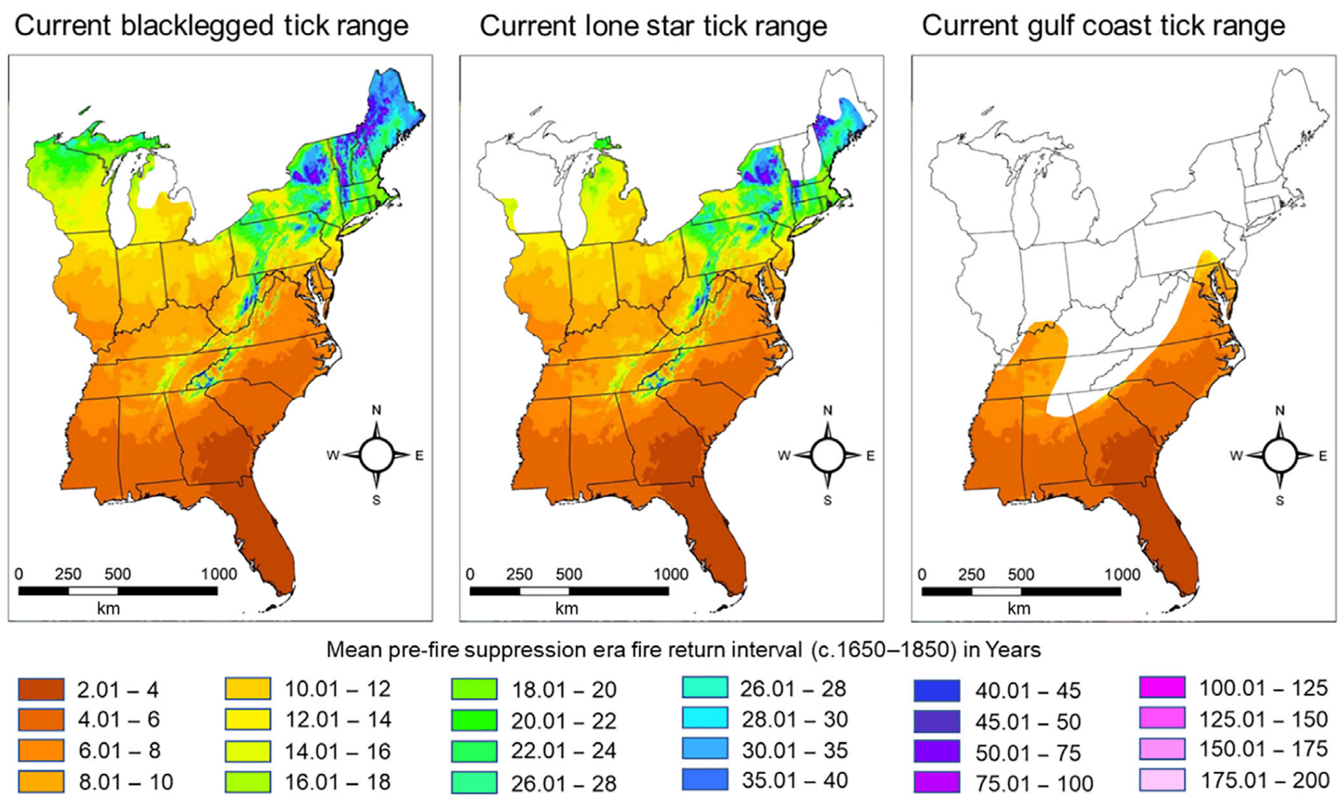

FIGURE 2 Mean fire return intervals before fire-suppression era (Guyette et al., 2012) within current ranges of blacklegged tick (Eisen & Eisen, 2018), lone star tick (Monzón et al., 2016), and gulf coast tick (Sonenshine, 2018). Present fire return intervals in much of these ranges exceed 50–100 years except where landscape-scale prescribed fire programs exist (Nowacki & Abrams, 2008; Stambaugh et al., 2018).

Dormant-season burning can typically achieve maintenance phase objectives, but repeated burning, aggressive prescriptions, or firing techniques that drive fires of greater intensity may be required to achieve more dramatic effects necessary to meet restoration objectives and directly impact ticks during the dormant season (Clark et al., 2020; Skowronski et al., 2020; Warner et al., 2020). Alternatively, growing-season fires may allow more precise targeting of specific questing ticks and can be aligned with plant phenology to achieve specific regeneration or reduction objectives (Reilly et al., 2017; White & Gaff, 2018). Thus, planning burning to coincide with conditions that target specific ticks and life stages or ecological effects on tick habitat is important for achieving desired outcomes and may require nuance in planning that focuses on target organism phenology.

Spatial variation

Heterogeneity of fire regime characteristics within or between discrete areas can be complex and can be influenced by ignition sources, such as lightning and anthropogenic sources (Cattau et al., 2020; Stambaugh et al., 2018), social constraints or influences on prescribed fire application patterns (Kobziar et al., 2015; Lee et al., 2019), effectiveness of fire suppression (La Puma et al., 2013; Nowacki & Abrams, 2008), vegetation–fire feedbacks (Nowacki & Abrams, 2008), and environmental factors like topography and weather (Lafon et al., 2017). For instance, effective fire suppression around a wildland–urban interface can reduce fire frequency in corridors of forest surrounding those areas, promoting forest type conversion (La Puma et al., 2013) and dense accumulations of vegetation where tick and fuel management likely matters most (Skowronski et al., 2016). In the restoration of fire-dependent landscapes and tick reduction, understanding specifically where spatial variation in fire regimes needs adjustment, such as around communities, can be beneficial in guiding the patterning of prescribed fire treatments and help elucidate what policy developments could facilitate prescribed burning for ticks.

FUTURE RESEARCH

Gaps in our understanding limit our ability to optimize prescribed burning treatments and other restoration efforts to reduce ticks in harmony with meeting other management objectives. Mechanistic research that focuses on (1) the ecology of ticks and their hosts, (2) direct and indirect effects of fire on ticks and their interactions with other organisms and (3) the impacts of long-term prescribed burning on tick populations and disease risk will be beneficial in guiding the use of prescribed fire and ecosystem restoration in tick mitigation strategies.

Tick and host ecology

A stronger understanding of tick ecology, especially with respect to interactions with their environments, hosts, and predators could enhance our ability to manage ticks and tick-borne disease transmission. Greater knowledge defining how variation in vegetation structure, vegetation composition, and microclimate influences tick survival, availability of tick hosts, and tick–host interactions can improve how land managers target treatment effects and applications. For instance, limited knowledge exists on how specific host species use and behave in the contrasting vegetation compositions, structures, or microclimates resulting from prescribed burns. A better understanding of tick use of refugia and questing space during different periods of the year would also help inform specifically when ticks will be most vulnerable to treatments and their effects. Likewise, better monitoring is needed to understand natural tick and wildlife dynamics in the eastern United States given the mosaic-like patterning of eastern forest conditions that influence ticks and wildlife habitat (e.g., fragmentation characteristics, proximity to wildland–urban interface, land-use and land-cover patterns, soils, latitude, and elevation). Such information would elucidate opportunities and areas to prioritize for management on landscapes where management could have the greatest effects, while information on temporal dynamics of ticks and hosts would inform when applications could have the greatest effects. Although there are clearly many responses and variables associated with tick and host dynamics in eastern forests, machine learning approaches to distilling patterns from large data sets are being successfully used in other facets of ecology and have untapped potential for better analyzing tick and host dynamics in their environments.

Direct fire effects

Further research on the direct effects of fire on ticks, their habitat, and hosts can provide fire managers with the information they need to hone the application of fire to reduce targeted tick life stages in a vegetation-specific context. For instance, greater research is needed to determine when direct effects on ticks are most successful and when heat transfer of typical cool-season burns is insufficient to reduce questing ticks. Similarly, in a restoration context, there is limited knowledge specific to mesophitic species regarding their sensitivity or resistance to direct effects on fire to help guide the appropriate application of burning to reduce these species. For instance, a greater understanding of variation in direct effects due to plant phenological state, weather conditions that enhance plant susceptibility to damage, and fire intensity would improve the timing and tactics of fire applications to achieve targeted goals, such as forest structural change, mesophitic species mortality, woody invasive species control, and soil preparation that supports the natural re-establishment of fire-dependent species. Similarly, studies rarely compare direct effects of burning between forest types (e.g., pine, oak, varying degrees of mesophication) or at different stages of restoration and often postulate conclusions that may not apply to all forest types given our understanding of how vegetation species and structure drive both fire behavior and susceptibility (see ecology of fuels concept). A firmer understanding of common fire behavior dynamics in different forest types and at different stages of management (e.g., restoration or maintenance) can help in synchronizing the timing and prescription of burning treatments to directly impact targeted ticks and vegetation and elucidate limitations of direct effects at different phases of management. A novel approach to synthesizing such knowledge would be to incorporate the use of new physics-based fire behavior models, such a QUIC-Fire (Linn et al., 2020), when planning tick and forest restoration management. These models allow fire managers to simulate real-world prescribed fire treatments under differing environmental conditions and with complex ignitions to predict fire behavior and outcomes in order to better plan effective burns.

Indirect fire effects

The indirect effects of fire build on the direct effects with a complementary suite of opportunities to influence ticks, their hosts, and forest conditions through prescribed burning over time. Additional research must be undertaken to understand the magnitude of shifts needed from burning to produce the desired indirect effects, such as microclimate and changes to vegetation structure, that are sufficient to reduce tick success, limit reinvasion rates into burned areas, and support the restoration or maintenance needs of fire-dependent forest communities.

Further, greater research is needed to fine-tune the applications of treatments to efficiently reverse mesophication effects while also promoting suitable regeneration of fire-dependent species. There is a need for a more resolved understanding of how fire effects influence the temporal and spatial variations of microclimatic extremes (e.g., hot, cold, and moisture) to better understand when and where indirect effects are likely to be mechanistically impactful on ticks and vegetation. Again, considering fire effects within the ecology of fuels concept is necessary: fires and their effects feed back such that these effects will vary with community type, geography, and stage of restoration. For instance, the opportunity to bring about additional winter freezing mortality on ticks would be most useful at northern latitudes or high elevations, whereas the opportunity to exceed extreme heat or dryness thresholds of ticks may be more widespread. Similarly, a refined understanding of how understory vegetation height and density and canopy openness influences tick questing success is needed in the context of ticks' ability and effort required to reach desired vertical positioning and the likelihood of encountering a host given vegetation influences on host behavior. Also, forest understory air flow conditions are heavily influenced by forest density such that thinned and burned forests better disperse and dilute chemical cues used by arthropods. Ticks use hosts' chemical cues as part of their host-seeking strategy, yet the potential role of forest-mediated chemical cue dilution has yet to be explored in terms of tick questing success.

Fire regimes

Despite numerous field studies focused on fire regimes, a refined knowledge of how fire regime characteristics and their interactions drive variation in fire effects can improve how fire managers leverage the patterns and processes of fire to reverse forest conditions that support the success of ticks. For instance, fire regime components have often been investigated independently in experiments rather than as important interacting factors, resulting in limited applicability to the understanding of actual fire regime influences. Studies that examine broader ranges of burning prescriptions, fire return intervals, and definitions of seasonality based on species-level phenology and that characterize intensity quantitatively in terms of heat flux rather than qualitatively could support the development of model-based decision-support tools to guide fire managers to better achieve ecosystem restoration and maintenance goals with prescribed burning. Integrating the ecology of fuel concept, that each fire influences future fuel and fire, would help maximize the utility of future decision-support tools and would help illustrate the ways in which fire-dependent ecosystems and tick reduction depend on fire as a long-term process rather than a single treatment or limited collection of treatments. While field focuses are extremely useful, numerical modeling approaches remain untapped as an approach to learning about fire regimes and their effects but could reduce some of the need for long-term field experimentation required to explore fire regimes. Similarly, greater attention must be paid to the spatial variability of fire behavior and effects, with regard to fire ignition and fuel conditions, and the spatial patterning of prescribed fire treatments on landscapes. Recent work highlights the potential for fire effects on ticks to spill over into adjacent unburned areas, presumably due to microclimate and host activity influences (Gleim et al., 2014); however, the mechanisms and extents of fire edge effects that extend into unburned areas and how they may be leveraged around homes to reduce tick exposure remains poorly understood.

Prescribed fire limitations

There are limitations to prescribed fire as a tick management or landscape restoration method. In general, suitable burning weather, smoke management challenges, and limited staffing of experienced fire personnel can limit the application of prescribed fire (Kobziar et al., 2015). Similarly, legal or social impediments, which include insufficient funding, liability, laws, and regulations, can also serve as important cultural obstacles to burning in some areas (Kobziar et al., 2015; Melvin, 2018; Quinn-Davidson & Varner, 2012). Prescribed burning in urban or suburban residential areas or park spaces (e.g., wooded parks, meadows) can be challenging where fire is not widely used, fire managers are inexperienced in the application of prescribed fire, and public perceptions of fire are negative. However, in areas that already have strong prescribed fire programs, burning in or adjacent to urban/suburban environments is common, with examples of such management in southern New Jersey (Warner et al., 2020), Albany, New York (Lee et al., 2019), around Charleston, South Carolina (Coates et al., 2020), and throughout much of Florida (Teske et al., 2021). Similarly, federal financial and planning assistance supports prescribed burning on private lands in these areas (e.g., the USDA Natural Resources Conservation Service), either by consultants or private landowners themselves; however, legislation and a general lack of landowner understanding of prescribed fire remains a limitation on private land burning (Wilbur et al., 2021).

We directly acknowledge that prescribed fire may not immediately provide the same magnitude of tick reduction as some other options and that it may require multiple applications to achieve tick reduction goals. Other integrated pest management (IPM) options for tick control can be very effective on small scales but also have important limitations, particularly on large scales (White & Gaff, 2018). Several nonfire tick control options cannot be easily implemented by the general public (e.g., many acaricides or rodent bait boxes that require professionals to apply), are no longer available (e.g., Met52), require host reduction or exclusion that is often not possible because of local or state regulations, or require wildlife baiting, which may be illegal or unadvisable in some states owing to hunting regulations or restrictions due to potential disease transmission (e.g., chronic wasting disease in white-tailed deer). Many IPM options primarily target *I. scapularis* or have only been evaluated on this species, leaving gaps in our approaches to controlling other increasingly important tick species that transmit disease.

Prescribed fire also has limitations as a tool for forest restoration. In cases where fire exclusion has enabled major changes in community composition, structure, and regeneration patterns, additional treatments in conjunction with prescribed fire may be required to regenerate fire-dependent community species assemblages and structure. For example, prescribed fire reduces competition and prepares seedbed conditions for fire-tolerant species but can be insufficient in creating the requisite canopy gaps to enable regeneration in long-excluded forests where forest density and overstory composition require substantial modification. In such scenarios, mechanical treatments (e.g., cutting, mowing, mastication) can be extremely beneficial for reducing vegetation density and competition and creating canopy gaps necessary for enabling regeneration (Lee et al., 2019; Reilly et al., 2017). In some cases, herbicide treatments combined with mechanical treatments can be more effective at controlling target species than burning or mowing when first beginning restoration work, especially when target species are clonal or sprout prolifically (Bried & Gifford, 2010; Hanberry et al., 2017). Likewise, prescribed fire alone may not be sufficient where target restoration species are too depleted to produce ample seed sources (Diaz-Toribio & Putz, 2017) or if soil seed banks have become depauperate of restoration target species (Vander Yacht et al., 2020). Particularly in areas with strong legacies of agriculture, logging, overgrazing, fire suppression, or other methods of controlling undesirable species and seeding or planting of target restoration species may be necessary to restore the composition and function of severely degraded fire-dependent communities (Diaz-Toribio & Putz, 2017; Löf et al., 2019).

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

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