Chapter 4
Fire Ecology and Management in Eastern Broadleaf and Appalachian Forests

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Abstract The role of fire in the eastern broadleaf and Appalachian forest regions, until recently, was poorly understood or minimally examined, as this region was long overlooked as a flammable landscape and fire was seen primarily as a threat to the timber resource and wildlife. In the past few decades, a significant body of research has enhanced our understanding of fire and its effects. We now recognize that fire has strongly shaped many ecosystems of this region along complex geomorphological gradients, and that returning fire, or its absence, has significant consequences for forest structure, species composition, and ecosystem function. This chapter synthesizes the state of knowledge regarding the prehistoric and historical roles of fire in these ecosystems; presents research demonstrating the effects of contemporary prescribed fire and wildfire on forest structure, species composition, and consequences for wildlife; examines evidence for shifting flammability of these ecosystems; and discusses the implications for both fire management and ecosystem sustainability in the twenty-first century.

Keywords Oak-pine · Woodlands · Savannas · Maple · Anthropogenic fire · Pyrophytic · Mesophication · Prescribed fire

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4.1 Introduction

The eastern broadleaf and Appalachian (EBA) forests of the USA were long overlooked as a region whose ecosystems, and the plant and animal communities within them, were strongly influenced by fire. In the past several decades our understanding of the critical role that fire played in shaping these ecosystems has come to light through the unearthing of rich archaeological and paleoecological records from the region (Delcourt and Delcourt 1997; Lafon et al. 2017). These records reveal a complex history of fire use over ~9000 years, and serve as a foundation for foresters, ecologists, geographers, and wildlife biologists in building stronger understandings of the past role of fire across the landscape and the potential for management that includes fire to restore forest structure, species composition, and ecosystem

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function. This chapter synthesizes our current understanding of the important role of fire in forest ecosystems within this region.

The EBA region occurs at mid-latitudes: from west to east it extends from the Mississippi River to the Appalachian Mountains, including the Blue Ridge, Central and Western Appalachians, and Ridge and Valley ecoregions; from south to north it extends from the Interior Plateau in north Alabama to western Indiana, southeastern Ohio, and the Western Allegheny Plateau in the western portions of Pennsylvania and New York (Chap. 1, Fig. 1.1). Topography is highly variable across mountain ranges (Appalachians), eroded plateaus (Western Allegheny and Interior Plateaus), and river valleys (Mississippi and Ohio Rivers). A temperate, continental climate with four distinct seasons characterizes the region. Summers are long and warm, and winters are cold (Brandt et al. 2014; Butler et al. 2015). In the easternmost portion of the region, annual precipitation is most variable in areas with diverse topography, ranging from ~90 cm in valleys to >175 cm on high peaks, but generally highest during the growing season when evapotranspiration is highest (Butler et al. 2015). West of the Appalachians, rainfall is more evenly distributed throughout the year. Snowfall is variable across the region (Bailey 1994). Soils range from Alfisols in the north, Ultisols in the western portion of the region, intermountain basins, and on ridges in the south, to Inceptisols in steep areas and plateaus (Bailey 1994). The role of fire across these complex topo-edaphic gradients is not monolithic, but varies in response to flammability. Fire-adapted mixed-oak and oak-pine communities occur in upland landscapes where fire can be frequent to moderately frequent, whereas low fire return intervals (FRI) characterize communities such as high-elevation spruce-fir (*Picea rubens-Abies fraseri*) forests and mesic hardwood and eastern hemlock (*Tsuga canadensis*) coves. In this chapter, we focus our discussion of fire primarily on the mixed-oak and oak-pine communities that occur throughout the EBA region.

EBA forests exhibit high biodiversity, structural complexity, biomass, and productivity associated with long-term geological stability, favorable climate for plant growth, moderately high to high soil productivity, and variability in soils and topography that provide for high diversity in microclimates and sites (Davis 1981; Stein et al. 2000; Belote et al. 2011; Rogers et al. 2017). Overstory and midstory (≥12.7 cm diameter at breast height; dbh) tree species richness often exceeds 20 species in Forest Inventory and Analysis (FIA) plots (0.067 ha in area) (Elliott and Swank 2008; Belote et al. 2011). Groundlayer plant richness frequently surpasses 10 species/m^2 (McEwan and Muller 2011), especially in the absence of a dense sapling or midstory stratum (Hammond et al. 1998) and heavy leaf litter accumulation (Gilliam and Roberts 2003).

Forest species distributions overlap across the region but often stratify along topographical gradients in elevation, aspect, terrain shape, and soil moisture (Day et al. 1988; Bolstad et al. 1998), though fire, wind, and storm disturbances also create forest patches of different ages and composition (Greenberg et al. 2015a, b). In the Central and Southwestern Appalachian and Interior Plateau ecoregions, mixed oak (*Quercus* spp.) and pine (*Pinus* spp.) forests occupy low-elevation mountain slopes, and include dry-site oak species like white oak (*Q.alba*), chestnut oak

(*Q. montana*), and scarlet oak (*Q. coccinea*), along with shortleaf pine (*P. echinata*) and Virginia pine (*P. virginiana*) (Williams and Johnson 1990). Mid-elevations with cool, moist north and northeast facing slopes and coves support mixed mesophytic forests of hardwoods like sugar maple (*Acer saccharum*), American beech (*Fagus grandifolia*), tuliptree (*Liriodendron tulipifera*), American basswood (*Tilia americana*), and northern red oak (*Q. rubra*), and conifers, including eastern white pine (*P. strobus*) and eastern hemlock. American chestnut (*Castanea dentata)*, once a dominant species across much of the landscape until the 1930s when it was extirpated by the chestnut blight (*Cryphonectria parastica*)*,* influenced community composition and ecosystem function in this region (Kane et al. 2020). At mid- to high elevations (700–1400 m) on south-facing slopes and ridgetops, fire-dependent woodlands and forests comprised of pitch pine (*P. rigida*), Table Mountain pine (*P. pungens*), and fire-tolerant oaks, especially chestnut and scarlet oak, often occur (Williams 1998). The evergreen, ericaceous shrub mountain laurel (*Kalmia latifolia*) is often an important understory species on these and other dry, fire-prone sites (Monk et al. 1985; Elliott et al. 1999). Without periodic fire, however, this species can form dense thickets that hinder hardwood and pine regeneration (Brose 2016). Spruce-fir forests, along with occasional heath balds, cap the highest mountainous elevations (>1700 m), where conditions are cold, moist, and generally fire-free, such as in the Great Smoky and Allegheny Mountains in the Blue Ridge and Western Allegheny Plateau ecoregions (Stephenson and Clovis 1983; Jenkins 2007).

Human influence transformed these forests in many ways. Prior to Euro-American settlement, Native Americans affected forests through intentional burning to create open woods and facilitate hunting and agricultural activities (Maxwell 1910; Williams 1989; Delcourt and Delcourt 1997). Drier sites occupied by upland oaks and pines often experienced periodic (every 4–6 years; Frost 1998), low- to moderate-intensity surface fire (Nowacki and Abrams 2008), ignited by humans and lightning (Chap. 1, Table 1.1; Guyette et al. 2006). Mature tree species on these sites were fire-tolerant, with adaptations to limit fire damage and properties that reinforced fire occurrence (Abrams 1992). Progressive deforestation occurred on the landscape as Euro-American settlement expanded, starting in the 1600s. Forest logging and conversion to agriculture, urbanization, or other uses left <45% of total forestland in the eastern USA intact by 2001, despite a trend of afforestation over the last century (Riitters et al. 2012). Since the early twentieth century, historically pyrophytic and open-canopied upland oak and pine savannas and woodlands have undergone densification to closed-canopy forests occupied by fire-sensitive, shade-tolerant (i.e., mesophytic) and/or generalist species (Hanberry et al. 2020b). Large overstory oaks, and in some places pines, still dominate many forest stands across the region (Fei et al. 2011), and oak seedlings continue to establish in the understory. However, sapling and midstory oaks are largely absent (e.g., Dyer and Hutchinson 2019; Izbicki et al. 2020), leading to a regeneration “bottleneck”. Instead, mesophytic species, such as sugar maple and American beech, and generalist species like red maple (*A. rubrum*), proliferate (Knott et al. 2019). Pine regeneration is also failing, and pine forests are transitioning to oaks and other hardwoods (Williams and Johnson 1990).

Federally mandated fire exclusion policies enacted in the 1930s strongly influenced forest regeneration patterns, as many declining oaks and pines are fire-dependent species; however, other human-driven changes that co-occurred with fire exclusion likely exacerbated the shift away from pines and oaks. Although there was regional variation in dominance by American chestnut (Rentch and Hicks 2005; Thomas-Van Gundy and Strager 2012), where it dominated, the loss of chestnut caused a dramatic shift in tree species dominance (Elliott and Swank 2008) that likely transformed the fire regime because of declines in chestnut's highly flammable litter (Kane et al. 2019). Increased herbivore pressures, especially from white-tailed deer (*Odocoileus virginianus*), lowered the regeneration potential of many tree species on some sites, altering competitive interactions among tree species and successional trajectories both in the presence and absence of fire (Hanberry and Abrams 2019). Contemporary second- and third-growth forests in much of the region are now denser and composed of fast-growing species like tuliptree and red maple (Elliott et al. 1999; Dyer 2006, 2010). Trees in these second- and third-growth forests generally have smaller crowns leading to smaller canopy gaps when individual trees die or are removed in partial harvests (Clebsch and Busing 1989), lowering light availability and regeneration potential of species with higher light requirements, like oaks and pines. In addition, invasive non-native species have increased in abundance and range, often hindering native plant regeneration (Marshall et al. 2009). It is against this backdrop of change that we explore the past, present and future roles of fire in these ecosystems.

4.2 Abundance of Fire-Adapted Traits

Plants of the region have traits reflecting selection pressures that long preceded the contemporary landscape, including traits that display adaptation to fire regimes (Table 4.1). In addition to climate, soils, and other disturbances (e.g., wind, ice, tropical storms), fire has shaped the composition and structure of savannas, woodlands, and forests in the region (Stambaugh et al. 2015). Other syntheses have focused on traits that enhance survival in fire-prone EBA communities (*cf.* Johnson et al. 2019). Our approach here is also to bring forward recent work on how these species influence fire and how they resist and repair injuries caused by past and future fire regimes.

The primary protective trait of trees globally is bark. Heat is transferred to the outer bark via radiation and vertically convected along the bole where it is conducted through the outer bark to the underlying cambium. Thick bark provides substantial protection from heat that would otherwise damage vascular cambium and impair water and nutrient use, hormone transfer, and photosynthate delivery; this damage can cause acute stress, and cumulatively, tree death (O'Brien et al. 2018). Pines (pitch pine, shortleaf pine and Table Mountain pine) and many upland oaks (chestnut oak, and to a lesser extent black oak (*Q. velutina*), scarlet oak, white oak and northern red oak) are notable for their thick bark as adults (Starker 1934; Babl

Table 4.1 Tree species in the eastern broadleaf and central Appalachian forests and their fire-adaptive traits

Species	Strategy†	Fire-adaptive Traits‡			Notes
		Sprouting	Bark Allometry	Litter Flammability	
Acer rubrum	Mesophyte	+	–	Low	
Acer saccharum	Mesophyte	+	–	Low	
Carya spp.	Pyrophyte	+	0	High	Variable among
Castanea dentata	Pyrophyte	+	0	High	
Cornus florida	Intermediate	+	0	Low	
Fagus grandifolia	Mesophyte	+	0	Medium	
Liquidambar styraciflua	Mesophyte	+	–	Medium	
Liriodendron tulipifera	Mesophyte	+	0	Medium	
Nyssa sylvatica	Intermediate	+	–	Low	
Pinus echinata	Pyrophyte	+	+	High	
Pinus pungens	Pyrophyte	0	0	High	Serotinous
Pinus rigida	Pyrophyte	+	+	High	Serotinous
Pinus strobus	Mesophyte	–	–	Low	
Pinus taeda	Pyrophyte	–	+	High	
Pinus virginiana	Mesophyte	–	–	Low	
Prunus serotina	Mesophyte	+	–	Low	
Quercus alba	Pyrophyte	+	0	High	
Quercus coccinea	Pyrophyte	+	0	High	
Quercus falcata	Pyrophyte	+	+	High	
Quercus macrocarpa	Pyrophyte	+	+	High	
Quercus marilandica	Pyrophyte	+	+	High	
Quercus montana	Intermediate	+	0	High	
Quercus muehlenbergii	Pyrophyte	+	0	High	
Quercus rubra	Pyrophyte	+	–	High	
Quercus stellata	Pyrophyte	+	0	High	
Ulmus alata	Mesophyte	+	–	Low	

†Strategy refers to the suite of fire-adaptive traits including sprouting, bark allometry, litter flammability, and others listed in the text. Fire-adaptive traits are based on published values in Jackson et al. (1999), Varner et al. (2015), Kreye et al. (2018a), and Babl et al. (2020). In general, '+' corresponds to positive, '0' intermediate, and '-'negative values for each listed trait. We differentiated "strategy" into three coarse categories, acknowledging that species exist across a continuum representing their ability to persist in fire-prone environments

‡Table adapted from Varner (2018)

et al. 2020). Species that rapidly allocate carbon to bark as juveniles can survive fires, enabling establishment and ascension into the canopy (Varner 2018). Sapling bark thickness is notable in pitch pine, shortleaf pine, and Table Mountain pine; slow bark accumulation typifies the patterns of Virginia pine and eastern white pine (Jackson et al. 1999). Thick bark on juvenile stems (so-called positive bark allometry; Jackson et al. 1999) characterizes blackjack oak (*Q. marilandica)*, post oak (*Q. stellata)*, southern red oak (*Q. falcata)*, and bur oak (*Q. macrocarpa)*, and less so on chestnut oak and white oak. Most other oaks in the region are slower to add bark with age (negative bark allometry; Jackson et al. 1999; Hammond et al. 2015; Table 4.1). Red maple lacks investment in juvenile and mature bark, making it more susceptible to fire-caused injury (Hammond et al. 2015; Babl et al. 2020), though this species has exceptionally pronounced resprouting capacity with increasing size. Bark roughness can also help protect trees from fire. For example, white oak has rugose bark, which maximizes surface area, dissipates radiant heat, and introduces turbulence to "shield" against convective heat (Hengst and Dawson 1994). Bark roughness and thickness are also important determinants of the amount of water that a tree's surface absorbs during rainfall events. Rougher barked oaks and pines tend to absorb more water, which acts as another mechanism for protecting these trees from fire.

In addition to defensive traits, species diverge in the flammability of their senesced litter, a trait that increases local fire intensity and overwhelms fire-sensitive competitors. Oaks, American chestnut, and pines in the region are notable for their litter flammability. The leaves of upland white oaks (white, chestnut, post, and bur oak) and red oaks (northern red, southern red, scarlet and black oak) are mostly long, deeply lobed, and curl when dried, characteristics that enhance their flammability (Kane et al. 2008; Babl et al. 2020). American chestnut was among the most flammable upland species in the region (Kane et al. 2019); its loss was important for several ecological processes, fire among them. The upland pines of the region, particularly the yellow pines (*Pinus* section *Pinus;* shortleaf, pitch, and Table Mountain), are also notably flammable. The suite of species in the region with less flammable litter includes white pine, eastern hemlock (the least flammable of species in the eastern USA tested to date), winged elm (*Ulmus alata*), eastern hophornbeam (*Ostrya virginiana*), flowering dogwood (*Cornus florida*), sweetgum (*Liquidambar styraciflua*), and red maple (Mola et al. 2014; Varner et al. 2015; Kreye et al. 2018b). Litter of most of these species also dries slowly, which magnifies the relative differences in their flammability (Kreye et al. 2018b). Of 17 species studied, red maple litter was the slowest to lose moisture (Kreye et al. 2013). Many pyrophytic oaks have leaf litter that decomposes slowly (Alexander and Arthur 2014), which also keeps fine fuels drier, fuel loads higher, and fuel beds more aerated (Dickinson et al. 2016). Differential flammability has been proposed as a primary mechanism of mesophication in the region (Nowacki and Abrams 2008; Kreye et al. 2013). Prior to Euro-American settlement, many upland areas were open-canopied woodlands with a groundlayer covered with herbaceous species (Hanberry et al. 2020b). The high light on the ground and productivity of grasses and other herbaceous species further acted to increase flammability (Kreye et al. 2018a).

Beyond bark and flammable litter, numerous other traits confer advantages in frequent fire regimes in the region. Resprouting from the base, along the bole, and in the crowns is common in the angiosperms, enabling survival following a spectrum of injuries. Oaks in particular are notable root, crown (branch and bole), as well as basal sprouters when topkilled. Individually, mesophytic species can have some of these traits (as in red maple, which sprouts vigorously), but fire can differentiate pyrophytes that invest more in belowground carbohydrate storage (Kruger and Reich 1997; Brose et al. 2006). While resprouting is a generalized response among many angiosperms to aboveground damage, the commonness of resprouting in response to fire in eastern deciduous forest species (including even the dominant upland pines, shortleaf, and pitch pine) is remarkable.

Compartmentalization of fire injuries through the bark allows trees to occlude and protect wounded xylem from fungal infections and inhibits decay development in the tree bole (Smith and Sutherland 1999; Stambaugh et al. 2017). Several oaks are notable for their resilience to fire-caused wounds (e.g., white, chestnut and northern red oak; Smith and Sutherland 1999; Stambaugh et al. 2017). Cone serotiny, sealed cones that store seeds until triggered to open by fire's heat, is found in Table Mountain pine and pitch pine, which are found on ridges and dry slopes in the EBA region. Once mature, these two pines and shortleaf and eastern white pine all self-prune lower branches, simultaneously decreasing the amount of less productive photosynthetic biomass and diminishing the possibility that fires could ignite the crowns. Generally, though, it is the collective suites of these traits that enable these species to dominate where fires are frequent and tolerate the stresses and injuries caused in fires (Keeley and Zedler 1998; Varner et al. 2016).

Given the traits detailed here, the persistence of the myth that the region's flora lack fire adaptations is surprising (Matlack 2013; Oswald et al. 2020). Examples noted here and elsewhere (Johnson et al. 2019) stand as classical adaptations that are mirrored by some fire-adapted forbs (e.g., Baskin and Baskin 1997; Bourg et al. 2015) and many upland animals (see Sect. 4.7) that reflect the long history of fire in the region (Stambaugh et al. 2015).

4.3 Fire History

The wide distribution of fire-adapted taxa throughout the region implies that fire was common in the past and suggests a need to restore fire-dependent communities where they historically occurred. Paleoecological and historical evidence of past fires, including the roles of lightning ignitions and people in shaping past fire regimes, provides a basis for interpreting past fire regimes and managing fire today.

Charcoal fragments in lake and wetland sediments and soil provide evidence of the antiquity of fire in the region, and of changes in the importance of fire with changes in climate, vegetation, and land use (Lafon et al. 2017). The earliest fires in the EBA burned forests that grew under the cooler climate of the last full glacial period between 23,000 and 20,000 ybp, and which were dominated by northern pines and spruce throughout the EBA (Jackson et al. 2000). These fires are documented by sparse macroscopic charcoal in high-resolution charcoal records developed at Pine Swamp, Maryland, and Spring Pond, Virginia (Lynch and Clark 2002), and by charcoal used for radiocarbon dates and quantified on pollen slides at Anderson Pond, Tennessee (Liu et al. 2013; Ballard et al. 2017; Driese et al. 2017; Horn et al. 2019). Sediments from these sites and from Jackson Pond, Kentucky (Liu et al. 2013), and Browns and Spring Ponds, Virginia (Kneller and Peteet 1999; Lynch and Clark 2002), also preserved evidence of fires during the late glacial from 20,000 to 11,700 ybp, although hiatuses in some records hinder interpretation. As oaks and other hardwood species expanded through the late glacial and early Holocene, charcoal deposition decreased at some sites, but increased at others. Site to site variability also characterizes charcoal records from the Holocene (last 11,700 years). Sediment charcoal records confirm the ubiquity of fire across the Holocene, but indicate that fire regimes were spatially and temporally variable (Hart and Buchanan 2012; Lafon et al. 2017). Intervals of increased or decreased burning at some sites appear linked to prehistoric and historic human activity. At the Cliff Palace Pond site in eastern Kentucky, for example, charcoal accumulation increased ca. 3000 ybp as aboriginal people began using fire for agricultural purposes (Delcourt et al. 1998). However, changes in climate and vegetation independent of humans also affected fire regimes.

Charcoal records developed by dating and identifying charcoal in soils provide stand-specific records of fire occurrence and forest composition (Hart et al. 2008; Horn and Underwood 2014). In Great Smoky Mountains National Park, charcoal is present in soils across a wide range of modern forest composition (Underwood 2013; Horn et al. *unpubl. data*). Dates on individual fragments span the Holocene, but most are late Holocene (last 4200 years), as found in soil charcoal work at Wine Creek, North Carolina (Fesenmyer and Christensen 2010). Identified fragments include both fire-dependent taxa such as yellow pines, oak, and chestnut, and fire-sensitive taxa such as white pine, maple, and hemlock, confirming the variability in fire regimes indicated by sediment charcoal records.

Fire histories have been reconstructed for recent centuries across the region using fire-scarred oak and yellow pines that decay slowly and yield long fire records. Fire history is best documented for the oak-pine mosaic covering mountain slopes of the Ridge and Valley and Blue Ridge Ecoregions (Lafon et al. 2017), where resinous old pines are common. These trees yield fire-scar records extending back to the 1600s–1700s, at or before early Euro-American settlement. Estimates of FRI range from 2–3 years in southern portions of these ecoregions to 4–8 years in northern sections (Bale 2009; Lafon et al. 2017; Stambaugh et al. 2018; Chap. 1, Fig. 1.5, Table 1.2). These FRI estimates apply to the oak-pine mosaic that covers the open mountain slopes, but would not apply to the mesophytic forests of valleys, ravines, and lower slopes, where fire was undoubtedly less common. Outside the Blue Ridge and Ridge and Valley Ecoregions, fire-scar sites are sparsely scattered, and/or most of the records extend only to the middle-late 1800s. FRI estimates are 2–20 years for oak-dominated forests of the Appalachian Plateau (Lafon et al. 2017; Hutchinson et al. 2019) and 2–5 years for oak savannas of the Interior Plateau (Guyette et al. 2003; Stambaugh et al. 2016).

These site-level FRIs have certain limitations (e.g., Van Horne and Fule 2006), including the possibility of underestimating the typical fire interval if fires were small and did not burn the whole study site. Therefore, conservative estimates are sometimes calculated using more intense or widespread fires that scarred at least 25% of trees (Lafon et al. 2017). These estimates, applied primarily in the Ridge and Valley and the Blue Ridge ecoregions, yield FRIs of 5–13 years and confirm that fire was frequent before exclusion in the montane oak-pine mosaic. After the early to middle twentieth century, however, fire frequency dropped sharply across the whole EBA region due to fire exclusion, coupled with other factors like changing climate and loss of American chestnut (e.g., Lafon et al. 2017; Stambaugh et al. 2018; Hutchinson et al. 2019).

Dormant season fires, illustrated by scars that formed during fall or spring when the weather and vegetation favor burning (Lafon et al. 2017), dominated the historical fire regime. Dormant season scars compose 70–100% of scars from studies conducted in the Appalachian Plateau and 100% from the Interior Plateau (Stambaugh et al. 2016; Lafon et al. 2017; Saladyga 2017; Hutchinson et al. 2019). They are also the most common scar seasonality in the Ridge and Valley and the Blue Ridge (Lafon et al. 2017; Stambaugh et al. 2018), but earlywood scars that formed later in spring are abundant at several sites, accounting for as many as 35–70% of scars. Latewood scars, which likely formed during summer, are rarer but account for 15–40% of scars at a few sites in the mountains. The prevalence of dormant season scars probably indicates that humans were the primary ignition source, as dormant season scarring matches the seasonality of anthropogenic fires today (Lafon et al. 2017).

Witness tree records from initial land surveys indicate that fire-adapted taxa were abundant and widespread at the time of Euro-American settlement. Four such taxa—*Quercus*, *Pinus*, *Carya*, and *Castanea*—accounted for 65–80% of witness trees in landscapes of the Blue Ridge escarpment in Georgia (Siskind 2020); the Ridge and Valley of Alabama, Virginia, West Virginia, and Pennsylvania (Nowacki and Abrams 1992; Shankman and Wills 1995; Thomas-Van Gundy and Nowacki 2013; Flatley and Copenheaver 2015); the Western Allegheny Plateau of southeastern Ohio (Dyer 2001); and the Interior Plateau of Kentucky (McEwan et al. 2005). These genera did not owe their abundance solely to fire but would have been less abundant without it. Fire apparently enabled them to extend from dry ridgetops and upper slopes to lower slopes and even valleys and ravines (e.g., Nowacki and Abrams 1992; Shankman and Wills 1995). In contrast, mesophytic taxa (e.g., *Acer*, *Fagus*) were largely restricted to the wettest, most fire-sheltered topographic positions, such as streamsides and lower north-facing slopes, and cove sites (e.g., Fralish et al. 1991; Abrams and Ruffner 1995; Shankman and Wills 1995). They were also common in cool, wet climates, such as the high elevations of the Central Appalachians in West Virginia and Pennsylvania, where fire was probably infrequent (Rentch and Hicks 2005; Thomas-Van Gundy and Strager 2012).

The presence of fire-adapted plants on the landscape implies a long history of lightning ignitions that predate anthropogenic fires (Noss 2012). Lightning ignitions are less common than human ignitions today but remain an important source of late-spring and early-summer fires in some ecoregions. Lightning ignites approximately 5–8 fires/400,000 ha per year in the southern Blue Ridge Mountains (Barden and Woods 1974; Greenberg et al. 2016), including as many as 18 fires/400,000 ha along the Blue Ridge escarpment in northwestern North Carolina (Lafon et al. 2017). Farther north, lightning accounts for approximately 10 fires/400,000 ha, or 24% of all wildfires, on the northern Blue Ridge of Virginia and 5 fires/400,000 ha (18% of fires) in the Ridge and Valley of Virginia, but only 0.5 fires/400,000 ha (8% of fires) along the high eastern Appalachian Plateau in West Virginia (Lafon and Grissino-Mayer 2007). Lightning ignitions are uncommon on both the Appalachian and Interior Plateaus, accounting for only 1% of wildfires in National Forests of these ecoregions (Yaussy and Sutherland 1994). However, lightning frequently coincides with mid-summer dry spells in the oak forests of southern Ohio and may have been an important ignition source before landscape fragmentation and fire suppression (Petersen and Drewa 2006).

Among the ecoregions, lightning probably played the greatest prehistoric role in the fire regimes of the Blue Ridge, where ignition densities resemble those in fire-prone areas of the Rocky Mountains and much of the Coastal Plain outside Florida (Schroeder and Buck 1970). Blue Ridge ignitions reflect mountain-atmosphere interactions that generate lightning strikes that readily ignite dry fuels, e.g., under synoptic high pressure or accompanying the passage of dry cold fronts (Denman 2016; Lafon et al. 2017). Historically, some lightning-ignited fires likely grew to large size and helped maintain the short fire intervals evidenced by fire scars. These ignitions would have been especially important in remote areas and during periods when human population density was low.

Humans have been the primary source of ignitions, accidental or deliberate, since they arrived in North America 13,000 ybp or more ago, especially in the temperate zone of the eastern USA (Delcourt and Delcourt 1997; Pyne 1982; Pinter et al. 2011). The early nomadic hunter-gatherers burned to clear travel corridors, defend encampments, fight enemies, attract wildlife and facilitate hunting, and culture native plants used for food and other purposes (Delcourt et al. 1998; Delcourt and Delcourt 2004). By about 7000 ybp, Native Americans were cultivating native plants in fields and growing trees in orchards—the beginning of agriculture and horticulture in the Midwest and Northeastern USA—and by 1000 ybp they had developed complex agricultural systems to grow corn, beans, and squash (Hurt 1987). They used fire to manage land in this subsistence economy of expansive grazing lands and shifting agriculture, and burned to meet their subsistence goals whenever fuels and weather enabled fire ignition and spread. Additionally, an accidental human-caused fire was not likely to be actively controlled, resulting in fires that would continue to burn until extinguished by change in fuels, weather, or topography. The resulting anthropogenic fire regime strongly shaped vegetation structure, composition and distribution (Pyne and Goldammer 1997; Delcourt et al.

1998; Anderson et al. 1999; Guyette et al. 2002; Anderson 2006; Scott et al. 2014; Johnson et al. 2019).

Early Euro-American settlers adopted Native American fire practices and also brought their own heritage of burning to expand open lands for domesticated crops and livestock (Pyne 1982; Johnson and Hale 2002). These cultural uses of fire maintained frequent burning except where permanent settlement, land development, and fragmentation of the fire-scape by European agricultural systems decreased the ability of fire to start and spread, and increased the demand and ability to suppress unwanted fires. From about the 1850s to 1930s, many of the forests were indiscriminately harvested, and some of the deadliest and most destructive wildfires in the USA raged through the slash left after logging (Pyne 1982). These destructive wildfires added to public demands for wildfire control.

Large, catastrophic fires such as the Peshtigo (1871) in Wisconsin (Chap. 7) and the Great Blowup of 1910 in Montana and Idaho (Chap. 8) raised the demand for wildfire suppression, which became the policy for the US Forest Service and many state forestry agencies in the 1920s and 30s (Pyne 1982; USDA/USDI 2001). National Forest personnel vigorously pursued fire control throughout Appalachia through a dual strategy of prevention to reduce the number of ignitions and suppression to halt the spread of fires before they could grow to a large size (Pyne 1982; Sarvis 1993). Effective fire suppression across the region proved successful. Fire-scar records illustrate a plunge in fire frequency from the historical levels of 1–5 fires per decade to virtually no burning after ca. 1930 (Lafon et al. 2017; Stambaugh et al. 2018). The scarcity of fire is also seen in agency fire-occurrence records, which indicate that present fire cycles are 200–11,000 years across different Appalachian landscapes (Lafon et al. 2017).

The loss of fire from these landscapes has contributed to contraction of oak and pine forests and woodlands and a shift toward mesophytic vegetation (Nowacki and Abrams 2008). These changes have prompted resource managers to reintroduce fire to promote desired tree regeneration (e.g., oak and pine), conserve native biodiversity, and restore oak and pine forests and woodlands and associated wildlife (e.g., USFS 2014, 2020). Considerable progress has been made to reintroduce fire, particularly on the extensive public lands of the Ridge and Valley and the Blue Ridge ecoregions. However, prescribed burning is limited in frequency and extent by significant challenges, including weather, agency capacity, air quality and smoke management, risk management, firefighter and public safety, social and cultural attitudes toward fire and land management, rural and urban development, and legal regulations (Ryan et al. 2013).

4.4 Ecological Consequences of Fire Exclusion

Across the EBA region, upland forest landscapes dominated by pyrophytic oaks and pines are shifting to less fire-tolerant and more shade-tolerant species that were historically limited primarily to mesic sites. These trends are hypothesized to be driven by multiple historic and ongoing factors (reviewed in McEwan et al. 2011), including land use changes (Foster et al. 1998), shifts in precipitation and drought severity (Pederson et al. 2014; Pederson et al. 2015), increases in herbivores (McEwan et al. 2011; Kane et al. 2019), loss of the flammable American chestnut (McEwan et al. 2011), and atmospheric nitrogen deposition (Thomas et al. 2010; BassiriRad et al. 2015). However, the dramatic decrease in fire since the early 1900s is arguably the dominant driver of the pathway of forest change in our region (Brose et al. 2001; Nowacki and Abrams 2008; Hanberry et al. 2020a). Here we again focus primarily on mixed-oak and oak-pine forests, as these are most likely to be altered significantly by fire exclusion.

Many of today's mature forests (stand age >80 yrs) regenerated ca. 1870 to 1930, after heavy industrial logging coupled with high-severity wildfires (Whitney 1994), which favored the establishment and sustained dominance of oaks, and yellow pines on more xeric sites. Forest succession has occurred on these sites for nearly a century with little or no fire. Stands lacking recent major canopy disturbances are dense, closed-canopied, and multi-layered, with basal area (BA) and tree density typically ranging from 25–30 m^2/ha and 300–400 trees (>10 cm dbh)/ha, respectively (e.g., Hutchinson et al. 2005b; Waldrop et al. 2008; Arthur et al. 2015; Thomas-Van Gundy et al. 2014). In pre-Euro-American forests, trees were larger (e.g., Dyer and Hutchinson 2019) and presumably uneven-aged, as they are in current old-growth stands (e.g., Hart et al. 2012). In adjacent western central hardwoods (Chap. 5), analyses of General Land Office (GLO) witness tree distances indicate that open oak and pine woodlands and savannas, rather than closed-canopy forests, dominated the pre-Euro-American landscape (Hanberry et al. 2014; Hanberry et al. 2020b). Similar quantitative analyses are lacking from our region, but historic traveler/pioneer accounts suggest that relatively open woodlands and forests were common (Whitney 1994; Brewer 2001).

Across most upland landscapes, the overstory of mature stands is dominated by a matrix of oaks, often with associated hickories (*Carya* spp.). On lower north- to east-facing slopes and coves, mesophytic species (e.g., red maple, sugar maple, American beech, and tuliptree) may dominate, whereas on xeric ridges and upper S- to W-facing slopes, yellow pines (e.g., pitch, shortleaf, and Table Mountain pine; Fig. 4.1) are common, particularly in the Southwestern and Central Appalachian Ecoregions. Regional Forest Inventory and Analysis (FIA) data document widespread oak abundance in the overstory. However, those data also show a decline in the relative density of overstory oaks and yellow pines in recent decades (Fei et al. 2011; South and Harper 2016; Knott et al. 2019). This trend is partly due to an increase in red maple in the overstory (Fei and Steiner 2007), as well gains in tuliptree, which now ranks first in sawtimber volume by species in multiple states (Indiana, Ohio, West Virginia, Kentucky, and Tennessee; FIA data). Fire exclusion also led to the accelerated loss of yellow pines often due to southern pine beetle outbreaks and subsequent poor regeneration (Kuykendall 1978; White 1987). In addition to topo-edaphic factors, current overstory composition has been influenced by past land use. Sites that have succeeded to forest after historic agricultural use (row crops, improved pasture) are more likely to be dominated by wind-dispersed

Fig. 4.1 Table Mountain pine stands: on the top (**a**) unburned stand with a dense understory of shrubs, hardwood trees, and eastern white pine; (**b**) a neighboring stand immediately after a spring burn in May 2001, Little Walker Mountain, Bland County, Virginia with blueberries (*Vaccinium* spp.) resprouting and many small Table Mountain pine seedlings (invisible in the photo); and on the bottom left and right (**c**) the same burned stand 17 years after burning, showing pine saplings amid remaining overstory pines (photos Charles Lafon)

species, including red maple (Dyer 2010) and yellow pine species (White 1987). Timber harvest history can also drive current composition. Oak-dominated stands logged since the mid-twentieth century, after several decades of fire exclusion, may transition more rapidly to dominance by non-oaks, particularly on more mesic sites (Nowacki and Abrams 2008).

In the absence of periodic fire or other management, a well-developed midstory (i.e., pole-sized trees 10–25 cm dbh) comprised mostly of shade-tolerant tree species is typically present, comprising 15–20% of BA (e.g., Arthur et al. 2015). Red maple is the quintessential midstory tree of mixed-oak forests in this region and across much of the eastern USA (Lorimer 1984; Abrams 1998), and its abundance and range have increased in the last few decades (Fei and Steiner 2007; Knott et al. 2019). Red maple thrives on varied sites, including the drier and less fertile locations where oaks are dominant, and can persist for decades in the understory and then grow rapidly when canopy gaps occur (Abrams 1998; Tift and Fajvan 1999). On more mesic/fertile sites, sugar maple often is abundant in the midstory (Jenkins and Parker 1998; Palus et al. 2018). Midstory maples of both species were shown to have established immediately after the cessation of periodic fires in the early twentieth century (Hutchinson et al. 2008).

A dense layer of saplings and/or shrubs (>1.5 m tall) is common beneath the midstory and is almost always dominated by shade-tolerant species. Stem densities are often quite high: 1500–3500 stems/ha >1.5 m tall (Waldrop et al. 2008; Hutchinson et al. 2016). In addition to maples, a variety of other shade-tolerant saplings may be abundant, depending on site conditions (e.g., American beech, blackgum (*Nyssa sylvatica)*, sourwood (*Oxydendrum arboreum)*, eastern hop hornbeam, and striped maple *(Acer pensylvanicum;* see also Palus et al. 2018; Vander Yacht et al. 2019*)*. Oak saplings are typically sparse to absent, except on the most xeric sites. Tall ericaceous shrubs, primarily the shade-tolerant and evergreen mountain laurel (xeric sites) and rosebay rhododendron (*Rhododendron maximum*; mesic sites), are abundant on acidic soils in the central and southern Appalachians and usually occur in dense thickets 2–4 m tall which pose increased risk of high-severity fire (Waldrop et al. 2007; Huebner et al. 2014). Their expansion in the mid-twentieth century has been linked with fire cessation (Baker and Van Lear 1998; Brose et al. 2002) though other factors, including American chestnut mortality, have been cited (Elliot and Vose 2012; Brose 2016).

The dense structure that develops without periodic fire or other management greatly limits light to the understory; full sunlight is typically <5% (e.g., Brose 2008). While the overstory intercepts most incoming radiation, midstory/sapling removal increases understory light to a modest 10–15% of full sunlight (Lorimer et al. 1994; Brose 2008; Parrott et al. 2012). Historically, where low-intensity fires occurred frequently, the midstory/sapling layer was sparse to absent (Hanberry et al. 2018).

The seedling/herbaceous layer, consisting of tree seedlings, shrubs, and herbaceous plants <1.5 m tall, is critically important for tree regeneration and plant diversity (Gilliam 2007). The low understory light levels in unburned and/or unmanaged stands limit the persistence and growth of all but the most shade-tolerant tree seedlings. Poor survival and growth of mid shade-tolerant oak seedlings are largely due to heavy shade (Johnson et al. 2019). However, with the continued importance of oak in the overstory, small oak seedlings are often present at moderate to high densities, establishing after heavy mast years and then persisting for some time, depending on site conditions (Johnson et al. 2019).

In many cases, oak seedlings are present and even abundant on the forest floor, as expected over succession, but in the absence of large-scale disturbance (including fire) small canopy gaps are almost always filled by poles and saplings of shade-tolerant species (Izbicki et al. 2020), resulting in a gradual patch-scale decrease in oak canopy dominance (Hart and Kupfer 2011; Hutchinson et al. 2012a). When larger canopy openings occur, fast-growing shade-intolerant trees, newly established from seed (e.g., tuliptree, sweet birch (*Betula lenta*)) are highly competitive and further limit the probability of future oak dominance, particularly on mesic sites (Loftis 1983; Jenkins and Parker 1998). Notably, after overstory removal on fire-excluded xeric sites or drought-affected areas, oak dominance may be evident 2–3 decades post-harvest, likely ensuring oak dominance through stand development (Gould et al. 2005; Morrissey et al. 2008). In highly xeric, fire-suppressed pine stands, canopy disturbance (e.g., ice storm damage, pine beetle infestation) can result in succession to oak dominance (Lafon and Kutac 2003).

The herbaceous layer varies substantially across topo-edaphic gradients, with the richness and abundance of herbaceous plants increasing from xeric nutrient-poor sites to mesic high-fertility sites (Hutchinson et al. 1999). In unburned and unmanaged stands, heavy understory shade filters out forbs and grasses that require partial to full sunlight, limiting occupation primarily to shade-tolerant species and/or spring ephemerals. However, many shade-tolerant and spring ephemeral forbs are mesophytes, and thus uncommon on the drier upland landscapes; this, coupled with the absence of forbs and grasses requiring partial to full sunlight, often results in a depauperate upland herbaceous flora. Historically, periodic fire on drier upland sites would have created more open forests and the capacity to support more grasses, forbs, and shrubs requiring partial to full sunlight. Some of the most diverse and unique plant communities in the eastern USA, characterized by a robust herbaceous flora, occur in open oak and pine woodlands and savannas, where frequent fire has been continuous or restored (e.g., Walker and Peet 1984; Leach and Givnish 1999; Chaps. 2, 5; Fig. 4.2).

The compositional and structural shifts through succession following fire exclusion as described above have inevitably led to a suite of ecosystem-level consequences. Abiotic conditions in closed-canopy forests with a well-developed midstory and sapling stratum occupied mostly by shade-tolerant species differ markedly from those on sites that historically held sparse-canopied oak woodlands throughout the region. During the growing season in closed-canopy forests, densely packed trees with deep crowns and high leaf area moderate air temperatures and wind speeds and increase relative humidity (Hanberry et al. 2020b) and precipitation interception (Siegert et al. 2019), creating more spatially homogeneous conditions than those in woodlands. The thin, smooth bark of many fire-intolerant species

Fig. 4.2 Fire-dependent forbs of the Appalachian mountains: from left (**a**) hill cane (*Arundinaria appalachiana*) and fire-scarred pine, Georgia (photo Charles Lafon); (**b**) Peters Mountain mallow (*Iliamna corei*; photo Jennifer Hoss), and; (**c**) Eastern turkeybeard (*Xerophyllum asphodeloides*) and fire scarred pine, Virginia (photo Charles Lafon)

funnels precipitation down the branches and trunk as stemflow, concentrating large amounts of nutrient- and carbon-rich water in a narrow region near the bole of these trees (Alexander and Arthur 2010; Siegert and Levia 2014). This water then either percolates (~0.5 m) into soils along roots near trees (Gonzalez-Ollauri et al. 2020) or remains in shallow soil horizons, creating temporary patches of high surface soil moisture adjacent to the tree (Liang 2020). However, the greater leaf area in closed-canopy forests, along with a shift to more mesophytic species, ultimately means more water uptake from soils, and relatively lower soil moisture throughout the soil profile than would be expected in woodlands (Ma et al. 2014; Von Allmen et al. 2015). The shift in composition also changes the primary zone of water withdrawal from soils because oaks tend to root deeper in soils compared to species like red maple (Gaines et al. 2015; Matheny et al. 2017).

Higher leaf area in closed-canopy forests creates a relatively continuous cover of leaf litter on the forest floor. This litter can create an inhospitable seedbed for many plant taxa, including oak (Royse et al. 2010; Brose 2011), and interacts with low light to hinder the establishment of an herbaceous groundlayer (Maynard and Brewer 2013). Because of marked differences in leaf litter chemistry (e.g., lignin content and C:N ratio) between many mesophytic species and oaks, mesophyte litter often decomposes faster than oaks and alters the cycling of nitrogen (Finzi et al. 1998; Finzi and Canham 1998; Washburn and Arthur 2003; Alexander and Arthur 2014), a key limiting nutrient in these systems. For example, red maple leaf litter on sites in Kentucky had lower lignin content and higher C:N ratio than that of co-occurring oaks, leading to immobilization of nitrogen from soils (Alexander and Arthur 2014). Because nitrogen is often limiting in these systems, a decrease in plant available nitrogen could affect growth and survival of plants with relatively high nitrogen needs, potentially accelerating further shifts in forest composition.

There are numerous ecosystem consequences of fire exclusion for wildlife populations. Acorns are a critical winter food source for many species, comprising a portion of the diet of at least 96 avian and mammal species (McShea 2000; McShea et al. 2007). Oaks are the most important North American genus for insect herbivores and an essential base for terrestrial food chains (Tallamy and Shropshire 2009). Changes in forest pond chemistry due to leaf litter differences among oaks and maples can dramatically alter forest ponds through changes in aquatic microbial food beds, with cascading negative impacts on amphibian biomass and survival (Rubbo and Kiesecker 2004). Sugar maple-dominated forests are more susceptible than oak-dominated ecosystems to invasion by exotic earthworms, which can increase leaf litter decomposition rates and reduce substrate availability for ground-nesting sites for songbirds (Fox et al. 2010).

All of these changes combined indicate that transition to increasingly closed-canopy stands with increased abundance of fire-sensitive, shade-tolerant species alters light, water, and nutrient availability, and plant-fauna interactions. Ultimately, these impacts also reduce the potential for fire restoration and maintenance of historically fire-prone ecosystems, regardless of where on the spectrum of woodland to closed forests these sites were historically.

4.5 Fire as an Emerging Management Tool

There is widespread recognition that oak, oak-pine and pine-oak savannas, woodlands, and open forests are being lost throughout the eastern USA as forests undergo succession following land use changes in the early twentieth century (Fei and Steiner 2007; Fei et al. 2011; Dey 2014; Johnson et al. 2019). Beyond plant composition change, the losses in landscape diversity and key habitat for wildlife species are important management issues (Dey and Kabrick 2015; Dey et al. 2017; Johnson et al. 2019; Hanberry et al. 2020b). It is widely acknowledged that significant effort will be required to restore historical conditions to forests where structural and compositional changes have transpired for over a century with fire exclusion. There is much to learn about the application of fire, both alone and in combination with other silvicultural practices, to restore and maintain historical forest conditions. Further, although there is growing use of prescribed burning in the EBA region for a range of management purposes, fire is applied to an insufficient portion of the acreages identified by managers as needing treatment.

Prescribed fire is often used as a tool to alter species composition and structure. In the EBA region, a common goal is to create conditions conducive to recruiting oak and pine into more competitive understory positions, thereby increasing the probability of attaining future canopy dominance (McEwan et al. 2011; Guldin 2019). Thus, the basic tenets of oak silviculture remain at the forefront when burning is used as a management tool with this goal (Brose et al. 2014). Regeneration of oaks and yellow pines is advance growth dependent; the abundance and stature of oak and pine reproduction dictate their response to disturbance. On more productive, mesic sites, competition is more robust and oak-pine regeneration success less robust, compared to drier, lower productivity portions of the landscape (Carvell and Tryon 1961; Sander 1972; Brose and Van Lear 2004; Dey and Hartman 2005; Brose et al. 2013; Guldin 2019).

From a management perspective, an initial fire is typically part of a larger plan designed to unfold over decades of repeated burning. Not only is a single low-intensity, dormant season fire insufficient to reduce competitor densities and create openings large enough for oak recruitment (McEwan et al. 2011; Brose et al. 2013), single fires result in prolific stump sprouting in many species (Arthur et al. 1998; Arthur et al. 2015). While repeated fire has been suggested to reduce resprouting (Van Lear and Watt 1993), even repeated fires beneath a closed canopy may be insufficient to increase dominance of oak regeneration (Hutchinson et al. 2005a, b; Waldrop et al. 2016). Annual burning, which is possible in some areas due to the annual re-accumulation of leaf litter, limits fire intensity, reducing the capacity of fire to alter composition and structure of the overstory (Waldrop et al. 1992; Hutchinson et al. 2005b). However, long-term application of annual fire, especially when applied in the growing season, can effectively eliminate understory hardwoods over decades (Knapp et al. 2015). Burning intervals of 2–3 years generally result in greater fire intensities than annual burns, opening stand structure through greater midstory mortality (Waldrop and Lloyd 1991; Hutchinson et al. 2005b; Waldrop et al. 2008; Brose et al. 2013; Arthur et al. 2015; Schweitzer et al. 2016).

Red maple is a widespread competitor in many EBA upland oak-pine forests, thus a focus of many prescribed fire studies, with disparate results. While red maple dominance can persist in the sapling layer after multiple burns (Waldrop et al. 2008; Arthur et al. 2015; Schweitzer et al. 2016), other studies have shown that multiple fires reduced red maple density (Hutchinson et al. 2005b; Blankenship and Arthur 2006; Fan et al. 2012; Hutchinson et al. 2012b). Persistence of red maple after repeated fires may be attributable to its rapid aboveground growth. Red maple also sprouts prolifically after fire; external parts of a clump are damaged from subsequent fires, whereas internal sprouts are less susceptible to topkill (aboveground death followed by resprouting or suckering). This sprout clump phenomenon allows escape from the fire trap (*sensu* Grady and Hoffman 2012) as red maple stems grow into sizes less impacted by subsequent fire. Prescribed fire (the "inciting" disturbance, *sensu* Hutchinson et al. 2012b) interacting with other disturbances, though difficult to plan for, may be the most effective scenario for improving the competitive status of oaks relative to red maple and other mesophytic competitors.

Growing season burns may reduce the competitive capacity of persistent mesophytes, including red maple (Waldrop and Lloyd 1991; Brose and Van Lear 1998; Blankenship and Arthur 2006; Keyser 2019). Barnes and Van Lear (1998) suggested that on some sites, three dormant season burns are similar in impact to one growing season burn. Multiple mid-to-high-intensity summer burns reduced red maple and tuliptree densities more than one low-intensity winter burn (Barnes and Van Lear 1998), but regardless of season of burn, oak and red maple densities did not differ, and red maple reproduction remained taller than oak (Brose and Van Lear 1998; Keyser 2019). Burning later in spring when sprout carbohydrate reserves are lowest during leaf expansion, and when higher ambient temperature promotes medium to high-intensity fire, may be key (Blankenship and Arthur 2006; Brose 2010). Growing season fires are more difficult to implement across the region, however (Chiodi et al. 2018). Effective management with fire throughout the region requires flexibility in timing of prescribed fire to stand and environmental conditions, but standard prescription parameters, limited burn days, and coincidence of good burning conditions with wildfires (limiting the availability of burn crews), can all limit implementation.

Low- to moderate-intensity dormant season fires most commonly used by EBA forest managers, typically topkill trees <10 cm dbh. As a result, dual disturbances are often required to increase and maintain understory light levels to stimulate oak-pine reproduction development and recruitment, reduce density and dominance by mesophytes, and increase cover of groundlayer plants (Reich et al. 1990; Kruger and Reich 1997; Brose and Van Lear 1998; Kinkead et al. 2013), but not in all cases (Wendel and Smith 1986; Franklin et al. 2003). Burning in combination with overstory density reduction is most successful when there is adequate oak-pine advance reproduction before treatment to give some certainty that desired stocking at stand maturity will be met (Dey and Fan 2009). In many forests, oak-pine advance reproduction is small in stature and low in number due to low light conditions. As a result, targeted disturbance that increases light to >20% full sunlight for oak and >50% for pine, and allows development of competitive reproduction prior to burning, is needed (Reukema 1959; Lorimer et al. 1994; Brose and Van Lear 1998; Miller et al. 2008; Dey and Fan 2009; Motsinger et al. 2010).

Repeated fires can result in the inability of oaks or pines to recruit beyond the seedling-sprout stage for several reasons. Although repeated fires can reduce midstory densities and improve seedbed conditions, understory sprouting by mesophytes rapidly occupies any transient growing space (Chiang et al. 2005; Blankenship and Arthur 2006; Brose 2010; Green et al. 2010; Keyser et al. 2017). Targeting small tree and shrub competitors with herbicide or chainsaw felling followed by canopy density reduction and prescribed fire can promote advance oak and pine regeneration, enhancing the likelihood of recruitment into the canopy during a sufficient fire-free period (Waldrop et al. 2016). Shade intolerant and mid-tolerant hardwoods require a longer fire-free period to recruit into the overstory than pines. Once oak and pine recruit into midstory positions, the canopy can be reduced (via mechanical felling and/or herbicides) to fully release the saplings. This prescription, despite being relatively intensive, may be a path forward for restoring oak- and pine-ecosystems across upland sites in the EBA region.

Variable responses of oak-pine reproduction to prescribed burning, thinning, and their combination may be attributed to many site factors that impact reproduction responses to disturbance (McEwan et al. 2011; Hutchinson et al. 2012b; Brose et al. 2013; Keyser et al. 2017). Shelterwood-burn prescriptions entailing harvests with retention of large overstory trees followed by burning after a few years to reduce competition (Brose and Van Lear 1998) may work in systems with adequate sizes and numbers of advance oak-pine reproduction (Brose et al. 1999; Dey and Fan 2009; Brose 2010). To promote recruitment, oaks and pines must be free to grow and of a sufficient size to resist topkill from subsequent fire (Arthur et al. 2012; Brose et al. 2013; Dey and Schweitzer 2018). For example, repeated fires over 13 years in Ohio reduced the dominance of shade-tolerant saplings; small light gaps caused by drought-induced overstory mortality facilitated the growth of large oak and hickory seedlings (Hutchinson et al. 2012b). These complex interactions among disturbances often result in complex outcomes (Cannon et al. 2017).

Management with fire in the EBA region is also somewhat idiosyncratic across sites, ecosystems and management goals. It is becoming increasingly clear that timing fire with other disturbances, natural and prescriptive, as well as the time between canopy reduction and burning, is critical to reaching management objectives (Kelty 1988; Kolb et al. 1990; Brose and Van Lear 1998; Keyser et al. 2017). Where increased oak and/or pine regeneration is a key goal, managers must consider how the interactions between fire and canopy reductions may impact the stand. For example, if canopy reduction is conducted under conditions of inadequate advance reproduction of desired species, it may be necessary to chemically treat competing mesophytic species prior to burning to promote advance regeneration of target species. In forest types where nontarget species (e.g., red maple and tuliptree, among others) will rapidly germinate or resprout and grow, burning prior to or immediately after canopy reduction may be warranted. These management complexities add to the need to bring nuanced understanding of when and how to use fire across the landscape.

4.6 Mechanisms and Patterns of Fire-Caused Tree Mortality

Fire effects in EBA savannas, woodlands, and forests are numerous and vary in importance depending on management objectives. Fire effects may also differ with the spatial extent of prescribed burns. For example, prescribed fire as a stand-level silvicultural tool intended to retain timber value may conflict with landscape level fire management objectives where canopy mortality may be desired to create a mosaic of forest structures (Lorber et al. 2018). Regardless of spatial scale, the most apparent fire effect is the response of trees and other woody species via stress that leads to mortality. Fire-caused injury results from heating of crown, stem, or root tissues (Hood et al. 2018). Crown injury in response to radiant and convective heat can involve damage to leaves, buds, or branches. Foliar damage (most commonly apparent as crown scorch) can cause short-term stress, whereas foliar consumption and bud or branch injuries can be substantial and lead to topkill or tree mortality. Because many fires in the region either occur in the dormant season (i.e., leaf-off) or are of low-intensity, crown injuries primarily impact small trees. High-intensity prescribed fires and wildfires during severe drought can cause high-severity fires in hardwoods (Fig. 4.3). Stem injuries cause short- and mid-term stress from reduced conducting tissues, and compartmentalization and repair, respectively (O'Brien et al. 2018). Increasing circumferential injury results in topkill or mortality. Where present, smoldering of large woody and surface organic fuels conducts heat through surface organic and mineral soils, causing fine and coarse root necrosis and reducing access to carbohydrate storage that stresses or kills trees (often death rather than topkill; Brose and Van Lear 1999). Crown, stem and root injuries often co-occur, leading to interactions among tissues and organs that exacerbate stress and increase tree mortality (Hood et al. 2018).

Past research on EBA postfire tree stress and mortality reveals divergent outcomes among species and general patterns across tree sizes. Nearly all tree species within the region are capable of resprouting. Small trees (both in stature and diameter) have buds within or near the flaming zone and have less protective outer bark than older and larger trees, hence mortality rates are higher in small seedlings for a given fire intensity and behavior (Dey and Hartman 2005). Trees tend to suffer less mortality as bark accumulation accelerates with age and size. The capacity for resprouting after topkill often increases with increasing stem diameter from seedlings to large saplings and pole-sized trees, but begins to decline as trees reach maturity and larger diameters (Johnson et al. 2019). For small seedlings and saplings, understory light and competition in the regeneration layer influence this relationship (Keyser and Zarnoch 2014). Effects of fire(s) on seedling mortality vary greatly by species. Fire-adapted *Quercus* and *Carya* seedlings experience much lower mortality over time in response to repeated fires relative to the less

Fig. 4.3 Shown here is a range of fire severity following a wildfire in the Daniel Boone National Forest, three years after an early dormant season fire. Burn severity ranges from high-severity (**a**, **b**) to (**c**) moderate burn severity, to (**d**) very low-severity surface fire (photo Mary Arthur)

fire-tolerant sugar maple, flowering dogwood, and blackgum seedlings (Dey and Hartman 2005; Brose et al. 2013; Short et al. 2019).

For adult canopy trees, species in the region differ widely in their resistance to injury from fires, and fire-caused mortality or topkill interacts with other disturbances. For example, wind disturbances before fire increase fuel loading that may lead to increased fire intensity and injury of surviving trees (Cannon et al. 2017). Fire, stresses, and disturbances exacerbated by climate change will be increasingly more common across the region (Vose and Elliott 2016). Keyser et al. (2018) reported two-year post-seedling stem mortality (topkill) for 10 Appalachian species. Among the species, white oak suffered only 6.9% mortality whereas less fire-tolerant species such as blackgum, flowering dogwood and red maple all exceeded 25% and sassafras (*Sassafras albidum)* experienced 58.9% topkill. Regelbrugge and Smith (1994) found chestnut oak and blackgum had the highest rates of survival compared to red maple, mockernut hickory (*C. tomentosa*) and northern red, scarlet, and black oak following wildfire. Species tend to vary along Hengst and Dawson's (1994) bark thickness scale: those with thick bark and large size exhibit greater survival than those with thinner bark and smaller stature. Mortality and topkill have cascading effects on species composition, structure, and resulting ecosystem processes.

4.7 Fire Effects on Wildlife

A key goal for using prescribed fire in the EBA region is to create, enhance, or maintain habitat for specific wildlife (Harper et al. 2016). As with any disturbance, some wildlife species benefit from fire and others do not, as species require different structural and compositional vegetation characteristics. Hence, the natural history and habitat requirements of focal wildlife species determine the ideal frequency, season, and severity of a prescribed fire program designed to meet their habitat requirements. Burn prescriptions for one focal species may conflict with that for others.

Wildlife respond to changes in vegetation structure and composition created by fire and altered over time via stand development or succession. Local fire effects are also tempered by larger-scale environmental conditions such as land cover, topography, and the broader landscape context. Harper et al. (2016) provided a synthesis of fire effects on a suite of wildlife species and guilds, and how fire can be applied to affect plant communities and promote focal wildlife.

Direct effects of fire on wildlife are poorly documented, but observations of animal fire-caused mortality or injury are relatively rare in the region. However, some species are more vulnerable during particular times of the year and may be adversely affected by certain firing techniques. For example, eastern box turtles (*Terrapene carolina*) and timber rattlesnakes (*Crotalus horridus*) are more vulnerable to fire soon after emerging from hibernacula in spring when they are relatively lethargic and less able to escape (Beaupre and Douglas 2012; Harris et al. 2020). Nests of ground- and shrub-nesting birds, and upland salamanders, may be susceptible to early growing season fire, but population effects are unlikely unless burns are large-scale (Ford et al. 1999; Moorman et al. 2011; Harper et al. 2016). Local populations within relatively small areas (<40 ha) are more likely to be negatively affected if burning occurs repeatedly during spring (or late winter if burning around hibernacula of some snake species) when individuals are most vulnerable. Adjusting season of burn and firing technique can reduce risk of direct effects on wildlife. For example, fire can be prescribed later in the growing season, and backing, flanking, and strip-heading fires can reduce the risk of trapping wildlife compared to heading or ring-fires.

Fire regimes affect vegetation structure and composition, thereby creating, modifying, or eliminating habitat for specific wildlife species. Generally, high-severity fire reduces overstory canopy closure and promotes understory cover for wildlife via increases in light penetration that promote rapid regrowth of stump sprouts and understory woody and herbaceous plants (Fig. 4.4). Conversely, frequent (1–3 year FRI) low-intensity fire limits woody midstory development, but rarely causes overstory mortality (Marschall et al. 2014; Dey and Schweitzer 2018). Frequent low-intensity fire may increase the herbaceous component and reduce the woody component of the understory over time, especially when at least 20–30% sunlight reaches the forest floor (Fig. 4.4; McCord et al. 2014). Frequent low-intensity fire in the absence of canopy reduction creates open understory conditions and promotes

Fig. 4.4 Frequently burned woodland (**a**) photo taken the spring after a late growing season fire; characterized by a lush herbaceous layer, sparse midstory, and open canopy. This condition provides habitat for woodland birds such as red-headed woodpecker (*Melanerpes erythrocephalus*) and eastern wood-pewee (*Contopus virens)*, brooding cover for wild turkey, and forage for white-tailed deer; (**b**) high-severity fire kills overstory, resulting in high snag density that provides nest sites for woodpeckers and other cavity-nesting species for years after the fire. The dense understory provides habitat for shrubland birds, lizards, and eastern cottontails (photo Craig Harper)

low-growing, often sparse groundcover which may benefit some species, such as loafing wild turkeys (*Meleagris gallopavo*). Less-frequent fire (3–6 year FRI) that maintains a sparse midstory and a dense woody understory of stump sprouts and few herbaceous plants can benefit shrub-nesting species such as hooded warbler (*Setophaga citrina*). High-severity fire that reduces or eliminates the overstory often results in dramatic shifts in the abundance, occurrence, and composition of wildlife communities including breeding birds, in particular (Greenberg et al. 2018c).

Timber harvests that reduce the overstory (e.g., shelterwood harvest, thinning) avoid the risks associated with high-intensity prescribed fire and generate income for the landowner. In this way, timber harvests can generate short-term change in the wildlife community similar to high-severity fire. Incorporating repeated prescribed fire following canopy-reducing timber harvest creates savanna and woodland conditions and habitat for the associated wildlife community (Lashley et al. 2011; McCord et al. 2014; Raybuck et al. 2015; Greenberg et al. 2016; Nanney et al. 2018). Fire-maintained woodlands are characterized by vegetation structure and composition that provide habitat for a diversity of wildlife species that may otherwise be rare in unburned landscapes (Vander Yacht et al. 2016). Shelterwood harvests increase light penetration to the forest floor, increasing understory structure while maintaining some overstory (Vander Yacht et al. 2017b). Repeated prescribed fire then can be implemented to diminish hardwood resprouting and seedlings from reaching the midstory, while maintaining a diverse understory of forbs, grasses, woody sprouts, and shrubs that provide food and cover for shrub- and canopy-nesting birds, white-tailed deer, wild turkey, and numerous other species (Fig. 4.4; Matthews et al. 2010; Lashley et al. 2011; McCord et al. 2014; Vander Yacht et al. 2017a).

High-severity fire that kills many overstory trees creates a large pulse of snags and downed logs, used by many animal species for nesting, foraging, and cover until the wood decays (Fig. 4.4; Perry 2012). Fire also consumes dead wood, especially small-diameter pieces but sometimes also large downed wood (e.g., during droughts); this may decrease habitat quality for shrews, mice, and other ground-dwelling wildlife that rely on downed wood for cover or on prey that use downed wood for cover or food (e.g., invertebrates). Abundance of lizards and possibly other reptiles increase after high-severity burns because of greater light and warmer conditions (Matthews et al. 2010; Greenberg et al. 2018a). Similarly, shrubland and some woodland birds, as well as some bat species, increase postfire, because of increased shrub layer, more snags, and reduced canopy and midstory clutter (Johnson et al. 2009; Johnson et al. 2010; Loeb and O'Keefe 2014; Ford et al. 2016; O'Keefe and Loeb 2017; Greenberg et al. 2018c). High-severity fire may reduce habitat for salamanders because of greater light penetration and a warmer, drier microclimate (Matthews et al. 2010). However, research has yielded mixed results, with some demonstrating no or temporary changes in the salamander community, especially where postfire leaf litter recovery was rapid (Ford et al. 2010; Moorman et al. 2011; Greenberg et al. 2018a).

Low-severity fires that consume the litter layer with little overstory mortality may nonetheless negatively affect litter-dwelling species (e.g., shrews, some ground-nesting birds, and possibly salamanders), but effects seem to be temporary, as many species return to prefire levels within a year as leaves senesce from deciduous trees and shrubs in the fall (Fig. 4.5; Matthews et al. 2009; Raybuck et al. 2012;

Fig. 4.5 (**a**) Unburned upland hardwood forest typically has a dense leaf litter layer, a well-developed midstory, and a sparse herbaceous cover. This condition favors leaf litter associates such as woodland salamanders and shrews and midstory birds such as wood thrush; (**b**) forest upland burned with an infrequent return interval of every 3–6 years typically is characterized by a dense understory of woody sprouts, which provides cover for songbirds, browse for white-tailed deer, and nesting sites for wild turkey (photo Craig Harper)

Raybuck et al. 2015; Greenberg et al. 2016; O'Donnell et al. 2016). Shrub-nesting birds may also decrease as shrub densities are reduced by fire, but generally return to prefire levels rapidly as the woody vegetation resprouts (Greenberg et al. 2007, 2018c). When fire is excluded for 10–15 years, woody stems grow taller and their density declines, reducing availability of dense, low shrubs required by shrub-nesting bird species, but enhancing the taller structural requirement for other species, such as white-eyed vireo (*Vireo griseus*) and ruffed grouse (*Bonasa umbellus*).

Precisionism should be avoided when setting target fire frequency for a prescribed burn program (see Hiers et al. 2016). Historically, variable fire frequencies led to heterogeneous forest composition and structure and thereby diverse wildlife communities. Annual and biennial burns typically eliminate the structural requirements for shrubland birds and other species associated with woody cover but maintain herbaceous-dominated understories that generate high-quality forage for deer and elk (*Cervus elaphus*; Fig. 4.4; Vander Yacht et al. 2017b; Nanney et al. 2018). Fire may promote soft mast production in upland hardwood forests starting about two years postburn, especially when coupled with canopy-reducing silvicultural treatments (McCord et al. 2014; Wood et al. 2019). However, frequent fires may eliminate or greatly reduce understory fruit availability, especially if a large portion of the landscape is burned homogeneously (Lashley et al. 2017; Wood et al. 2019). A fire mosaic within and among burn units ensures cover and food remain available across the landscape. Fire shadows – areas that remain unburned within burn units due to fuel or weather conditions – increase structural heterogeneity and may allow persistence of less pyrophytic flora and woody vegetation (Lashley et al. 2014).

Heterogeneity in fire season also offers options for multiple wildlife species and increases the "burn window" (Knapp et al. 2009; Lashley et al. 2015; Harper et al. 2016). Growing season fire has been promoted widely in the EBA region because it aligns with the dominant season of lightning-caused fire and may provide better control of hardwood sprouts than dormant season fire (Sect. 4.5), with important implications for restoring some imperiled plant communities and habitat for focal wildlife species (Knapp et al. 2009; Ryan et al. 2013). Research on season-of-burn effects on vegetation and wildlife in the EBA region is scant, but suggests that single, low-intensity dormant- versus early growing season burns do not differ in their effects on forest structure and tree regeneration (Keyser et al. 2019, Sect. 4.5), or bird and herpetofaunal communities (Greenberg et al. 2018b, 2019). Dendrochronological fire scar evidence reveals that most fires in this region were ignited in early and late dormant season (Lafon et al. 2017). Without a discernible difference in plant community response (and thus no improvement in habitat quality) between early growing- and dormant season fire, it is difficult to provide an ecological rationale for conducting prescribed burns during the reproductive season of many wildlife species when they are most vulnerable, especially when prescription windows are constrained during the growing season (Chiodi et al. 2018). More research is needed to address tradeoffs between the vegetation response to early growing season burns, and direct effects on vulnerable wildlife.

Burning later in the growing season (August – October) and into the dormant season may be used to avoid the reproductive season of many species, or to alter vegetation composition (Gruchy et al. 2009; Knapp et al. 2009; Harper et al. 2016). Moreover, that timeframe is the most underutilized part of the burn window in the EBA region (Chiodi et al. 2018). Even dormant season burning can reduce or degrade both cover and food resources for various species, but when conducted on a 3–6 year FRI, conditions can be maintained for species that require woody structure as well as provide diverse food resources for game species such as white-tailed deer, elk, black bear (*Ursus americanus*), and wild turkey (Fig. 4.5; Van Manen and Pelton 1997; Lashley et al. 2011; McCord et al. 2014; Nanney et al. 2018). Unburned patches diversify both food and structural components, which may represent critical nesting sites or refuge for vulnerable species during or immediately after a burn (Harris et al. 2020).

The spatial scale of burning is critical when assessing population-level effects of fire on focal wildlife. Prescribed burns on small sites (<40 ha) may have minor or only temporary effects on wildlife populations, though individual animals respond behaviorally at extremely small spatial scales relative to their individual habitat requirements (e.g., white-tailed deer behaviorally respond to fires <0.2 ha; Westlake et al. 2020). Conversely, large (>200 ha) burns are more likely to have negative effects on local populations of some species, especially if implemented during periods of increased vulnerability, and may have diminishing returns in terms of wildlife use of the burn interior (Mason and Lashley 2021). For example, large-scale, early growing season burns (depending on burn coverage and intensity) in the southern Appalachians could negatively affect ruffed grouse because of low re-nesting rates. Grouse populations are already declining because of reduced regeneration harvests over the past few decades that eventually provide young forests with high stem-densities required by grouse (Tirpak et al. 2006; Devers et al. 2007; Jones et al. 2015). Alternatively, large-scale intensive burning during the dormant season could enhance habitat for ruffed grouse by promoting greater small-stem density while allowing individuals to escape without direct negative effects.

The diverse topography in the EBA region - especially the Appalachians - affects soil type, moisture, temperature, and vegetation, which in turn affect fire intensity and frequency. When burn units are relatively large and extend into multiple aspects, drainages, and forest types, fire intensity is variable, often resulting in a burn mosaic with many patches left unburned (Lorber et al. 2018). Those unburned patches promote a heterogeneous forest structure and composition, especially important when burning large areas relative to the habitat requirements of targeted wildlife. Using topography to their advantage, managers in the region may target more frequent and intense fires on dry south- and west-facing slopes and ridgetops, and less-frequent, lower-intensity fires on moister lower slopes and north- and east-facing aspects (Moorman et al. 2011; Thomas-Van Gundy and Nowacki 2013; Harper et al. 2016). This "landform fire planning" allows wildlife associated with cool, moist microclimates and dense litter layers, such as shrews and salamanders, to persist in areas less prone to burn (Ford et al. 1999; Harper and Guynn 1999; Ford et al. 2002).

Intensity, frequency, severity, and season of burning are intertwined with regard to effects on wildlife. The scale of a prescribed fire program should match the objectives and risks associated with focal wildlife. Where maximum wildlife diversity is the conservation objective, managers should promote heterogeneity in fire characteristics at multiple spatial and temporal scales (Lashley et al. 2014; Lashley et al. 2015; Taillie et al. 2018). This pyrodiversity will promote heterogeneity in the structure and composition of plant communities, providing habitat for more wildlife species.

4.8 Future Conditions

Maintaining a diversity of community types across the landscape is a key goal of forest managers, and promotes forest resilience, plant and animal diversity, and forest productivity. This goal is increasingly important and more challenging in the face of a rapidly shifting climate and accompanying extreme weather events, invasive species, and insect and disease outbreaks (Chap. 12). The unprecedented rate of climate change has already reorganized many forest communities (Fei et al. 2017), leading to increased vulnerability of some species to the direct effects of warmer temperatures and altered precipitation patterns (Brandt et al. 2014; Butler et al. 2015), and indirect effects including drought (Allen et al. 2015), pest and pathogen outbreaks (Rogers et al. 2017), and increased probability of fire occurrences (Iverson et al. 2019). Of course, shifting climate also affects some species positively, effectively expanding the range of suitable climate. Upland oak and pine species most impacted by fire exclusion are those predicted to experience range expansion with climate warming because of their high drought and fire tolerance (Iverson et al. 2019). All of these changes have dramatically shifted forest processes, and understanding the role that fire plays in the future of these stands is inherently tied to this contemporary reality. Landscapes diverse in forest structure and composition are deemed more resilient to environmental stresses and biotic threats (Brandt et al. 2014; Butler et al. 2015; Guldin 2019).

Whether prescribed or the result of unplanned wildfire, burns in the EBA region are often of mixed-severity and result in varied community-level responses. Unplanned wildfires provide perhaps the best illustration of this pyrodiversity potential. Following an early-dormant season wildfire along the Cumberland Plateau, oak and pine saplings, oak sapling density, and non-woody understory species richness were positively associated with fire severity (Fig. 4.3; Black et al. 2018). With increasing prevalence of unplanned fires predicted with shifting climate and greater incidence of drought, these extreme fire events are likely to occur more often, with tangible and long-term consequences for species composition and forest structure. While some of these events may lead to increased regeneration by species whose ranges are predicted to expand with changing climate (upland oaks and pines; Iverson et al. 2019), higher fire severity also creates conditions conducive to invasion by non-native species (Black et al. 2018). Fortunately for forest managers in the region, the dramatic increase in research over the past several decades elucidating fire history, the relationship between dominant species and fire-adapted traits, the ecosystem consequences of fire and fire-exclusion, the silvicultural underpinnings for understanding the role of fire as a key disturbance agent, and the interacting effects of fire and fire exclusion on wildlife species, strongly informs our collective ability to infuse ongoing management with increasingly strong science.

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