Chapter 1
Introduction to Fire Ecology Across USA Forested Ecosystems: Past, Present, and Future

Cathryn H. Greenberg, Beverly S. Collins, Scott Goodrick, Michael C. Stambaugh, and Gary R. Wein

Abstract Fire has, does, and will shape forest structure, composition, and biodiversity. In this book, we introduce the driving forces, historical patterns, and future management challenges of fire in forested ecoregions across the continental USA. Climate warming and decades of fire suppression or exclusion have altered historical fire regimes and threaten diversity of fire-adapted forest vegetation into the future. Historical fire regimes ranged from frequent, low-severity fires in some ecosystems to infrequent, high-severity fires in others. They were driven by interactions among climate, drought cycles, topography and soils, fuel type and accumulation, and ignition frequencies by lightning; and increasingly by humans as Native American populations expanded in many ecoregions. Fires burned across large landscapes in ecosystems where fuels were continuous, such as pine-savanna ecosystems of the Southeastern Coastal Plain or ponderosa pine forests of the Southwest. Today, decades of fire exclusion have led to divergent outcomes: succession toward forests less apt to burn (*mesophication*), or more frequent or higher-severity wildfires. Management of fire toward future forests will require careful definition of

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desired future and reference conditions, establishing priorities, and working across agency boundaries to implement prescriptions.

Keywords Ecoregions · Fire-adapted plant traits · Fire history reconstruction · Fire regime · Humans and fire

1.1 Introduction

Fire is integral to shaping the structure, composition, and biological diversity of many forest types in ecoregions across the USA. Fire regimes – the frequencies, severities, seasons, and spatial patterns of fire over a long period of time – vary with vegetation across broad climate and topographic gradients. In this book, we take a regional approach to examine fire ecology of forest types across the USA, and the driving forces, historical patterns, and future management challenges within each region. Regions covered (Fig. 1.1) include the Piedmont (PDMT; Chap. 2), Southeastern Coastal Plain (SCP) Uplands (SCPU; Chap. 3) and Floodplains (SCPF; Chap. 6), Eastern Broadleaf/central Appalachians (EBA; Chap. 4), Western Central Hardwood Forests (WCHF; Chap. 5), Northeastern Forests (GL-NEF;

Fig. 1.1 Regions covered by the chapters. From east to west, these are the Northeast (GL-NEF), uplands (SCPU) and floodplains (SCPF) of the Southeastern Coastal Plain, Piedmont (PDMT), Eastern Broadleaf/Central Appalachian Hardwoods (EBA), Western Central Hardwoods (WCHF), Southwest (SWF), Rockies (RCKS), California Mediterranean (NAMCZ), and Pacific Northwest (PNW). See Table 1.1 for ecoregions within each chapter region

Table 1.1 The Environmental Protection Agency Level III ecoregions (https://www.epa.gov/eco-research/level-iii-and-iv-ecoregions-continental-united-states) and major vegetation types (NatureServe 2018) for each region covered in this book, total number of wildfires/100 ha (TFPA), ratio of lightning- to human-caused (other) wildfires (L/O), and the correlation (r) between monthly lightning and other wildfires (COR). Wildfire data includes 1992-2011 (Short 2013)

Regions, ecoregions, and major vegetation	TFPA	L/O	COR
GL-NEF: NORTHEAST: 49, 50, 51, 52, 53, 54, 55, 56, 57, 58, 59, 60, 61, 62, 82, 83			
Eastern Forest & Woodland	2.15	0.04	0.55
Appalachian-Northeast Oak-Hardwood-Pine	2.96	0.05	0.51
Central Midwest Mesic Forest	1.58	0.02	0.69
Appalachian-Interior-Northeast Mesic Forest	1.93	0.04	0.79
Central Midwest Oak Woodland & Savanna	1.85	0.01	0.78
Laurentian-Acadian Mesic Hardwood-Conifer Forest	2.17	0.04	0.50
Laurentian-Acadian Pine-Hardwood	7.21	0.01	0.49
Boreal Conifer Poor Swamp	–	–	–
PDMT: PIEDMONT: 45, 64			
Eastern Forest & Woodland	12.00	0.02	−0.16
Appalachian-Interior-Northeast Mesic Forest	11.76	0.02	−0.18
Southern & South-Central Oak-Pine	13.66	0.02	−0.04
Southeast Flooded & Swamp Forest	–	–	–
Eastern Grassland & Shrubland	6.03	0.74	0.96
Appalachian Rocky Felsic/Mafic Scrub/Grassland	20.55	0.02	0.11
SCPU: SOUTHEASTERN COASTAL PLAIN UPLANDS: 34, 35, 63, 65, 73, 74, 75, 76			
Southeast Forest & Woodland	12.17	0.1 4	−0.26
Southeast Coastal Plain Evergreen Oak-Mixed Hardwoods	12.45	0.11	−0.35
Eastern Forest & Woodland	7.48	0.03	−0.16
Southern & South-Central Oak-Pine	7.49	0.03	−0.16
Southeast Grassland & Shrubland	14.75	0.18	−0.37
Florida Peninsula Scrub & Herb	18.70	0.36	−0.27
Southern Barrens & Glade	13.17	0.07	0.62
SCPF: SOUTHEASTERN FLOODPLAINS: 34, 35, 63, 65, 73, 74, 75, 76			
Southeastern North American Flooded & Swamp Forest	10.60	0.05	−0.37
Atlantic & Gulf Coastal Plain Pocosin	7.68	0.11	−0.18
Southern Coastal Plain Evergreen Hardwood-Conifer Swamp	16.23	0.12	−0.34
Atlantic & Gulf Coastal Wet Meadow & Shrubland	25.96	0.13	−0.35
Southern Coastal Plain Basin Swamp/Flatwoods	8.92	0.05	−0.44
Pond-Cypress Basin Swamp	11.36	0.46	−0.10
EBA: EASTERN BROADLEAF / APPALACHIANS: 66, 67, 68, 69, 70, 71			
Eastern Forest & Woodland	2.15	0.04	0.55
Appalachian-Interior-Northeast Mesic Forest	1.95	0.05	0.79
Appalachian-Northeast Oak-Hardwood-Pine	2.96	0.05	0.51
Southern & South-Central Oak-Pine	7.48	0.03	−0.16
Eastern Grassland & Shrubland	1.24	0.00	–
WCHF: WESTERN CENTRAL HARDWOODS: 29, 32, 33, 36, 37, 38, 39, 40, 72			

(continued)

Table 1.1 (continued)

Regions, ecoregions, and major vegetation	TFPA	L/O	COR
Central Midwest Mesic Forest	1.75	0.02	0.44
Central Midwest Oak Woodland & Savanna	1.85	0.01	0.782
Laurentian-Acadian Mesic Hardwood-Conifer	2.15	0.04	0.50
Laurentian-Acadian Pine-Hardwood	6.97	0.01	0.31
Southern & South-Central Oak Pine	7.48	0.03	−0.16
Great Plains Forest & Woodland	1.88	0.15	0.26
Central Grassland & Shrubland	1.09	0.30	0.66
RCKS: ROCKIES: 15, 16, 17, 19, 2, 41			
Central Rocky Mtn. Dry Lower Montane-Foothill Forest	6.77	1.46	0.89
Central Rocky Mtn. Mesic Lower Montane Forest	5.68	1.00	0.95
Rocky Mtn. Subalpine-High Montane Forest	2.87	2.58	0.84
Southern Rocky Mtn. Lower Montane Forest	10.87	2.40	0.70
SWF: SOUTHWESTERN FORESTS: 22, 23, 24, 25, 26, 79, 81			
Rocky Mtn. Forest & Woodland	10.87	2.40	0.68
Southern Rocky Mtn. Lower Montane Forest	10.87	2.40	0.68
Western Pinyon-Juniper Woodland & Scrub	4.27	2.56	0.74
Southern Rocky Mtn-Colorado Plateau Pinyon-Juniper	4.27	2.56	0.74
Western Interior Chaparral	3.33	0.96	0.57
NACMZ: CALIFORNIA MEDITERRANEAN: 5, 6, 7, 8, 85			
Californian Forest & Woodland	10.94	0.05	0.84
Californian Scrub & Grassland	11.93	0.06	0.86
Californian Chaparral	11.93	0.06	0.86
Vancouverian Forest	8.97	0.93	0.94
PNW: PACIFIC NORTHWEST: 1, 2, 3, 4, 9, 11, 77, 78			
Vancouverian Forest	5.98	0.75	0.96
Southern Vancouverian Dry Foothill Forest	8.59	0.38	0.92
Southern Vancouverian Montane-Foothill Forest	9.11	0.90	0.94
Vancouverian Coastal Rainforest	3.75	0.34	0.95
Vancouverian Subalpine-High Montane Forest	7.58	2.82	0.84

Chap. 7), Rockies (RCKS; Chap. 8), North American Mediterranean Climate Zone (NAMCZ; Chap. 9), Pacific Northwest (PNW; Chap. 10), and Southwestern Forests (SWF; Chap. 11). The final chapter (Chap. 12) provides a comprehensive discussion of managing for resilience under changing climates and fire regimes in USA forests.

Over the past 30 years land area burned by wildfires has increased fourfold (Vose et al. 2018) and federal wildfire suppression costs have escalated accordingly. This increased wildfire risk is due to warming temperatures and extreme drought, along with fuel accumulation from decades of active fire suppression or exclusion of human ignitions. Predicted increases in drought duration and frequency, along with greater risk of other disturbances (e.g., insect pest outbreaks; wind blowdowns), further add to fuel accumulation. Accordingly, models suggest the *severity* (a measure of impact estimated from plant biomass consumed or killed; Keeley 2006) and area of wildfires might increase 2–6 times by mid-century in some western forest types and boreal forests of Alaska and the northern GL-NEF (Vose et al. 2018). In other regions, such as the SCPU, future fire seasons may be lengthened and prescribed burn days reduced, increasing the risk of wildfire (Chaps. 3 and 12). These changing fire regimes may, in turn, alter ecosystem services such as carbon storage, water resources, biodiversity, and wildlife habitat.

Climatic gradients of temperature and precipitation, modified by elevation, topography, and soil moisture retention capacity, strongly influence the distribution of ecoregions and forest types. These gradients also influence the amount, type, moisture content, and temporal and spatial distribution of fuels that affect fire regimes and area burned within and across the regions considered in this book (Fig. 1.1). Temperatures generally decrease from south to north latitudes, and decrease locally with increasing elevation. Based on long-term climate normals (1981–2010), average annual minimum temperatures reach as low as −6 °C in the most northerly latitudes of the contiguous USA and −12 °C at the greatest elevations (NOAA 2020). Long-term average maximum temperatures exceed 38 °C in the most southerly latitudes and southwestern desert (NOAA 2020). Precipitation generally decreases from east to west, but is modified by physiographic features such as mountain ranges and oceans that affect local weather patterns. Average annual precipitation ranges from <13 cm in parts of the SWF, to >500 cm along the PNW coast. Average monthly precipitation during the growing season (May–October) over the last 5 years (2015–2019) ranged from a high of 15.9 cm/mo in Florida, northward to around 10.2 cm/mo in the GL-NEF (NOAA 2020). Westward, precipitation between May and October reached as low as 1.8 cm/mo for Nevada (SWF). The chapters in this book cover a broad range of this climate variability. Moving from the southeast, chapter regions lie within the Subtropical Division (SCP(U,F)), PDMT), Hot Continental Division and Mountains (EBA, GL-NEF), Warm Continental Division (GL-NEF), and Prairie Division (WCHF) of the Humid Temperate Domain (Bailey 2014). In the Intermountain West, regions include the Tropical/Subtropical Desert, along with the Tropical/Subtropical and Temperate Steppe and associated mountains (SWF, RCKS) of the Dry Domain (Bailey 2014). Farthest west, along the Pacific coast, they include the Mediterranean Division and Mountains to the south (NAMCZ), northward through the Marine and Warm Continental Regime Mountains of the Humid Temperate Domain (Bailey 2014).

The timing and frequency of meteorological droughts (low precipitation) and periods when evapotranspiration exceeds precipitation are main drivers of fire frequency and severity across regions considered in this book. Historically, frequent, less severe fires occurred in forest types or ecoregions with pronounced dry seasons or growing season droughts (NAMCZ, Chap. 9; PNW, Chap. 10), especially where high productivity leads to rapid accumulation of fuels (SCPU, Chap. 3; SWF, Chap. 11). At the other end of the spectrum, episodic or cyclic droughts triggered moderate to high-severity or large-area fires (depending on drought frequency, drought intensity, and the rates and types of fuels accumulated) in forest types or ecoregions without pronounced dry seasons and where productivity is sufficient to accumulate enough fuels to carry fire. For example, infrequent large fires are associated with periodic droughts in the WCHF (Chap. 5), GL-NEF (Chap. 7), and bottomland hardwood forests of the SCPF (Chap. 6), especially following windstorms that increase downed fuels. In the northern RCKS, where fuels are abundant, droughts can trigger fires, and the failure of monsoons to bring summer precipitation can lead to large fires in the southern RCKS (Chap. 8). Across regions, predicted changes in the frequency or duration of droughts will certainly have consequences for future fire regimes.

The frequency and timing of lightning strikes, especially with respect to dry periods and fuel loads, affect the frequency, *intensity* (the rate of heat energy released by the fire) (Lippincott 2000; Brooks et al. 2004), and extent of *natural* (lightning-caused) fire within and across forest types, ecoregions, and regions considered in this book. Based on data from 2009 to 2018 (Vaisala 2018), average annual cloud to ground lightning flash density is highest in the SCP, especially in Florida and along the Gulf coast, and in the WCHF, along the prairie-forest margin. Areas in these regions average ≥12 lightning flashes/km^2/year (Vaisala 2018). In general, lightning density decreases from the southeast and south-central USA to the north and west, such that the GL-NEF, NAMCZ, and PNW regions average <1 flash/km^2 per year (Vaisala 2018). Seasonality of lightning strikes and lightning-ignited wildfires also varies among regions (Fig. 1.2). July is the peak month for lightning in most regions, including the northeastern-most region, the GL-NEF; in contrast, May and June are peak lightning months in the PNW. In general, eastern regions show weaker lightning seasonality, especially the SCP and WCHF where lightning strike densities are high. Western regions have stronger lightning seasonality, especially the PNW, where lightning strike densities are low.

Historically, lightning was a prime ignition source for fires in some forest types and locations, such as pine ecosystems of the SCPU (Chap. 3) and upper montane forests of the NAMCZ (Chap. 9). In landscapes with flat topography and continuous, dry forest types with long-needled and grassy fuels that facilitated fire spread, such as pine savannas of the SCPU, a single lightning strike could ignite large fires that spread across the landscape. Conversely, more rugged topography or natural fire breaks such as rivers (SCPF, Chap. 6; WCHF, Chap. 5) limit fire extent. Further, where fuels are moist during months when thunderstorms are common (e.g., EBA, GL-NEF), lightning flash density does not always correspond with the number or timing of lightning-ignited fires. Thus, at the ecoregion or region scale, lightning flash density, and even wildfire density, may not be a complete metric for historical fire frequencies.

Historically and currently, lightning was not the only, or even the primary source of total fire ignitions. Table 1.1 provides an overview of the current state of wildfires across the country based on fire occurrence data (1992–2011), gathered as part of the National Fire Program Analysis, and integrated fire reports from federal, state and local fire organizations (Short 2013). The regions can be loosely grouped into four classes (Fig. 1.3) based on the total fire density (number of wildfires per area; TFPA), ratio of lightning fires to fires from other causes (L/O) (excluding prescribed fire, unless escaped), and the similarity, or correlation (COR) in seasonality of the lightning fires compared to the other causes (Table 1.1). The first class, including

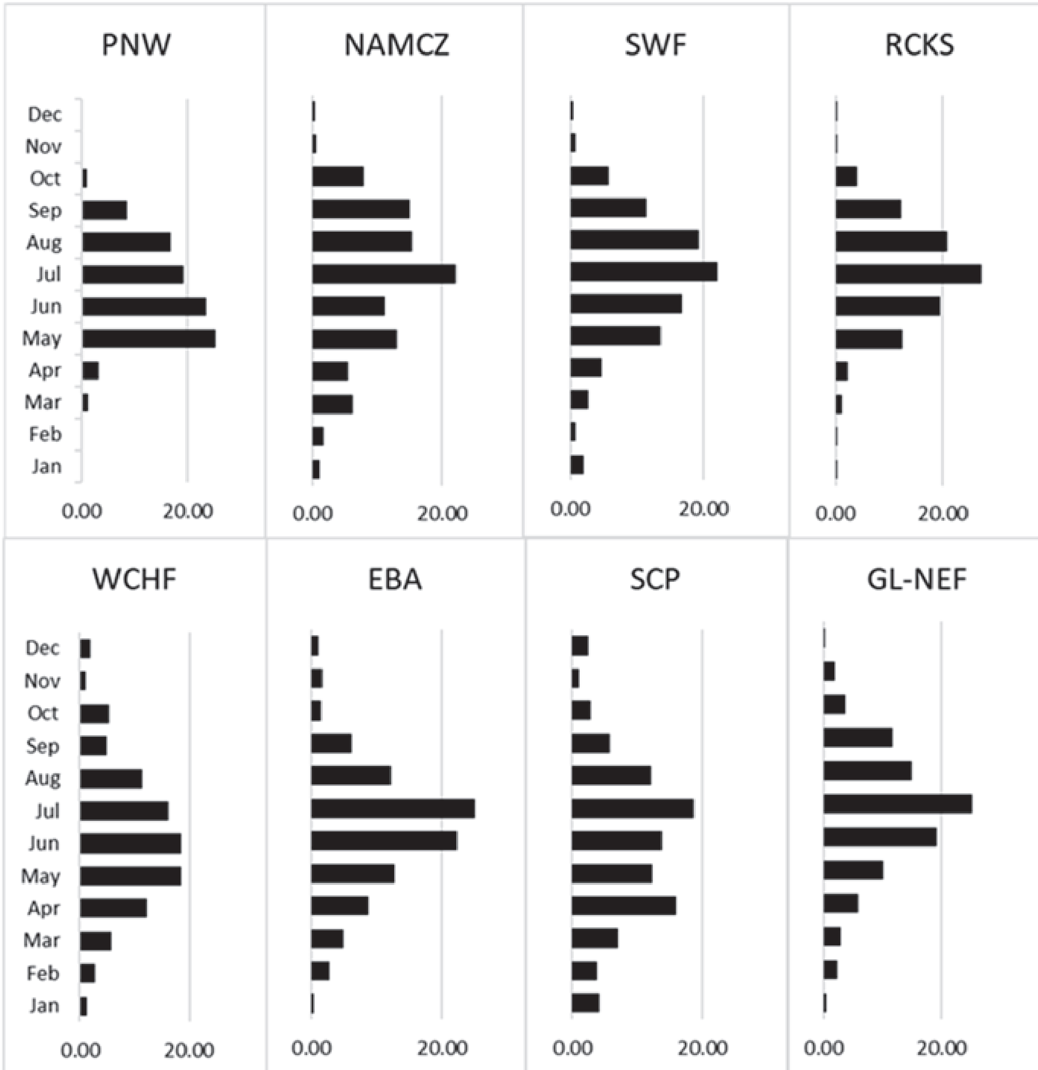

Fig. 1.2 Mean frequencies of lightning strikes per month within each region (2015–2019). (Data source: Vaisala National Lightning Detection Network (https://www1.ncdc.noaa.gov/pub/data/swdi/database-csv/v2/))

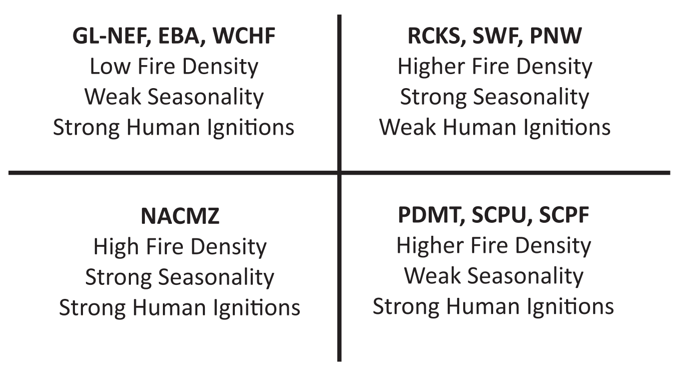

Fig. 1.3 Wildfire categories based on fire density, ratio of lightning fires to fires from other causes (excluding prescribed burns unless escaped), and the similarity in seasonality of lightning fires compared to other causes (see Table 1.1)

the GL-NEF, EBA, and WCHF reflects low fire density (regional TFPA means 2.84–3.16), very low L/O (regional means of 0.03–0.09), and a weak positive relationship between the timing of lightning and other wildfires (regional COR means 0.38–0.62). The low L/O ratio indicates fires in these regions are predominantly human-caused (also see Greenberg et al. 2015a, Table 1.6). The timing of lightning fires tends to be constrained by seasonal factors (fuels are generally moist and less ignitable during "lightning season" when summer thunderstorms are usually accompanied by rain), and COR indicates the degree to which these climatic factors may also be constraining other ignitions. The weak positive relationship for this class indicates some degree of seasonal similarity between lightning fire season and that of other ignitions. The second class consists of the RCKS, SWF, and PNW regions, and is characterized by slightly higher fire densities (TFPA 6.35–7.01), lightning as the dominant ignition source (L/O 1.04–2.18), and strong correlation between the timing of lightning and other ignitions (COR 0.68–0.92) due to seasonal constraints on fuel ignitibility after spring snow melt and "green up". The third class, including the PDMT, SCPU, and SCPF regions, is differentiated by higher fire density (TFPA 10.70–13.04), a predominance of human-caused fires (L/O 0.14–0.26), and little relationship between the timing of lightning and other fires (COR −0.31−0.14). For this class, human-caused fires dominate despite high lightning flash densities, and human-caused fires occur in all months, with little relation to the highly seasonal lightning fires. The final class consists of the NACMZ region, and is characterized by a high fire density (TFPA 11.09), strong influence of human-caused fires (L/O 0.28), and a strong, climate-constrained seasonal linkage between lightning and other fires (COR 0.88). We again emphasize that fire density is not necessarily reflective of area burned; today, most wildfires are rapidly extinguished, burning only a fraction of the landscape that might historically have burned in unfragmented ecosystems where topography and fuels permitted.

The four general classes (Fig. 1.3) are based on regional means which reflect the interplay of lightning strike density and timing, the relative strength of human ignitions, and fire density among vegetation types within the regions. We illustrate this interplay by comparing Oak-pine (*Quercus-Pinus*) forests (Southern & South-Central Oak-Pine; SSCOPF) of the PDMT, which has high lightning strike density, with low-mid elevation conifer forests (Southern Vancouverian Montane Foothills Forest; SVMFF) of the PNW, which has the lowest lightning strike density among regions (Table 1.1). As expected from the comparative lightning strike densities, TFPA is higher for SSCOPF (13.66) than SVMFF (9.11). However, the majority of fires in SSCOPF are not lightning-caused (L/O 0.02), while fires are more evenly distributed between lightning and other causes in SVMFF (L/O 0.90). The monthly distribution of fires by cause for each of these systems is also quite different (Fig. 1.4). The distribution of lightning fires and other ignition sources coincide over seasons (COR 0.94) for SVMFF. For SSCOPF, lightning fires and other ignitions peak at different times of the year (COR −0.04) and the predominance of other ignitions in suggests a shift in the seasonal timing of most fires away from the "natural" lightning-caused seasons.

Complex interactions between natural and human causes of fire, the historical forest conditions these interactions created, and changing variation in fire regimes

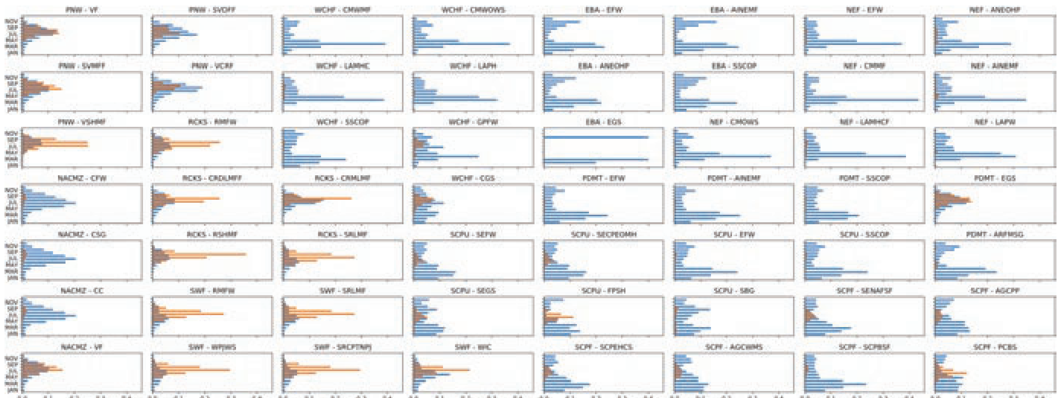

Fig. 1.4 Fraction of total wildfires due to lightning (orange) versus human causes (blue). Graphs are arranged quasi geographically, i.e., the PNW is in the upper left and the SCP is in the lower right, to illustrate the dominance of lightning-caused fires in the west and human-caused wildfires in the east. Wildfire data includes 1992–2011 (Short 2013)

(and thus forest conditions and fuels) have highlighted the need to consider the role of fire in forest management. Recent policies mandate that National Forests sustain or restore "ecological integrity" to forests, and manage them within the "historical range of variation" of natural disturbances, including fire (USFS 2012). Other federal land management agencies within the US Department of Interior (Dale 2006), state natural resource agencies, and conservation groups such as land trusts and conservancies, also aim to manage lands within the context of historical disturbance regimes and in consideration of safeguarding biodiversity, human safety, protection of property in an expanding wildland-urban interface, and other forest values. For example, the National Fire Plan and subsequent forest legislation (HFRA 2003) provides guidance for a coordinated wildland fire response by the US Forest Service and many land management agencies within the US Department of Interior. These documents focus on improving and coordinating fire suppression efforts among agencies, but also recognize the important role of fire in maintaining process and function in fire-dependent ecosystems (Dale 2006). Below, we briefly review scientific approaches to reconstructing short- and long-term fire histories and regimes, and the historical drivers of these regimes, across forest types and ecoregions covered in this book.

1.2 Fire History and Adaptations

1.2.1 Reconstructing Fire History: The Science and the Art

Reconstructing fire histories and long-term fire regimes requires an integrated, "multi-proxy" approach that combines physical evidence with inference based on past climate shifts, vegetation, and the population levels and cultural practices of

Native Americans and Euro-American settlers (Conedera et al. 2009). Physical evidence of multi-centennial fire history can be provided by fire scars – healed tissue of fire-caused injuries near the base of trees – dated by annual tree-rings. Tree-rings are typically crossdated with older trees, or decay-resistant snags, logs, and stumps (e.g., Fulé et al. 2012); rarely subfossil fire-scarred woody material from peat bogs or buried soils have been used to extend fire histories (Chambers et al. 1997; Conedera et al. 2009). Studies of long lived tree species, such as giant sequoia (*Sequoiadendron giganteum*) in the California Sierra Nevada, have shown linkages between fire frequency and climatic fluctuations over a 2000-year period (Swetnam 1993). Radiocarbon dating of charcoal layers within the stratigraphy of sedimentary profiles in water bodies or, less commonly, soil, assess fire regimes by detecting fire intervals over millennia with coarser temporal resolution (Couillard et al. 2013; Grissino-Mayer 2015). In addition, paleoecology, archaeology, and original (pre-settlement) land survey data provide indirect evidence of historical fire regimes and their linkages to past climate shifts, vegetation, and the potential influence of humans (Delcourt and Delcourt 2004; Nowacki and Abrams 2015). Indirect evidence of fire history and fire dependence also is provided by the forests themselves: plant-soil-climate interactions, plant adaptations to fire, regeneration ecology, and forest dynamics including species composition, forest structure, and stand age structure, are critical in "reading" clues about fire history and fire dependence of different forest types. In sum, determining fire histories and regimes, and discerning the relative influence of natural drivers (e.g., climate and lightning-caused ignitions) versus intentional use of fire by humans, is not a precise science, but rather a combination of physical evidence, indirect evidence, and expert judgement.

As modeled by Guyette et al. (2012), coarse-scale historical fire frequency broadly follows precipitation and temperature gradients among regions: mean fire return intervals (FRIs) range from <2.01 years in parts of the SCP to >1000 years in desert regions of the SWF and cool-moist high elevation sites of the PNW (Fig. 1.5). At the ecoregional scale, mean FRIs range from 4.3 years (2.1–5.8 years among ecoregions) for the SCP to 57.6 years (14.4–199.7 years among ecoregions) for the PNW (Table 1.2). High variability in mean FRI among ecoregions within the PNW and RCKS and low variability among ecoregions within the SCP (Table 1.2) appear related to the differing elevation and precipitation gradients within these regions. Certainly, local factors such as ignitions or edaphic controls (e.g., substrate, water) can further modify fire probability, creating finer-scale complexity for specific sites. Overall, spatial scale must be considered when describing fire frequencies or FRIs for particular forest types or ecoregions.

As illustrated by the large standard deviations and differences between minimums and maximums (Table 1.2), there is wide variation in FRIs at the ecoregion scale. This variation may reflect local-scale differences in fire frequencies or how we measure them. For example, FRI for a given region may be considered "annual" if yearly fires were recorded at a regional scale, when in fact any given land unit within that region may have burned much less frequently (Falk et al. 2007; Chap. 5). Similarly, fire scar, charcoal, pollen, or other records may reveal fire frequencies at a local scale but may, or may not, apply to a broader landscape or ecoregion.

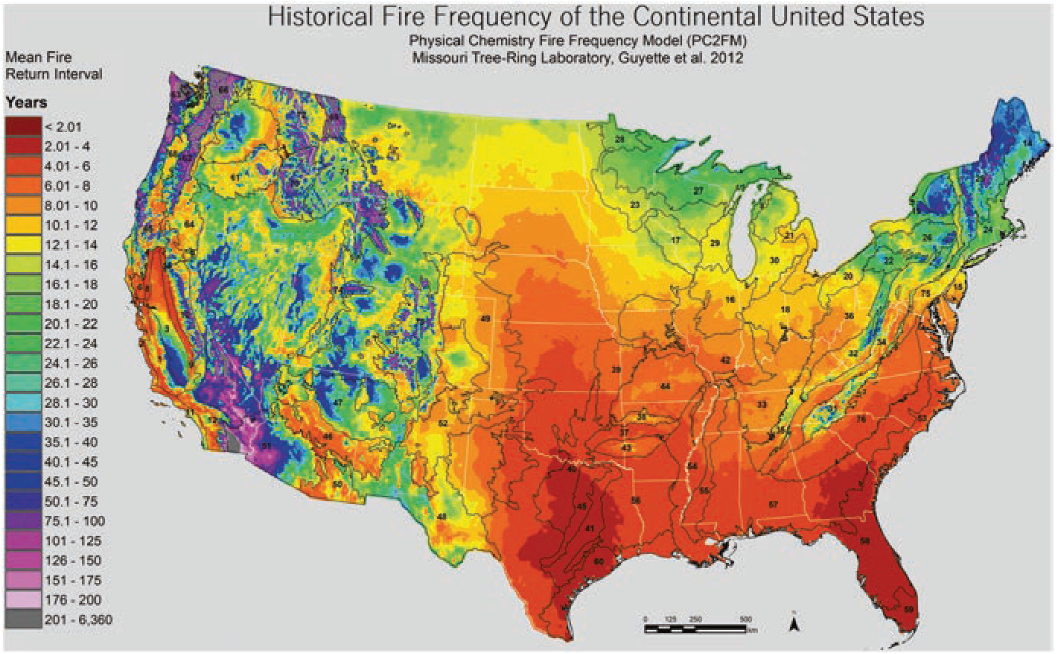

Fig. 1.5 Physical Chemistry Fire Frequency Model of historical mean fire return intervals in forested ecoregions considered in this book. Numbers in ecoregions refer to Table 1.2 below

Table 1.2 Means, standard deviations, minimums, and maximums of fire return intervals in forested ecoregions covered in this book. Map code corresponds to ecoregions in Fig. 1.5

		Mean fire return interval			
MAP CODE		MEAN	STD	MIN	MAX
	NAMCZ				
1	Central California Coast Ranges	15.8	13.2	4	64
2	Central California Coast	6.7	2.0	4	20
3	Great Valley	18.7	15.1	3	63
4	Klamath Mtns.	7.1	2.6	4	21
5	Modoc Plateau	17.3	6.0	8	38
6	N. California Coast Ranges	5.8	2.6	3	26
7	N. California Coast	6.1	2.0	4	17
8	N. California Interior Coast Ranges	4.8	0.9	3	11
9	Sierra Nevada Foothills	6.8	4.4	3	44
10	Sierra Nevada	32.4	36.8	4	508
11	S. California Coast	9.8	3.9	4	33
12	S. California Mtns. & Valleys	24.1	37.7	4	257
13	S. Cascades	27.0	16.4	8	62
	GL-NEF				
14	Acadian Plains and Hills	30.0	4.2	19	55
15	Atlantic Coastal Pine Barrens	12.3	3.4	8	22
16	Central Corn Belt Plains	10.2	1.4	8	14
17	Driftless Area	14.2	1.2	11	19

(continued)

Table 1.2 (continued)

		Mean fire return interval			
MAP CODE		MEAN	STD	MIN	MAX
18	E. Corn Belt Plains	10.3	0.9	7	14
19	E. Great Lakes Lowlands	17.8	5.1	10	56
20	Erie Drift Plain	14.6	4.2	9	34
21	Huron/Erie Lake Plains	10.8	1.0	9	16
22	N. Central Appalachians	22.6	5.3	11	48
23	N. Central Hardwood Forests	14.8	1.7	11	22
24	Northeastern Coastal Zone	18.3	2.9	12	30
25	Northeastern Highlands	37.1	22.4	12	1302
26	N. Allegheny Plateau	20.2	5.5	9	61
27	N. Lakes and Forests	18.7	3.6	11	42
28	N. Minnesota Wetlands	17.4	1.3	14	21
29	Southeastern WI Till Plains	13.1	0.7	11	17
30	S. Michigan/N. Indiana Drift Plains	12.2	1.0	10	16
	EBA				
31	Blue Ridge	15.2	9.6	6	142
32	Central Appalachians	14.7	7.9	6	71
33	Interior Plateau	8.3	0.9	6	13
34	Ridge and Valley	11.2	5.5	5	58
35	Southwestern Appalachians	9.7	3.1	5	22
36	W. Allegheny Plateau	10.1	2.5	6	26
	WCHF				
37	Arkansas Valley	5.1	0.8	4	11
38	Boston Mtns.	7.5	1.6	5	14
39	Central Irregular Plains	7.4	1.4	4	10
40	Cross Timbers	3.6	0.7	3	6
41	E. Central Texas Plains	3.2	0.4	2	4
42	Interior River Valleys and Hills	8.0	1.0	6	11
43	Ouachita Mtns.	6.0	1.3	4	15
44	Ozark Highlands	6.8	0.8	5	9
45	Texas Blackland Prairies	3.2	0.4	2	4
	SWF				
46	Arizona/New Mexico Mtns.	9.3	4.0	4	181
47	Arizona/New Mexico Plateau	22.2	9.7	6	68
48	Chihuahuan Deserts	15.2	5.3	6	35
49	High Plains	8.9	1.8	5	15
50	Madrean Archipelago	9.7	3.4	4	44
51	Sonoran Basin and Range	69.3	64.7	5	317
52	Southwestern Tablelands	8.7	3.1	4	22
	SCPU				
53	Middle Atlantic Coastal Plain	5.8	1.5	3	11
54	Mississippi Alluvial Plain	5.3	0.7	4	8

(continued)

Table 1.2 (continued)

		Mean fire return interval			
MAP CODE		MEAN	STD	MIN	MAX
55	Mississippi Valley Loess Plains	5.9	1.0	4	8
56	S. Central Plains	4.2	0.7	3	6
57	Southeastern Plains	4.8	1.2	3	10
58	S. Coastal Plain	3.0	0.9	2	6
59	S. Florida Coastal Plain	2.1	0.3	2	3
60	W. Gulf Coastal Plain	3.6	0.7	2	5
	PNW				
61	Blue Mtns.	17.7	20.5	7	443
62	Cascades	89.9	184.3	4	7216
63	Coast Range	76.2	107.8	4	2005
64	E. Cascades Slopes and Foothills	15.4	16.3	6	330
65	Klamath Mtns./California High N. Coast Range	27.2	33.2	4	342
66	N. Cascades	199.7	287.9	7	7385
67	Puget Lowland	20.3	14.2	8	256
68	Willamette Valley	14.4	6.3	9	67
	RCKS				
69	Canadian Rockies	120.7	140.6	10	1861
70	Idaho Batholith	42.4	37.5	7	441
71	Middle Rockies	37.9	47.0	8	1327
72	N. Rockies	34.2	48.9	6	1223
73	S. Rockies	27.8	34.7	7	510
74	Wasatch and Uinta Mtns.	24.0	21.0	7	232
	PDMT				
75	N. Piedmont	10.4	2.3	7	22
76	Piedmont	5.7	1.2	3	16

Regional networks of fire scar data are advancing examination of low and mixed-severity fire histories across multiple spatial scales (Falk et al. 2011). Fire scars cannot address frequencies of low-intensity groundfires that don't damage trees or high-severity burns in which most trees are killed, but can be paired with dead and living tree age data to infer stand-replacing burns based on new cohorts developing near the timing when an older cohort died (Falk et al. 2011). All trees may not be scarred in every fire event, allowing for estimates of fire frequency or area burned in each fire over time (Falk et al. 2011). Because pines generally record fire scars better than hardwoods, fire history ecologists in hardwood ecoregions are likely to select pine or mixed pine-hardwood stands in a hardwood matrix (e.g., Aldrich et al. 2014; Saladyga 2017) at the risk of overestimating fire frequencies or making incorrect inferences regarding fire regimes on the broader landscape. For example, yellow pine or mixed pine-hardwood forests in the EBA, PDMT, and WCHF regions may have established and been perpetuated by frequent past burning (Chaps. 2, 4 and 5), and typically occur on lower quality sites in which fuels and edaphic conditions may be more conducive to frequent burns than higher-quality hardwood sites (e.g., Saladyga 2017). Finally, regardless of fire history time periods or the spatial scale covered, neither fire scar nor charcoal history can, by themselves, determine whether fires were ignited by lightning or humans; most chapters discuss how both factors affect FRIs, and use of the term may vary accordingly.

1.2.2 Fire Regimes: Variability in Frequency and Severity Across USA Forests

The term *fire regime* refers to long-term fire histories, including fire type and severity, spatial extent and pattern, and average frequency and season, that were characteristic of different vegetation types (Chap. 12). Historically, fire varied widely among USA forest types in average frequency, type, severity, and ecological response (Schmidt et al. 2002). Fire regimes differed among forest types distributed across topographic and edaphic gradients within ecoregions as well. For example, within the NAMCZ, historic fire regimes vary from high-severity fires in sclerophyllous shrublands (where obligate seeding, soil seed-banking, and serotiny contribute to a persistent plant community), to a high frequency, low-severity fire regime in yellow pine and mixed conifer forest types (Chap. 9). In the EBA, frequent or moderately frequent, low-severity fires burned in upland mixed-oak forests, but FRIs were long in high-elevation spruce (*Picea*)-fir (*Abies*) forests and mesic cove hardwood forests in topographically sheltered positions (Chap. 4). Even within forest types, characteristic FRIs were variable, leading to spatially and temporally heterogeneous structure and composition.

Throughout the USA, frequent, low-intensity fires were characteristic of many forest types; examples include longleaf pine (*P. palustris*) forests and slash pine (*P. elliottii*) savannas (Huffman et al. 2004) in the SCPU; shortleaf pine (*P. echinata*) forests throughout the SCPU, PDMT, EBA, and WCHF (Stambaugh and Guyette 2006), and ponderosa pine (*P. ponderosa*) forests in the SWF, RCKS, and PNW regions (Sackett et al. 1996; Chap. 10). This fire regime generally maintained an open grass/herbaceous-dominated understory and promoted uneven-age pine regeneration by killing encroaching shade-tolerant conifer or hardwood competition and creating suitable seedbed conditions for pine regeneration. In contrast, episodic high-severity fires were characteristic of forest types such as multi-decadal FRIs in peninsular Florida sand pine (*P. clausa clausa*) scrub (Freeman and Kobziar 2011), jack pine (*P. banksiana*) forests of the GL-NEF (Spaulding and Rothstein 2009), lodgepole pine (*P. contorta*) of the RCKS, and multi-century fires in cool, moist Sitka spruce (*Picea sitchensis*) and Douglas-fir (*Pseudotsuga menziesii*) forests of the RCKS (Chap. 8) and Pacific coastal range (Chap. 10). Recovery mechanisms after stand-replacing fires in these forest types include windborn seeds from nearby refugia, which promote slow establishment over time, and serotinous cones that open and shed abundant seed, resulting in episodic, even-age regeneration.

Infrequent or moderately frequent high-severity fires in the GL-NEF initiated early successional spruce and red- (*P. resinosa*) and white- (*P. strobus*) pine forests or birch-aspen (*Betula-Populus*)-mixed wood forests that eventually succeeded to northern hardwoods-hemlock (*Tsuga canadensis*) and spruce during long intervals between fires (Chap. 7). In the upland mixed-oak or oak-hickory (*Quercus-Carya*) hardwood forests of the EBA, PDMT, and WCHF regions, moderately frequent, low-severity fires historically played a role in keeping forest *mesophication* at bay by killing more fire-sensitive species such as red maple (*Acer rubrum*), and maintaining understory light conditions conducive to oak regeneration (Abrams 1992). Similarly, current trends in fire-excluded western forests indicate that fire prevented shade-tolerant trees such as grand fir (*Abies grandis*) from replacing ponderosa pine on moist to wet sites in the PNW (e.g., Mershel et al. 2014), or Douglas-fir from invading low elevation ponderosa pine forests in the RCKS (Chap. 8). Thus, many fire-maintained forest types are technically mid-successional, in that they eventually would be – and are being, in many cases – replaced by more fire-sensitive hardwood or shade-tolerant conifer species. These forest types are *fire-dependent* in that community composition and structure would fundamentally change in the absence of their associated fire regime.

1.2.3 Fire-Adapted Plant Traits: Resistance, Recovery, and Regeneration

In fire prone environments, characteristic plant species exhibit traits that enable them to survive or regenerate after fire (Keeley et al. 2011). Fire-adapted "resistance, recovery, or regeneration" traits (Gagnon et al. 2010; Thomas-Van Gundy and Nowacki 2013; Pausas 2015; Kidd and Varner 2019) are often suited to – and in some cases even promote – particular fire regimes, and likely reflect evolutionary pressure over millennia (Keeley et al. 2011; He et al. 2012). Fire *resistance* traits such as thick bark to protect from heat injury, and self-pruning branches that prevent fire from reaching tree crowns, are associated with trees such as longleaf pine in the southeast (Chap. 3), and ponderosa pine in the west (Chaps. 8, 11 and 12). In these forests, fallen, highly flammable pine needles and rapid postfire recovery of a continuous, grassy-herbaceous understory provide fuels conducive to frequent, low-severity fires that create bare mineral soil seedbed conditions for pine regeneration from seed. Similarly, highly flammable litter shed by species such as Oregon white oak (*Quercus garryana*) and California black oak (*Q. kelloggii*) fuels fast-spreading, but low to moderate intensity, surface fires in the NACMZ and PNW (Engber and Varner 2012). In contrast, tree species such as sand pine in peninsular Florida, jack pine and balsam fir (*Abies balsamea*) in the GL-NEF, and lodgepole pine in the RCKS that evolved with infrequent, stand-replacing fire are typically thin-barked; sand and jack pines also retain low branches that serve as "ladder fuel" for fire to reach the tree canopy. Hot fires cause serotinous cones to open, shedding abundant seed onto a recently burned forest floor conducive to pine regeneration, virtually assuring the species' persistence (Freeman and Kobziar 2011). Long intervals between stand-replacing fires allow for heavy buildup of fuels, often including dense, highly flammable shrubs or scrubby tree species (e.g., scrub oaks in sand pine scrub (Freeman and Kobziar 2011)) that promote future crown fires under suitable weather and fuel conditions.

Plant germination and sprouting traits provide for recovery after fire. Some species such as rabbit bells (*Crotalaria rotundifolia*) and narrow-leaved bush clover (*Lespedeza angustifolia*) in longleaf pine forests regenerate after fire-generated heat or smoke stimulates germination from long lived soil seedbanks (Wiggers et al. 2017). Other species have windblown seeds that disperse into recently burned forests, such as white spruce (*Picea glauca*) (Gärtner et al. 2011) and paper birch (*Betula papyrifera*) (Ilisson and Chen 2009) in Northeastern and boreal forests. Many plant species flower and fruit soon after fire, producing new seed to recolonize burned areas; these include wiregrass (*Aristida stricta*) (Uchytil 1992), saw palmetto (*Serenoa repens*), and scrub palmetto (*Sabal etonia*) (Abrahamson 1999) in SCPU pine ecosystems, and snowbrush (*Ceanothus velutinus*) in the PNW. Other fire-adapted recovery strategies by woody species include epicormic sprouting from live buds beneath the bark of damaged tree boles, or resprouting from basal shoots, lignotubers, or underground roots or rhizomes (e.g., scrub oaks in California chaparral and Florida sand pine scrub) (Chaps. 3 and 9). Some species, such as quaking aspen (*Populus tremuloides*) in the GL-NEF, western USA, and Canada vigorously spread clonally, especially following the death of aboveground stems (Mitton and Grant 1996).

Although some plant species are strictly fire-dependent in that they could not persist (without human intervention) in the absence of fire, many recovery and regeneration strategies also allow a species to persist after other natural (e.g., wind blowdowns, ice storms; Greenberg et al. 2015a) or anthropogenic (e.g., timber harvests) disturbances (e.g., Greenberg et al. 1995a). Most chapters in this book use the term *fire-dependent* to describe how ecosystem-specific fire regimes maintain characteristic composition and structure of specific forest types, rather than implying that most individual species could not persist without fire. For example, the prevalence of eastern broadleaf oak and oak-hickory forests expanded with increasing use of fire as a management tool by Native Americans and Euro-American settlers (Delcourt and Delcourt 2004), but oaks do not require fire to regenerate *per se* (Chap. 7). On the other hand, presence of even a few trees of species with fire-specific traits, such as Table Mountain pine (*P. pungens*), in which cones open after fires, suggests that fire may have historically occurred on that site. Further, among forest types and ecosystems, a preponderance of species having postfire persistence strategies that "match" specific fire regimes within their geographic range suggests that fire was an important evolutionary driver of these traits (Gagnon et al. 2010; Keeley et al. 2011; Pausas 2015).

1.3 Examining the Influence of Humans on Fire Regimes

The long-term influence of humans on fire history must be inferred from archaeological studies, charcoal records, or pollen records that show evidence of changing Native American population densities and corresponding changes in fire frequencies (e.g., Guyette et al. 2006). Descriptions by early explorers and knowledge of cultural practices by Native Americans and Euro-American settlers are also important (Greenberg et al. 2015b). In the eastern USA, early explorers describe what is now termed *humanized pyroscapes* throughout much of the SCPU, PDMT, and EBA (e.g., Nowacki and Abrams 2008; Grissino-Mayer 2015). In the SCPU and drier sites of the PDMT and EBA, frequent burning by Native Americans altered forest types and structure, creating and maintaining savannas, prairies, open woodlands, and yellow pine or pine-oak forests that would otherwise succeed to dense hardwood-dominated forests (Flatley et al. 2013). On other sites, burning by Native Americans shifted species composition of hardwood forests. For example, at Cliff Palace Pond on the Cumberland Plateau in Kentucky, Delcourt and Delcourt (2004) found that increases in charcoal influx and the proportion of large charcoal particles – indicators of increased fire frequency – coincided with Woodland-age occupation of the surrounding area. Forest composition on the surrounding upper hillslopes shifted from fire-intolerant tree species associated with cove or mixed mesophytic forest types, to fire-tolerant species, such as oaks, American chestnut (*Castanea dentata*), walnut (*Juglans*), and hickories (*Carya*) – even as the regional climate was becoming cooler and wetter (Delcourt and Delcourt 2004).

The relative contributions of climate and human activities to historical forest structure and composition vary across forest types and ecoregions. Nowacki and Abrams (2015) compared original land survey data on forest composition to predicted composition based on tree species' climatic, shade, and pyrogenicity associations, to examine the relative impacts of climate and early Euro-American settler disturbances on eastern USA forests. Their analysis found that intensive, widespread disturbance by Euro-American settlers – primarily burning – overrode climatic influence, increasing abundance of maple, aspen, and oak and substantially reducing abundance of conifers in the northern hardwood region. In the WCHF, frequent burning by early Euro-American settlers increased oak until the mid-twentieth century, when fire exclusion led to forest mesophication, including greater abundance of maple (Nowacki and Abrams 2015). In the western USA broadly (PNW, NAMCZ, SWF, RCKS), multi-proxy studies and modelling show climate, primarily temperature and drought, controlled fire frequency prior to Euro-American settlement (Brown and Hebda 2002; Marlon et al. 2012; but see Chap. 8). However, burning by Native Americans overrode the influence of climate alone at local sites with concentrated populations. For example, Brown and Hebda (2002) reported increased charcoal influx beginning 2000 ybp at several densely populated sites on southern Vancouver Island in Canada, despite a moist, cool climate where frequent fires would otherwise be unlikely. In the SWF, Native Americans used fire and coexisted with the fire regime over the landscape (Chap. 11). Beginning with

Euro-American settlement in 1800, and peaking between 1850 and 1870, humans were associated with changes in burning frequency and severity. Generally, there was a broad increase in biomass burning across the west (Marlon et al. 2012); however, in the SWF, fire was excluded from most forests (Chap. 11).

Historical data, such as land survey records, have been combined with current forest inventories to investigate the lingering effects of human activities on forest composition (Thompson et al. 2013). For example, in the GL-NEF (Maine to Pennsylvania), land survey records and forest inventories revealed a shift from greater abundance of late successional trees such as hemlock and beech (*Fagus grandifolia*) prior to Euro-American colonization, to early and mid-successional trees such as red maple, along with a more homogeneous forest composition and less correlation with local climate associated with historical clearing for agriculture (Thompson et al. 2013). In northern Minnesota, survey records combined with forest inventory data revealed declining landscape diversity and shifts from greater abundance of tamarack (*Larix*), spruce, and paper birch in presettlement forests where fires were the primary disturbance, to trees such as aspen and balsam fir after logging and fire suppression; some forest dominants, such as jack pine and red pine (*P. resinosa*), were largely replaced by aspen (Friedman and Reich 2005). Recent analysis of an expanded area (Minnesota, Wisconsin, Michigan) documented five classes of "lost" forests (e.g., tamarack (*Larix laricina*)-pine-birch-spruce-poplar (*Populus*), and cedar (*Thuja*)/juniper-pine-maple-hemlock) as well as "novel" forest types, such as ash-maple-cedar/juniper-birch (Goring et al. 2016). In the Missouri Ozarks, a combination of land survey and inventory data revealed densification of historically open, oak-dominated forests with periodic fire through increasing establishment of fire-sensitive trees such as eastern redcedar (*Juniperus virginiana*) and maples (Hanberry et al. 2014). In sum, multiple lines of evidence indicate that humans have been an important driver of fire regimes and associated shifts in forest composition in some ecosystems for thousands of years (e.g., Delcourt and Delcourt 2004; Nowacki and Abrams 2008, 2015; Greenberg et al. 2015b).

1.4 Today's Forests: A Legacy of the Past

1.4.1 Today's Forests Reflect Past and Present Land Uses and Natural Disturbances

In addition to historical, widespread use of fire to manage forests, other past and present human activities have altered forest structure directly at multiple scales. Land clearing and abandonment (as soil fertility declined) over millennia by Native Americans and (later) Euro-American settlers for home sites, villages, or agriculture has altered forest age-classes and seral stages (Greenberg et al. 2015b). Widespread logging beginning in the late 1800s altered forest age structure, fuels, fire frequencies, and fire intensities across much of the USA (e.g., Chap. 10). Historically and into the present, activities associated with railroads and agriculture provided major sources of ignition (e.g., Fusco et al. 2016). Since the early 1900s, active suppression of both human- and lightning-ignited fires (USNPS and USFS 2001; Dale 2006), along with changes to the historical pattern of frequent burning by Native Americans and Euro-American settlers, has led to fuel accumulation (e.g., ponderosa pine forests; Pyne 1996; Marlon et al. 2012) and denser forests (termed "*densification*"; e.g., Hanberry 2014; Hanberry et al. 2014). In some areas of the west (e.g., ponderosa pine, western yellow pine and mixed conifer), heavy livestock grazing has reduced grassy fuels leading to altered fire regimes and increased densities of small trees (Bock and Block 2005; Chap. 11). Where agricultural land was abandoned once fire suppression began, succession has led to forests with composition and structure that reflect a history of little to no fire (e.g. PDMT, Chap. 2; PNW, Chap. 10).

Effects of human activities on forest structure and changing fire regimes extend beyond those due to direct land use and management. Climate change attributed to heavy use of fossil fuels is causing warming summer temperatures and increased drought duration and frequency that is increasing the frequency, size, and severity of fires (Vose et al. 2018). Warming temperatures and earlier snowmelt associated with climate change have led to increases in the number of fires and area burned in western forests (Dennison et al. 2014). Non-native invasive plants have altered forest structure, fuels, and biological diversity (Brooks 2008), and entire species of forest trees have been decimated by introduced insects, fungi, and pathogens. Examples in eastern forests include American chestnut by the chestnut blight (*Cryphonectria parasitica)*, ash (*Fraxinus* spp.) by the emerald ash borer (*Agrilus planipennis)*, and hemlock by the hemlock wooly adelgid (*Adelges tsugae*); examples in western forests include oaks and other species by sudden oak death (*Phytophthora ramorum*) (Rizzo et al. 2002), and many five-needled pine species by white pine blister rust (*Cronartium ribicola*) (Lovett et al. 2016). Since World War II, the USA population has increased from 132.12 million (1940) to 309.32 million (2010) [US Census Bureau (www.census.gov)], resulting in forest loss, fragmentation, and urban sprawl.

Human activities have interacted with natural disturbances in shaping today's forests. In addition to lightning-ignited fires, episodic or recurring windstorms, ice storms, drought, native insect pests and pathogens, oak decline, floods, and landslides kill or damage trees at multiple scales, creating mosaics and gradients of structural conditions and canopy openness within stands and across large landscapes (Greenberg et al. 2015a). The occurrence, frequency, spatial extent, and severity of these natural disturbance types varies among and across ecoregions in relation to climate, latitude, topography, elevation, and soil type. Together with human-caused disturbances, they alter fire regimes and otherwise impact forest structure and composition. For example, extreme drought may precipitate outbreaks of southern pine beetles in eastern pine-dominated forests; drought and warmer temperatures associated with climate change are likely promoting the frequency, scale, elevation, and latitude of mountain pine beetle (*Dendroctonus ponderosae*) outbreaks in many pine forest types of the western USA (Creeden et al. 2014; Chap. 12). Heavy pine mortality may alter successional trajectories (Nowak et al. 2015), and increase vulnerability to wildfires through heavy fuel loading.

1.4.2 Forest Age Class and Stand Structure Provide Clues to Fire History or Past Land Use

More recent anthropogenic and natural disturbance history, including fire history, are reflected in forest composition, age, and structure. For example, an even-aged 50-year old stand of largely serotinous pine species, such as jack pine in the GL-NEF (Smirnova et al. 2008), sand pine in the SCPU (Drewa et al. 2008), or lodgepole pine in the RCKS (Axelson et al. 2009), could indicate a stand-replacing fire occurred around 50 years prior. Over time, such high-severity fires create a mosaic of diverse age-classes of even-aged stands across the landscape (Trammell et al. 2017). In presettlement coast redwood (*Sequoia sempervirens*) forests, human-caused fire, along with frequent, episodic flooding and slope failure resulted in relatively even-aged stands (Lorimer et al. 2009). Even-aged eastern hardwood forests also could indicate past stand-replacing fires, but widespread clearcutting in the early twentieth century is a more likely alternative given the low likelihood of high-severity wildfires in these moist, deciduous forest types (Van Lear and Harlow 2002). Even-aged stands of Virginia (*P. virginiana*), shortleaf, or loblolly (*P. taeda*) pine in the EBA, WCHF, PDMT, and SCPU, or white pine in New England often originate on abandoned agricultural fields and pastures as part of "old field succession" (Oosting 1942; Bormann 1953). In general though, recent history of low-severity fires leads to uneven-aged stands. For example, a stand of mature, uneven-aged shortleaf pine or mixed oak-shortleaf pine in the PDMT, EBA, or WCHF with no pine seedlings, saplings, or young trees would suggest that frequent, low-severity fires routinely created bare mineral soil seedbed conditions necessary for shortleaf pine regeneration, followed by a long absence of fire leading to leaf litter accumulation and lower light conditions not conducive to pine regeneration. Similarly, an abundance of young, fire-susceptible trees, such as hardwoods in mature longleaf pine-wiregrass forests in the SCPU, pinyon-juniper woodlands in the SWF, or Douglas-fir in western ponderosa pine forests would indicate a long absence of low-severity fire that would otherwise kill encroaching woody vegetation, thereby maintaining an open, savanna-like understory. Overall, the complex forest outcomes from multiple, interacting disturbances reflected in forest composition and structure present an additional challenge to restoring forests and fire regimes to historical levels.

1.4.3 Fire and Invasive Plants

The interaction of fire, climate change, and the spread of non-native invasive species is an increasing concern over all ecoregions covered in this book (Chap. 12). Fire can promote establishment or growth of invasive species such as princess tree (*Paulownia tomentosa*) over complex topography in Southern Appalachian forests (Kuppinger et al. 2010) and Russian thistle (*Salsola kali*) in ponderosa pine woodlands (Rice et al. 2008). Invasive grasses can increase fine fuel load and lead to hotter, longer, more spatially continuous, or more frequent fires, and greater fire susceptibility in forests across the ecoregions (D'Antonio and Vitousek 1992). For example, in SCPU pine sandhills and savannas, cogongrass (*Imperata cylindrica*) increased fire intensity. In southeastern Indiana, prescribed fires set in mixed hardwood forests invaded by Japanese stiltgrass (*Microstegium vimenium*) burned hotter and longer, resulting in lower survival of planted seedlings of native tree species, including white oak (*Q. alba*) and black oak (*Q. velutina*) (Flory et al. 2015). In California riparian woodlands, fire promoted dominance of giant reed (*Arundo donax*), which increased susceptibility to further wildfire (Coffman et al. 2010). And, in pinyon-juniper woodlands, increased fire frequency attributed to increasingly hot, dry conditions promotes invasion by annual grasses such as cheatgrass (*Bromus tectorum*) that in turn create continuous fuels, promoting more frequent and widespread burns that further inhibit tree establishment (Brooks et al. 2004; Chap. 9). Further, non-native invasives, including tall grasses, vines, and flammable trees, can shift the distribution of flammable biomass, creating ladder fuels that result in groundfires moving into the canopy (Brooks et al. 2004; Stocker and Hupp 2008). In such forests, non-native invasive species can create a positive feedback with fire; fire may not be an effective management tool, and future climates that promote more frequent fire may facilitate their spread. By contrast, in some fire-adapted ecosystems, non-native invasive species can decrease fire frequency or intensity. This can lead to less establishment of native species and lower diversity. For example, Brazilian pepper (*Schinus terebinthifolius*) can create a fire suppression feedback in fire prone SCPU savanna (Stevens and Beckage 2009). In northeastern oak forests, dense shrub thickets of buckthorn (*Rhamnus cathartica*) create humid conditions that, in combination with non-native, litter (fuel)-consuming worms, virtually preclude fire (Chap. 7). Where these species are fire-sensitive, fire can be an effective management tool for inhibiting non-native invasive species (Stevens and Beckage 2009), and their spread may be slower in future climates with more frequent drought and fire.

1.4.4 Wildlife

Fire, along with other natural and anthropogenic disturbance, is an important driver of the composition and structure of USA forests that in turn shapes the community composition and relative abundance of many wildlife species. Many species are closely associated with forest structure; mature forest species occur primarily in relatively closed-canopy forests, whereas disturbance-dependent species are found in forests with reduced canopy cover or other disturbance-created vegetation types such as open woodlands and savannas (Chaps. 2, 3, 4 and 5). Some specialist bird species are closely linked to specific forest types and structures historically created by fire regimes characteristic of those vegetation types. For example, federally threatened Florida scrub jays (*Aphelocoma coerulescens*) are restricted to low-growing scrub or scrubby flatwoods with few or no canopy trees that were historically created and maintained by stand-replacing fires (Breininger et al. 1999; Chap. 3). Similarly, the federally endangered Kirtland's warbler (*Setophaga kirtlandii*) is found only in large stands of dense, young jack pine, in the upper Midwest (Michigan and Wisconsin) that also were created historically by stand-replacing fires (Spaulding and Rothstein 2009; Chap. 7). In contrast, a frequent, low-intensity fire regime in SCPU longleaf pine forests historically maintained an open understory with few hardwood trees required by the once widespread and now federally endangered red-cockaded woodpecker (*Leuconotopicus borealis*), along with Bachman's sparrow (*Peucaea aestivalis*), bobwhite quail (*Colinus virginianus*), brown-headed nuthatch (*Sitta pusilla)* (Wilson et al. 1995), gopher tortoise (*Gopherus polyphemus*), and several other wildlife species (Chap. 3).

Many other disturbance-dependent species are not as specialized but are nonetheless closely associated with heavily disturbed forest or successional habitats. In eastern hardwood forests, low-severity fires typical of most prescribed fires has little effect on most wildlife species, as changes to forest structure are few and transient (Greenberg et al. 2018a, b). Uncharacteristic, high-severity fires in eastern hardwood forests cause heavy tree mortality, resulting in more individuals and species of breeding birds; this includes an influx of disturbance-dependent species even while most species of mature forest birds persist (Greenberg et al. 2018a; Rush et al. 2012; Rose and Simons 2016). Abundance of some lizard species also increases following high-severity fire (Greenberg et al. 2018b). In general, fire severity in western conifer forests affects bird species and nesting guilds differently, with open-cup nesters favoring moderate and low-severity fires, open-cup canopy-nesting birds preferring unburned western forests, and cavity-nesting woodpeckers and other cavity-nesting species responding positively to moderate-to-high-severity fires or areas of heavy beetle-kill with abundant snags (Saab et al. 2005, 2011; Matseur et al. 2018; Taillie et al. 2018).

1.5 Managing Forests of Today and Tomorrow Within the Context of Fire Ecology

Historically, today, and into the future, fire regimes are a consequence of complex interactions among climate, especially the frequency and duration of drought; biophysical characteristics of the landscape, including forest type, topography, and productivity; and ignition sources, including the timing of lightning strikes or human-caused ignitions (Fig. 1.6). As explored more fully in Sect. 1.1, the frequency and timing of drought or dry periods interacts with overall climate and ecosystem productivity to influence the frequency and severity of fire; in general, more seasonal or more frequent dry periods promote a more frequent, lower-severity fire regime, while long intervals between droughts promote less frequent, higher-severity fires where fuel buildup is adequate. Topography and source of ignition can influence fire size, with rugged topography and human-caused ignitions promoting smaller fires. Finally, sites with longer growing seasons, especially those that are warm with low humidity, may carry fire for longer periods during the year, contributing to a more aseasonal fire regime (Fig. 1.6).

Across many of the regions considered in this book, the frequencies or durations of droughts and disturbances such as blowdowns and pest outbreaks are predicted to increase (Chap. 12). At the same time, continuing increases in atmospheric CO_2 may change forest productivity and increase the rate of succession or growth of later succesional species (Mohan et al. 2007; Miller et al. 2016). These predicted changes may have different consequences for fire regimes of the future. Combined with more frequent or prolonged drought, added fuels from disturbances or faster forest growth could increase the frequency or intensity of fires. In sites where succession (in the absence of fire) is bringing mesophication, more frequent drought and fire may slow succession and allow fire-tolerant species to persist. Overall, although broad-scale factors such as rising CO_2 or drought drive fire regimes, management of today's forests into the future will require localized knowledge of how these factors

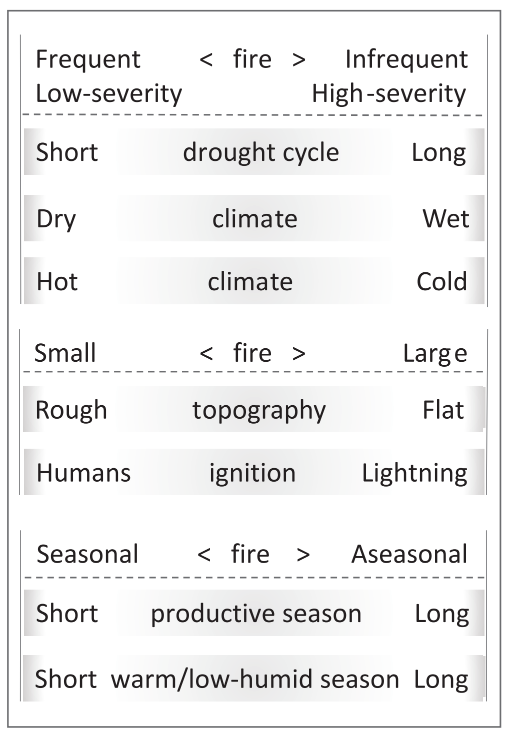

Fig. 1.6 Conceptual diagram of the interplay of climate, weather, the biophysical landscape (topography, productivity), and ignition sources with fire characteristics (frequency, severity, size, seasonality) within and across regions. See text for more information

interact with the biophysical landscape (topography, forest type) and ignition sources (Fig. 1.6).

Fire management of today's forests within the context of historical fire regimes may not be possible given their altered current condition and the warming climate (Vose et al. 2018). Land ownership patterns constrain the size and frequency of prescribed burning (Chap. 5), and an ever-growing urban expansion and wildland-urban interface impedes the use of prescribed fire, presents smoke management issues, and mandates suppression of wildfires to protect lives and property (Ryan et al. 2013). Further, prescribed burning alone may not attain restoration objectives or maintain healthy populations of some plant and animal species in forests that already deviate from historical structure and composition due to past land use or management practices (e.g. Fiedler et al. 1996; Ryan et al. 2013) and invasive species (Kerns et al. 2020).

A first step in forest and fire management planning will be clear and careful definition of management objectives (e.g., desired future conditions) and reference conditions. Reference conditions, and the historical range of variation in natural disturbance regimes (Greenberg et al. 2015a), clearly differ among ecoregions and forest types, and extend across a range of historical human influence. Similarly, appropriate fire and (or) silvicultural prescriptions differ among USA forest types according to site conditions, historical fire regimes, wildfire risks, and desired future conditions. With careful planning, multiple objectives can often be attained with the same fire, or fire combined with other silvicultural prescriptions, for a given forest type in accordance with its historical fire regime (Arthur et al. 2012). These may include creating habitats for target wildlife species, fuel reduction to reduce wildfire risk, creating open forest structures, promoting regeneration of target tree or herbaceous plant species, or increasing biotic and landscape diversity. A recent approach to forest management for a changing climate emphasizes *resistance* (the ability to retain forest structure, composition, and functions despite disturbances) and *resilience* (the ability to "bounce back" or absorb disturbance) (DeRose and Long 2014; Chap. 12). In this approach, prescriptive silviculture treatments or location-specific management may be needed. For example, simulations of forest response to future fires revealed that climate suitable planting (i.e., proactively planting species suitable for the predicted future climate) provided greater resilience than other silvicultural treatments in northern Great Lakes forests (Duvenek and Scheller 2015).

Myriad social, political, cultural, and budgetary priorities, environmental factors, and land ownership patterns complicate a comprehensive approach to wildfire management and effective ecosystem restoration at a landscape level (USFS 2018). Where the risk of wildfire is high, silvicultural additions or alternatives to prescribed burning might be considered when assessing the most expedient and safe pathways to attain target composition and structure of USA forest types. For example, clearcutting followed by pine-planting in both SCPU Florida sand pine scrub and GL-NEF jack pine forests create an even-aged stand structure and composition similar to that created by historical high-severity, stand-replacing burns, and are readily colonized by forest type/structure specialist Florida scrub jays (Greenberg et al. 1995b) or Kirtland's warblers, respectively (Donner et al. 2008). Various combinations of thinning, prescribed fire, and herbicide have been used successfully to initiate oak woodland and savanna restoration in some closed canopy upland hardwood EBA forests (Vander Yacht et al. 2017; Chap. 4), and to increase resilience to climate-accelerated disturbances such as drought and bark beetle outbreaks in the western USA (e.g., ponderosa pine restoration) (Chap. 12; Fiedler et al. 1996).

A collaborative approach among government and nongovernmental agencies, Tribes, private landowners, and other stakeholders is needed to identify management priorities and share resources, funding, and monitoring data across ownership boundaries (Chaps. 5 and 12). Completed in 2014, the National Cohesive Wildland Fire Management Strategy (Council 2014) provided a foundation for collaborative wildland fire management. Subsequently, the 2014 Farm Bill enhanced the ability of the US Forest Service to work with States through the Good Neighbor Authority, and the 2018 omnibus bill provided additional tools to enhance cross-boundary wildland fire management (USFS 2018). Additional federal programs include the Collaborative Forest Landscape Restoration Program and the Joint Chiefs' Landscape Restoration Partnership, and improved awareness, training, and coordination for prescribed burning on private lands provided by Prescribed Fire Councils and Prescribed Burn Associations (Chap. 5). Ultimately though, as these collaborative programs are implemented, it is important to remember that tradeoffs will be required to maintain forest services along with resilient, or adaptable, forests for the future (Wagner et al. 2014).

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