Chapter 5
Fire Ecology and Management of Forest Ecosystems in the Western Central Hardwoods and Prairie-Forest Border

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Abstract The ecotone between the Great Plains and the Eastern Deciduous Forest region is characterized by transitional grassland-forest ecosystems with a robust history of frequent fire regimes and fire-adapted natural communities. Historically, fires created a mosaic of prairies, savannas, woodlands, and forests juxtaposed by landscape controls. Humans have been strong determinants of fire regimes, causing frequent fires in historical times and an extended period of fire exclusion for nearly the last century. In recent decades, interest has increased in understanding the region's fire ecology and management. This interest is driven by management objectives to promote and maintain plant and animal diversity, restore ecological processes, and increase ecosystem resilience. Plant species in the region exhibit adaptation to frequent fire regimes and wildlife species are associated with habitats maintained by fire. However, exclusion of fire over the past century has left a long-lasting mark on ecosystems by changing ecosystem structures and compositions and, in some cases, by eliminating fire-adapted natural communities. In the future, the rise of campaigns that promote appropriate fire uses will be contingent upon science, demonstrated management successes, public perspectives, and the broader challenges associated with global changes.

Keywords Fire regime · Humans · Native plants · Wildlife · Grasslands

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Ecoregions 29, Cross Timbers; 32, Texas Blackland Prairies; 33, East Central Texas Plains; 36, Ouachita Mountains; 37, Arkansas Valley; 38, Boston Mountains; 39, Ozark Highlands; 40, Central Irregular Plains; 72, Interior River Valleys and Hills

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5.1 Introduction

In the center of North America, the Great Plains intersects the Eastern Deciduous Forest (EDF) (Fig. 5.1). The Great Plains is an expansive grass-dominated biome

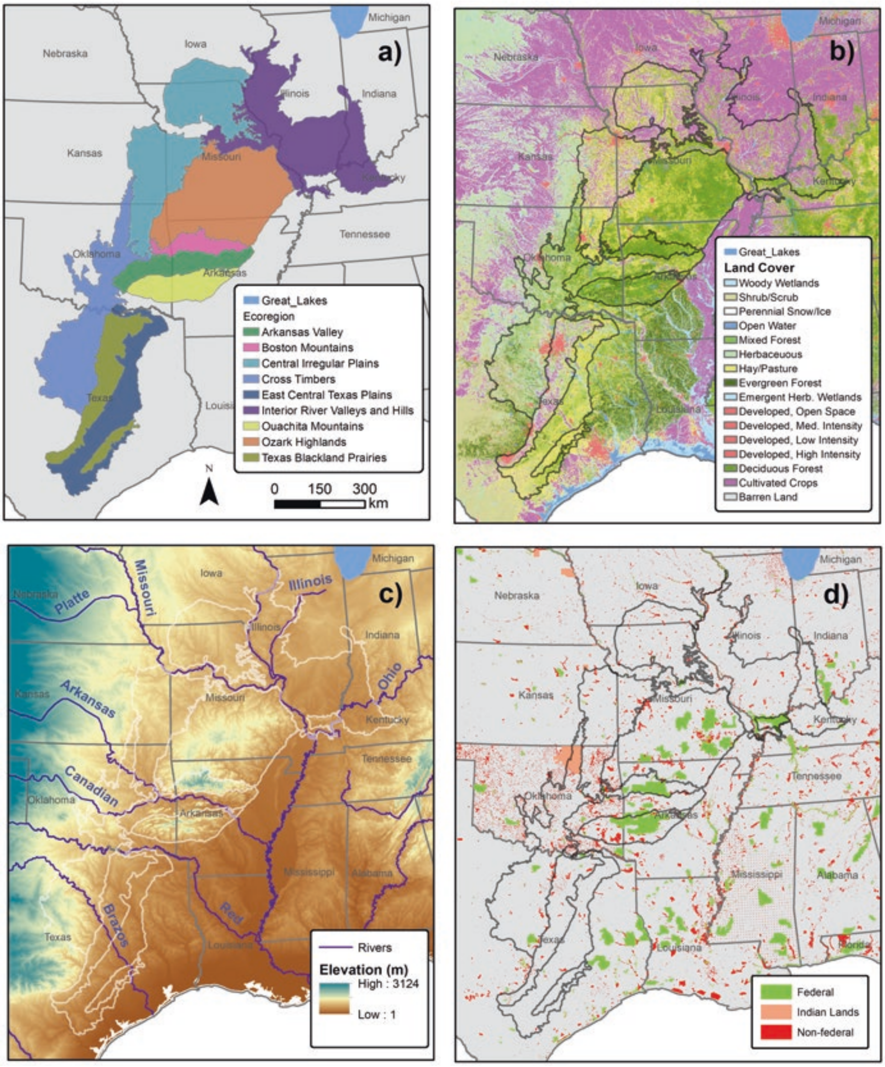

Fig. 5.1 (**a**) level-III ecoregions used to define the study region (Omernik and Griffith 2014); (**b**) land cover based on the National Land Cover Database (NLCD) and 16-class legend modified Anderson Level II classification system; (**c**) major rivers and elevation based on the GTOPO30 elevation dataset (Danielson and Gesch 2011), and; (**d**) federal, Indian, and non-federal ownerships (USGS 2018)

covering 18% of the contiguous USA. The EDF extends to the Atlantic Ocean and is one of the largest temperate deciduous forest biomes in the world. In the southern portion of their intersection, the ecotone is broad and transitions from mixed-grass prairies in the west to oak-hickory (*Quercus*-*Carya*) forests in the east (Braun 2001). The ecotone has likely persisted since the Cenozoic Period (25 myr) and, as such, is globally recognized as the Central Forest-Grasslands Transition Ecoregion (Ricketts et al. 1999).

As an ecotone located in the center of the continent, fire in this region can be viewed from many perspectives. In all directions, forests and fire regimes grade into diverse environments as described in chapters of this book to the southeast (Chap. 2), east (Chaps. 3, 4, and 6), and north (Chap. 7). Fire has long been present and controlled by humans (Sauer 1950) and continues to be relevant to the region's ecosystems, economics, and society (Chap. 1). In this chapter, we describe the region's fire environment, fire regime attributes, influences of humans on fire regimes, and the response of plant and animal species to fire.

5.2 The Fire Environment

The fire environment is defined by the major controlling factors of climate and weather, topography, vegetation, and fuels. Fire environment conditions dictate fire regime characteristics, fire behavior, and fire risk. The details of the fire environment aid in understanding complex fire interactions that underlie the region's fire ecology and management.

5.2.1 Climate and Weather

Climate conditions set the stage for the physical chemistry that constrains fire regimes and fire frequency (Guyette et al. 2012). In this region, the climate is humid-subtropical, with the exception of the northern extents where conditions shift to be hot-summer / humid continental (Beck et al. 2018). South to north, mean annual temperatures steadily decrease from 22.2 to 9.3 °C (Period: 1980–2010; Daly et al. 2004). Mean annual precipitation ranges from 66 to 172 cm. The driest areas are in south-central Texas and the wettest in the Boston and Ouachita Mountains (Fig. 5.1); on average, January and May are the driest and wettest months, respectively.

Atmospheric general circulation patterns cause regional climate variability to be strongly influenced by the Gulf of Mexico and Pacific Ocean. Central USA summers are commonly warm and humid when air is drawn northward from high pressure systems in the Gulf of Mexico and subtropical Atlantic Ocean. Pacific sea surface temperatures (e.g., El Niño Southern Oscillation [ENSO]) can affect precipitation amounts with strong La Niña events corresponding to dry winter conditions and El Niño events corresponding to wet summers (Stahle and Cleaveland

1988). Droughts and pluvials lasting months to multiple years are common (Fye et al. 2003). Droughts, particularly in summer, strongly affect plant productivity and fine herbaceous fuel loading. Drought periods are quasi-periodic at an 18–20 year interval and have lasted for multiple decades over the last millennium (Stahle and Cleaveland 1988; Stambaugh et al. 2011a).

Elevated fire activity can result from either ENSO mode (El Niño or La Niña). La Niña conditions often present broader burn windows and more consecutive days within burn prescriptions (Sparks et al. 2012). In 2011, extreme summer drought corresponding with La Niña conditions existed across Oklahoma and Texas when over 30,000 fires burned more than 1.6 million ha. For some fires, weather with high wind speeds from a tropical storm further accentuated drought impacts by causing extreme fire behavior and ignitions (e.g., powerline failure). In 2015, summer El Niño conditions resulted in wet conditions that increased fine-fuel production. When followed by a fall flash drought and corresponding with a post-frontal air mass, extreme fire behavior and high-severity fire effects occurred (2015 Hidden Pines Fire) (Jackson 2015).

Drought-induced fire potential is influenced by long- and short-term atmospheric conditions. In summer, thunderstorms with lightning are common; however, compared to human ignitions, lightning ignition rates remain low due to moderation by accompanying rains, high humidity, and high moisture contents of deciduous vegetation (Fig. 5.2; Schroeder and Buck 1970). In recent decades, only a small portion (<1%) of modern fires have been caused by lightning (Chap. 1, Table 1.1). Extreme weather events accentuate fire through instantly increasing fuel loading. High winds, tornadoes, and ice storms can cause extensive branch breaking and tree falls that, in turn, interact with extreme drought and potentially result in high-severity fires (e.g., 2011 Ferguson Fire in Oklahoma). In 2009, a derecho caused heavy damage across >45,000 ha from southern Missouri to Illinois. Even without weather events, extreme and prolonged droughts can cause widespread vegetation mortality across the region (Rice and Penfound 1959). Drought has also been a major inciting factor of oak decline in Arkansas and Missouri following the years 1999 and 2006 (Fan et al. 2012) and more recently across Texas and Oklahoma following the drought of 2011 (Moore et al. 2016).

Assessing and refining drought and weather tools are important to fire management of grasslands and forests. Assessments of drought conditions utilize a variety of metrics including the Palmer Drought Severity Index (PDSI), Cumulative Drought Index (CDI; Fig. 5.2), the Keetch-Byram Drought Index (KBDI), and the Energy Release Component (ERC), among others. Within grasslands, drought metrics (i.e., soil moisture) are good predictors of herbaceous fuel moisture content and probability of large (>405 ha) wildfires. For closed canopy forests, fuel moisture contents vary significantly by slope aspect until a precipitation event (i.e., all aspects equally wet) or until drought conditions exceed approximately −2.0 PDSI (i.e., moderate drought) when all aspects are dry (Stambaugh et al. 2006a).

In recent decades, drought and other weather data have become increasingly available and integrated into fire management and decision support systems (e.g., Remote Automated Weather Stations [RAWS], Interagency Fuel Treatment Decision

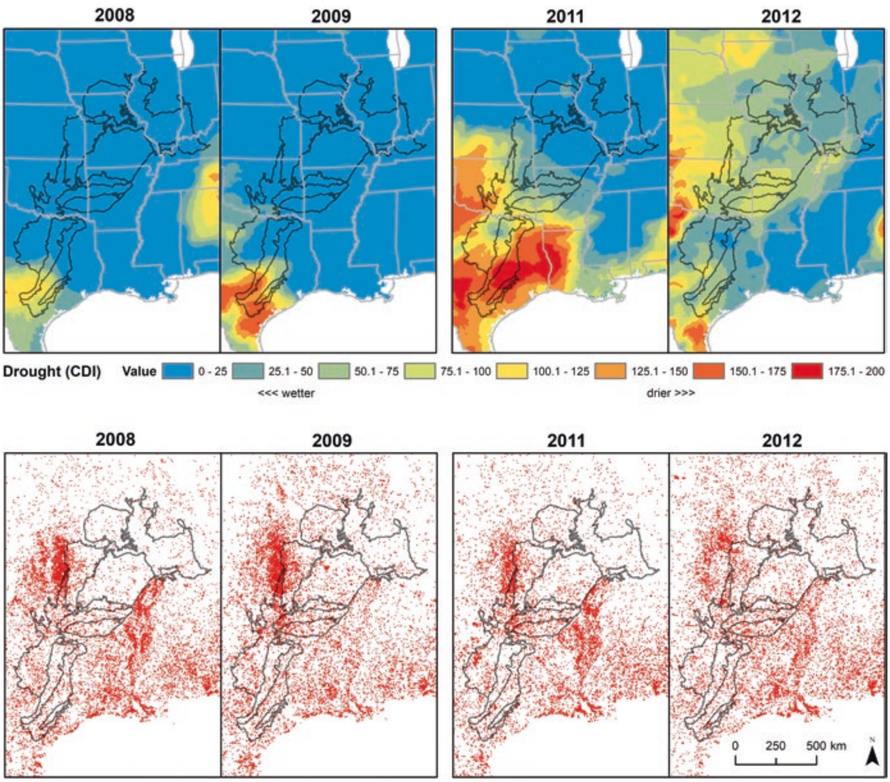

Fig. 5.2 Top: Maps of drought for two subsequent wet years (2008, 2009) and drought years (2011, 2012). Drought values are the annual Cumulative Drought Index (CDI) representing the combination of drought intensity and duration of drought, tabulated over the course of the year (Peters et al. 2014; Data source: National Drought Mitigation Center, National Integrated Drought Information System, and National Centers for Environmental Information). Bottom: Fire locations (red dots) for corresponding years are satellite detections (Data source: MODIS/Aqua+Terra Thermal Anomalies/Fire locations 1 km V006 NRT (Vector data)). Black line polygons correspond to ecoregions in Fig. 5.1

Support System [IFTDSS]). Weather conditions for burn prescriptions are relatively similar across the region regardless of fuel types. For fire control, common desirable weather conditions are 30–45% relative humidity, 7–10 mph midflame wind speed, with a minimum mixing height of 610 m. Finer-scaled weather parameters are used to address more specific objectives. For example, monitoring short-term drought and 10-h fuel moisture can help predict topkill of woody understory and midstory stems (Sparks et al. 2012). Monitoring longer-term drought conditions is useful for managing heavier fuels such as opportunities for consumption.

5.2.2 Topography

The region covers approximately 604,550 km^2 extending from northwestern Illinois and southern Indiana in a southwesterly direction to east-central Texas. The region comprises nine ecoregions based on distinct biophysical conditions (Fig. 5.1). In the north, The Interior River Valleys and Hills and Central Irregular Plains are broad expanses of relatively flat and productive lands making them well-suited for agriculture (Fig. 5.3a). Topography is diverse in the more forested Ozark Highlands,

Fig. 5.3 Regional landscapes and vegetation patterns: (**a**) flat terrain and heavily agricultural areas of the Interior River Valleys and Hills; (**b**) low mountains and closed canopy deciduous forests of the Ozark Highlands; (**c**) oak-pine forests on linear ridge lines of the Ouachita Mountains, and; (**d**) intermixing of prairies and oak woodlands at the western edge of the region in the Cross Timbers

Boston Mountains, Arkansas Valley, and Ouachita Mountains (Fig. 5.3b, c). Further west, large plains landscapes comprise the Cross Timbers, East Central Texas Plains and Texas Blackland Prairies (Fig. 5.3d).

Taken together, the topography is flat to gently sloping; elevations range from 13 to 785 m asl. Steep long slopes and higher elevations occur mostly in the Ozark Highlands and Boston and Ouachita Mountains. Major rivers drain primarily south and westward including the Illinois, Mississippi, Missouri, Arkansas, Canadian, Red, and Brazos Rivers (Fig. 5.1). These riverways are typically productive, less flammable, and more forested than adjacent lands. Major riverways are sources of loess that, via wind transport, overlays adjacent lands with dominant soil orders such as Mollisols, Alfisols, Ultisols, and, to a lesser extent, Vertisols.

North of the Missouri River, most of the region was glaciated during the Last Glacial Maximum approximately 20,000–25,000 ybp (Clark et al. 2009) resulting in flat and broad landscapes more analogous to landscapes of the Cross Timbers and central Texas prairies and plains. South of the Missouri River extending to the Ouachitas (approximately 550 km), topography is distinctly more variable. The general effect of this surface variability is less frequent fire with increasing topographic roughness (i.e., variability in aspects, slopes, and slope positions; Stambaugh and Guyette 2008). Topographic roughness is considered a master variable for determining fire frequency since it is strongly associated with species occurrence (Batek et al. 1999), forest density, and anthropogenic factors (e.g., human population density, road density). Aspect can also affect microclimates and forest species compositions, especially in the Ouachitas where slopes are strongly north-south oriented with higher densities of pine (*Pinus* spp.) on southerly aspects.

5.2.3 Vegetation

Deciduous vegetation is dominant throughout the region. Semi-deciduous vegetation (e.g., live oak; *Quercus virginiana*) exists in southernmost locales and evergreen vegetation, primarily pines and junipers (*Juniperus* spp.), can be found as primary tree components. The growing season is approximately March to October; this season is reduced slightly in more northern locales. Several genera provide a unifying coverage for the region, for grasslands this is often bluestem grasses (*Andropogon* spp.) and for forests, this is often oaks (Fig. 5.4).

Grasslands (e.g., tallgrass, mixed-grass, and shrublands) are a dominant cover type along the western and northern portions of the region (Fig. 5.1). In addition, large bottomland grasslands historically existed in some riparian zones major rivers (e.g., Missouri and Mississippi Rivers). Tallgrass prairies include species that grow 2 m or more in height such as Indiangrass (*Sorghastrum nutans*) and big bluestem (*Andropogon gerardii*). Mixed-grass areas contain increased mixing of cool and warm-season species such as little bluestem (*Schizachyrium scoparium*), western wheatgrass (*Agropyron smithii*), and grama grasses (*Bouteloua* spp.). Forbs can represent three times more species than grasses. Common forbs include coneflowers

Fig. 5.4 Natural vegetation communities and fuel structures north to south across the region: (**a**) forbs, grasses, and shrubs in an oak (*Quercus* spp.) savanna in the Central Irregular Plains; (**b**) forb-dominated ground cover in an oak woodland of the Ozark Highlands; (**c**) glade with abrupt transition to forest in the Ozark Highlands; (**d**) shortleaf pine-bluestem (*Pinus echinata* - *Andropogon* spp.) savanna in the Ouachita Mountains; (**e**) post oak (*Q. stellata*) savanna in the Cross Timbers, and; (**f**) sand post oak – bluestem (*Q. margaretta* - *Andropogon* spp.) woodland in the East Central Texas Plains

asters (*Symphyotrichum* spp.), sunflowers (*Helianthus* spp.), goldenrods (*Solidago* spp.), and ragweeds (*Ambrosia* spp.) (Fig. 5.4a). Woody species (trees and shrubs) are minor components of grasslands, occurring primarily in riparian zones and abandoned agricultural lands and consisting of species such as elms (*Ulmus* spp.), sumac (*Rhus* spp.), hackberry (*Celtis* spp.), cottonwood (*Populus* spp.), mesquite (*Prosopis* spp.), and various junipers.

Due to suitable climate and soils, most of these grasslands have been converted to agricultural lands. Conversion to hay / pastures has occurred throughout the region, particularly in the Central Irregular Plains, Ozark Highlands, and East

Central Texas Plains. Grassland conversion has emphasized planting of non-native cool-season grasses (e.g., tall fescue [*Lolium arundinaceum*]) that present fuel, fire management, and woodland restoration challenges (McGranahan et al. 2012). Conversion to cultivated crops essentially removes a fire regime. Cultivated croplands cover large proportions of the Central Irregular Plains of northern Missouri and southern Iowa and Interior River Valleys and Hills of Illinois and Indiana. In some areas, fall burning is used to remove crop residues and reduce pests, but this practice is more common outside of the region (e.g., Mississippi Alluvial Plain).

Moving eastward from the Great Plains prairie landscapes, vegetation transitions to more forested conditions with various types of structures (Fig. 5.4). Forest structures are commonly defined by the degree of canopy closure; savannas (0–30%), woodlands (30–100%), and forests (100%) (Nelson 2010). In the ecotone, forested areas are associated with increased topography and sites of lower productivity (e.g., shallow soils) or protected from disturbances (e.g., wetlands). Large areas of old, relict savannas, woodlands, and forests occur in the ecotone, especially within the Cross Timbers and Texas plains and prairies (Fig. 5.4e, f). In the Cross Timbers exists one of the largest areas of uncut forests in the USA (>323,750 ha; Therrell and Stahle 1998), and trees in this region are hotspots of rarity and evolutionary distinctiveness (Potter 2018). From the Ouachita Mountains northward to the Interior River Valleys and Hills, expansive forest areas exist despite being mostly cutover by the beginning of the twentieth century. Currently, some landscapes may be more forested than anytime during the last 500+ years and many areas continue to increase in forest cover (Sect. 5.5.4).

The primary forest type across the region is oak-hickory. Mixed hardwoods occur as both associates to oak-hickory forests and as a separate forest type. Shortleaf pine (*Pinus echinata*), a relatively slow-growing pine with an ability to resprout following topkill when young, was historically more common in the Ouachita Mountains and Ozark Highlands (Fig. 5.4d) but failed to regenerate following the initial cutover. The dominance of open forest communities composed of oaks, hickories, and shortleaf pine forest types before Euro-American settlement were largely the result of frequent fire regimes and, to a lesser degree, disturbances such as wind, ice storms, and animal browsing. Repeated burning maintained open canopy communities including prairies, savannas, and woodlands (Hanberry et al. 2014a), but many of these have succeeded to closed-canopy forests due to fire exclusion during the last century. Current forest ages and species mixes largely result from the history of late nineteenth to early twentieth century logging.

Though the majority of the region can be classified as a matrix of prairies and forests, unique natural communities also exist associated with cliffs, glades, barrens, talus slopes, river scours, and wetlands. These communities often show greater potential for edaphic controls due to wider ranges of moisture and temperatures, while fire may be a less important driver of function and composition. Of these, glades have received management and restoration through fire and thinning because they have declined in area and lost unique flora and fauna due to encroachment by fire-sensitive tree species (Sect. 5.5.3).

5.2.4 Fuels

Depending on ecoregion, current fuel type dominance varies from grass to timber (source: Landfire 2014, 13 Anderson Fire Behavior Fuel Models). More detailed fuel models are available that improve fuel bed uniformity characterization and accuracy of fire behavior predictions (Scott and Burgan 2005). A minimum of 1.68 Mg/ha of fuel is needed to carry a typical grass fire (Stevens 2005), and short grass fuel models (Model 1; Anderson 1982) assume this as an average loading. Currently, shortgrass is the dominant grass fuel in all ecoregions except the Cross Timbers. Prior to land conversions primarily due to agriculture, a higher proportion of tallgrass likely existed. Tallgrass fuels (Fuel Model 3) are least common across the ecoregions reaching up to a maximum of 10% coverage within the Texas Blackland Prairies. At the Tallgrass Prairie Preserve in Oklahoma, Leis and Kopek (2013) reported tallgrass fuel loadings between 2.2 and 6.7 Mg/ha for grasslands 8–32 months postfire, respectively. The Cross Timbers has a higher proportion of grass with timber fuels (Fuel Model 2) that includes the potential for producing fire brands.

Among the ecoregions, the greatest concentrations of grass fuels exist within the Cross Timbers, Texas plains and prairies, and southcentral plains; each with 50–60% coverage of grass fuels. The ecoregions with the most mixed-fuels (grass%:timber%) are the Arkansas River Valley (40:49), Cross Timbers (55:28), and Ozark Highlands (32:60). Fire management within mixed fuels necessitate multiple fuel models to predict fire behavior (Sparks et al. 2012). Static fuel models have limited utility for predicting fire behavior, particularly in grassland fuels whose properties show high temporal variability (aside from surface area-to-volume ratio and bulk density; Starns et al. 2019). In contrast, dynamic fuel models that are conditioned based on time of year and drought condition would provide more utility in prediction.

Within the more forested Boston and Ouachita Mountains and Ozark Highlands, 60–80% of fuels are timber types. The primary fuel contributing to fire behavior is deciduous leaf litter (Model 9) (Fig. 5.5b, c). Up to 60% of the fuels in the Boston Mountains and Ozark Highlands is leaf litter with an additional 15–20% being compact timber litter (Model 9). Leaf litter loadings average around 10.1 Mg/ha (4.5 tons/ac); annually burned forests may maintain up to 3.4 Mg/ha (1.5 tons/ac) (Fig. 5.5b). Following fire, it can be expected that 50% of the maximum litter loading level (approximately 5.6 Mg/ha [2.5 tons/acre]) reaccumulates after 2 years and 99% after 12 years (Stambaugh et al. 2006b).

In forests, smaller woody fuels (e.g., 1- and 10-h) also vary seasonally with larger inputs during leaf fall and winter. Inputs of larger, 100- and 1000-h fuels are more associated with stand development stages, disturbance events, and management activities (Pregitzer and Euskirchen 2004). Fuel loading across mature upland forests is relatively homogeneous while fuel loading in riparian forests is more highly variable (Stambaugh et al. 2007a, 2011b). Total forest fuel loading may range from 0.2 to 157 Mg/ha (0.1–70 tons/ac).

Other fuel types in the region included those associated with agricultural lands (non-hay or pasture lands), and to a very small extent, shrub fuels. Shrub fuels are

Fig. 5.5 Examples of fire behavior in the region: (**a**) low-intensity September growing season prescribed fire in grass, forb, and timber litter fuels in an oak-pine woodland in the Boston Mountains; (**b**) dormant season prescribed fire in the Ozark Highlands in an area has been burned annually since 1949 (65th burn entry shown). Note the lack of midstory vegetation, limited fuels (primarily leaf litter from previous fall), and low-intensity; c) first entry March prescribed fire through timber litter of chinkapin oak-hickory forest with dense understory sugar maple (*Acer saccharum*) in the Central Irregular Plains, and; d) high-severity wildfire during extreme drought in oak-pine forest in East Central Texas Plains (photos Jeff Sparks)

typically absent but can comprise up to 6% of fuel type coverage in the Cross Timbers. Agricultural lands are a dominant cover (44–46% of area) for the Interior River Valleys & Hills, Mississippi Alluvial Plain, and Western Corn Belt Plains. Fuels would typically be crop residues and currently it is uncommon practice to burn these, especially in situations where residues have wildlife benefits.

5.3 Fire Regimes

Multiple historical archives inform the characterization of regional fire regimes, including records from archeological sites, charcoal, phytoliths, pollen, tree-rings and fire scars, documents, and vegetation studies (Chap. 1; Sect. 1.6). Each of these archives differs in their properties such as number, resolution, temporal scale, and spatial extent. Archive properties are critical to consider when characterizing fire regime. Resolution relates to the increment sizes of temporal scales or spatial extents. Temporal scale is often greatest for the lowest resolution data and vice versa

(Swetnam et al. 1999). Spatial extent is perhaps the most important property for fire regime characterization, especially because fire frequency increases with spatial extent of observation (Falk et al. 2007).

Debate and confusion about fire regimes often arises due to comparisons that mix resolutions and scales. For example, it is possible that a historical documentary account of fire in a region recorded annual fire, but because the fire coverage varies across landscapes, all areas were not affected. In this example, at finer scales (e.g., 1 km^2) the fire frequency may vary from 1 to 12 years. Based on documents in the region, there are many areas that "burned annually". Based on tree-ring records of fire scars (commonly collected within 1 km^2 areas), although annual burning did occur in some places, it was relatively uncommon and often associated with strong human influences.

Archeological data and charcoal reconstructions of fire regimes are extremely limited in the region (source: Global Paleofire Database; paleofire.org). In the Ozarks, archeological studies and charcoal and pollen records extend back at least 2000 ybp and show continuous fire activity marked with human influences; vegetation changes tracked along with fire and climatic variability (Jurney 2012; Nanavati and Grimm 2020). In a northeastern Texas oak-pine-hickory forest, more evidence exists for past climate variability and controls on fire frequency and extent during the last 3500 years (Albert 2007). Though charcoal records are limited in number, they confirm that fire regimes have changed over thousands of years due to climate and humans. However, in the context of contemporary conditions, these records lack details of local ecology relevant to the scales of natural resource management. For this reason, in this description of fire regime characteristics we focus on fire regime characteristics during the last five centuries and their relevance to the future. Fire regime characteristics of the last five centuries are informed by annual resolution archives that are more numerous including tree-rings and fire scars, documents, and measurements of vegetation conditions. From these archives, detailed datasets of fire regime characteristics demonstrate the ecological potential of ecosystems with metrics at a resolution that can guide fire management.

5.3.1 Fire Frequency

The vast majority of the region is characterized as having frequent historical fire regimes during the last five centuries or more. This is detailed by records of fire scars from over 50 sites, studies of vegetation changes (Miller 1972; Nuzzo 1986; DeSantis et al. 2011; Hanberry et al. 2014a, b), experiments with varying fire frequency (Masters and Waymire 2012; Knapp et al. 2015), and models of fire regimes (Frost 1998; Keane et al. 1999; Guyette et al. 2012). Areas with lower levels of historical fire frequency exist within this matrix such as those with extreme moisture conditions (e.g., swamps, riparian areas) (Chap. 6) or those with little to no fuels (e.g., cliffs, some barren glades). The most fire-sensitive and longest-lived organisms often occur in these protected locations (e.g., bald cypress [*Taxodium distichum*] in swamps, eastern redcedar [*J. virginiana*] on cliffs).

Outside of protected areas, fire frequencies can be surprisingly homogeneous across large portions of the region. Fire frequencies prior to Euro-American settlement (pre-EAS) ranged from 3 to 12 years on average for woodland sites across the prairie-forest ecotone (Rooney and Stambaugh 2019). In the mid-1800s, fire frequencies often reached maximum burning frequencies (annual) due to intensive human activities. Nearly all fire scar history records in the prairie-transition show intermittent annual burning during this period, and in some locations it continued for decades. Some data are from woodland sites that are embedded within large grassland landscapes, and these data likely reflect characteristics of Great Plains grassland fire regimes.

Fire scar studies in the Ozarks of Oklahoma, Arkansas, and Missouri have focused on shortleaf pine and oak forest ecosystems. In these areas, pre-EAS fire frequencies ranged from 3 to 20+ years (Guyette et al. 2006a; Stambaugh and Guyette 2008; Stambaugh et al. 2013). Spatially, the historical frequency of fire reflected topographic variability. In some cases, fire breaks were created by rivers, mountains, and barren lands, likely separating fire regimes into “fire compartments”. Compartment boundaries likely were dynamic and less defined during times of drought when extreme fire behavior and extensive fires occurred. In the Ozark Highlands, historical fire frequencies across the Current River landscape decreased as the roughness of the topography increased (Stambaugh and Guyette 2008). This effect was likely the result of lowered potential for fire spread as fuel type, moisture, continuity, and loading changed with aspect and vegetation type.

Fire regimes in the Current River watershed are among the most studied in the world and have provided key insights into fire regime dynamics. As more is learned about its historical fire regimes and associated vegetation, it has become clear that increasing care is needed for their interpretation for both ecology and management. For example, average or mean fire intervals do not fully characterize fire frequency conditions, particularly the wide range of short and long individual fire intervals that existed. Occasionally very frequent annual or even biannual burning occurred that would have promoted herbaceous vegetation. Conversely, periods of 20 years or longer without fire also occurred that would have allowed survival of woody vegetation (Stambaugh et al. 2014). The historical heterogeneity of fire intervals is attributed to vegetation communities composed of a mix of coexisting plant types (e.g., woody and herbaceous plants) and community structures (e.g., savanna vs. forest).

Due to a lack of research effort, little data about historical fire regimes exist for the Ouachita Mountains, despite having similar vegetation types to the Ozark Highlands (forests dominated by oaks, hickories, and shortleaf pine). Observations of old fire-scarred trees across the region indicate historical evidence of recurring fires. Long, east-west oriented linear ridges likely impart north-south facing aspect effects on fire frequency and severity based on strong species composition differences between aspects. Long slopes enhance potential for convective pre-heating leading to greater potential for fire occurrence on higher landscape positions.

Even less data documenting historical fire frequency exist in the Interior River Valleys and Hills. Here, pre-EAS fire regimes appear to be comparable to those of the prairie-forest border. Fire frequencies of less than two years and sustained for centuries as reported by McClain et al. (2010) represent the most frequent reported north of the southeastern USA. In Iowa, along the Mississippi River, fire scars from white oak trees recorded an average fire frequency of five years from 1714 to 1810 (Site: Nye Cabin, Muscatine County; Missouri Tree-Ring Laboratory *unpubl. data*). Fire scar records further east and north outside of this region, but with comparable vegetation, show pre-Euro-American mean fire intervals from three to ten years (Guyette et al. 2003; Stambaugh et al. 2006a).

Dramatic and highly variable alterations in fire frequency occurred as a result of EAS (see Sect. 5.4). The impacts appear to differ strongly among forests and grasslands. Generally, forests underwent very frequent burning coincident with the timing of settlement activities (e.g., establishment of towns, roads) while fire in grasslands was suppressed. Most areas in the region experienced fire suppression by the 1910s to 1930s and have now undergone nearly a century without fire.

5.3.2 Fire Seasonality

Fires during most months of the year are possible within the recent range of climate conditions, but fire seasonality is largely driven by factors associated with ignition sources (anthropogenic factors) and fuel properties (e.g., Chap. 1, Figs. 1.2, 1.4, Table 1.1). Generally, weather patterns and vegetation conditions force fire seasons to be predominantly in the late winter / spring (January to April) and late summer/ fall (September to November; Knapp et al. 2009). In the northern portion of the region, fire seasonality is more strongly split into spring and fall seasons, however more recent efforts at expanding burn windows have resulted in increased burning outside of the spring season throughout the region. Drought years can alter this split fire season and promote conditions favoring more fires during summer months. Extreme and widespread droughts result in increased growing season fire activity (e.g., 1980, 2011, and 2012) and strong La Niña conditions often correspond with dry climate conditions, particularly in more southerly portions of the region. Short-term dry conditions in summer are common but rarely result in increased fire activity except for July 4th (ignitions from fireworks; Balch et al. 2017). Increased moisture content of herbaceous fuels caused by increased presence of live fuels is the major factor limiting fire activity in the growing season, while high humidity can further lessen fire activity and potential.

In the coldest months, between the fall and late winter/spring fire seasons, fire activity is reduced due to short day lengths, low temperatures and evaporation rates, and high fuel moisture content. Frozen precipitation during these months directly reduces fire activity, especially in more northern extents. Persistent snow cover is more of a limiting factor in winter fire occurrence from mid-Missouri northward. However, smoldering fires can persist through precipitation events by burning large fuels. These fires may reactivate if conditions allow. In this case, prior to fire suppression and exclusion fires may have been long duration continuing to burn over multiple seasons.

Many documentary accounts suggest dormant season fires of mixed seasonalities have occurred through time. Natural archives such as fire scars are somewhat limited in their ability to distinguish seasonality of historical fires. Growing versus dormant season fire scars are determined by the position of the scar within the ring. Growing season scars occur within a ring while dormant season scar occur between rings. For fire scars, dormant seasonality could be from September through the following March for much of the region. More southerly regions have a shorter dormant season and therefore greater potential to distinguish fall versus spring events. Even so, throughout the region the majority of fire scar records are dominated by dormant season events. The highest proportion of historical growing season fires recorded is 15% within the prairie-forest border (Rooney and Stambaugh 2019). It is not clear whether dormant season fires tended to be fall or spring or mixed and, being largely anthropogenic fires, this likely depended on human activities. Burning in the fall (often noted as "Indian summer") is reported by Native Americans. In the Ozarks during the early 1900s, burning occurred near or on Easter. Historical accounts depict active human ignitions:

> *And every spring, especially on Easter Sunday, the woods were always burnt. I mean, there were fires ***Easter Sunday was the big day for burning, which I don't know why. [They burned] they said to get rid of the ticks. We had one neighbor who would just get out and start walking to the store and if he had a match in his pocket and saw a pile of leaves, he would just set it on fire. Take off and let it burn.***Only time you got into trouble was if you burnt someone's fence posts up.*
>
> Alan Anderson interview response in Jacobson and Primm (1997)

In recent decades, more dormant season fires typically occur in late winter/spring compared to fall. The tendency towards more fires in the spring are likely due to factors of human ignitions as opposed to fuel properties. Late winter to spring burning begins a month or two earlier in the south than the north (Balch et al. 2017). Fires occurring in spring are due to desired effects (e.g., increased forage, tradition and habit), and for agencies, due to more burn days in prescription, budget, workforce availability, and planning factors. The vast majority of burning on federal and state lands occurs during the late winter/spring season.

Fuel types, conditions, and amounts influence fire seasonality. Generally, fuel production is adequate to support annual burning in grasslands and forests, but grasslands present larger burn windows throughout the year due to more rapid curing and drying. In grasslands, vertical fuel orientation provides potential for burning aerial fuels even with some snow on the ground; in some cases these sites can be reburned through ignition of underlying thatch within months following snowmelt. In forests, where leaf litter is the primary fuel, prolonged snow cover compacts the litter layer causing a dense litter mat that is less flammable. In exposed and windy areas, leaves can arrange in piles, creating a less uniform fuel bed.

Timing of fuel production varies between grasslands and deciduous forests, which creates burn opportunities that are unique to the ecosystems. In grasslands, savannas, and woodlands, dead herbaceous fuels (thatch) can be available to burn many seasons of the year while the standing crop of herbaceous fuels tend to be less available until cured. Growing season burns in these fuels are mostly possible through burning of the thatch layer accumulated from previous years; these are often patchy fires with short flame lengths (Fig. 5.5a). In conditions when thatch layers burn hot enough, live herbaceous fuels may become available for consumption. By comparison, in closed canopy deciduous forests with minimal herbaceous ground cover, leaf drop constitutes the primary fuel for fire spread and becomes mostly available within a few weeks (fall leaf drop) when it is also most flammable. On sites with heavy litter fuel accumulation, it may be possible to conduct multiple light burns within weeks or months, each burn removing a portion of the litter layer.

Savanna and woodland communities, like those that once dominated the region, often have mixed plant functional groups (e.g., woody species, forbs, grasses, vines). Trees and herbaceous ground cover provide the greatest potential for varying fire seasonality because the timing of fuel availability and flammability are diverse. In some cases, it may be possible to burn more than one time per year by relying on the varied fuel types and input timings. For example, in a woodland, a fire may occur in summer consuming herbaceous fuels and then again in the fall or following spring consuming leaf litter. In this case, fire seasonality could plausibly be in the growing season, dormant season, or both. Other characteristics of fuels are also important in determining fire seasonality such as chemical, physical, and fuelbed properties (Varner et al. 2015).

Much of the current interest in fire seasonality and plants relates to life cycles and mortality. Spring ephemeral plants have short growing seasons and can be consumed in spring burns. However, effects of spring burns on herbaceous plant communities are poorly understood. In the Ouachita Mountains, Sparks et al. (1998) found that fire seasonality had little effect on herbaceous species richness, but a larger effect on density and cover. Effects were more pronounced for grasses, which increased with dormant season burns. Seasonal fire effects can be species specific and timing of fire can affect certain herbaceous species directly through injury or mortality, especially during vulnerable phenological stages. A chaotic array of burn seasonality may increase biodiversity as a mixed season regime could reduce dominance of a single species group by favoring a variety of life history traits across the community.

Often grasses are classified into two primary growth periods; cool season (peak growth March through May) and warm season (peak growth April through Oct). Burning in spring can kill, damage, or inhibit growth of early cool-season species that are active (Howe 1994) because new plant tissues are most sensitive to heat (Bond and van Wilgen 1996) and carbohydrate reserves in the roots are lower after spring shoot and leaf flush, and therefore plants have reduced sprouting potential. Burning during the middle of summer is more detrimental to warm-season grasses and favors early-flowering cool-season species that have finished growth and dropped seed (Howe 1994). Many grasses flower more vigorously after growing season burns. Fire in communities with mixed warm-cool grasses may not change competition. Studies focused on livestock management have reported grass productivity gains with early growing season burns, however overall plant biomass production is greater with fall than spring burns. For warm season grasses, positive gains in vegetative production may be made, especially in areas or years with cooler winters. However, plants may also senesce earlier in these conditions (Ehrenreich and Aikman 1963).

Burning of surface and live fuels releases nutrients that can be leached from the system if not taken back up by micro-organisms or growing vegetation. Prescribed fire close to the onset of growth may reduce leaching. More nutrients could be volatilized when actively growing tissues are burned than when tissues are burned during the dormant season. In the dormant season, some nutrients from aboveground structures have been translocated to underground storage structures and therefore escape from being volatilized. Boring et al. (2004) showed greater nitrogen loss with growing season burns while phosphorus was not typically affected by season because temperatures were not high enough to volatilize. In Massachusetts, Neill et al. (2007) reported organic horizon reductions more from summer than spring burns which caused soil bulk density to increase. In the same study, soil pH, acidity, base saturation, total exchangeable cations, carbon, or nitrogen did not differ by season of burning.

Seasonal effects of fire on vegetation are linked to seasonal effects on wildlife through food and habitat alterations. Wildlife response to fires depends on species specific life history traits and habitat requirements. Smith (2000) provided a national overview of fire effects on wildlife while Harper et al. (2016) provided more up-to-date information specific to various wildlife species and fire management scenarios of the region. Prescribed fire objectives often focus on seasonal effects that improve wildlife habitat and forage (type, palatability, nutrition, availability).

Season of burn effects on wildlife are especially dependent on fire characteristics such as severity and size. Generally, seasons when wildlife are most vulnerable to direct effects from fire are during critical reproductive stages (nesting, brood-rearing, fawning) or when immobile or slow (e.g., salamanders, bats soon after emerging from hibernacula) (Perry 2012; O'Donnell et al. 2015; Harper et al. 2016). In prescribed fires, few direct effects on wildlife are typically observed as most animals move away from direct contact. At the other extreme, high-severity wildfires can cause high wildlife mortality rates on large scales. Perhaps the most sensitive species to direct fire effects are those that are least mobile such as herpetofauna. Howey and Roosenburg (2013) reported 20% of box turtles (*Terrapene* spp.) were injured during a September prescribed fire in Kentucky. Harris (2020) reported similar rates of injury and mortality from growing season burns in Tennessee, and noted that turtles avoided injury by occupying areas that did not burn, moving to unburned areas, and burrowing. In Arkansas, Beaupre and Douglas (2012) reported population declines in timber rattlesnakes following an April fire in Arkansas. This study was particularly important as it indicated that measured population declines may have resulted from movement, not reduced survival. Subsequent work has shown that burning at the site resulted in overall improved habitat quality. Many studies have shown that dormant season burning has no overall negative effects on herpetofauna, and several found positive effects through increased abundance as a result of improved habitat (Harper et al. 2016).

Additional concerns about burn seasonality extend to mammals and birds, particularly game bird species such as northern bobwhite quail (*Colinus virginianus*), ring-necked pheasant (*Phasianus colchicus*), and wild turkey (*Meleagris gallopavo*; Chap. 4). Recent work has addressed concerns for spring burning and turkey nesting since fire may directly affect ground nests and burning may cause hens to renest. From a synthesis of ninety sources, Wann et al. (2020) concluded that growing season burns pose little risk to turkey nests or broods if fire extent and frequency concerns are properly addressed. Diverse habitats created by landscape heterogeneity of burn effects are ideal for a multitude of activities from nesting, to foraging, to loafing.

5.3.3 Fire Extent, Pattern, and Duration

Fires in the Great Plains have potential to be extensive. Multiple interacting conditions facilitate extensive fires including recurring dry periods in a region with productive herbaceous fuels, high wind speeds, and relatively low topographic variability. With east to west prevailing winds, historical fires likely commonly burned hundreds of thousands of hectares and had a significant effect on the vegetation patterns, types, and structures transitioning into the EDF. In very dry years with abundant ignitions, fires likely had the potential to enter more eastern regions. It is assumed, but undocumented, that historical fires in grasslands were expansive events due to the lack of roads, fire suppression technology, and possibly human concerns for fire risk. The extent of historical grazing and human population effects are unknown factors that would have strongly dictated fire sizes and patterning.

The earliest fire scar history records in the prairie-forest border extend back to the mid-1600s, but most records extend to the early 1700s. From the 1700s to the mid-1800s, fires appeared to increase in extent across the prairie-forest border region (Rooney and Stambaugh 2019). A similar increase was documented in the Ozark Highlands. This result is based on an increased number of sites burning in individual calendar years, and it is assumed that more sites burning was the result of many different small fires as opposed to an increased frequency of large, landscape- to regional-scale fires. Analyses of climate and fire events show fires prior to EAS were more closely associated with drought conditions than modern fires. For this reason, pre-EAS fires were likely larger on average than in more modern times post-nineteenth century.

In the Ozark Highlands, Guyette and Kabrick (2002) suggested that, in years when fires were extensive, they were also potentially high-severity and stand-replacing (this was observed in 2011 in Texas). Though limited, some stand origin dates correspond with historical years with extensive fires. Few studies have addressed the association between historical fire extent and fire severity in the eastern USA. Marschall et al. (2019) found historical fire extent and severity were not correlated because some small fires were also high-severity and some large fires were low-severity.

Within the Ozarks Highlands, historical fire sizes likely ranged from small spot fires (<1 ha) to fires with landscape or larger coverage. Lightning strikes likely ignited trees and produced small fires; potentially larger fires occurred if no rains accompanied lightning. Dry and hollow lightning-ignited trees can smolder for long periods allowing them to potentially be sources of ignitions later once conditions are favorable for fire spread (Cohen et al. 2007). Slow spreading fires can persist for weeks or longer if allowed; a summer fire in the Ozarks lasted for over a month before being extinguished. Historical fires that were not suppressed may have also lasted for months and, in this case, may have had different seasonalities between locations of ignition and extinction.

Annual burned areas exceeding 40,000 ha are estimated to have occurred across the Boston Mountains and Ozark Highlands prior to 1810 (Guyette et al. 2006a) as fires were synchronous in years when drought conditions were near normal (1808) to extreme (1772). Stambaugh et al. (2013) later found many of these same fire years corresponding to areas further westward into Oklahoma. Fires were widespread in 1780, the same year that smoke from fires in the Great Lakes region darkened the sky over much of New England (McMurry et al. 2007); a year of sub-continental scale fire activity involving the central USA and southern Ontario.

In recent decades of prescribed fire management, fire operations typically begin and end in a single day. On days when potential fire behavior is low (e.g., combustion, rate of spread), fires are often confined to mid-day when relative humidity is lowest and desired fire behavior can be achieved. In a single day and utilizing ATVs and helicopters, these burns can encompass thousands of ha in forests (e.g., Ozark Highlands and Ouachita Mountains) to tens of thousands of ha in grasslands (e.g., Flint Hills, Kansas). In the Flint Hills, over 40,000 ha of prescribed fire regularly occurs each year. In 2010, when over 80,000 ha of the Flint Hills were burned, smoke visible from satellite imagery reached the northeastern USA coast.

Large wildfires are relegated to periods of drought. Longer, multi-year droughts have occurred as recent as the 1950s and resulted in widespread fire activity, large fire events, and drought induced vegetation changes (Rice and Penfound 1959). In the last decade, large multi-week fires have occurred near the western edge of the region, particularly in the spring. The Anderson Creek Fire in Kansas in March 2016 burned 1600 km^2 and in March 2017, the Northwest Complex Fire in Oklahoma burned 3360 km^2, and in 2018 the Rhea and 34 Complex Fires burned over 1400 km^2. As expected, these fires were fought and suppressed, however in historical times (i.e., without suppression) they would presumably have burned much larger areas. Most modern wildfires are small and average fire sizes have been trending downward in the last century. In Missouri, across a mix of forests and grasslands, average fire size has decreased exponentially from about 40 to 6 ha during the period 1939 to 2001.

5.3.4 Fire Intensity, Severity, and Types

Fire intensity is defined as the product of the available heat of combustion per unit of ground and the rate of spread. From grasslands to forests, fire behavior parameters vary widely both between and within fuel types (Engle et al. 2007). Andrews et al. (2011) demonstrated that shortgrass and timber litter with understory fuels had similar maximum flame lengths (2 m) and fireline intensities (1176 kJ/m) while other properties of the fires were very different. In this example, fire in shortgrass was fast spreading (max 66 m/min) with low heat per area (1044 kJ/m^2) while timber litter with understory was slow spreading (max 5 m/min) with high heat per area (15,096 kJ/m^2). For forests, more typical desired prescribed fire behavior parameters might be shorter leaf litter flame lengths (<0.6 m) and slower rates of spread (<1.5 m/min; strip headfires reported by Brose et al. 2014; Fig. 5.5c).

Understanding relationships between fire behavior and desired effects is critical to achieving prescribed fire objectives. In grasslands, fires move fast, are short duration, have relatively low heat and thus belowground heating is minimal. However, burning can increase soil heating indirectly by removing litter and thatch thereby promoting earlier emergence of warm season grasses. In many forested areas, fires that move slow and have long residence times are key to topkilling small woody stems – a common objective in creating a woodland canopy structure. Towards this objective, it is estimated that a fire line intensity of 500 kW/m is needed to control (topkill) woody understory stems ≥1 m tall (Sparks et al. 1999).

Fire intensity can cause preferential mortality of both flora and fauna. In fire management, flora, especially trees, are described along a gradient of fire tolerance. Fire can cause injury and mortality to trees through several pathways, including root damage due to conduction through the soil, damage to the vascular cambium via conduction through tree bark, direct combustion of foliage or live buds, or tissue damage through convection or radiation (Hood et al. 2018). In the Western Central Hardwoods, low to moderate intensity fires common to woodlands and forests were unlikely to cause crown damage under normal conditions, especially for hardwoods burned during the dormant season. Mortality models for hardwood trees in the eastern USA have included maximum bole char height and diameter at breast height (dbh) as predictor variables (Keyser et al. 2018). Dbh is considered a surrogate for bark thickness, due to positive relationships with bark thickness. In general, the bark of mature trees is thick enough to provide protection from surface fires, but there is considerable interspecific variation in bark thickness of seedlings and saplings (Schafer et al. 2015). The development of relatively thick bark at a young age confers a potential competitive advantage for tree recruitment by avoiding topkill with low-intensity surface fire.

Similar fire effects can be seen on fauna, particularly arthropods occupying surface soils. In the Ozark Highlands, Verble-Pearson and Yanoviak (2014) showed that increased fire intensity led to reduced abundance in arthropod populations and less species richness in ant (*Formicidae*) populations immediately after fire. In this way, managing fire intensity may select for those arthropods that are better at seeking refugia and can therefore affect community structure and composition.

As a result of fire intensity and residence time, effects of fire are typically classified along a gradient of severity. Fire severity is the degree to which a site has been altered or disrupted by an individual fire. Fire severity can be used to classify fire regimes such as their proportions of low-, mixed-, or replacement-severity fires (in reference to vegetation). LandFire (version 1.4.0) fire severity classification shows regional fire severity is strongly divided between grasslands (primarily replacement severity) and forests (primarily low-severity). High intermixing of low and replacement severity patches characterizes the grass and timber mosaic of Cross Timbers. Mixed-severity fire regimes are the least common in the region, mostly located along lower reaches of the Red River in Oklahoma and scattered throughout the Central Irregular Plains in northern Missouri and southern Iowa.

Despite fire regime severity being mostly low for forests of the region, small potential exists for mixed- and high-severity fires, especially during dry conditions (Figs. 5.5d and 5.6). The largest areas with the greatest potential for high-severity fires exist within the Arkansas Valley. Here, and in the Ouachita Mountains, long slopes and south aspects provide potential for 11–15% of fires to be high-severity. In the Ouachita Mountains, areas of replacement-severity potential are largely arranged west-to-east following southerly aspects of long linear mountains. Despite there being similar vegetation types in the Boston Mountains and Ozark Highlands, these areas display less distinct landform-based patterns in fire severity.

Recent wildfires provide evidence that replacement (high)-severity fires can indeed occur in both hardwood and pine forests during droughts (Fig. 5.6d). Replacement severity classification includes high-intensity surface fires, not just canopy fires. Replacement-severity fires often occur on sites with steep long slopes, heavy and/or ladder fuels, and fire-sensitive species. Replacement canopy fires occur in dense conifer stands (especially of eastern redcedar) and in short-statured deciduous forests during late summer/fall when leaves are on trees and dry enough for scorching or torching. In September 2011, replacement-severity fires occurred in oak woodlands throughout the Cross Timbers and Texas prairies and plains ecoregions. In some of these fires, canopy fires burned through oak-juniper forest types with a severity that discolored substrates (soil and rock) (Fig. 5.6). In other cases, canopy fires burned through mixed pine-oak forests (2011 Bastrop Complex Fire, Fig. 5.5d).

Following individual fires, field measurements can be made to quantify fire severity based on the degree to which a site has been altered from prefire conditions. A common burn severity measurement system is the Composite Burn Index (CBI; Key and Benson 2006), part of the Landscape Assessment of the Fire Effects Monitoring and Inventory System (FIREMON; Lutes et al. 2006). Although few studies have utilized the CBI field protocol in the eastern USA, it has utility for linking ground-based measurements vegetation change to remote sensing imagery, and thus expanding to whole fire extents at a relatively fine spatial resolution (e.g., 30 m). In the Cross Timbers, Stambaugh et al. (2015) tested CBI and showed that it

Fig. 5.6 Top: Sand post oak (*Quercus margaretta*) woodland in the East Central Texas Plains with a dense midstory invasion by native yaupon (*Ilex vomitoria*) and eastern redcedar presents high potential for stand replacement fire. Bottom: Stand-replacement fire in an area of the Cross Timbers composed of post oak, live oak (*Q. fusiformis*), mesquite (*Prosopis glandulosa*), Ashe juniper (*Juniperus asheii*)

performed well in oak woodlands. Among the five soil and vegetation layers used to rate burn severity, the shrub layer is a particularly good indicator of fire severity.

Despite being dangerous, high-severity fires were likely characteristic of some locations and vegetation types historically and had unique and important ecological effects. In Oklahoma and Texas, high-severity fires have converted closed canopy forests to early successional low brushy thickets that are preferred by some declining wildlife species (e.g., black-capped vireo [*Vireo atricapilla*]). In some of the higher-severity patches, survival among tree species has been highest for species such as post oak (*Q. stellata*) and blackjack oak (*Q. marilandica*). Relatively little attention has been placed on the ecology of blackjack oak, and it is commonly failing to regenerate throughout its range under closed canopy / fire-excluded conditions. In some areas, its presence may be an indicator of sites with high replacement severity fire potential.

5.4 The Human-Fire Connection

Throughout the world, fire regimes are strongly dependent on humans. The human-fire connection has persisted for millennia and changed with cultures and populations. Likely only in the last century has landscape burning been so removed from human survival and well-being. Understanding the long-standing relationship between humans and fire regimes provides examples for how modern-day fire ecology and management is linked to humans and can provide benefits to society.

5.4.1 Paleo and Historical Period Before European Colonization

People migrated into eastern North America and settled into the region some 10,000–15,000 ybp, and additional evidence is occasionally revealed that points to even earlier occupations, for example, in Texas (Driver and Massey 1957; Goebel et al. 2008; Morse and Morse 2009; Chaput et al. 2015; Perttula et al. 2020). Human populations increased since the initial migration and estimates of pre-European contact populations for North America range wildly from less than 1 million to 18 million, with 3–8 million being commonly reported (Goebel et al. 2008; Koch et al. 2019). In the early Holocene, the Native American population was centered in Texas and the southeastern USA, with people moving northward and westward after 9500 ybp (Chaput et al. 2015). Substantial population increases occurred around 3500 ybp in the central and eastern temperate deciduous forests, perhaps as a result of agricultural advancements when people adopted the culture of maize (*Zea mays*), squash, beans and other cultivated crops from MesoAmerica. From 2000 to 500 ybp, populations continued to increase throughout eastern North America reaching their greatest densities before European contact. During this Mississippian Period, the largest populations were centered along the Big Rivers (e.g., Ohio and Mississippi) in the greater Cahokia Region located in the Interior Valley Rivers and Hills (Fig. 5.1).

Humans brought the knowledge and ability to use fire to manage the land so that it provided for their benefit and well-being. They quickly became the dominant source of fire on the landscape in eastern temperate forests, significantly adding to natural lightning fires, transforming climate driven fire regimes to anthropogenic ones (Pyne 1982; Delcourt and Delcourt 1997, 1998; Nelson et al. 2006; Pinter et al. 2011; Abrams and Nowacki 2015). Even small groups of nomadic people could affect the nature of vegetation on landscape or regional levels when their fires burned without suppression, and spread rapidly to large extents on plains and flatter topography, especially in seasons of drought (Abrams and Nowacki 2008; Stambaugh and Guyette 2008; Springer et al. 2010; Denevan 2011; Pinter et al. 2011; Gajewski et al. 2019). In warmer periods during the Holocene, frequent fire-dependent ecosystems such as prairies and oak-pine savannas and woodlands (Fig. 5.4) dominated landscapes in the tallgrass prairie-eastern deciduous forest border region (Winkler et al. 1986; Nordt et al. 1994; Winkler 1994; Baker 2000; Nelson et al. 2006). These types of ecosystems provided for a high diversity of plant and animal species, seed, fruit and berry production, other plant-based foods, medicines and utensil manufacture, and forage and browse for game species that provided food, shelter and clothing.

During the Paleolithic Period (prior to 11,000 ybp), humans were hunter-gatherers who used stone tools to hunt megafauna, and large and small game. This diet was supplemented by harvesting wild plants. They were nomadic, moving in small groups across the landscape, taking advantage of animal migrations and seasonal plant availability. Fire was the tool they had that could affect landscapes to promote the plants and animals that were vital to their well-being. Climate during the Holocene was variable but generally favorable to human occupation and expansion (Mayewski et al. 2004). During warmer and drier periods, increases in charcoal and pollen in sediments indicate the increase in fire frequency and expansion of C_4 (warm season) grasses, oaks and pines in prairies, savannas and open woodlands (e.g., Winkler et al. 1986; Nordt et al. 1994; Winkler 1994; Baker 2000; Nelson et al. 2006). Even in cooler and wetter periods, human fires maintained the dominance of species and frequent fire ecosystems (Delcourt and Delcourt 2004; Abrams and Nowacki 2008) that supported an abundance of bison (*Bison bison*), elk (*Cervus canadensis*), deer (*Odocoileus virginianus*), wild turkey, quail and other small game, in addition to a diverse banquet of plants to sustain human population growth and prosperity.

During the Archaic Period that began about 10,000 ybp, human populations increased, as did their use of fire across the region (Fowler and Konopik 2007; Gajewski et al. 2019). By now the megafauna were extinct, and bison became a prime game species that inhabited fire-maintained prairies, savannas and woodlands throughout the region (Hornaday 1887; Nelson 2010). Technology advancements (e.g., invention of the atlatl) increased hunting success. Through the Middle Archaic

Period (approx. 8000–5000 ybp), people continued to live as nomadic hunter-gatherers. But by the Late Archaic Period (approx. 5000–3000 ybp), they became more sedentary, living in semi-permanent settlements, practicing horticulture and domesticating native plants. Native trees that produced nuts such as hickory, oak, and walnut (*Juglans nigra*), and trees and shrubs that produced fruits and berries were developed into orchards by thinning and burning natural stands or sowing seeds in created openings, in either case, fire was used to maintain the orchard and facilitate harvesting of the crop (Abrams and Nowacki 2008). They domesticated native plants such as sunflower (*Helianthus*), squash (*Cucurbita*), and sumpweed (*Iva annua*) and began producing crops in a shifting slash and burn agriculture system. They also developed pottery and other methods for long-term storage of any food surplus from their cultivation and foraging that allowed them to live in semi-permanent locations. They continued seasonal travelling to gather plants, seeds, berries and other edibles, and to hunt deer, elk, small game, and fish.

The Late Archaic Period (approximately 3000–500 ybp) includes the Woodland and Mississippian Cultures in this region up to the time of European contact. During the Late Archaic Period, continued developments in agriculture were made and by 1000 ybp, the Three Sisters, maize, beans and squash, were being grown in family gardens and by communities in extensive bottomland fields where sandy loam alluvial soils made cultivation easier (Hurt 1987). Some fields would be cropped for 5 or 15 years, then left fallow while new fields were developed by slash and burn methods (Hurt 1987), others were extensive, permanent and intensively managed (Doolittle 1992). Fire was the key tool for developing and maintaining agricultural openings and horticultural groves of nut and fruit bearing trees and shrubs.

Permanent villages became more common, and large urban cities were established in the Mississippian period (approximately 1150–350 ybp). One of the largest cities in the world at the time, and the center of the Mississippian Culture was Cahokia, which was located along the Mississippi River near the confluence of the Missouri and Illinois Rivers. From about 1400 to 600 ybp, Cahokia rose to prominence as a religious, governmental and economic leader of a cultural complex of people that occupied much of the eastern USA. Its population has been estimated at 6000–40,000 in the city center, which was surrounded by outlying villages (Woods 2004). Its extensive trade network and sphere of influence extended from the Gulf of Mexico to the Great Lakes, along the major tributaries of the Mississippi River, and throughout the southeastern USA. But sometime between 1300 and1400 Cahokia and other mound building villages and cities collapsed due to a complex of factors including severe flooding, unfavorable climate of The Little Ice Age that caused crop failures, resource overuse, pollution, food shortages and political and social unrest and upheaval (Emerson 2002; Emerson and Hedman 2016; Tainter 2019).

By the end of the Mississippian Period, the western portion of the Central Hardwood Region was inhabited by Native Americans from numerous tribes. Populations were at their highest level before European contact. The tribes were a mix of the Plains and Eastern Woodland cultures. The Caddo and Illinois confederacies were of the woodland culture, being influenced by their ancestors, the mound builders who lived in large cities and villages along the major tributaries of the Mississippi River (Perttula et al. 2020). They lived in more permanent locations and subsisted on a system of agricultural production and trade. For example, at the time of French contact with the Illinois people in the late 1600s, there were 20,000 people living in Grand Village on the Illinois River (Morrissey 2015). They also hunted, fished and harvested native plants, both wild and domesticated. Tribes of the Plains culture such as the Osage, Kansa, Iowa, Missouria, Quapaw, Wichita and Tonkawa were also dominant in this region. They lived in semi-permanent villages, grew crops such as corn, beans and squash, but were more nomadic as the bison resource was prominent in their way of living. Development of the bow and arrow and advances in pottery manufacture increased hunting success and ability to store food, and hence, permitted living in more permanent locations.

Beginning in the mid-1500s to late 1600s, early European explorers, fur trappers and missionaries encountered a cultural landscape that had been shaped with fire by the hand of Native Americans for millenia (Pyne 1982; Butzer 1992; Denevan 1992; Krech 2000; Stewart 2002; Delcourt and Delcourt 2004; Mann 2006; Harkin and Lewis 2007). Fire was used for numerous reasons including agriculture, horticulture, range management, warfare, hunting, defense, habitat management, wild plant production, and facilitating travel. Its use was not limited to the vicinity of villages, rather it was used on a daily basis around villages and while traveling on nomadic expeditions. Fire histories along major travel corridors such as rivers have unique signatures in the consistency of fires over long time periods due to the frequent presence of travelers whose purposeful or accidental fires spread through the valleys and into the uplands whenever fuels and weather were conducive to fire spread (e.g., Dey and Guyette 1996). In more remote areas, fire was used for seasonal hunting and gathering. Fires were set to maintain prairie, savanna or open woodland habitats for bison, elk, deer, turkey, quail and other small game, and for managing areas for berry, fruit and nut production, and other plant materials from sun-loving species.

Historically, human-set fires were typically frequent, low-intensity, low-severity surface fires that burned in the dormant seasons (fall to spring) across landscapes (Guyette et al. 2006b, 2016; Clark et al. 2007; Brose et al. 2013; Lafon et al. 2017). We know from modern day observations that such fires over 10–30 years have minimal effect on overstory density (Hutchinson et al. 2005; Dey and Fan 2009; Arthur et al. 2012, 2015; Fan and Dey 2014). However, such fires are effective in setting back succession by topkill or mortality of the woody understory and midstory. Thus, we can surmise that a history of frequent low-intensity fires resulted in a landscape mosaic of forests, woodlands, and savannas depending on the frequency of occasionally severe fires or other disturbances that reduce overstory density, such as insects, disease, and windthrow. By frequent burning, Native Americans opened up the forest and set back succession, thereby promoting species diversity, forage and browse production, herbaceous biomass, seed production, and overall productivity throughout the food web. By promoting development and productivity of the ground flora, they made more resources accessible to animals and humans compared to mature forests where the tree canopy is high (18–30 m or more), the understory has relatively low diversity and biomass, and much of the biomass is inaccessible in large coarse woody material (Dey and Kabrick 2015).

Fire burned frequently in oak-pine forests throughout the region with average mean fire intervals ranging from <2 years in central and eastern Texas to 6–8 years in Missouri, southern Illinois, and western Kentucky and Tennessee from 1650 to 1850, which encompasses the end of the Native American and initial EAS periods (Guyette et al. 2012). This long-term fire frequency would definitely have produced widespread open forest conditions that included savannas and woodlands (Butzer 1992; Hanberry and Thompson 2019) interspersed with prairies on the plains (e.g., Schroeder 1982). Hanberry et al. (2014a) estimated that 65% of the Ozark Highlands in Missouri (about 6 million ha) were historically oak-pine woodlands based on analyses of early surveyor witness tree records. In the Midwest and southern Great Lakes (approximately 88 million ha), Hanberry and Abrams (2018) reported that 35%, 38% and 25% of the area was either grasslands, open forests, or closed forests, respectively, in the early 1800s. Nuzzo (1986) stated that there were 11–13 million ha of oak savannas in the Midwest originally, before EAS. The highly fire-adapted genera *Quercus* and *Pinus* dominated forest composition in prehistory (Hanberry and Nowacki 2016). Native Americans had a significant influence on forest structure and composition across the region by their use of fire.

The first European explorers came into this region with the travels of Hernando de Soto (1539–1542), and Father Jacques Marquette and Louis Joliet (1673). Along with European exploration and immigration came diseases that decimated Native American populations (Dobyns 1983; Ubelaker 1988; Verano and Ubelaker 1992). For example, the Caddo population in eastern Texas declined from an estimated 200,000 to 8500 shortly after contact with de Soto's expedition, and by the 1700s it had fallen to 1400 survivors (Perttula p. 109 in Mann 2006). Heavily populated urban centers were wiped out. Associated with this widespread decline in Native population is a decline in fire frequency, with some local fire-free intervals extending for 50–100 years (Guyette et al. 2003; Brose et al. 2015). Concurrently, traditional tribal territories and land use were disrupted by the Beaver Wars during the seventeenth century in which the Iroquois waged war successfully on surrounding tribes in the Ohio Valley and Great Lakes region in an effort to control the fur trade with Europeans. Tribes such as the Osage moved westward into the region, displaced by Iroquois aggression. Fire frequency often increases in areas during warfare and conflicts, but also decreases in the aftermath when areas become depopulated due to the displacement of local people and retreat of the conquering tribe.

Populations rapidly returned with Euro-American immigration in the nineteenth century following the Louisiana Purchase (1803) and land treaties with Native Americans that opened up the country for EAS. The 1830 Indian Removal Act accelerated the effort to relocate Native Americans further west to make way for EAS. By 1839, one of the largest tribes in the area, the Osage Nation, had ceded by treaty the major portion of their ancestral lands in Missouri, Arkansas, Kansas and Oklahoma (https://www.kshs.org/kansapedia/osage-treaties-with-the-united-states/19293 accessed 8/31/2020). Subsequently, the population of Missouri increased rapidly from 20,000 in 1810 to 682,000 by 1850 (https://en.wikipedia.

org/wiki/List_of_U.S._states_and_territories_by_historical_population#Total_population,_1790–1860 accessed 8/31/2020). Similar trends in population growth occurred throughout the region during this century. From 1818 to 1907, the six states that represent the core of this region were admitted to the union. Plains and eastern woodland Native American cultures were replaced by the emerging Euro-American culture having a dramatic effect on the role of fire.

Initially, European settlers, who brought with them their own fire culture and history (Pyne 1997), adopted Native American fire practices but modified them for their own purposes in farming and livestock production. They permanently settled more remote areas that had up to then only been impacted by humans on a seasonal or multiple year cycle of use and temporary occupation. They used fire to clear forests, convert native vegetation to agricultural crop production, and manage open range grazing of livestock. Rivers were initially the major highways of transportation, but after the Civil War, expansion of railroads opened up new areas for settlement and connected farms and forests to city markets. Bison were hunted to near extinction for eastern markets by the 1880s, being replaced by domestic cattle, hogs, sheep and goats. A common pattern of increasing fire frequency with initial EAS has been reported throughout the eastern USA, including annual burning in some places, which was accompanied by reductions in variability in fire occurrence and a lack of association between fire occurrence and climate conditions (Frost 1998; Guyette and Spetich 2003; Guyette et al. 2006a; McEwan et al. 2007; DeSantis et al. 2010; Flatley et al. 2013; Brose et al. 2015; Stambaugh et al. 2017, 2018). In forested areas, settlers were starting fires wherever and whenever they could, saturating the landscape with fire, and their land use practices became a greater influence on vegetation than climatic factors (Nowacki and Abrams 2015).

With further settlement and developments, through time the landscape became fragmented by land uses (i.e., roads, crop fields, and cool-season grass pastures), and this increased barriers to landscape fire spread and improved access for fire suppression in rural areas (Guyette et al. 2002). People now had more reasons to protect their property and buildings from wildfires. Fire was quickly becoming seen as a threat and gaining a bad reputation for its ability to destroy property and resources such as forage and timber (Pyne 2010). Catastrophic fires that raged through expanses of logging slash from the timber boom era (circa 1850–1920), such as the Peshtigo (1871) and the Hinckley (1894) burned thousands of km^2, destroyed villages, and killed thousands of people (Pyne 1982). Public reaction was for more fire control, which became a primary mission of the US Forest Service and other state forestry agencies, and it still is today. For much of the twentieth century, there has been an all-out war on wildfires and a prevailing attitude among forestry leaders that wildfire can be defeated and eliminated from the land (Pyne 2015). In 1935, the US Forest Service adopted the 10 am policy by which all fires were to be controlled by 10 am the morning after they were discovered.

The prolonged period of twentieth century fire exclusion and suppression continues for most forestlands up to present. Conversely, some of the largest acreages of burned grasslands in the USA exist within and just west of the region. Some lands managed by agencies and private individuals began reintroducing fire in the late

1970s and early 1980s, primarily for natural community management. Presently, it is estimated that, in the region, nearly 400,000 ha of forestland are burned annually through prescribed fire.

5.5 Effects of Human Fire Exclusion on Ecosystems

The era of fire exclusion and suppression since approximately the 1930s has had pronounced and lasting effects on the development of terrestrial ecosystems. Combined with other anthropogenic factors, including land use decisions and urban development, the character and distribution of natural communities across the contemporary landscape is notably different from historical accounts. Across ecosystem types, the reduction in fire had common effects of increasing the abundance of woody vegetation (encroachment or densification), changing the composition of plant communities, and altering ecosystem functions.

5.5.1 Shifting Ecosystems

Fire exclusion contributes to several mechanisms of plant community change. Fires of high frequency and/or intensity inhibit the development or expansion of native woody vegetation. However, the ability to reproduce vegetatively allows many woody species to persist until an interruption in the fire regime (or other disturbance) provides opportunity for recruitment (Bond and Midgley 2001; Hoffmann et al. 2020). Once woody vegetation establishes, fires of higher intensity or frequency may be required to control further development or spread, although the rates of woody encroachment and specific fire regimes needed for control vary across the ecoregions and ecosystem types. The development of woody stems reduces the availability of light energy available to herbaceous plants, shifting competitive dominance towards woody vegetation and reducing the abundance and diversity of the herbaceous community.

In addition to the effects of competition from woody vegetation, fire exclusion results in accumulation of detritus that creates a barrier to herbaceous plant establishment. Studies have reported reductions in productivity of herbaceous vegetation following fire exclusion even without development of woody vegetation in prairies (Knapp and Seastedt 1986) and have attributed greater effects of detritus accumulation than woody vegetation abundance in pine woodlands (Hiers et al. 2007; Veldman et al. 2014). The development of woody vegetation provides additional inputs of leaf litter to the detritus layer, which can subsequently modify the nutrient dynamics of the ecosystem. Eastern redcedar, a common species to increase abundance with fire exclusion throughout the region, has been found to alter nitrogen cycling (Norris et al. 2007), carbon accumulation (McKinley and Blair 2008), and microbial communities (Williams et al. 2013).

The period of fire exclusion has coincided with increased abundance of non-native, invasive plants, which have additionally contributed to ecosystem shifts and management challenges with reintroduction of prescribed fire regimes (Fig. 5.6). However, it is difficult to disentangle whether plant invasions are: (1) a direct result of fire exclusion; (2) correlated with fire exclusion practices through direct effects of other land use legacies, or; (3) an indirect result of fire exclusion through other changes to plant communities or ecosystem functions. Overgrazing or agricultural land use followed by abandonment provide opportunity for invasion by non-native plants. Changes in the diversity, dominance, and productivity of native plant communities associated with such disturbances, as well as fire exclusion, may further increase invasibility (Hobbs and Huenneke 1992; Tilman 1999). The non-native, invasive species of the region vary widely in their autecological response to fire. Species such as Russian olive (*Elaeagnus angustifolia*), Chinaberry (*Melia azedarach*), Asian bittersweet (*Celastrus orbiculatus*), and sericea lespedeza (*Lespedeza cuneata*) persist after burning through vegetative reproduction. Species such as cogongrass (*Imperata cylindrica*), cheatgrass (*Bromus tectorum*), and Japanese stiltgrass (*Microstegium vimineum*) are well-adapted to fire, serving as fuels that alter fire behavior to favor their postburn expansion and dominance (Chap. 12). There are few opportunities to evaluate the dynamics of plant invasion on sites without a history of fire exclusion, making it difficult to know the direct effect of fire exclusion on invasion.

Effects of fire exclusion on plant communities have complex effects on and interactions with other ecosystem functions. Wildlife populations are impacted by habitat characteristics of vegetation structure and composition. The increase in tree density and complex vertical structure reduces habitat for species associated with open forest ecosystems and early successional habitats (Hanberry and Thompson 2019). Species such as the red-cockaded woodpecker (*Picoides borealis*) and northern bobwhite quail have become symbolic of frequent-fire ecosystems, but a diverse assemblage of other species are associated with or dependent on open ecosystems. Effects of fire on microbial communities and their feedbacks on vegetation communities are relatively poorly understood drivers of ecosystem function (Eivazi and Bayan 1996; Hartnett and Wilson 1999; Dove and Hart 2017). Persistent effects of long-term fire exclusion on interactions between soil microbial communities and associated plant species may impede restoration efforts through reintroduction of fire.

Ecosystem changes that perpetuate after long-term fire exclusion are often difficult to reverse. Gradual changes over time eventually reach a tipping point, where change accelerates, leading to altered ecosystem functions and an alternative state (Suding et al. 2004). These changes may manifest in the altered fire ecology of the system. For example, frequent fire regimes in tallgrass prairies historically limited the expansion of native shrubs, and long-term fire exclusion allowed them to expand. Reintroducing annual burns did not reduce shrub abundance, and moderate (4-year) fire intervals further promoted shrub expansion (Heisler et al. 2003); high-intensity burns were required to control shrubs. Fuel loads and types may also change during long-term fire exclusion, in some cases increasing risk of extreme fires. For example, eastern redcedar expansion within oak woodlands increase the risk of stand replacement fires, further altering the ecosystem (Stambaugh et al. 2014).

5.5.2 Tallgrass Prairies

The tallgrass and mixed-grass prairie ecosystems of the Central Irregular Plains and Cross Timbers ecoregions have been classified as endangered or critically endangered due in large part to conversion to agricultural uses (Noss et al. 1995; Hoekstra et al. 2005). Remaining areas of prairie are often small and highly fragmented, degraded by overgrazing, the invasion of non-native species, and conversion to shrubland or developing forest (Davison and Kindscher 1999). The removal of fire has played a critical role in the expansion of woody vegetation within grasslands; without frequent and, in some cases, high-intensity fires, woody vegetation can quickly increase in abundance and distribution, spreading from small populations within existing prairie or from boundary populations. For example, at Konza Prairie Biological Station (KPBS) in Kansas, USA, the expansion of woody vegetation from riparian zones into tallgrass prairie nearly doubled forested areas from 1939 through 2002 (Briggs et al. 2005; Knight et al. 1994). Within upland areas, native shrub species such as roughleaf dogwood (*Cornus drummondii*) and smooth sumac (*Rhus glabra*) can spread via vegetative reproduction to create dense shrub thickets or “islands” across prairie landscapes (Briggs et al. 2005; Tunnell et al. 2006). The encroachment of eastern redcedar into tallgrass prairie has been of particular concern given the ubiquity of the species and the scale and rate of expansion. Briggs et al. (2002) reported a maximum expansion rate of 5.8% per year during a period of expansion at KPBS, resulting in transition from prairie to eastern redcedar forest within a 40-year period. Eastern redcedar has been documented as a problem within grasslands across most states of the region and was the forest type with the greatest increase in forestland from 2005 through 2012 within an eight-state region of the central USA (Meneguzzo and Liknes 2015).

With increased abundance of woody vegetation, fire exclusion from tallgrass prairies results in loss of plant diversity. High densities of woody stems restrict light energy from penetrating through to the groundlayer where herbaceous plants abound (Fig. 5.6). Within the shrub islands created by native species such as roughleaf dogwood or smooth sumac, low light levels have been associated with decreased plant species richness and diversity, as well as reduced abundance of grass species (Lett and Knapp 2003, 2005). Similar responses have been observed with encroachment of eastern redcedar. Herbaceous species are nearly eliminated from directly beneath the foliage of redcedar trees, creating locally depauperate plant communities (Briggs et al. 2002). As the canopy cover of eastern redcedar increases, species richness and abundance have been shown to decrease with either linear relationships (Limb et al. 2010) or non-linear relationships that suggest potential threshold levels of canopy cover for accelerated diversity loss (Briggs et al. 2002).

The importance of fire in the development and maintenance of the tallgrass prairie is well established, but a refined understanding of specific fire regimes under contemporary conditions is complex. Frequent fires are critical to preventing the expansion of woody vegetation within prairies, with return intervals >3 years resulting in transitions to shrublands or woodlands (Briggs et al. 2005; Ratajczak et al. 2014). In eastern portions of the tallgrass prairie, species richness increased with increasing fire frequency, likely due to the need for high frequency burning to control woody vegetation on productive sites (Bowles and Jones 2013). In contrast, increasing fire frequency to annual burning reduced species richness by favoring competitive C_4 grasses throughout western portions of the tallgrass prairie ecosystem (Collins et al. 1995). Historically, fire may have occurred throughout the year, with the timing of burning affecting the abundance and dominance of the plant community (Howe 1994). Given the diversity of species within prairies, burning at any particular time will likely favor certain species at the expense of others. Generally, growing season or summer burns reduce dominance of C_4 grasses and dormant season or winter burns increase their dominance, often resulting in increased dominance of forbs (Davison and Kindscher 1999).

The vegetation structure and diversity of prairies are associated with assemblages across trophic levels. Insect communities are responsive to fire-induced changes in vegetation composition within prairie ecosystems (Swengel 2001), with the prevalence of grasshopper guilds responding to the abundance of forbs or grasses associated with fire frequency (Evans 1988). With the encroachment of woody vegetation into prairies, habitat-specialist butterflies have declined throughout the region (Swengel et al. 2010). Similar patterns have been described for bird communities, with declines in grassland bird species associated with the increase in woody vegetation in prairie communities (Coppedge et al. 2004; Grant et al. 2004). Heterogeneous habitats that include some structural complexity contributed by woody vegetation support a mixture of grassland- and woody-dependent bird species (Zimmerman 1992). Thus, aspects of the fire regime, including fire frequency and season, can indirectly affect bird populations by affecting the abundance of vegetation types and directly affecting populations by interacting with important life cycle stages. For example, spring burning can negatively impact greater prairie-chicken (*Tympanuchus cupido*) nest success whereas summer burning, which occurs after the nesting period, has minimal negative effects (Reinking 2005).

The maintenance and restoration of contemporary tallgrass prairies are challenged by limits to management options. Twidwell et al. (2016) demonstrate that policies of prescribed fire management, including the range of conditions under which burning is conducted today, result in a narrow range of fire behaviors that do not approximate the historical range of variability by reducing fire intensity. Consequently, fire intensities produced by prescribed fire programs may not be sufficient to overcome effects of historical fire exclusion through fire management alone. Integrating controlled grazing with fire provides additional opportunities to manage prairie ecosystems, especially if fire management is limited by external factors.

5.5.3 Glades

The term "glade" has been used to describe a variety of ecosystems throughout the eastern USA (Baskin et al. 2007). In the Ozark region of Missouri and Arkansas, glade ecosystems are relatively small areas (often <1 ha but can be >500 ha) that are scattered throughout woodland or forest landscapes (Fig. 5.4c). Over 30,000 individual glades have been identified across the Ozark Highlands, and Boston and Ouachita Mountains (Nelson et al. 2013). Glades are defined by shallow soils and exposed bedrock, often sandstone, dolomite, and granite, and commonly occur on exposed slopes or ridges. The transition into glade communities can occur abruptly within forest and woodland ecosystems. Given their thin soils and generally xeric conditions, glades are associated with drought-tolerant species and often support unique plant and animal communities. Plant communities within glades commonly correspond to variation in soil depth, with surfaces of bare exposed bedrock supporting only mosses and lichens, extremely shallow soils (<1 cm depth) supporting annual forbs and grasses, and greater abundance of perennial species occurring where soil depths reach 5 cm (Nelson et al. 2013). Through time, the development of soil or organic matter within cracks in the bedrock, ledges or shelves, or the areas between rock exposures create opportunities for the establishment of woody species (Ware 2002; Baskin et al. 2007). Unlike truly edaphic glade communities of the southeastern USA (Chap. 3), which are dominated by C_3 grasses and annual plant species, glade communities of the central region have greater abundance of C_4 grasses and perennial plants and are prone to transition to woodland or forest ecosystems in the absence of disturbance (Baskin and Baskin 2000). Glades are associated with diverse herbaceous plant communities that include unique or endemic species. Many glade species require high light levels to remain competitive and are adapted to the dry, shallow soils (Baskin and Baskin 1988). There are several species, such as limestone adders tongue (*Ophioglossum engelmannii*) and western wallflower (*Erysimum capitatum*), that associate with calcareous soils within glades of the region.

Decreased fire over much of the last century has primarily changed glade plant communities through the encroachment of woody vegetation. Eastern redcedar is the most problematic tree species, with other common species including chinkapin oak (*Q. muehlenbergii*) on calcareous soils of limestone or dolomite glades and post oak or blackjack oak on sandstone or igneous glades (Erickson et al. 1942; Jeffries 1987; Weaver and Bornstein 2012). Using remote sensing information, Miller et al. (2017) found that woody encroachment, primarily from eastern redcedar, increased seven-fold from 1939 through 2014 in dolomite glades of the Missouri Ozarks. Similarly, Knapp and Pallardy (2018) reported steady increase in the density of eastern redcedar and chinkapin oak from 1968 through 2016 in unburned glade-like habitats of mid-Missouri.

The encroachment of woody vegetation is understood to reduce the abundance and diversity of glade ecosystems, but few studies have directly quantified effects of fire exclusion on glade vegetation. Prescribed burning and mechanical removal of woody vegetation are commonly used to restore glade ecosystems. There are many examples of successful glade restorations using these methods, such as the Stegall Mountain complex in southeastern Missouri (Templeton et al. 2011). Reintroducing fire into glades can reduce the density of woody stems, primarily due to topkill of saplings (Jenkins and Jenkins 2006). However, if trees get large enough to withstand topkill, prescribed burning may be ineffective at reducing woody cover. For example, repeated prescribed burning over a 30-year period did not reduce the abundance of woody stems following encroachment of a glade complex by eastern redcedar of Missouri (Miller et al. 2017). Preventing canopy closure is important for maintaining heliophytic herbaceous species common to glades. Short-term studies have found that prescribed burning to either increase or have no effect on herbaceous plant communities (Jenkins and Jenkins 2006; Comer et al. 2011), but this topic has not been studied extensively.

The open structure and dry conditions associated with glades support unique wildlife. Bird species include those associated with shrublands and early successional habitat, such as prairie warbler (*Dendroica discolor*) and yellow breasted chat (*Icteria virens*; Fink et al. 2010). Efforts to restore glades through the reintroduction of fire and removal of eastern redcedar can increase the abundance of some these species (Comer et al. 2011). Bachman's sparrow, a species associated with open pine ecosystems of the southeastern USA, also occurs within glades of the Missouri Ozarks, although populations have declined with fire exclusion (Hardin et al. 1982). The greater roadrunner (*Geococcyx californianus*) and collared lizard (*Crotaphytus collaris*) are typically southwestern species that occur up through glades habitats in the Ozark Highlands of Missouri due to the dry conditions (Nelson et al. 2013). Fire exclusion was particularly impactful on collared lizards, due not only to the reduction of glade habitat but also the restriction of movement of individuals among glades (Brisson et al. 2003). The reintroduction of prescribed burning created stabilized metapopulations through the ability to disperse throughout glade networks (Templeton et al. 2011).

5.5.4 Upland Savanna, Woodland, and Forest

Much of the vegetated area of the region is classified as mixed forest (Fig. 5.1). Increased precipitation across the west-east gradient is associated with general increases in site productivity and changes in tree species composition. Across much of the region, however, upland sites are dominated by oak-hickory forests. Common oak species include white oak (*Q. alba*), black oak (*Q. velutina*), scarlet oak (*Q. coccinea*), northern red oak (*Q. rubra*), post oak, blackjack oak, chinkapin oak, and bur oak (*Q. macrocarpa*); common hickory species include pignut hickory (*C. glabra*), mockernut hickory (*C. tomentosa*), shagbark hickory (*C. ovata*), black hickory (*C. texana*), and bitternut hickory (*C. cordiformis*). Historically, shortleaf pine was also a dominant species in pure stands or in mixture with oak species across the Ozark region. A variety of other species occur in association with oak and pine dominance, including maples (*Acer* spp), ashes (*Fraxinus* spp.), elms, cherry (*Prunus* spp.), black gum (*Nyssa sylvatica*), and eastern redcedar.

The contemporary forested landscape is a reflection of past land use and management decisions. Shortly prior to the fire exclusion policies of the early twentieth century (Sect. 5.4.1) was a period of exploitative timber removal and intensive land use associated with settlement and agricultural enterprise. This cut-over period initiated the regeneration of second-growth forests, and the frequent anthropogenic fire of the time likely favored stress- and fire-tolerant species, such as oaks and hickories, in the regeneration layer. The widespread fire exclusion policies then provided a "release" of that regeneration, setting the trajectory for the development of forest composition and structure we see today. Across much of the region, the dominance of closed-canopy oak forests, commonly aged to 80–100 years old, reflects these legacies.

The period of fire exclusion has been associated with two commonly observed patterns across upland ecosystems: (1) increased density of trees compared to historical conditions, and; (2) compositional shifts towards more fire-sensitive species through time. Several studies contrast contemporary conditions to those at the time of Public Land Surveys (PLS) in the 1800s to demonstrate these changes (Fralish et al. 1991; Batek et al. 1999; Hanberry and Abrams 2018). In the Ozark Highlands of Missouri, Hanberry et al. (2014b) report that contemporary forests have 2–3 times the number of trees as those recorded by the PLS data, with mean dbh around 35 cm in the historical records and 23 cm now. The greater number of trees observed today can, in part, be traced back to the release of second-growth regeneration at the time fire exclusion began, as these trees developed within even-aged cohorts to create closed-canopy forests. During the subsequent period of fire exclusion, the establishment and recruitment of new trees was no longer disrupted by the topkill induced by surface fire. A long-term burning study from Missouri found that prescribed burning with a 4-year return interval was frequent enough to inhibit recruitment of any new trees to the canopy over a 50-year period (1964 through 2013), while adjacent unburned areas developed several layers of vertical structure due to tree recruitment through time (Knapp et al. 2017). As a result, fire exclusion has allowed these ecosystems to "fill in" with the establishment and recruitment of new trees through time. In addition to increasing stand density, the open vertical structure of savannas and woodlands has largely been replaced by multi-layered forests.

In recent decades, forested ecosystems have experienced compositional shifts from dominance of fire-adapted species, such as oaks, hickories, and pine, to increases in the abundance of more fire-sensitive species such as maples, ashes, and elms. Fire exclusion provided opportunity for the establishment and recruitment of these trees. Their presence can moderate ecosystem conditions to reduce fire frequency or intensity by retaining moisture in the leaf litter, increasing sub-canopy humidity, and altering physical or chemical properties of fuels. This positive feedback system, termed mesophication, has been associated with successional transitions from oak-hickory forest to maple forests throughout the eastern USA (Nowacki and Abrams 2008). In addition, low light levels to the forest floor associated with increasing stand densities favor shade-tolerant species rather than the mid- to low-tolerant oak and pine species. Consequently, the relative abundance of oaks and pines have decreased compared to historical records, with changes continuing in recent decades (Fei et al. 2011; Hanberry et al. 2014b; Knapp and Pallardy 2018).

In the southwestern portion of the Western Central Hardwoods Region lie the Cross Timbers, a unique region of Kansas, Oklahoma, and Texas that is a xeric ecotone from grassland to oak-dominated woodlands and forests. The low productivity of the region results in short-statured trees of poor timber value, which contributed to extensive areas spared from widespread timber harvest during settlement. The region is dominated by xeric oak species, primarily post oak and blackjack oak, that may exceed 300 years old yet remain <15 m tall. Regeneration of the dominant oak species is associated with fire; although acorns infrequently contribute new individuals, sprouting from stumps, seedlings, or root systems following fire primarily provides the source of succession regeneration (Clark and Hallgren 2003). Following fire exclusion, encroachment of fire-sensitive tree species, including eastern redcedar, elms, and hackberries (*Celtis* spp.), has been documented throughout the region (Hoff et al. 2018a). Greater biomass in the forest understory and midstory has increased fuel loading and created ladder fuels that pose wildfire risk and limit options for prescribed burning, particularly in this drought-prone region (Hoff et al. 2018b; Stambaugh et al. 2014).

Moving east to the Ouachita Mountains through the Ozark Highlands ecoregions, shortleaf pine becomes an important tree species that historically dominated upland ecosystems. Although present across a wide range of the eastern USA, shortleaf pine occurs in greatest abundance in Oklahoma, Arkansas, and Missouri (Moser et al. 2007). Prior to the exploitative logging practices of the late 1800s and early 1900s, shortleaf pine was vastly more abundant, particularly in Missouri, where various estimates indicate shortleaf pine today represents approximately 20% of the historical condition (e.g., areal extent, stand density; Guyette et al. 2007).

While logging removed much of the seed source for shortleaf pine regeneration, the period of fire exclusion further limited regeneration success. Shortleaf pine seeds germinate best in contact with mineral soil, and the accumulation of leaf litter on the forest floor results in low densities of shortleaf pine seedlings (Grano 1949; Yocom and Lawson 1977). Seedlings and saplings can resprout following fire due to a morphological adaptation of the root collar, known as the basal crook, in which dormant buds are located on lateral root tissue just below the soil surface. Shortleaf pine seedlings require high light levels for sustained growth, however, and are unlikely to do well in shaded understories of dense stands. Following canopy disturbances, abundant competition from hardwood sprouts reduces the success of shortleaf pine regeneration (Kabrick et al. 2015). In the absence of fire, contemporary forest management practices in Missouri are unsuccessful at increasing shortleaf pine regeneration, even with shortleaf pine in the canopy to serve as a seed source (Olson et al. 2017). Frequent surface fire provides opportunity for shortleaf pine seedling establishment and competition control, although an appropriate fire-free period is necessary to help promote shortleaf pine recruitment (Stambaugh et al. 2007b). In some areas of Texas where shortleaf pine is well established, regeneration can be high despite fire intervals of 2–3 years.

The Interior River Valleys and Hills ecoregion features greater site productivity and the presence or increased abundance of mesic species such as sugar maple (*A. saccharum*), tulip poplar (*Liriodendron tulipifera*), and American beech (*Fagus grandifolia*). Challenges with oak regeneration are more pronounced in this ecoregion than on the more xeric sites of the Ozark Highlands. Consequently, shade-tolerant mesic species commonly accumulate within the understory and midstory forest layers, with canopy recruitment following small-scale disturbance events that create canopy openings (Lin and Augspurger 2008; Knapp and Pallardy 2018). With canopy disturbances of greater intensity, tulip poplar can dominate the regeneration layer (Groninger and Long 2008). In this region, prescribed burning can be incorporated into forest management to favor success of oak regeneration, similar to other sites within the eastern USA (Brose 2014).

Fire exclusion has reduced the extent of open ecosystems across ecoregions within the western Central Hardwoods Region, converting savannas and woodlands to closed-canopy forests with concurrent losses of herbaceous vegetation abundance and diversity. Many studies have shown that reintroducing fire into upland ecosystems increases the abundance of herbaceous vegetation (Nuzzo et al. 1996; Knapp et al. 2015; Maginel et al. 2019). The response of species or functional groups is dependent on interactions with the canopy structure and characteristics of the fire regime. For example, legumes are typically more responsive to prescribed burning under shade than grasses, and C_4 grasses in particular, which require greater light levels for response (Peterson et al. 2007). In the Missouri Ozarks, reintroducing fire into closed-canopy oak forests resulted in the open structure characteristic of woodlands but favored forbs over graminoids (Knapp et al. 2015; Maginel et al. 2019). In shortleaf pine grasslands of Arkansas, Sparks et al. (1998) reported that legumes increased in abundance following dormant season burning, whereas *Panicum* spp. grasses decreased in abundance with growing season fire. Responses to fire also vary by site. Landscape-scale burning in the Missouri Ozarks over a 20-year period increased species richness on exposed sites but decreased or had no effect on species richness on protected sites (Maginel et al. 2019). Consequently, landscape scale burning may homogenize species diversity by eliminating fire-sensitive species, despite increases in local species richness (Myers et al. 2015).

Fire can significantly improve forage abundance, nutritional carrying capacity, and palatability for grazers and browsers, including both wildlife and domestic animals (Allen et al. 1976). Within this region, emphasis is often placed on management for game species. In the Ouachita Mountains, Masters (2006) reported forage production to be 10–25 times higher in the first 6–8 years postfire in an oak-pine stand as compared to a mature stand. Reducing canopy closure by 30–40% in mature closed-canopy forests increased soft mast production and improved cover preferred by wild turkey hens (McCord et al. 2014). Recurring prescribed fire following canopy reduction maintained desirable cover and food resources for wild turkey poults. However, recurring low-intensity prescribed fire without canopy reduction did not reduce basal area, influence understory composition or structure, or improve conditions for wild turkeys. Lashley et al. (2011) suggest that a fire return interval of 3–5 years may maintain forage availability, soft/hard mast production, and fawning cover, and Wann et al. (2020) found turkeys preferentially select areas burned within the previous 3 years. Fire managed areas should not be so large to eliminate infrequently burned areas, such as hardwood forests, from the home range of individual turkeys.

The vegetation structure and composition of open ecosystems provides habitat for a wide variety of bat and bird species. Declines in bat populations has increasingly limited the use of prescribed burning throughout the region in the last decade. For bats, it is important to consider the needs of individual species in land management because each has differing morphological characteristics and habitat requirements. In a regional study of prescribed burned areas and bats in the Ozarks, evening bats were most positively associated with habitat features characteristic of savannas and woodlands but, in general, all species had high occupancy rates across savanna, woodland, and forest habitat types (Starbuck et al. 2014). Across a restoration gradient from savanna to woodland to forest in Missouri, Reidy et al. (2014) found that mature forest birds such as Acadian flycatcher (*Empidonax virescens*) and worm-eating warbler (*Helmitheros vermivorum*) were more common in high-density forest stands with no recent fire. However, both woodland species (e.g., eastern wood pewee (*Contopus virens*), summer tanager (*Piranga rubra*)) and early-successional species (e.g., eastern towhee (*Pipilo erythrophthalumus*), indigo bunting (*Passerina cyanea*)) were associated with low canopy density and recent or frequent fire. For both canopy-nesting and shrub-nesting species, lower stand density associated with woodlands resulted in greater nest survival when compared to forests in the same region (Roach et al. 2018). Species such as the red-cockaded woodpecker, Bachman's sparrow, pine warbler (*Setophaga pinus*), and brown-headed nuthatch (*Sitta pusilla*) are associated with open pine habitats and have been lost or greatly reduced due to historical land use and fire exclusion (Eddleman et al. 2007).

5.6 Fire Management Today

In general, there is a need for increased prescribed burning across the USA for reasons ranging from ecosystem restoration and management to climate adaptation to wildfire management. Today, on average 1–2% or less of the region burns each year including all grasslands and forestlands from both prescribed and wildfires. For forestlands, some of the primary reasons for prescribed fire management are to improve wildlife habitat, increase early successional communities and open forest structures, favor desired species of trees, and increase plant and animal diversity. Many of these objectives can be achieved in unison and necessitate the same fire management prescription.

Prescribed fire management occurs across private and public lands for a wide diversity of objectives. Within the forested ecoregions, the largest acreages of prescribed burning occur on federal and state ownerships (e.g., national forests and refuges, state parks and forests), while in grasslands a larger proportion of burning occurs on private ownerships. Due to broad variations in climate, soils, and competing species, one fire management prescription for all regions does not fit; regional-, site-, and species-specific factors should be considered (Arthur et al. 2012), and therefore detailed and site-specific fire regime information is valuable to guide management.

For prescribed fires, much of the year-to-year burning occurs on the same land parcels and most of these fires are small (e.g., <12 ha). Sizes of fires can be constrained by land ownerships and capacity (e.g., personnel, equipment) for burning large areas. However, weather is the leading impediment for prescribed fire use, while capacity and air quality/smoke are also important (Melvin 2018). In the last two decades, prescribed fire sizes have become larger to include landscape-scale burns, particularly on federal lands such as national forests. Support for prescribed fire management in the region has grown to include national programs (e.g., Collaborative Forest Landscape Restoration Program [CFLRP], Joint Chiefs' Landscape Restoration Partnership) and non-governmental agencies (NGOs) with complimentary land management objectives. In the Ozark Highlands and Ouachita Mountains, these programs have supported over 200,000 ha of prescribed fire management annually with some individual burns encompassing over 2000 ha. Similar increases in capacity have occurred for prescribed fire management on private lands, partly driven by increased programmatic support, but also due to improved coordination (e.g., Prescribed Fire Councils, Prescribed Burn Associations), training, and awareness and motivation, especially for wildlife management. The potential to increase use of prescribed fire is substantial based on the extent of former fire-dependent ecosystems that could be restored, the need for quality habitat for wildlife species of conservation concern, recovery of habitat for threatened and endangered species, and need for active management to increase landscape diversity, productivity and resilience.

Despite being supported by scientific studies, prescribed fire management of large forest landscapes, particularly with large individual burns, is a reversal of campaigns, policies, and attitudes that arose with the fire suppression era circa the 1930s. As such and expectedly, new science and information needs and challenges have arisen. Increases in prescribed fire management have required new workforce capacity, new management policies, new inter-agency coordination, new science, and new public information campaigns, among other needs. For forest management in this region specifically, challenges have related to industry and professional perceptions of appropriate land use, land management practices, and the associated fire effects. Fire effects on timber quality and site conditions have been a leading concern, and this has likely always existed, not just in the last few decades or century. To address this concern and the associated information needs, new silvicultural systems have been emerging (e.g., shelterwood-burn technique; Brose et al. 1999, silvicultural approaches to woodland management; Dey et al. 2017) and additional experiments and demonstration sites are underway. New fire management techniques and systems may also help meet these objectives. For example, more work is needed that demonstrates how and what types of prescribed fires (e.g., season, intensity, behavior) can be incorporated in management plans for not only tree objectives, but also for objectives related to overall plant species diversity, wildlife food and cover, water quality, recreation, and others. Fire alone will seldom be sufficient to manage and restore desired vegetation and habitats, rather it must be integrated with other practices to achieve goals and address public concerns.

Clearly, diverse challenges face fire management going forward (Ryan et al. 2013) and current and historical fire regimes differ due to human factors and goals in land management. Some human factors are personal (e.g., ethics), some are inherent to professions and agencies, and others are associated with publics and stakeholders. Little information exists outlining land ethics related to prescribed fire and this may be a major impediment underlying resistance to prescribed fire campaigns. Overall, public opinion for prescribed fire management is positive and not a major limiting factor to its use. McCaffrey (2006) reported that public support of prescribed fire was strongly shaped by familiarity with the practice, trust in land management agencies, and concerns about smoke and fire control. Interaction between agency personnel and the public was the most helpful way to build acceptance amongst those surveyed. Agency efforts to increase public familiarity with prescribed fire as a management tool may increase public approval.

In the future, new challenges for fire management are anticipated. Current major challenges in the region included prescribed fire and silviculture integration, fire effects on threatened and endangered species (e.g., bats), and smoke management, particularly near major population centers and travel corridors. Important unknown questions also relate to longer-term factors such as understanding fire regime and vegetation relationships, nutrient cycling, invasive species, and climate change. Nearly all of these concerns are not specific to fire management but are also important to other types of forest management practices and treatments as well (e.g., mechanical harvesting, herbicide applications).

Ultimately, the future of fire management will be determined by human factors. For millennia, humans have been the primary driver of fire activity and fire regimes were dynamic across landscapes and through time. Humans historically burned to receive benefits and this continues to underlie our land management objectives today. Today, human needs and perceived benefits from fire are very different than in the past; in many ways fire on the landscape seems less directly linked to our survival (e.g., food source, shelter, safety) but it is intricately linked to intangible benefits from natural resources, environmental quality, biodiversity conservation, and ecosystem resilience, which all contribute to our well-being. Knowledge of fire regimes, the role of humans, and the response of ecosystems to fire, or the lack thereof, will aid in determining the value of fire management. Certainly, historical precedence exists for fire management, and human-driven fire regimes will be part of the ecology of the region in the future.

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