

Cathryn H. Greenberg
Beverly S. Collins *Editors*

Natural Disturbances and Historic Range of Variation

Type, Frequency, Severity, and Post-
disturbance Structure in Central
Hardwood Forests USA

Managing Forest Ecosystems

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Aims & Scope

Well-managed forests and woodlands are a renewable resource, producing essential raw material with minimum waste and energy use. Rich in habitat and species diversity, forests may contribute to increased ecosystem stability. They can absorb the effects of unwanted deposition and other disturbances and protect neighbouring ecosystems by maintaining stable nutrient and energy cycles and by preventing soil degradation and erosion. They provide much-needed recreation and their continued existence contributes to stabilizing rural communities

Forests are managed for timber production and species, habitat and process conservation. A subtle shift from *multiple-use management* to *ecosystems management* is being observed and the new ecological perspective of *multi-functional forest management* is based on the principles of ecosystem diversity, stability and elasticity, and the dynamic equilibrium of primary and secondary production.

Making full use of new technology is one of the challenges facing forest management today. Resource information must be obtained with a limited budget. This requires better timing of resource assessment activities and improved use of multiple data sources. Sound ecosystems management, like any other management activity, relies on effective forecasting and operational control.

The aim of the book series *Managing Forest Ecosystems* is to present state-of-the-art research results relating to the practice of forest management. Contributions are solicited from prominent authors. Each reference book, monograph or proceedings volume will be focused to deal with a specific context. Typical issues of the series are: resource assessment techniques, evaluating sustainability for even-aged and uneven-aged forests, multi-objective management, predicting forest development, optimizing forest management, biodiversity management and monitoring, risk assessment and economic analysis.

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 Springer

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Preface

This edited volume addresses the historic range of variation (HRV) in types, frequencies, severities, and scales of natural disturbances, and how they create heterogeneous structure within upland hardwood forests of Central Hardwood Region (CHR). The idea for this book was partially in response to a new (2012) forest planning rule which requires national forests to be managed to sustain ‘ecological integrity’ and within the ‘natural range of variation’ of natural disturbances and vegetation structure. This new mandate has brought to the forefront discussions of HRV (e.g., what is it?) and whether natural disturbance regimes should be the primary guide to forest management on national forests and other public lands. Natural resource professionals often seek ‘reference conditions,’ based on HRV, for defining forest management and restoration objectives. A large body of literature addresses changes in forest structure after natural disturbance, but most studies are limited to a specific site, disturbance event, forest type, or geographic area. Several literature reviews address a single natural disturbance type within a limited geographic area (often not the CHR), but do not address others or how their importance may differ among ecoregions. Synthesizing information on HRV of natural disturbance types, and their impacts on forest structure, has been identified as a top synthesis need.

Historically, as they are today, natural (non-anthropogenic) disturbances were integral to shaping central hardwood forests and essential in maintaining diverse biotic communities. In addition to a ‘background’ of canopy gaps created by single tree mortality, wind, fire, ice, drought, insect pests, oak decline, floods, and landslides recurring or episodically killed or damaged trees, at scales ranging from scattered, to small or large groups of trees, and across small to large areas. Additionally, some animals, such as beavers, elks, bison, and perhaps passenger pigeons, functioned as keystone species by affecting forest structure and thus habitat availability for other wildlife species. Prehistoric anthropogenic disturbances – fire and clearing in particular – also influenced forest structure and composition throughout much of the CHR and therefore the distribution of disturbance-dependent wildlife species. The spatial extent, frequencies, and severities differed among these natural disturbance types and created mosaics and gradients of structural conditions and canopy openness within stands and across the landscape.

A full-day symposium, organized by the editors, at the 2014 Association of Southeastern Biologists conference in Spartanburg, South Carolina, was the basis for this book. Our goal was to present original scientific research and knowledge synthesis covering major natural disturbance types, with a focus on forest structure and implications for forest management. Chapters were written by respected experts on each topic with the goal of providing current, organized, and readily accessible information for the conservation community, land managers, scientists, students and educators, and others interested in how natural disturbances historically influenced the structure and composition of central hardwood forests and what that means for forest management today.

Chapters in this volume address questions sparked by debated and sometimes controversial goals and ‘reference conditions’ in forest management and restoration, such as the following: What was the historic distribution, scale, and frequency of different natural disturbances? What is the gradient of patch sizes or level of tree mortality conditions created by these disturbances? How do gradual disturbances such as oak decline, occurring over a long period of time and across a broad landscape, differ in effects from discrete disturbances such as tornadoes? How does topography influence disturbance regimes or impacts? How do native biotic (insects or fungi, keystone wildlife species) and abiotic (precipitation, drought, temperature, wind, and soil) agents interact to alter disturbance outcomes? What was the diversity of age classes and gradient of forest structure created by natural disturbances alone? How might disturbance-adapted plants and animals have fared in the hypothetical historic absence of anthropogenic disturbances? How might climate change alter disturbance regimes and structure of upland hardwood forests in the future? And finally, should, and how, can land managers manage these forests within the HRV of natural disturbance frequencies, spatial extents, and gradient of conditions they create?

We sincerely thank all those who encouraged and aided in the development of this book. Each chapter was peer-reviewed by at least two outside experts and both coeditors, and we thank these colleagues for their useful suggestions: Chris Asaro, Robert Askins, Francis Ashland, Bart Cattanach, Steven Croy, Kim Daehyun, Dianne DeSteven, Chris Fettig, Mark Harmon, Matthew Heller, Louis Iverson, John Kabrick, Tara Keyser, Scott Lecce, William MacDonald, Henry McNab, Manfred Mielke, Billy Minser, Scott Pearson, Duke Rankin, Jim Rentch, John Stanturf, Scott Stoleson, Ben Tanner, and Thomas Wentworth. We also thank the Association of Southeastern Biologists for allowing us to host a conference symposium on this important topic, and the National Forests of North Carolina for assistance with travel costs for speakers. We especially thank each author for contributing, and for timely chapter revisions, which made this book possible.

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Chapter 12

The Historic Role of Humans and Other Keystone Species in Shaping Central Hardwood Forests for Disturbance-Dependent Wildlife

Cathryn H. Greenberg, Kendrick Weeks, and Gordon S. Warburton

Abstract Multiple natural disturbance types historically created conditions that were suitable for many, but not all, disturbance-dependent wildlife species in the Central Hardwood Region (CHR). In addition, some wildlife species, such as beavers, passenger pigeons, elk, and bison, historically functioned as keystone species by creating or maintaining unique disturbed habitats that otherwise would be rare. For millennia, humans (Native Americans, and later European settlers) also created and maintained early successional habitat variants (estimated at 7–43 % of the CHR landscape in 1500 AD) including farmlands, old fields in different stages of succession, grasslands, and open woodlands by clearing for cultivation and settlements, frequent burning, and old field abandonment. In this chapter, we argue that humans were a keystone species in the CHR, having a major influence on the diversity, distribution, and abundance of many disturbance-dependent wildlife species by creating, maintaining, or greatly expanding specific, unique types of early successional habitats and some mature forest types dominated by shade-intolerant pioneer species, such as yellow pine. Determining the largely unknowable historic range of variation of natural disturbances, selecting an arbitrary moment on a temporally and spatially dynamic landscape as a reference, and subjectively deciding what should

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or should not be included as ‘natural’ may not serve as the most productive guide for conservation. Alternatively, forest and land use planning for diverse wildlife conservation might more logically start with clear objectives, and proceed with management activities targeted toward attaining them.

Keywords Wildlife • Keystone species • Humans • Ecosystem engineers • Disturbance-dependent birds

12.1 Introduction

Disturbance-dependent wildlife species require open structural conditions created immediately after forest disturbances or at some point early in the dynamic process of recovery and maturation. Historically, natural disturbances (e.g., Chaps. 1, 2, 3, 4, 5, 6, 7, 8, 9, this volume) provided habitats for many disturbance-dependent species by creating patches of young forest structure, from small canopy gaps to large swaths of partial or complete canopy removal, within a mature upland hardwood forest matrix of the Central Hardwood Region (CHR). In addition, some wildlife species, such as beavers (*Castor canadensis*), passenger pigeons (*Ectopistes migratorius*), elk (*Cervus canadensis*), and bison (*bison bison*), historically functioned as keystone species by creating or maintaining unique disturbed habitats such as wetlands or prairies that would otherwise be rare, thereby increasing the abundance, diversity, and distribution of wildlife species that required them. Hence, multiple natural disturbance types historically created conditions that were suitable for many, but not all, disturbance-dependent wildlife species. However, several breeding birds (Askins 2001) and other wildlife species of the CHR such as woodchucks (*Marmota monax*) and rabbits (*Sylvilagus floridanus*) require specific variants of disturbance-created habitats that were created, maintained, or expanded in large part by humans (*Homo sapiens*) through active land management by clearing, frequent burning, and land abandonment in and surrounding inhabited areas, for thousands of years (Delcourt and Delcourt 2004).

In this chapter, we argue that humans were a keystone species in the CHR, having a major influence on the diversity, distribution, and abundance of many disturbance-dependent wildlife species by creating, maintaining, or greatly expanding specific, unique types of early successional habitats and some mature forest types dominated by shade-intolerant pioneer species, such as yellow pine (*Pinus spp.*). Through land use and active land management by clearing, farming, and frequent burning Native Americans (and later European settlers) created settlements, gardens, farmlands, meadows and prairies, open woodlands, [river] canebreaks (*Arundinaria gigantea*), and old fields at varying stages of succession that included successional yellow pine forests (Delcourt and Delcourt 2004). We use results of studies on natural disturbances, paleoecology, archeology, and historical accounts by early explorers to illustrate and discuss likely dynamic scenarios of prehistoric (prior to European settlement) CHR landscapes, and availability of different early successional

habitat variants required by disturbance-dependent wildlife. We focus our discussion on disturbance-created habitats rather than wildlife species per se, because habitat availability likely governed the distribution of many disturbance-dependent wildlife species historically, as it does today. We use disturbance-dependent breeding birds to illustrate possible scenarios of historic wildlife distribution because they are among the most thoroughly studied taxa, and many species are specialized in their associations with specific variants of early successional habitat (MacArthur and MacArthur 1961) that include disturbed young forests, but also other land uses and conditions commonly created by humans (Askins 2001).

12.2 Origin and Early History of Central Hardwood Forests: Climate, Megafauna, and Humans

Human arrival in the CHR coincided with retreating ice sheets and a warming climate more than 13,000 years before present (BP), as open tundra-boreal ‘parklands’ dominated by spruce (*Picea* sp.) and jack pine (*P. banksiana*) were slowly being replaced by temperate, deciduous forest migrating north from warmer more southerly refuges (Delcourt and Delcourt 2004). During the last ice age, glaciers in North America extended south as far as the Missouri and Ohio Rivers, and east to New England (Clark et al. 2009), and a colder, drier climate resulted in alpine tundra in the Blue Ridge Mountains above 1,450 m (Delcourt and Delcourt 2004). Between 18,000 years and 5,000 years BP, climate in the CHR shifted from arid-cool to the warm-humid climate of today (Carroll et al. 2002), interrupted by glacial re-advancing with associated cold and drought during the Younger Dryas period (12,800–11,500 years BP) (http://en.wikipedia.org/wiki/Younger_Dryas), and a rapid warming (more than 7° C in 50 years) around 11,500 years BP (the Pre-boreal transition phase) ([http://en.wikipedia.org/wiki/Boreal_\(age\)](http://en.wikipedia.org/wiki/Boreal_(age))). Warmer temperatures during the hypsithermal (7,500–5,000 years BP) were followed by a cooling trend (5,000–120 years BP) that included the Little Ice Age (600–120 years BP) (Carroll et al. 2002). Oak-chestnut-hickory (*Quercus-Castanea-Carya*) forests became widespread in the CHR by 3,000 years BP (Dickinson 2000; Delcourt and Delcourt 2004). Past climate change and associated disturbance regimes, even in recent millennia, has been a major ‘background’ natural disturbance in the CHR and resulted in major shifts in forest composition and habitats, as well as extinctions and reassembly of wildlife communities.

When humans first arrived, megafauna including ancient and modern bison (*Bison antiquus* and *B. bison*), elk, primitive horses (*Equus* spp.), woolly mammoths (*Mammuthus* sp.), mastodons (*Mammot* sp.), stag-moose (*Cervalces scotti*), and giant ground sloth (*Megalonyx* sp. and others), as well as extant modern wildlife species associated with boreal forest and tundra, such as muskox (*Ovibos moschatus*) and caribou (*Rangifer tarandus*) inhabited much of the CHR (Carroll et al. 2002; O’Gara and Dundas 2002; http://exhibits.museum.state.il.us/exhibits/larson/ice_age_animals.html; <http://parks.ky.gov/parks/historicsites/big-bone-lick/history>).

aspx). A mere 14,000 years ago or less, grazing, browsing, and trampling by keystone megafauna herbivores were important natural disturbances, shaping forests and maintaining open habitats (e.g., Svenning 2002) for many disturbance-dependent species.

Most of these megafauna are now extinct; the relative roles of an overall warming climate, associated shifts in vegetation composition and structure, and the arrival of big-game hunting humans (the Clovis culture) to their extinction is hotly debated (Burney and Flannery 2005; Koch and Barnosky 2006; Askins 2014). Theories that extinctions were precipitated through over-hunting by humans are supported by archaeological evidence at multiple sites, showing human arrival just prior to local extinctions of remaining megafauna (many populations collapsed from 14,800 to 13,700 years BP; Gill et al. 2009). Mosimann and Martin (1975) hypothesized and developed simulations illustrating how even a small founding population of humans could multiply quickly enough to extirpate the slow-reproducing megafauna under a steady hunting regime, with extinctions progressing in a front, beginning in Alaska where humans first entered North America, and moving slowly south and east (Burney 1993). The coincidental timing of extinctions of many megafauna species with the arrival humans is corroborated by a study of spores in lake sediments in upstate New York, Ohio, and Indiana (Gill et al. 2009). The study showed that the abundance of *Sporomiella*, a fungus that grows on the dung of herbivorous mammals, declined dramatically between 14,000 and 13,000 years BP, indicating that large mammals also declined during that period and coinciding with human arrival. This decline was followed by an increase in deciduous trees (possibly released by the absence of grazing and browsing by keystone megafauna), and more frequent fires (possibly set by humans and/or fueled by denser vegetation), as evidenced by increased charcoal particles in the sediments (Gill et al. 2009). Many of the mammals that became extinct at the end of the Pleistocene had survived similar glacial-interglacial transitions for hundreds of thousands of years, suggesting that humans may have played an important and perhaps complex role in their demise (Burney and Flannery 2005; Koch and Barnosky 2006).

Whether through their hypothesized role in extinction of megafauna or (and) their documented role in the more recent extinction or local extirpation of modern fauna, the predatory activities of humans have dramatically and directly influenced many wildlife populations in the CHR. In the last 250 years or less, European settlers were directly responsible for the extinction of several species including the Carolina parakeet (*Conuropsis carolinensis*) and passenger pigeon; the regional extirpation of wolves (*Canis lupus*), cougars (*Puma concolor*), bison, elk, and other species; and dramatic population declines of other species such as beavers through excessive and unregulated hunting and trapping. By removing keystone wildlife species such as beaver (wetland creators), or elk and bison (grazers) whose activities historically created or maintained disturbed, open habitats, humans also indirectly influenced the distributions and populations of many disturbance-dependent wildlife species.

Perhaps most importantly, humans themselves have historically functioned as a keystone species through their management and use of land on inhabited landscapes

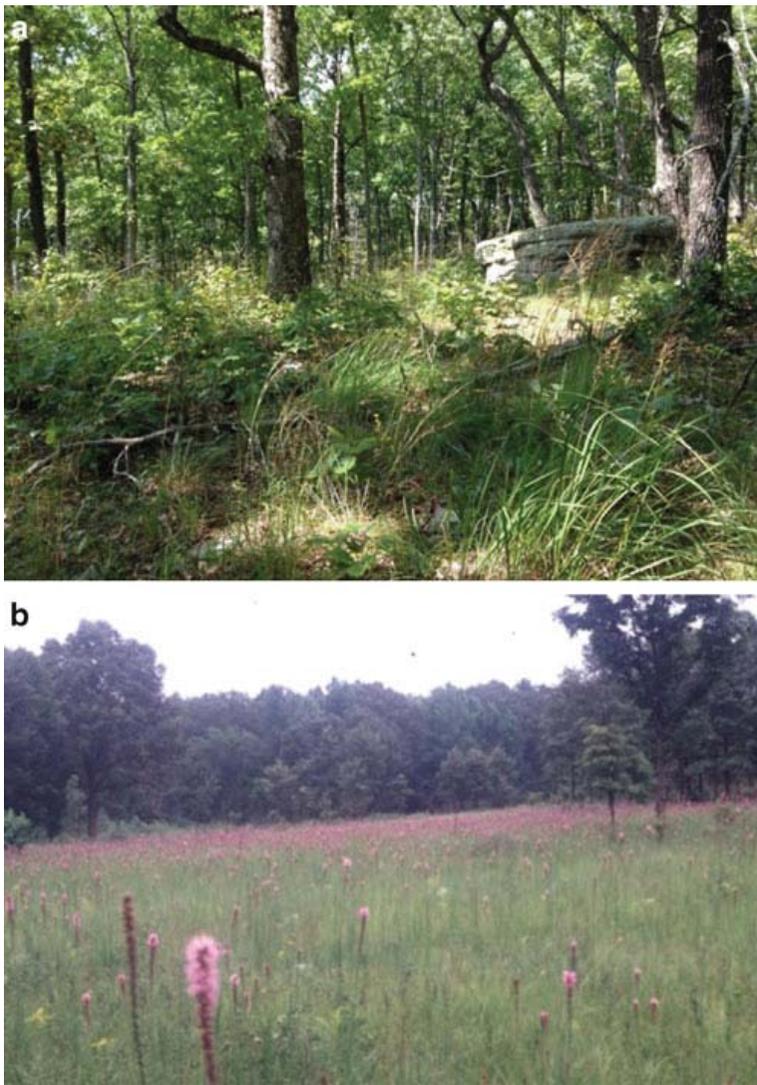


Fig. 12.1 (a) Open woodland with grass-forb-woody understory (Similar to descriptions by early explorers in the Cumberland Plateau, Piedmont of the Carolinas and Georgia, and Appalachians on South- and West-facing aspects of the southern Appalachians) on private land in Sequatchie County, Tennessee in 2013. The woodland, initially closed canopy forest, was not mechanically thinned, and was burned every 2–3 years since the late 1970s (Craig Harper pers. comm; photo courtesy of Craig Harper); (b) Native prairie vegetation at Ft. Campbell in Kentucky and Tennessee managed with burning or mowing at 1–3 year intervals (Daniel Moss pers. comm.) (Photo courtesy of William Minser)

since before central hardwood forests existed as we know them today. By regularly creating, maintaining, or expanding early successional habitats, including many variants that might rarely be created by natural disturbances alone such as agricultural fields, old fields in different stages of succession, open woodlands (e.g., Fig. 12.1a), meadows or prairies (e.g., Fig. 12.1b), and successional yellow pine-dominated forests, humans historically were a major influence on abundance, distribution, and species diversity of disturbance-dependent fauna.

12.3 Early Successional Habitats: One Size Does Not Fit All

The term ‘early successional habitat’ is commonly, albeit erroneously, used generically to refer to any open, recently disturbed habitat that is transient unless maintained by recurring disturbances (Greenberg et al. 2011a). Although both young forest and truly early successional habitats share the features of openness in common, they differ considerably in many ways in the structure and composition of plants (Lorimer 2001; Greenberg et al. 2011a) and, because of that, the wildlife species that use them. In the CHR, high-severity natural disturbances such as large blowdowns, or anthropogenic disturbances such as regeneration harvests, create young forest with high woody stem density and thick cover for wildlife, but generally do not create bona fide successional conditions with high plant species turnover. Even after high-severity natural disturbances that substantially reduce canopy cover, plant species composition usually remains similar to the original mature forest, often with a transient addition of blackberry (*Rubus* spp.) or pokeweed (*Phytolacca americana*), as pre-existing shrubs and fallen or damaged trees resprout prolifically and tree seedlings grow from pre-established advance regeneration or seed (Lorimer 2001; Greenberg et al. 2011b). In the CHR open, young forest conditions typically last 8–15 years before canopy closure (Loftis et al. 2011; Thompson and Dessecker 1997).

In contrast, truly successional habitats occur when pioneer plants colonize treeless areas that are no longer disturbed. In the CHR, most successional habitats originate from anthropogenic land uses, such as abandoned pasture or farmlands, as colonizing shade-intolerant pioneer tree species, including yellow pines (e.g., pitch (*P. rigida*), shortleaf (*P. echinata*), or Virginia pine (*P. virginiana*)), yellow-poplar (*Liriodendron tulipifera*), or black locust (*Robinia pseudoacacia*) (Delcourt and Delcourt 2004), and shrubs create conditions suitable for other, later successional species in a relay sequence toward a mature hardwood forest (Lorimer 2001; Greenberg et al. 2011a).

Disturbance-dependent breeding birds are associated with open habitats created by disturbances, but many are relatively specialized, requiring specific but different variants of early successional habitats ranging from young forest to grasslands (Askins 2001; Hunter et al. 2001) (Table 12.1). In this chapter we use the term ‘early successional habitat’ as it is commonly used and understood in the wildlife literature to denote open conditions created by either natural or anthropogenic disturbances (Greenberg et al. 2011a). However, we emphasize that ‘one size does not fit all’ for disturbance-dependent wildlife species, and therefore different variants of early successional habitats, created by both natural and anthropogenic disturbances, and interactions between them, are required to maximize diversity and abundance of native, disturbance-dependent breeding birds.

Table 12.1 Associations of select disturbance-dependent breeding bird species of the CHR with different early successional habitat variants^a created by natural or anthropogenic disturbances

Species	Early successional habitat variants ^a										
	GH	WM	OW	Sa	SS	SF	Pa	Ag	OF	Su	Ur
American goldfinch (<i>Carduelis tristis</i>)	X	X	X	X	X	X	X	X	X	X	–
American kestrel (<i>Falco sparverius</i>)	X	–	–	X	–	–	X	X	–	–	–
American robin (<i>Turdus migratorius</i>)	X	–	X	X	–	–	X	X	–	X	–
American woodcock (<i>Scolopax minor</i>)	–	–	X	–	X	X	–	–	–	–	–
Barn owl (<i>Tyto alba</i>)	X	–	–	X	–	–	X	X	–	–	–
Barn swallow (<i>Hirundo rustica</i>)	X	X	–	X	–	–	–	X	–	X	–
Bewick's wren (<i>Thryomanes bewickii</i>)	X	–	X	X	–	–	–	–	–	X	–
Blue grosbeak (<i>Passerina caerulea</i>)	–	–	X	–	X	–	–	–	X	–	–
Blue-winged warbler (<i>Vermivora pinus</i>)	–	–	X	X	X	–	–	–	X	–	–
Bobolink (<i>Dolichonyx oryzivorus</i>)	X	–	–	–	–	–	–	–	–	–	–
Brown thrasher (<i>Toxostoma rufum</i>)	–	–	X	X	X	X	–	–	–	X	–
Carolina wren (<i>Thyrothorus ludovicianus</i>)	X	–	X	X	–	–	–	–	–	X	–
Chestnut-sided warbler (<i>Setophaga pensylvanica</i>)	–	–	X	–	X	–	–	–	–	–	–
Chipping sparrow (<i>Spizella passerina</i>)	X	–	X	X	–	–	X	X	–	X	–
Common nighthawk (<i>Chordeiles minor</i>)	–	–	X	X	–	–	–	–	–	X	X
Common yellowthroat (<i>Geothlypis trichas</i>)	–	–	X	–	X	–	–	–	X	–	–
Dickcissel (<i>Spiza americana</i>)	X	–	–	X	–	–	X	X	–	–	–
Eastern bluebird (<i>Sialia sialis</i>)	X	–	X	X	–	–	X	X	–	X	–
Eastern kingbird (<i>Tyrannus tyrannus</i>)	X	–	–	X	–	–	–	–	–	–	–
Eastern meadowlark (<i>Sturnella magna</i>)	X	–	–	–	–	–	X	–	–	–	–
Eastern phoebe (<i>Sayornis phoebe</i>)	X	–	X	X	–	–	–	X	–	X	–
Eastern towhee (<i>Pipilo erythrophthalmus</i>)	–	–	X	X	X	X	–	–	–	X	–
Field sparrow (<i>Spizella pucilla</i>)	–	–	X	X	X	–	–	–	–	–	–
Golden-winged warbler (<i>Vermivora chrysoptera</i>)	–	X	X	–	X	–	–	–	–	–	–
Grasshopper sparrow (<i>Ammodramus savannarum</i>)	X	–	–	–	–	–	–	–	–	–	–
Gray catbird (<i>Dumetella carolinensis</i>)	–	–	X	–	X	X	–	–	–	X	–
Henslow's sparrow (<i>Ammodramus henslowii</i>)	X	X	–	–	–	–	X	–	–	–	–
Horned lark (<i>Eremophila alpestris</i>)	X	–	–	–	–	–	X	X	–	X	–
House wren (<i>Troglodytes aedon</i>)	X	–	X	X	–	–	–	–	–	X	–
Indigo bunting (<i>Passerina cyanea</i>)	–	–	X	X	X	–	–	–	–	X	–
Loggerhead shrike (<i>Lanius ludovicianus</i>)	X	–	X	X	–	–	X	X	–	–	–
Mourning dove (<i>Zenaida macroura</i>)	X	–	X	X	–	–	X	X	–	X	–
Northern bobwhite (<i>Colinus virginianus</i>)	X	–	X	X	–	–	–	–	–	–	–
Northern cardinal (<i>Cardinalis cardinalis</i>)	–	–	X	–	X	X	–	–	X	X	–
Northern mockingbird (<i>Mimus polyglotus</i>)	X	–	X	X	–	–	–	–	–	X	–

(continued)

Table 12.1 (continued)

Species	Early successional habitat variants ^a										
	GH	WM	OW	Sa	SS	SF	Pa	Ag	OF	Su	Ur
Northern rough-winged swallow (<i>Stelgidopteryx serripennis</i>)	X	X	–	–	–	–	–	X	–	–	–
Orchard oriole (<i>Icterus spurius</i>)	–	–	X	X	–	–	–	–	X	–	–
Prairie warbler (<i>Setophaga discolor</i>)	–	–	X	–	X	X	X	–	–	–	–
Purple martin (<i>Progne subis</i>)	X	X	–	X	–	–	X	X	X	–	–
Red-headed woodpecker (<i>Melanerpes erythrocephalus</i>)	–	X	X	X	–	–	–	–	–	–	–
Red-tailed hawk (<i>Buteo jamaicensis</i>)	X	–	X	X	–	–	X	X	X	X	X
Red-winged blackbird (<i>Agelaius phoeniceus</i>)	–	X	–	–	–	–	–	–	–	–	–
Ruffed grouse (<i>Bonasa umbellus</i>)	–	–	X	X	X	X	–	–	–	–	–
Savannah sparrow (<i>Passerculus sandwichensis</i>)	X	–	–	–	–	–	–	–	–	–	–
Song sparrow (<i>Melospiza melodia</i>)	X	–	X	X	–	–	–	–	–	X	–
Tree swallow (<i>Tachycineta bicolor</i>)	–	X	–	X	–	–	–	X	–	–	–
Vesper sparrow (<i>Poocetes gramineus</i>)	X	–	–	–	–	–	–	–	–	–	–
White-eyed vireo (<i>Vireo griseus</i>)	–	–	X	–	X	X	–	–	–	–	–
Yellow-breasted chat (<i>Icteria virens</i>)	–	–	X	–	X	X	–	–	X	–	–

^aGH grass-herbaceous, WM wet meadow, OW open woodland, Sa savanna, SS scrub-shrub, SF sapling forest, Pa pasture, Ag agricultural, OF old field, Su suburban, Ur urban

12.4 Natural Disturbances and Early Successional Habitats for Wildlife: Severe Weather, Weather-Related, and Biotic Agents

Historically, non-anthropogenic natural disturbances created variable age classes and structural conditions across small- to large areas, at different locations and times in a shifting mosaic of ephemeral patches, with young forest composing varying proportions of the vast CHR landscape at any given time. Mobile, disturbance-dependent wildlife species could use these transient young forest habitats opportunistically. However, in the hypothetical absence of human-caused disturbances, their populations would almost certainly have been variable, fluctuating spatially and temporally as conditions became available for brief periods before becoming unsuitable as forests recovered and matured.

12.4.1 Severe Weather

Based on records over the past 150 years or less, disturbance types, frequencies, and severities historically varied temporally and spatially within and among ecoregions, and locally across topography. For example, in the CHR hurricane-related winds are

more frequent in eastern ecoregions, whereas tornados are more frequent in western ecoregions but also commonly occur in the Piedmont, Ridge and Valley, and Southwestern Appalachians ecoregions (see Peterson et al. Chap. 5). Damage from hurricane-related winds is variable. For example in the Blue Ridge Mountains, Hurricane Opal (whose track did not enter the ecoregion despite considerable damage there) caused single- to multiple-tree windthrows from downbursts of wind (McNab et al. 2004), whereas damage from Hurricane Hugo included tens of thousands of hectares rated as “total timberland damaged” (Dogett 1993). Ice storms (Lafon Chap. 7) and landslides (Wooten et al. Chap. 9) are most common on steep slopes in mountainous ecoregions such as the Blue Ridge Mountains. The impacts of severe weather disturbances on central hardwood forests ranged from small gaps (Hart Chap. 2) to large swaths of broken limbs and (or) fallen trees, creating a gradient of young forest conditions potentially suitable for gap, edge, scrub-shrub, or sapling-stage breeding bird species (Table 12.1).

12.4.2 *Lightning-Ignited Fire*

Lightning-ignited fires are rare in the deciduous forests of the CHR because fuels are generally too moist, discontinuous, or otherwise inadequate to allow spread except under severe drought conditions (e.g., Schroeder and Buck 1970; Barden 1997; Delcourt and Delcourt 1997; Flatley et al. 2013; also see Sect. 12.7.1). Schroeder and Buck (1970) estimated that about 1–5 lightning ignitions occur annually per 4,000 km² in the CHR. The wildfire reporting database for National Forests shows that within CHR National Forests, lightning ignites an average of 0.3–7.8 fires per 2,000 km² annually; in contrast humans, accidentally or purposefully, ignite an average of 4.8–93.9 wildfires (not including prescribed burns) per 2,000 km² annually (Greenberg et al. Chap. 1, Table 1.6). Guyette et al. (2006a) estimated fewer than one in 200 wildfires in the CHR were lightning ignited; the rest were due to arson, cigarettes, unattended campfires, or other anthropogenic causes. Historic fire frequencies positively corresponded with human population densities and far exceeded probable frequencies attributable to lightning ignition (Guyette et al. 2006a, b; Hart and Buchanan 2012; also see Grissino-Mayer Chap. 6; Leigh Chap. 8).

Studies in the Boston Mountains ecoregion suggest that topographic heterogeneity, or ‘roughness’ reduces fire frequency in general (Guyette et al. 2006b). However, lightning-ignited fires occur more frequently and with higher severity in some topographic positions, such as ridgetops and dry south-, southwest-, or west-facing slopes in the Blue Ridge Mountains ecoregion that tend to be low-quality, drier sites (Flatley et al. 2013). Not coincidentally, these topographic positions are also where Table Mountain pine (*P. rigida*), pitch pine, mountain laurel (*Kalmia latifolia*), and other plant species associated with dry, low-quality sites and occasional fire most commonly occur (Zobel 1969).

Under most conditions, wildfires in hardwood forests of the CHR are low-intensity, and changes to forest structure and breeding bird communities are relatively minor and transient (Greenberg et al. 2013). Exceptions may occur during infrequent, extreme drought conditions, or on steep topography and ridgetops with xeric, low site quality conditions that are more conducive to hot, high-severity fires that result in heavy tree mortality. A combination of low lightning ignition frequency and the relatively random location of lightning strikes across the vast CHR render it unlikely that lightning-ignited fires alone would have repeatedly burned the same landscapes with sufficient frequency needed for the development and maintenance of prairies, savannas, open woodlands, or yellow pine forests (see Sect. 12.4.3) with occasional exceptions. When they did occur, lightning-ignited high-severity fires likely created open, young forest conditions with abundant standing snags potentially suitable for yellow pine regeneration (Jenkins et al. 2011) and for gap-, edge, scrub-shrub, sapling-stage, or open woodland breeding bird species (Table 12.1) (e.g., Greenberg et al. 2013).

12.4.3 Southern Pine Beetle

Historically, Native Americans (and later European settlers) promoted the development and maintenance of pine forests over mature, climax upland hardwoods on inhabited landscapes by actively managing with frequent fire, and by abandoning farmlands that were often colonized by yellow pines such as shortleaf, Virginia, and pitch pine (Ashe and Ayers 1901; Mattoon 1915; Ashe 1922; Balch 1928; Delcourt and Delcourt 2004). Such yellow pine-dominated forests are disappearing due to a combination of (1) southern pine beetle (*Dendroctonus frontalis*) attacks on yellow pine forests that established when Native Americans or European settlers (through the mid-1900s) were actively clearing, burning, and abandoning lands (see Nowak et al. Chap. 4), and (2) a dramatic reduction in the frequency of anthropogenic fire ignitions and (or) suppression of wildfires when they do occur (see Sect. 12.7.1). Without active land management by humans, yellow pine-dominated forests would likely have been limited in distribution to low quality sites and topographic positions where hardwood competition is reduced and lightning-ignited fires are more frequent. On a hypothetical CHR landscape without humans, the impact of southern pine beetles may have been minor across much of the landscape, because yellow pine forests would have been much more restricted in their distribution.

12.5 Keystone Wildlife Species: Bison, Elk, and Beaver as Agents of Disturbance and Ecosystem Engineers

Many animal species respond to, rather than drive, forest structure. However, some species were themselves agents of disturbance, functioning as keystone species by helping to create and maintain open, early successional conditions and wetlands

that enabled many other wildlife species to thrive. Elk, bison, beaver, and perhaps even passenger pigeons were especially notable ‘ecosystem engineers’ that historically had considerable impacts on the CHR landscape, often in close association with humans. In fact, a mutualism developed between Native Americans, and their large ungulate prey. Native Americans created prairies, open woodlands, and forest edge through frequent burning and clearing that enabled elk and bison to thrive; in turn, their grazing helped to arrest forest succession and maintain these grass-dominated habitats that ignited easily and carried fire across broad areas (Delcourt et al. 1998; McClafferty 2000; Delcourt and Delcourt 2004). This ‘graze and burn’ disturbance regime, co-managed by Native Americans and large ungulates, created structural conditions promoting higher densities and greater distributions of wildlife species requiring open, grassy habitats than would be possible in its absence (e.g., Table 12.1).

12.5.1 Passenger Pigeon

Passenger pigeons numbered 3–5 billion in eastern North America until the late 1800s when their population declined until their extinction in 1914 (Yeoman 2014). They ranged throughout most of eastern North America, wintering south of latitude 36° N and breeding in the northern part of the CHR including southern New York, west-southwest across Pennsylvania, northern West Virginia, and Kentucky as well as parts of the midwestern USA (Ellsworth and McComb 2003). Based on their massive numbers and collective mass, passenger pigeon flocks are thought to have been an important agent of low-intensity disturbance throughout much of the CHR, similar to that of ice storms or lower-intensity windstorms, by increasing light levels in forests through limb and tree breakage (Ellsworth and McComb 2003). They also covered the ground with several cm of feces at nesting and roosting sites, killing the understory vegetation and inhibiting plant growth for several years (see Ellsworth and McComb 2003), and potentially altering fuels structure by killing understory plants and creating coarse woody debris (Ellsworth and McComb 2003). Flocks, estimated at 105,000 pigeons per ha, commonly formed columns over 1 km wide and 400–450 km long (King 1866 as cited in Schorger 1955; Ellsworth and McComb 2003) and numbered in the millions (see Yeoman 2014). In 1871, naturalist A.W. Schorger estimated a communal nesting site covering 2,200 km² of sandy oak barrens in Wisconsin, with 136 million breeding adults (Yeoman 2014). Roosting and nesting areas, commonly 0.02–10 km² but sometimes as large as 130 km², were used by an estimated 27,000–36,000 kg per ha of pigeons (Ellsworth and McComb 2003).

Ellsworth and McComb (2003) estimated that historically, passenger pigeons affected approximately 0.5–0.8 % of their total winter range annually through their use of temporary and long-term roosts; breakage of smaller limbs and trees (lower-intensity disturbance) affected an estimated 8 % of their breeding area annually (Ellsworth and McComb 2003). Ellsworth and McComb (2003) suggest that low-intensity damage in nest areas likely resulted in a light environment favoring

shade-tolerant tree species such as American beech (*Fagus grandiflora*), eastern hemlock (*Tsuga canadensis*), and sugar maple (*Acer saccharum*), and establishment of intermediate (moderately shade-tolerant) species such as oaks, in gaps. In contrast, severe physical damage in roost areas may have resembled damage from high winds, or even hot fires that top-kill most plants and add nutrients to the soil, resulting in high light levels and release of intermediate tree species such as oaks or eastern white pine (*P. strobus*) (Ellsworth and McComb 2003). The gradient of structural conditions created by passenger pigeons were likely suitable for gap-associated breeding birds such as cerulean warblers (*Setophaga cerulea*) (Perkins 2006) where damage was relatively light, to edge- and open area species such as indigo buntings (*Passerina cyanea*) where damage was more severe. Passenger pigeons also may have played an important role in seed and nut dispersal. Hence, prior to their extirpation by humans, passenger pigeons may have functioned as a keystone species by affecting forest composition as well as forest structure that in turn affected other wildlife species.

12.5.2 *Beaver*

Historically, beavers inundated riparian forests by damming slow-moving streams, creating large areas of boggy scrub-shrub wetlands with dead standing trees, or beaver meadows (see Greenberg et al. Chap. 1, Fig. 1.2 h) that supported wetland-dependent plants and animals. Beaver populations were estimated at between 60 and 400 million in pre-colonial North America (Seton 1929), and they occurred virtually anywhere with suitable water and food plant resources (Baker and Hill 2003). In his travels, Bartram noted that beaver ‘abounded’ north of Georgia (Van Doren 1928). Given the extremely high populations of beaver in pre-European times, the entire CHR surely included an extensive mosaic of beaver ponds and swamps of various sizes and configurations. Hey and Phillippi (1995) estimated that 40 million beavers in 1600 would have maintained 206,795 km² of water surface in the upper Mississippi and Missouri River basins; current beaver populations there may pond about 2,023 km². In the eastern USA, heavy beaver trapping for the fur trade began in the 1600s (Naiman et al. 1988). Between 1853 and 1877 the eastern USA Hudson Bay Company alone shipped three million pelts to England (http://www.ohiohistorycentral.org/w/American_Beaver?rec=1124). Beaver populations nearly vanished throughout North America by the 1900s due to excessive trapping for the fur trade (Naiman et al. 1988; Baker and Hill 2003).

Inundation of dammed waterways provides multiple benefits for wildlife and increases local landscape diversity. Beaver pond complexes provide standing water, edge, standing snags killed by flooding, plant diversity, and vertical stem diversity all in one area (Baker and Hill 2003). Wetland vegetation including sedges (*Carex* spp.), bulrush (*Scirpus* spp.), and cattails (*Typha* spp.) rapidly colonize newly created wetland complexes. Many wildlife species including waterfowl, wading birds, red-winged blackbirds (*Agelaius phoeniceus*), woodpeckers, migrating songbirds,

raptors, aquatic furbearers such as mink (*Neovison vison*) and muskrat (*Ondatra zibethicus*), amphibians, and semi-aquatic reptiles such as bog turtles (*Clemmys muhlenbergii*) and water snakes colonize beaver ponds and wetlands, and use them for breeding and habitat (Baker and Hill 2003; Rosell et al. 2005). Historically, when beaver populations were high, at least some beaver ponds may have persisted for over 1,000 years (Ben Tanner unpubl. data). Abandoned beaver ponds eventually drain and are colonized by shrubs and grasses, sometimes lasting for years before eventually reverting to forest (Askins 2000). Historically, these beaver meadows and disturbed areas surrounding beaver ponds were likely extensive along floodplains, and provided habitats for shrub-scrub and some grassland bird species, rodents, lagomorphs, ungulates, and their predators (Askins 2000; Baker and Hill 2003).

Historically, frequent and continual creation and abandonment of beaver ponds across the CHR created diverse wetland habitats that facilitated a much higher local diversity, as well as abundance, landscape distribution and population connectivity for many more wildlife species than today. Some species with poor dispersal ability, such as bog turtles, have reached critically low population levels likely in part because of severely diminished beaver populations and the habitats they engineered (US Fish and Wildlife Service 2001); more than 90 % of mountain bog habitat has been lost (Walton 2006). Thus, prior to their near-extirpation by humans, beaver were historically perhaps one of the greatest animal agents of disturbance given the spatial extent and effects of their habitat alteration activities.

12.5.3 Elk

More than 10 million elk were estimated to have occurred in North America prior to the arrival of Europeans (Seton 1929). Modern elk have occupied the CHR for at least 20,000 years (McClafferty 2000; O’Gara and Dundas 2002), since (and for long after) boreal forest and tundra dominated the landscape (Delcourt and Delcourt 2004). There are many historical reports of large numbers of elk in the CHR. Place names such as Banner Elk, North Carolina (Blue Ridge Mountains ecoregion), Elk River in West Virginia (Central Appalachians and Allegheny Plateau ecoregions), and Elk Creek in Kentucky (Interior Plateau ecoregion) also suggest that elk were once widespread (VDGIF 2010). By the late 1800s or early 1900s they had been eliminated by over-hunting (O’Gara and Dundas 2002; Innes 2011).

Elk are grazers, primarily using grasslands or open prairies, but usually remaining within 400 m of mature forests which they use for cover (Peek 2003). They feed primarily on grasses, shrubs, and forbs depending on the season and location (Peek 2003). Although elk populations were likely controlled by hunting, predation by wolves, black bear (*Ursus americanus*), and cougars, and diseases, their numbers, as seen and reported, were clearly sufficiently high to impact vegetation structure and composition in and around the open areas where they occurred. At high densities elk can alter species composition and structure, reduce or eliminate shrubs or seedlings, decrease plant diversity, and create browse lines (McClafferty 2000).

Even at low to moderate densities, elk browsing can slow the rate of succession (Putnam 1996). Selective grazing can stimulate the growth of palatable grasses at moderate densities or favor undesirable forage species at higher densities (Woodward et al. 1994; Schreiner et al. 1996). Although elk play an important role in maintaining open grasslands by grazing and browsing, it is unlikely that they can create them from a starting point of mature hardwood forest. In all likelihood, Native Americans facilitated the presence of elk in the CHR through frequent burning that created and maintained meadows, prairies and open woodlands.

12.5.4 Bison

Modern bison have been present (until recently) in the CHR since at least the Pleistocene (http://exhibits.museum.state.il.us/exhibits/larson/ice_age_animals.html). As with elk, grasslands created by widespread clearing and frequent burning by Native Americans provided suitable conditions for bison to thrive (Rostlund 1960) for thousands of years (http://exhibits.museum.state.il.us/exhibits/larson/ice_age_animals.html), as the CHR landscape transitioned from boreal parkland to deciduous forest. Reports by early explorers, archeological finds, place names such as Buffalo Lick in the Piedmont ecoregion of northeastern Georgia (<http://www.bartramtrail.org/pages/articles.html>), and a buffalo wallow in central North Carolina (Simmons 1999), indicate that bison were widespread throughout much of the CHR. Buffalo traces were made and used during their seasonal migrations from the plains of central Illinois, through forests to the salt licks of Kentucky (Interior Plateau and Interior Valleys and Hills ecoregions). These traces were wide enough to be used as travel routes by Native Americans and later by European settlers (<http://keithbobbitt.com/Log%20Cabins/NorthCarolinaRoute.htm>).

Reports by early explorers indicate that bison were quite numerous, and grasslands and woodlands were sufficiently abundant to support them (Rostlund 1960). In 1722, Catesby noted “The buffalo. They range in droves feeding upon the open savannas morning and evening, and in the sultry time of the day they retire to shady rivulets and streams” in the Piedmont ecoregion (as cited in Rostlund 1960). Michaux (1805) reported seeing bison in groups of 150–200 in his travels through Kentucky in the early 1800s. Ramsey (1853, as cited in Moss 2001) described prairies around Nashville, Tennessee (Interior Plateau ecoregion) “luxuriant growth of native grasses, pastured over as far as the eye could see, with numerous herds of deer [*Odocoileus virginianus*], elk, and buffalo.” Captain Timothe de Monbreun, a French hunter and trapper from Illinois, traveling down the Cumberland River near Palmyra, Tennessee (Montgomery County) reported seeing large herds of buffalo in 1777 (Kellogg 1939 as cited in Moss 2001). In 1780, buffalo were killed by Colonel John Donelson and his party near the Cumberland River along the Kentucky-Tennessee line (Williams 1928 as cited by Moss 2001). Bison disappeared from the southeast in the middle 1800s largely due to over-hunting by European

settlers (Rostlund 1960). They were extirpated from North Carolina by 1765, Maryland by 1775, and Virginia by 1797 (Rostlund 1960). Michaux (1805) noted that bison were frequently shot by settlers for their tongues, with the remainder of the carcass wasted.

In the CHR, bison used fire-maintained prairies and shrub-grass woodlands for feeding (Tesky 1995). Bison are grazers, eating up to 14 kg of grass daily (Evans and Pobasco 1977), although they may switch to woody browse species if grasses are not available. Similar to elk, bison grazing pressure can lead to changes in plant composition and structure, impede forest succession (Reynolds et al. 1982) and help to maintain the grass-dominated communities they depend on. Bison can also affect local stands of timber by horning and thrashing during the rut (Reynolds et al. 1982). Trails on hillsides can drain upland areas and change vegetative composition (Reynolds et al. 1982), and wallows can become pools of water for other species to use (Tesky 1995). Prior to their regional extirpation by humans, both bison and elk were likely instrumental in retarding forest succession by grazing that, in conjunction with frequent burning by humans, helped to create and maintain open oak woodlands, prairies and savannas.

12.6 Humans as a Keystone Species and Ecosystem Engineer on the Historic Landscape

For millennia, *Homo sapiens* was a predominant keystone species and ecosystem engineer in the CHR that created and maintained many variants of open, early successional habitats and forest age classes for a wide variety of disturbance-dependent species in and surrounding their settlements (Carroll et al. 2002). Native Americans were active land managers, using fire to clear forests for settlements and agriculture, and to improve visibility, facilitate travel, increase native fruit production, and create edge and open, grassy habitats to attract game species (Van Lear and Waldrop 1989; Yarnell 1998; Carroll et al. 2002; Delcourt and Delcourt 2004). Social organization became more centralized and sophisticated over millennia, and by 1,000 BP concentrated settlement patterns and agriculture “generated a landscape patchwork of fragmented forests, cultivated land, and nutrient-depleted old fields abandoned as fallow land” (Delcourt and Delcourt 2004). Habitats created and maintained primarily by Native Americans included settlements, farmlands and gardens, abandoned fields of different age-classes, and forests of pioneer species colonizing abandoned fields including river cane (forming dense canebreaks) and yellow pines (Delcourt and Delcourt 2004). Through their land management activities across large landscapes adjacent to settlements, Native Americans – and later European settlers – created grassland, garden-residential ‘suburb,’ agricultural field, old-field, yellow pine forest, and open woodland habitats, thereby influencing species diversity, distribution, and abundance of many disturbance-dependent breeding birds with these specific habitat associations (Table 12.1).

12.6.1 *Historic Land Use and Forest Management by Native Americans in the Central Hardwood Region*

As early as 10,000 years BP Native Americans lived in long-term settlements in valleys and lowlands near rivers throughout much of the CHR. Archaeological evidence from the Shenandoah Valley of Virginia, the Little Tennessee River Valley of east Tennessee, eastern Kentucky, Watauga Valley of North Carolina, West Virginia, and the Valley and Ridge province indicate that such settlements were widespread. By the Late Archaic (4,500 years BP) Native Americans cultivated crops and managed forests surrounding and far beyond their settlements by burning frequently to facilitate travel and visibility, promote seed, berry, and nut production, and production of grasses and forage to attract elk, deer, bison, and other game species (Chapman et al. 1982; Williams 1989). These activities increased through the late Holocene, with a substantial increase in burning frequency by 3,000 years BP (Yarnell 1998; Delcourt and Delcourt 2004; Grissino-Mayer Chap. 6; Leigh Chap. 8). Delcourt and Delcourt (2004) suggest that by 3,000 years BP frequent burning by Native Americans promoted upland forests dominated by more fire tolerant oak, chestnut, hickory, and walnut (*Juglans* spp.), even as the prevailing climate would otherwise be expected to promote more fire-intolerant, mesophytic species. Frequent burning promoted the development and maintenance of savannas, prairies, open woodlands and pine forests that were once interspersed throughout the CHR (Flatley et al. 2013). By 1,000 BP Native American social organization was highly sophisticated in the CHR, with widespread dependence on agriculture (Delcourt and Delcourt 2004).

American Indians cleared land for villages and agriculture by girdling trees through peeling or burning away bark, and by burning. Older fields with declining soil fertility and productivity were abandoned to be reclaimed by forest, and new fields were cleared progressively and in rotation (Williams 1989), creating a mosaic of different-aged forests and forest structures in the areas surrounding settlements. Disturbances from agriculture, field abandonment, and frequent burning affected forest composition near settlements. Before agriculture became widespread, only 10 % of wood charcoal from archaeological sites was from pioneer species such as yellow-poplar, pine, red cedar (*Juniperus virginianus*), or river cane; subsequently (and prior to the arrival of Europeans) it rose steadily to 50 % (Chapman et al. 1982; Yarnell 1998).

Wood was used to build structures, and for fuel (Williams 1989). Assuming that fuel wood use by Native Americans was similar to that of European settlers in the Blue Ridge Mountains ecoregion, an average family used about 3.62 m³ (15 cords) per year for cooking and warmth, which was likely salvaged from cleared land, second growth forest in abandoned fields, cull and undersized trees, or the surrounding forest (Nesbitt and Netboy 1946; Williams 1989). Model simulations for the Little Tennessee River Valley (Baden 1987 as cited in Delcourt and Delcourt 2004) indicate that the area required for growing enough maize for one person increased from 0.1 to nearly 0.4 ha between 1,000 and 250 years BP as dependency

on maize increased. Soil fertility and harvest yield generally decline sharply within 10 years on maize fields, forcing abandonment of old and clearing of new fields.

Clearing, agriculture, and widespread burning by Native Americans influenced the forests and early successional habitats, but were almost certainly most pronounced near settlements along valley bottoms and surrounding uplands (Van Lear and Waldrop 1989; Milner and Chaplin 2010). By 3,000 years BP anthropogenic fire resulted in “a fine-grained patchwork of vegetation on upper hillslopes and ridgetops that include prehistoric garden plots, open patches with mixed crops of domesticated species, abandoned Indian old-fields reverting back into early-successional grassland barrens, thickets of shrubs, and even-aged stands of pitch pine or tulip poplar trees” on the Cumberland Plateau with mixed mesophytic forests in more sheltered topographic positions (Delcourt and Delcourt 2004). A schematic representation of land use by Native Americans illustrates the different variants of early successional habitats they created in and surrounding villages by clearing, burning, and agricultural activities (Fig. 12.2).

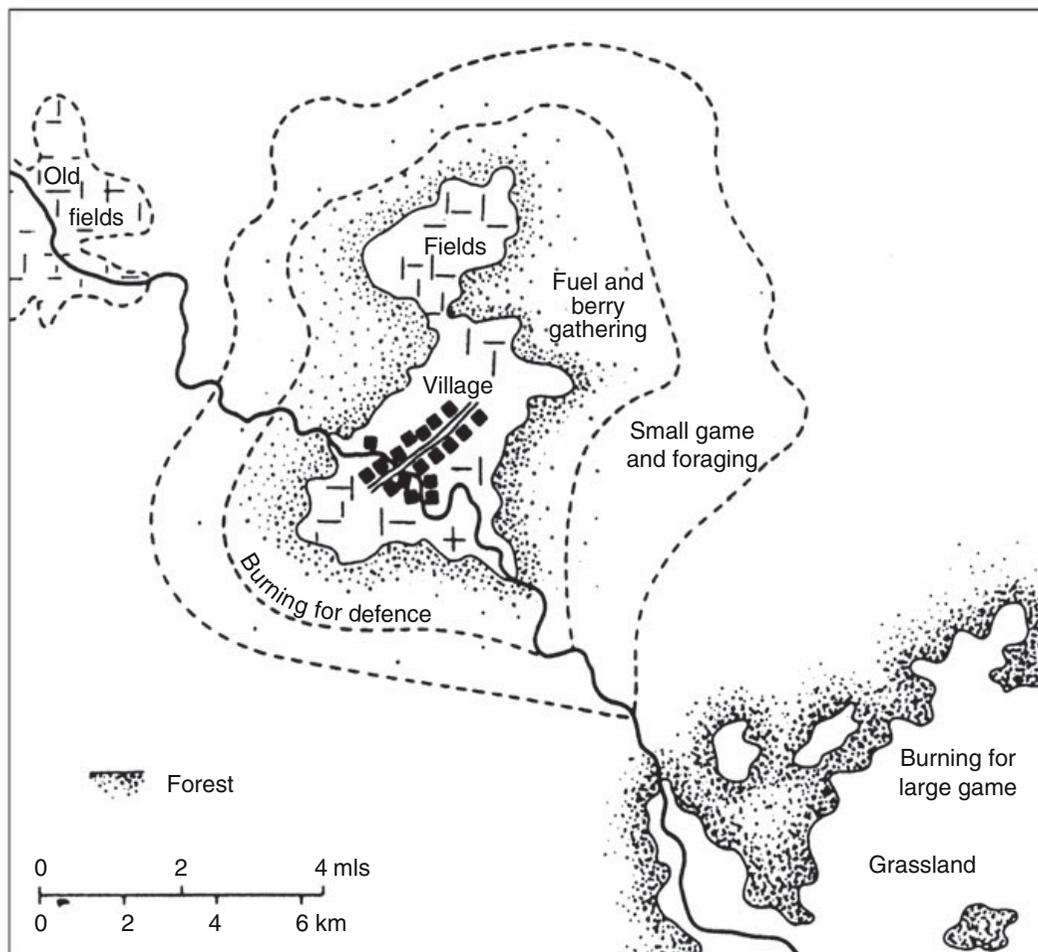


Fig. 12.2 Schematic of a Native American settlement and surrounding managed landscape (From Williams 1989)

Estimates of the Native American population ca. 1500 AD in the eastern USA range between 0.5 and 2.6 million, based on archaeological and historical information (Milner and Chaplin 2010). Their settlements and agricultural fields were located in spatially discrete, irregularly distributed aggregates across productive land, primarily along coastlines or (in the CHR) river valleys (Fig. 12.3) (Milner and Chaplin 2010). Nearly all Native Americans lived in villages of 50–1,000 people surrounded by fields (e.g., Fig. 12.2; Williams 1989). Some settlements were quite large; tens of thousands of people lived along a 100 km stretch along the Mississippi River and into the surrounding uplands in Cahokia, near east St. Louis (Ozark Highlands ecoregion), during the Mississippian period (800–1500 AD) (Denevan

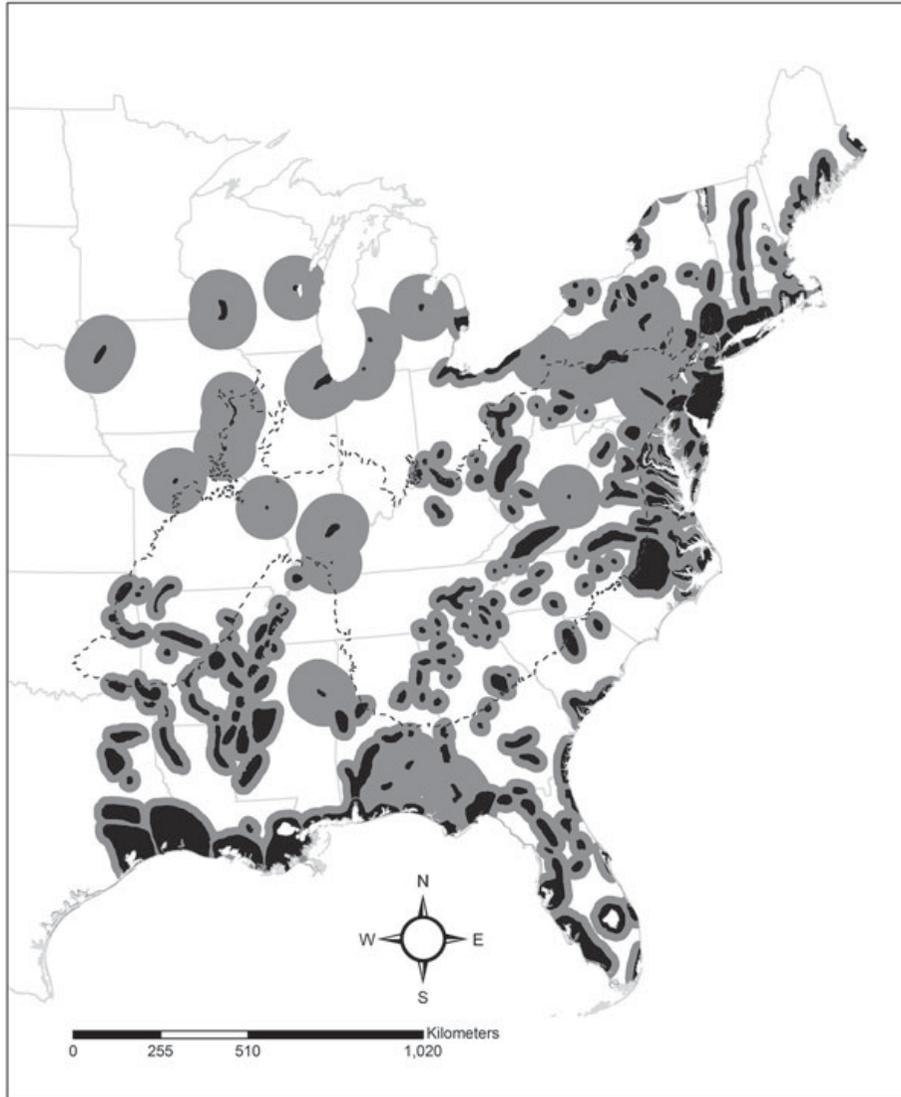


Fig. 12.3 Known population polygons of Native American settlements around 1500 AD based on archaeological and historical evidence (*black*), with buffers (*gray*) encompassing the potential zone of human influence, such as frequent fire, surrounding settlements (Adapted from Milner and Chaplin 2010)

1992; Milner and Chaplin 2010). Both population levels and the locations of settlements were dynamic over time. For example, a major depopulation occurred in the Midwest sometime between 1300 and 1500 AD, prior to European contact. Settlements sometimes relocated, likely as soil and fuel resource were depleted (Williams 1989).

Milner and Chaplin (2010) calculated the area of known Native American settlements ca. 1500 AD, and used nearest-neighbor statistics to calculate buffers surrounding them that incorporate the area of probable environmental impact. Based on their modeling, Native Americans impacted at least 7.1 % (settlements only), and up to 42.6 % (including buffers) of the landscape within the CHR ca. 1500 AD, prior to settlement by Europeans (Fig. 12.3). Landscapes heavily impacted by Native Americans likely expanded, contracted, and shifted with their populations and movements. Large tracts of mature or old-growth forest subjected primarily to non-anthropogenic natural disturbances likely created a matrix between populated areas and surrounding areas of environmental impact (Fritz 2000; Delcourt and Delcourt 2004). During this prehistoric moment, in a temporally and spatially dynamic landscape, suitable habitat was likely widely available for breeding bird species associated with mature- and young forests created by natural disturbances, as well as for species requiring different variants of land uses and early successional habitats that were created primarily by Native Americans.

12.6.2 Descriptions of Native American Land Use and Historic Landscapes by Early European Explorers

Accounts of pre-settlement landscapes by early naturalists and explorers are scant, and potentially biased, as most likely took routes most easily traversed and likely near or between Native American population centers. Nonetheless, several descriptions provide insight into landscape condition – thus the availability of different early successional wildlife habitats – at specific times and places, in different central hardwood ecoregions prior to or with minimal settlement by people of European descent.

In 1540, writings from Hernando DeSoto's expedition described the landscape of the Blue Ridge Mountains ecoregion inhabited by the Lamar and Qualla cultures as "including palisaded towns and large expanses of cultivated fields" ... "Ridges were well-wooded, and outside the cultivated valleys, the land was all forest" (as cited in Yarnell 1998). In Virginia, the Shenandoah Valley between the Blue Ridge Mountains and the Alleghenies was described in the mid-1700s as a vast grass prairie covering more than 2,590 km², which was burned annually by Native Americans (Van Lear and Waldrop 1989). In 1670 German explorer John Lederer described the Roanoke Valley along the Virginia-North Carolina border and along the border with West Virginia as forested, but "where it was inhabited by Indians, it lay in open in spacious plains," and "by the industry of these Indians as... very open and clear of wood" (John Lederer as cited in Williams 1989).

Prairie-like openings throughout the Piedmont ecoregion, some up to 40 km across, were described by several early explorers and traders (see Barden 1997). In 1540 Spanish and Portuguese narratives described “many fine fields... the forest was more open and there were very good fields along streams... They traveled a full league [5 km] through a garden-like land of fruit-bearing trees, among which a horse could be ridden without any trouble” near Camden, South Carolina. Further north along the Catawba River they describe several plains and “many fine fields of tilled lands” (Rostlund 1957 as cited in Barden 1997). In 1567 Spanish explorer Juan Pardo describes “very large and good plains... clear land... beautiful plains” including one near Charlotte North Carolina (Rostlund 1957 as cited in Barden 1997) during his travels through the Piedmont ecoregion. Other travelers (e.g., John Lederer in 1670; John Speed in 1676; John Lawson 1701; Catesby in 1720s (as cited in Barden 1997)) describe large savanna and prairie throughout the Piedmont ecoregion maintained by frequent burning. In winter 1701, John Lawson noted “the woods being newly burnt and on fire in many places,” and in the 1720s Mark Catesby observed many fires started by Native Americans, observing that “in February and March the inhabitants have a custom of burning the woods, which causes such a continual smoke, that not knowing the cause, it might be imagined to proceed from the fog... an annual custom of the Indians in their huntings, of setting the woods on fire many miles in extent” (as cited in Barden 1997).

The Coosa chiefdom, including an area from the confluence of the French Broad and Tennessee Rivers to around Talladega Alabama in the Southwestern Appalachians, Ridge and Valley, and Blue Ridge Mountains ecoregions, was described by the DeSoto expedition (1540) as “thickly settled in numerous towns with fields between, extending from one to another” (US Congress as cited in Williams 1989). Bartram (Van Doren 1928) describes endless savannas along the Tennessee River to the west of the Appalachians in the Interior Plateau ecoregion in his 1775 travels.

The first white settlers in western Kentucky encountered the Big Barrens (Interior River Valleys and Hills, and Interior Plateau ecoregions), encompassing an estimated 12,950–15,540 km². They described it as vast grassland with only occasional stunted trees unsuitable for building material, fences, and fuel (Owen 1856 and Hussey 1876 as cited in McInteer 1946). Early writers thought that the open prairie vegetation of the Big Barrens was created and maintained through frequent burning by Native Americans to attract game, and later by the first European settlers to maintain pasturage for cattle (Michaux 1805; McInteer 1946). The prairie vegetation of the Big Barrens may be partly explained by its unique limestone geology, but a rapid shift to forest vegetation as well as cultivated fields and pasture by the early 1800s – soon after white settlement – indicates that frequent fire was instrumental in maintaining these open, prairie conditions (see McInteer 1946; Baskin et al. 1994).

Historic accounts of the Ouachita Mountains ecoregion indicate that forests were more open, with lower tree density and basal area and more shortleaf pine than today; extensive prairies occurred in the western Ouachita Mountains (Foti and Glenn 1990). Le Page du Pratz of Natchez wrote of his travels from the Natchez to the St. Francis in the late 1720s “during the summer, the grass is too high for travelling;

whereas in the month of September the meadows, the grass of which is then dry, are set on fire and the ground becomes smooth, and easy to walk on: and hence it is, that at this time, clouds of smoke are seen for several days together to extend over a long track [sic] of country; sometimes to the extent of between 20 [100 km] and 30 [150 km] leagues in length, by two or three leagues in breadth, more or less..." and after rains "the game spread themselves all over the meadows and delight to feed on the new grass..." (du Pratz 1774 as cited in Foti and Glenn 1990). He writes further "The lands we find in going up the Black [Ouachita] River... in general may be considered as one very extensive meadow, diversified with little groves, and cut only by the Black River and little brooks, bordered with wood up to their sources" (du Pratz 1774 as cited in Foti and Glenn 1990). Dunbar and Hunter described the hills near the Ouachita River in 1804 and 1805 as being sometimes barren, with oak-dominated and pine woods variously in the area (Rowland 1930 as cited in Foti and Glenn 1990). In 1819–1820, botanist Edwin James described the Ouachita Mountains as covered with small and scattered trees or nearly treeless with some denser forests along the bases of mountains east of Hot Springs (James 1823 as cited in Foti and Glenn 1990). In 1844, Featherstonhaugh wrote that Indian fires thinned the forests but did not destroy them and "now that Indians have abandoned the country, the undergrowth is rapidly occupying the ground again" (Featherstonhaugh 1844 as cited in Foti and Glenn 1990).

During their 1818–1819 travels through the Ozark Highlands ecoregion, Henry Schoolcraft and Levi Pettibone noted valley bottoms of dense, pristine deciduous forest, valley walls covered with oak, hickory and pine forests, and uplands covered by a mosaic of prairie, oak savanna, oak woods with open undergrowth, and open grassy glades or barrens. These were probably enlarged and maintained by the Osage Indians who set fire to prairies to drive game into the wooded areas where the animals could be more easily killed (Rafferty 1996). Brackenridge wrote of his voyage up the Missouri River in 1811 that "... notwithstanding the ravages of fire, the marks of which are everywhere to be seen, the woods, principally hickory, ash, and walnut formed a forest tolerably close" (Brackenridge 1816 as cited in Spetich et al. 2011). Between the early nineteenth and late twentieth century, tree density in the Boston Mountains ecoregion tripled, increasing from 133 to 378 trees per ha, and from 123 to 287 per ha in the Ozark Highlands ecoregion, likely due to changes in the cultural practice of intentional burning (Foti 2004).

Clearly, Native Americans throughout the CHR created abundant open conditions in and surrounding their settlements by clearing for settlements and cropland, and by their frequent, widespread use of fire to manage fields, woodlands, and grasslands. Through their land management activities, Native Americans functioned as a keystone species by creating specific variants of early successional habitats required by different disturbance-dependent species. Without human-created habitats, species strongly associated with grasslands, savannas or prairies (e.g., elk, bison, bobwhite quail (*Colinus virginianus*), eastern meadowlark (*Sturnella magna*), field sparrow (*Spizella pucilla*), grasshopper sparrow (*Ammodramus savannarum*)), abandoned fields (e.g., yellow-breasted chat (*Icteria virens*), blue grosbeak (*Passerina caerulea*), or gardens and suburbs (e.g., song sparrow (*Melospiza melodia*), northern

mockingbird (*Mimus polyglotus*), or chipping sparrow (*Spizella passerina*) would likely have been uncommon or highly restricted in their distribution (e.g., beaver meadows) in the CHR (Table 12.1).

12.6.3 European Settlement

DeSoto's explorations in 1540 mark the first Native American contact with Europeans, and the start of Native American depopulation from newly introduced diseases and warfare (Yarnell 1998). European settlement of the CHR began in the mid- to late 1700s (Williams 1989). By the early 1800s most Native American populations had been severely reduced and secondary forests began to overtake their abandoned fields and farmlands (Yarnell 1998).

European settlers in the CHR continued the Native American practice of burning, and perhaps increased the area and frequency. Human habitation was concentrated in the river valleys and lowlands, where agriculture and burning made their greatest mark on the landscape and surrounding slopes. As the post-Civil War population of settlers increased in the CHR, so did populations of free-ranging cattle, pigs, and other domestic animals – even at higher elevations of the southern Appalachian ecoregion. The frequency – often annual – of burning large landscapes also increased to expand the area of woodlands and grasslands as pasturage (Ashe and Ayers 1901; Yarnell 1998). In 1885, ornithologist William Brewster (1886) wrote of the Blue Ridge Mountains ecoregion “Much of the low country, especially those portions bordering or near the larger streams, is under cultivation... Extensive areas, however, are everywhere still clothed in forest, either of vigorous second-growth or fine old timber.” Brewster (1886) also wrote “in many places... trees are scattered about in groups or singly at intervals of one or more hundred feet, with grassy openings in between, giving the country a park-like appearance.” Yellow pine forests, open woodlands, and grasslands remained abundantly available surrounding settled areas during this period due to the land management activities of European settlers (Ashe and Ayers 1901; Mattoon 1915; Ashe 1922; Balch 1928).

12.7 Recent Changes in Land Use and Condition: The Past 120 Years

Many variants of early successional or heavily disturbed habitats were likely at their historical high for several decades in the early 1900s for several reasons: (1) much of the CHR was systematically and progressively logged, resulting in large areas of young forest, with new areas cut as others grew up and matured; (2) large wildfires were common, ignited both intentionally and by sparks from trains using railroads built to extract timber, fueled by recently cutover, dry forestland; (3) family-run

farming practices commonly left weedy fencerows, fallow fields, and untilled patches; (4) the demise of American chestnut (*C. dentata*) created forests with large numbers of standing dead trees, followed by heavily perforated canopies lasting for many years as the ‘mighty giants’ fell and before their replacement in the canopy by oak and other forest tree species.

Conversely, both young forest and other early successional habitats may be at an historical low today because: (1) family-run farming operations have diminished since the 1960s, replaced by industrialized farming practices using equipment and herbicides that eliminate weed and brush cover; (2) forests on public lands have been allowed to mature for the past century, with dramatic reductions in regeneration harvest levels in recent decades (Shifley and Thompson 2011); (3) human population growth, land ownership patterns, urban sprawl, and second homes have fragmented forests and removed large areas from the wildland base.

Additionally, in the past century, humans have had substantial indirect impact on forest structure and tree species dominance by introducing non-native forest pests and pathogens that have effectively wiped out (or soon will) entire tree species within the CHR (Hicks 1998). In the early 1900s introduction of the non-native chestnut blight (*Cryphonectria parasitica*) gradually killed all mature American chestnut trees, then a dominant species throughout most of the CHR that composed up to 50 % of forest trees in some locations. Since then, gypsy moth (*Lymantria dispar*), balsam wooly adelgid (*Adelges piceae*), hemlock wooly adelgid (*Adelges tsugae*) and others have (or soon will) dramatically altered CHR by killing important tree species that are dominant in several forest types. Introductions of non-native wildlife species such as starlings (*Sturnus vulgaris*) and house sparrows (*Passer domesticus*), and increases in domestic and feral predators such as dogs (*Canis lupus familiaris*) and cats (*Felis catus*) also negatively affect wildlife populations and communities.

12.7.1 Reduced Fire Frequency: Suppression... or Changes in Cultural Burning Practices?

Many of the open woodlands, yellow pine forests, prairies, and other fire-maintained conditions in the CHR began to transition to closed canopy hardwood forests between the 1920s and 1940s, after the federal government began a campaign to curtail the use of fire across the landscape (Spetich et al. 2011). Fire suppression policies followed on the heels of several notable fires that burned vast areas of coniferous forest and killed people in the western USA or in northern states (e.g., upstate New York and Minnesota) (Spetich et al. 2011). Catastrophic crown fires are integral to the ecology of some coniferous ecosystems such as lodgepole pine (*P. contorta*) forests in the western USA, boreal forests in northern states (Schoennagel et al. 2004), and sand pine (*P. clausa*) scrub in Florida (Greenberg et al. 1995); in these ecosystems, mortality of mature pine trees is rapidly followed by release of their

seed onto the bare, fire-‘prepared’ seedbed, with regenerating forests developing directly back to the original pine forest type. In contrast, crown fires are nearly unheard of in hardwood forests of the CHR. Wildfires in the CHR are typically surface fires that generally do not kill mature trees, and result in few long-term changes to either fuels or forest structure as shrubs rapidly resprout, and leaf litter is replenished as deciduous leaves drop the following autumn (Stottlemeyer et al. 2006; Waldrop et al. 2007, 2010).

Historically, continuous, grassy fuels likely carried fire across frequently burned prairies, savannas and open woodlands that were locally interspersed with closed canopy forests throughout the CHR (Flatley et al. 2013) (e.g., Fig. 12.1). However, the relatively low frequency of lightning-ignited fire (e.g., Tuttle et al. Chap. 10; Greenberg et al. Chap. 1, Table 1.6), and the high fire frequency required to create and maintain a grassy ground cover, suggests that these habitats would have been rare in the absence of frequent, intentional burning by Native Americans (and subsequently by European settlers) (Lorimer 2001; Delcourt and Delcourt 2004; Guyette et al. 2006a; see Sect. 12.4.2). A hypothetical historical CHR landscape without forest management by Native Americans may have been dominated by primarily mature or old growth forest, interspersed with beaver-engineered wetlands and meadows along waterways, and subject to sporadic and varying natural disturbances (see Chaps. 1, 2, 3, 4, 5, 6, 7, 8, and 9, this volume) including occasional low-severity (e.g., low tree mortality) lightning-ignited fire; high-severity (e.g., heavy tree mortality) lightning-ignited fires were likely mainly limited to specific topographic positions and (or) under infrequent severe drought conditions. The decline of open, fire-maintained habitats in the CHR resulted from (1) eliminating the accepted cultural practice of frequently and repeatedly burning forests by Native American and (later) European settlers; and (2) suppressing wildfires that were predominantly ignited by humans, either intentionally or accidentally (e.g., Tuttle et al. Chap. 10; Greenberg et al. Chap. 1, Table 1.6 and Sect. 12.4.2), rather than suppression of natural (lightning-ignited) wildfires, or fire suppression policies per se.

12.8 Habitat Requirements of Disturbance-Dependent Wildlife: Were Natural Disturbances Enough?

Breeding bird species in the CHR differ in their associations with specific structural features (MacArthur and MacArthur 1961; Askins 2001), and across the gradient of conditions created by different natural and anthropogenic disturbances (Table 12.1). Many forest interior species, such as the wood thrush (*Hylocichla mustelina*) and ovenbird (*Seiurus aurocapillus*), are primarily associated with relatively large tracts of undisturbed closed-canopy forests but often use young, productive forests with abundant fruit and insect foods (Greenberg et al. 2011b) to forage during the post-fledgling period (Lanham and Whitehead 2011; Stoleson 2013). Others, such as the northern cardinal (*Cardinalis cardinalis*), eastern titmouse (*Baeolophus bicolor*),

Carolina chickadee (*Poecile carolinensis*), Carolina wren (*Thyrothorus ludovicianus*), eastern towhee (*Pipilo erythrophthalmus*), and American robin (*Turdus migratorius*) are generalists, able to thrive across a wide range of forest conditions and land uses.

Disturbance-dependent species are associated with open habitats created by disturbances, but may differ in their specific requirements. Some, such as indigo buntings, can thrive in most open habitats with adequate perch and nest sites, including small to extensive patches of young forest created by natural disturbances such as hurricane-related winds (Greenberg and Lanham 2001), tornadoes (Newbold 1996), or high-severity fire (e.g., Greenberg et al. 2013), or by anthropogenic disturbances such as recently harvested forest (e.g., Greenberg et al. 2014), shrubby pasturelands, or even utility rights-of-way (Lanham and Whitehead 2011). In contrast, requirements of many other CHR disturbance-dependent species are relatively specialized, and often associated with early successional habitats that are and historically were created primarily by humans (Table 12.1). On a hypothetical historical (Holocene) CHR landscape without humans, most of these more specialized species would likely have had lower population levels and narrower distributions. This suggests that many such species either co-evolved with Native American forest management, or were able to expand their ranges in response to land uses by Native Americans in the CHR.

12.8.1 Breeding Bird Response to Natural Disturbances

Our literature search indicates a paucity of studies on wildlife response to natural disturbances in the CHR. Studies of breeding birds in upland hardwood forests of the Ozark Mountains ecoregion of Arkansas (Prather and Smith 2003) and in the Ridge and Valley ecoregion of Tennessee (Newbold 1996) reported that the number and abundance of early successional species increased, and densities of most mature forest species remained high in tornado-damaged sites compared to mature forest. In the Blue Ridge Mountains ecoregion Greenberg and Lanham (2001) also reported higher species richness and relative abundance of breeding birds – including closed canopy-, edge-, and gap-associated species – in large (0.1–1.2 ha), ‘incomplete’ canopy gaps created by hurricane-related downbursts of wind that downed many, but not all trees. These studies of natural disturbances, together with studies of anthropogenically-disturbed (recently harvested) young forests in several different ecoregions indicate that the presence of a residual, partial canopy and dense shrubs or stump sprouts from damaged trees provide suitable habitat for forest canopy-, shrub-, and some disturbance-dependent species, resulting in higher species richness and density of breeding birds compared to mature forest (see Greenberg et al. 2014). However, many other disturbance-dependent breeding bird species of the CHR do not commonly occur in young forest, instead requiring more open ground, grass cover, or old field conditions (Table 12.1) that historically were created primarily by humans.

12.8.2 *Breeding Bird Response to Anthropogenic Disturbances*

Several breeding bird species in the CHR are uniquely associated with specific human-modified environments (Table 12.1). For example, eastern meadowlarks require open fields with tall, continuous grass cover. Bobwhite quail require continuous, tall grass and shrub cover with open- or no forest canopy. Golden-winged warblers (*Vermivora chrysoptera*) require open, grassy areas with some shrub and sapling cover in a forested matrix, at elevations greater than 850 m in the Blue Ridge Mountains ecoregion or lower elevations at higher latitudes (Rosenberg et al. [in press](#)). Chipping sparrows require open, mowed areas. Eastern bluebirds (*Sialia sialis*) require wide open fields where nest boxes are provided (or high-severity burns with standing snags (Greenberg et al. 2013), which are rare in the CHR). Field sparrows, yellow-breasted chats, and blue grosbeaks require abandoned pastures and old fields with mosaics of grass, shrubs, and saplings. Song sparrows and northern mockingbirds occur almost exclusively in garden habitats or suburban residential areas (Table 12.1).

By creating required habitat conditions for species that would otherwise be rare or limited in distribution, humans – first Native Americans and later European settlers – have functioned as a keystone species for thousands of years. Native Americans created and maintained savannas, prairies, and open woodlands by frequent, intentional burning; these habitats were used by elk and bison that helped to maintain them by grazing. Villages and agricultural fields were created by clearing and burning, and abandoned to revert to old fields, yellow pine forests, or other successional conditions. Historically, these anthropogenically-created habitats allowed many disturbance-dependent breeding bird species with specific requirements for differing variants of early successional habitats to occur and thrive within the CHR.

12.9 **Historic Abundance and Shifting Distributions of Breeding Birds**

Habitat availability affects both local and regional distributions of mobile species such as disturbance-dependent breeding birds that can opportunistically exploit ephemeral habitats. Historically, populations of breeding bird species dependent on anthropogenically-created habitats such as gardens, old fields, and grasslands likely tracked spatially and temporally dynamic Native American populations, settlement patterns, and increasing reliance on agricultural crops. Over the past several decades changes in land use and management practices have reduced the quantity and suitability of anthropogenically-disturbed habitats for many disturbance-dependent breeding bird species, with direct and indirect effects on their populations. The greater prairie chicken (*Tympanuchus cupido*), a grassland associate once common in the Big Barrens region of south-central Kentucky were extirpated largely due to the disappearance of vast, fire-maintained prairies within the region (Hunter et al. 2001). More than 70 % of eastern grassland-associated breeding bird species such

as grasshopper sparrow, savannah sparrow (*Passerculus sandwichensis*), Henslow's sparrow (*Ammodramus henslowii*), Vesper sparrow (*Pooecetes gramineus*), bobolink (*Dolichonyx oryzivorus*), and eastern meadowlark have significantly declined over the past several decades (Askins 1993, 2000, 2001; Knopf 1994; Sauer et al. 2000) due to intensive management of pasture and haylands and loss or fragmentation of agricultural grasslands to development.

Similarly, nearly half of shrub-early successional breeding birds have significantly declined over the past several decades (Sauer et al. 2000). The disappearance of family farms, where low-intensity livestock grazing created and maintained a mosaic of grass, shrubs, and saplings, has resulted in the steep decline in golden-winged warbler populations in the Blue Ridge Mountains ecoregion where they were once common (Rosenberg et al. *in press*). Other bird species that depend on scrub/shrub or other early successional habitats, such as blue-winged warbler (*Vermivora pinus*), prairie warbler (*Setophaga discolor*), yellow-breasted chat, common yellowthroat (*Geothlypis trichas*), chestnut-sided warbler (*Setophaga pennsylvanica*), American woodcock (*Scolopax minor*), field sparrow, indigo bunting, brown thrasher (*Toxostoma rufum*), and eastern towhee, have declined from 10 to 60 % in the eastern USA over the past 40 years (Partners in Flight 2013). Declines in ruffed grouse (*Bonasa umbellus*) populations are associated with a dearth of dense, sapling stage forest that develops 8–15 years after regeneration harvests (Thompson and Dessecker 1997). This is partly due to changes in federal land management policies that have greatly reduced timber harvests on National Forests. These strong correlations between land use change and populations of bird species associated with specific land uses or conditions suggests that their populations, and those of other wildlife species with similar habitat requirements, also likely increased or decreased historically with the shifting availability of suitable habitats created by weather-related natural disturbances, pests and pathogens, keystone wildlife species, and humans.

Historical shifts in the geographic distribution of some breeding bird species are documented, and are associated with changes in habitat availability corresponding with a dynamic climate and changing land uses or conditions. For example, red-cockaded woodpeckers (*Picoides borealis*) occurred until only a few decades ago at the northern extent of their range in isolated stands of shortleaf or Virginia pine or pine-oak in the Southwestern Appalachians and Blue Ridge Mountains ecoregions of Tennessee and Kentucky (Nicholson 1977). These small populations have disappeared as their fire-maintained yellow pine forest habitats declined due to southern pine beetle outbreaks (Nicholson 1977; see Nowak et al. Chap. 4), elimination of the cultural practice of intentional burning, and fire suppression. Historically, red-cockaded woodpeckers and other yellow pine forest associates such as brown-headed nuthatches (*Sitta pusilla*) and pine warblers (*Setophaga pinus*) may have been more widely distributed in the CHR in yellow pine forests that commonly established on farmlands and old fields abandoned first by Native Americans and later by European settlers through the mid-twentieth century.

Similarly, the breeding distribution of golden-winged warblers has expanded and contracted within some CHR ecoregions over the past 150 years in response to

regional changes in land use or condition, hence habitat availability (Rosenberg et al. [in press](#)). During the late nineteenth and early twentieth century widespread timber cutting and later abandonment of agricultural lands provided abundant early successional habitat for golden-winged warblers (Rosenberg et al. [in press](#)). In his visits to the Blue Ridge Mountains ecoregion Brewster (1886) wrote “Common in Jackson and Macon Counties, ranging 2,000–4,100 feet [610–1,250 meters], and haunting open oak woodlands, and second growth on hillsides. In many such tracts it seemed to be the most abundant and characteristic species...” Just a century later, golden-winged warblers only occur in isolated, higher elevation locations where habitat exists (Rosenberg et al. [in press](#)).

Brewster (1886) went on to describe abundant populations of other disturbance-dependent breeding bird species that today are relatively rare in the Blue Ridge Mountains ecoregion. Bobwhite quail were “Abundant everywhere, in grain fields in the valleys, oak woodland over the mountain sides, and throughout the balsam forests that cover the higher peaks and ridges...”; golden eagles [*Aquila chrysaetos*] were “frequently seen... said to breed on inaccessible cliffs and ledges of the higher mountains, whence they often descend into the valleys to prey on young geese, lambs, etc.” Bartram noted many species associated with early successional habitats such as blue linnet (indigo bunting), yellow-breasted chats, and golden-winged warblers (Van Doren 1928).

Just as some disturbance-dependent species have declined or even disappeared from large areas of the CHR, they may persist in patches of suitable habitat, or colonize or recolonize areas if suitable habitats become available. For example, Henslow’s sparrows were recorded on the Cumberland Plateau in Tennessee (Southwestern Appalachians ecoregion) for the first time after a large, local farm was left unmanaged for a few years, allowing suitable grassland conditions to develop (Lance 2014). American kestrels (*Falco sparverius*) and bobwhite quail are common in and near the large, open, grassy meadows at the Sandy Mush Game Lands in Buncombe County, but rare throughout most of western North Carolina. Prairie warblers (Greenberg et al. 2013) and red-headed woodpeckers (*Melanerpes erythrocephalus*) (Greenberg et al. unpubl. data) recently colonized tracts of upland hardwood forest in the Blue Ridge Mountains ecoregion, within several years after experimental high-severity burns killed most trees. Bobolinks, rare in the CHR, recently colonized hayfields managed with low-intensity mowing in Watauga County, North Carolina (K. Weeks, pers. obs.). These examples illustrate how ‘if you build it they will come,’ and suggest that managing for specific variants of early successional habitats could increase populations and distributions of targeted disturbance-dependent species.

12.10 Wildlife Conservation and Management within the Historic Range of Variation

Historically, humans were a keystone species, having a profound influence on the abundance, distribution, and diversity of disturbance dependent breeding birds and other wildlife species. Land management activities and land uses by Native

Americans such as clearing for settlements and agriculture, farmland abandonment, and frequent burning to create and maintain open grasslands and woodlands provided variants of early and later successional habitats for specialized species that would otherwise have been rare or absent in the CHR. On a hypothetical historical landscape without humans, mobile disturbance-dependent species that require edge and young forest conditions would likely have been transient in their distributions as natural disturbances created suitable conditions lasting only several years before canopy closure. However, except for those that could use once-common beaver meadows, breeding bird species requiring grassland, old field, garden-‘suburb,’ open woodland, and even yellow pine forest habitats (with some exceptions) would have been uncommon or absent within the CHR.

Forest management within the historic range of variation of natural disturbances first requires a subjective decision regarding whether prehistoric land management activities by humans should be regarded as a natural disturbance. If not, it becomes challenging to envision an historic CHR that approaches accuracy, because humans have occupied the CHR for more than 13,000 years; prior to human occupation, much of the CHR was in tundra-boreal forest with megafauna as primary agents of disturbance. Further, under that paradigm forest management is irrelevant; a *laissez faire* approach will allow non-anthropogenic disturbances to occur regardless, and any management would, by definition, be outside the historic range of variation. Both a ‘no management’ and a ‘manage for a landscape as it might have been without humans’ approach are confounded by a current forest condition that has been modified by humans for millennia and likely alters and influences the effects of natural disturbances. If so, then what moment in time should be selected to reference ‘historic conditions’ in a long and dynamic history of human population levels, settlement patterns, and land management practices – both Native American and European – on the landscape? Reference conditions including specific quantities, patch sizes, compositions, and structures simulating the gradient of conditions created by both anthropogenic and non-anthropogenic disturbances must be specifically defined.

Alternatively, forest and land use planning for diverse wildlife conservation might more logically start with clear objectives, and proceed with management activities targeted toward attaining them. Rather than debating an unknowable and dynamic historical condition, or what should or should not be considered a natural disturbance, a more pertinent question might be (1) do we want to maintain viable populations of diverse disturbance-dependent species? If yes, then (2) where, how much, and what methods should be used to attain targeted forest composition and structural conditions, and different variants of early successional habitats required by those species?

Clear conservation objectives and targeted management activities are confounded by the ‘real world’ of conservation planning, land management, and current forest condition (Foster and Aber 2004; Warburton et al. 2011; Zenner Chap. 14). The majority (90 %) of land within the CHR is in private ownership (see Greenberg et al. Chap. 1); its use and management is the decision of landowners, and may or may not be compatible with a landscape level conservation vision or strategy. Much of the land base that was historically mature or disturbed forest, or variants of early

successional habitats managed by Native Americans is now urban, suburban, plantation, even-aged forest, or industrialized agriculture; tracts of land that were once continuous wildlands are now fragmented by development. On public lands, where large tracts provide the greatest opportunity for wildlife and wildlands conservation, policy, public opinion, and human values other than biodiversity must also be considered including (among others) aesthetics, recreation, endangered species, and forest products. Conservation management on a landscape scale will require a multi-pronged strategy by citizens, local, state, and tribal governments, non-governmental organizations, and the federal government to address deficiencies in the conservation of natural resources that Americans value. An important, currently deficient component of conservation delivery is management for disturbance-dependent wildlife and their habitats.

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References

- Ashe, W. W. (1922). Forest types of the Appalachian and White Mountains. *Journal of the Elisha Mitchell Scientific Society*, 37, 183–198.
- Ashe, W. W., & Ayers, H. B. (1901). Forests and forest conditions in the southern Appalachians. In *A report of the secretary of agriculture in relation to the forests, rivers, and mountains of the southern Appalachian region* (pp. 45–68). Washington, DC: US Gov Print Office.
- Askins, R. A. (1993). Population trends in grassland, shrubland, and forest birds in eastern North America. *Current Ornithology*, 11, 1–34.
- Askins, R. A. (2000). *Restoring North America's birds*. New Haven: Yale University Press.
- Askins, R. A. (2001). Sustaining biological diversity in early successional communities: The challenge of managing unpopular habitats. *Wildlife Society Bulletin*, 29, 407–412.
- Askins, R. A. (2014). *Saving the world's deciduous forest*. New Haven: Yale University Press.
- Baker, B. W., & Hill, E. P. (2003). Beaver (*Castor canadensis*). In G. A. Feldhamer, B. C. Thompson, & J. A. Chapman (Eds.), *Wild mammals of North America: Biology, management and conservation* (2nd ed., pp. 288–310). Baltimore: The Johns Hopkins University Press.
- Balch, R. E. (1928). *The influence of the southern pine beetle on forest composition in western North Carolina*. Thesis, New York State College of Forestry, Ithaca.
- Barden, L. S. (1997). Historic prairies in the Piedmont of North and South Carolina, USA. *Natural Areas Journal*, 17, 149–152.
- Baskin, J. M., Baskin, C. C., & Chester, E. W. (1994). The big barrens region of Kentucky and Tennessee: Further observations and considerations. *Castanea*, 59, 226–254.
- Brewster, W. (1886). An ornithological reconnaissance in western North Carolina. *Auk*, 3(94–112), 173–179.
- Burney, D. A. (1993). Recent animal extinctions: Recipes for disaster. *American Scientist*, 81, 531–541.
- Burney, D. A., & Flannery, T. F. (2005). Fifty millennia of catastrophic extinctions after human contact. *Trends in Ecology and Evolution*, 20, 395–401.
- Carroll, W. D., Kapeluck, P. R., Harper, R. A., & Van Lear, D. H. (2002). Background paper: Historical overview of the southern forest landscape and associated resources. In D. N. Wear &

- J. G. Greis (Eds.), *Southern forest resource assessment* (General technical report SRS 53, pp. 583–605). Asheville: USDA Forest Service Southern Research Station.
- Chapman, J., Delcourt, P. A., Criddlebaugh, P. A., Shea, A. B., & Delcourt, H. R. (1982). Man-land interaction: 10,000 years of American impact on native ecosystems in the lower Little Tennessee River Valley, eastern Tennessee. *Southeastern Archaeology*, *1*, 115–121.
- Clark, P. U., Dyke, A. S., Shakun, J. D., Carlson, A. E., Clark, J., Wohlfarth, B., Mitrovica, J. X., Hostetler, S. W., & McCabe, A. M. (2009). The last glacial maximum. *Science*, *325*, 710–714.
- Collins, S. L., & Uno, G. E. (1985). Seed predation, seed dispersal, disturbance in grasslands: A comment. *The American Naturalist*, *125*, 866–872.
- Delcourt, H. R., & Delcourt, P. A. (1997). Pre-Columbian Native American use of fire on southern Appalachian landscapes. *Conservation Biology*, *11*, 1010–1014.
- Delcourt, P. A., & Delcourt, H. R. (2004). *Prehistoric Native Americans and ecological change: Human ecosystems in eastern North America since the Pleistocene*. Cambridge: Cambridge University Press.
- Delcourt, P. A., Delcourt, H. R., Ison, C. R., Sharp, W. E., & Gremillion, K. J. (1998). Prehistoric human use of fire, the eastern agricultural complex, and Appalachian oak-chestnut forests: Paleoecology of cliff palace pond, Kentucky. *American Antiquity*, *63*, 263–278.
- Denevan, W. M. (1992). The pristine myth: The landscape of the Americas in 1492. *Annals of the Association of American Geographers*, *82*, 369–385.
- Dickinson, W. R. (2000). Changing times: The Holocene legacy. *Environmental History*, *5*, 483–502.
- Dogett, C. A. (1993). A method to assess large-scale forest damage: A case study. *Southern Journal of Applied Forestry*, *17*, 197–199.
- Ellsworth, J. W., & McComb, B. C. (2003). Potential effects of passenger pigeon flocks on the structure and composition of presettlement forests of eastern North America. *Conservation Biology*, *17*, 1548–1558.
- Evans, K. E., & Pobasco, G. E. (1977). *Wildlife of the prairies and plains* (General technical report NC 29). St. Paul: USDA Forest Service North Central Forest Experiment Station.
- Flatley, W. T., Lafon, C. W., & Grissino-Mayer, H. D. (2013). Fire history, related to climate and land use in three southern Appalachian landscapes in the eastern United States. *Ecological Applications*, *23*, 1250–1266.
- Foster, D. R., & Aber, J. D. (2004). *Forests in time: The environmental consequences of 1,000 years of change in New England*. New Haven: Yale University Press.
- Foti, T. L. (2004). Upland hardwood forests and related communities of the Arkansas Ozarks in the early 19th century. In M. A. Spetich (Ed.), *Upland oak ecology symposium: History, current conditions, and sustainability* (General technical report SRS 73, pp. 21–29). Asheville: USDA Forest Service Southern Research Station.
- Foti, T. L., & Glenn, S. M. (1990, September 19–20). The Ouachita Mountain landscape at the time of settlement. In *Conference on restoring old growth forests in the interior highlands of Arkansas and Oklahoma* (pp. 49–65). Morrilton: Winrock International.
- Fritz, G. J. (2000). Levels of native biodiversity in eastern North America. In P. E. Minnis & W. J. Elisens (Eds.), *Biodiversity and Native America* (pp. 223–247). Norman: University of Oklahoma Press.
- Gill, J. L., Williams, J. W., Jackson, S. T., Lininger, K. B., & Robinson, G. S. (2009). Pleistocene megafaunal collapse, novel plant communities, and enhanced fire regimes in North America. *Science*, *326*, 1100–1103.
- Greenberg, C. H., & Lanham, D. J. (2001). Breeding bird assemblages of hurricane-created gaps and adjacent closed canopy forest in the southern Appalachians. *Forest Ecology and Management*, *153*, 251–260.
- Greenberg, C. H., Neary, D. G., Harris, L. D., & Linda, S. (1995). Vegetation recovery following high-intensity wildfire and silvicultural treatments in sand pine scrub. *The American Midland Naturalist*, *133*, 149–163.

- Greenberg, C. H., Collins, B. S., Thompson, F. R., III, & McNab, H. R. (2011a). What are early successional habitats, how can they be sustained, and why are they important? In C. H. Greenberg, B. S. Collins, & F. R. Thompson III (Eds.), *Sustaining young forest communities: Ecology and management of early successional habitats in the Central Hardwood Region, USA* (pp. 1–10). New York: Springer.
- Greenberg, C. H., Perry, R. W., Harper, C. A., Levey, D. J., & McCord, J. M. (2011b). The role of recently disturbed upland hardwood forest as high quality food patches. In C. H. Greenberg, B. S. Collins, & F. R. Thompson III (Eds.), *Sustaining young forest communities: Ecology and management of early successional habitats in the Central Hardwood Region, USA* (pp. 121–141). New York: Springer.
- Greenberg, C. H., Waldrop, T. A., Tomcho, J., Phillips, R. J., & Simon, D. (2013). Bird response to fire severity and repeated burning in upland hardwood forest. *Forest Ecology and Management*, *304*, 80–88.
- Greenberg, C. H., Franzreb, K. E., Keyser, T. L., Zarnoch, S. J., Simon, D. M., & Warburton, G. S. (2014). Short-term response of breeding birds to oak regeneration treatments in upland hardwood forest. *Natural Areas Journal*, *34*, 409–422.
- Guyette, R. P., Dey, D. C., Stambaugh, M. C., & Muzika, R. (2006a). Fire scars reveal variability and dynamics of eastern fire regimes. In M. B. Dickinson (Ed.), *Proceedings of fire in eastern oak forests: Delivering science to land managers* (General technical report NRS-P 1, pp. 20–39). Newton Square: USDA Forest Service Northern Research Station.
- Guyette, R. P., Spetich, M. A., & Stambaugh, M. C. (2006b). Historic fire regime dynamics in the Boston Mountains, Arkansas, USA. *Forest Ecology and Management*, *234*, 293–304.
- Hart, J. L., & Buchanan, M. L. (2012). *History of fire in eastern oak forests and implications for restoration. Proceedings of 4th fire in eastern oak forests conference* (General technical report NRS-P 102). Newtown Square: USDA Forest Service Northern Research Station.
- Hey, D. L., & Phillippi, N. S. (1995). Flood reduction through wetland restoration: The Upper Mississippi River Basin as a case study. *Restoration Ecology*, *3*, 4–17.
- Hicks, R. R. (1998). *Ecology and management of central hardwood forests*. New York: Wiley and Sons.
- Hunter, W. C., Buehler, D. A., Canterbury, R. A., Confer, J. L., & Hamel, P. B. (2001). Conservation of disturbance-dependent birds in eastern North America. *Wildlife Society Bulletin*, *29*, 440–455.
- Innes, R. J. (2011). *Cervus elaphus*. In *Fire effects information system*, [Online]. USDA Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory (Producer). <http://www.fs.fed.us/database/feis/>. Accessed 18 Nov 2014.
- Jenkins, M. A., Klein, R. N., & McDaniel, V. L. (2011). Yellow pine regeneration as a function of fire severity and post-burn stand structure in the southern Appalachian Mountains. *Forest Ecology and Management*, *262*, 681–691.
- Knopf, F. L. (1994). Avian assemblages on altered grasslands. *Studies in Avian Biology*, *15*, 247–257.
- Koch, P. L., & Barnosky, A. D. (2006). Late quaternary extinctions: State of the debate. *Annual Review of Ecology, Evolution, and Systematics*, *37*, 215–250.
- Lance, T. (2014). *The Henslow's sparrow thrives at Fort Campbell* (pp. 16–19). Tennessee Conservation, May/June 2014.
- Lanham, D. J., & Whitehead, M. A. (2011). Managing early successional habitats for wildlife in novel places. In C. H. Greenberg, B. S. Collins, & F. R. Thompson III (Eds.), *Sustaining young forest communities: Ecology and management of early successional habitats in the Central Hardwood Region, USA* (pp. 209–224). New York: Springer.
- Loftis, D. L., Schweitzer, C. J., & Keyser, T. L. (2011). Structure and species composition of upland hardwood communities after regeneration treatments across environmental gradients. In C. H. Greenberg, B. S. Collins, & F. R. Thompson III (Eds.), *Sustaining young forest communities: Ecology and management of early successional habitats in the Central Hardwood Region, USA* (pp. 59–71). New York: Springer.

- Lorimer, C. G. (2001). Historical and ecological roles of disturbance in eastern North American forests: 9,000 year of change. *Wildlife Society Bulletin*, 29, 425–439.
- MacArthur, R. H., & MacArthur, J. W. (1961). On bird species diversity. *Ecology*, 42, 594–598.
- Mattoon, W. R. (1915). *Life history of the shortleaf pine* (Bulletin of the U.S. Department of Agriculture 244). Washington, DC: U.S. Department of Agriculture.
- McClafferty, J. A. (2000). *An assessment of the biological and socioeconomic feasibility of elk restoration in Virginia*. Thesis, Virginia Polytechnical Institute and State University, Blacksburg.
- McInteer, B. B. (1946). A change from grassland to forest vegetation in the “Big Barrens” of Kentucky. *The American Midland Naturalist*, 35, 276–282.
- McNab, W. H., Greenberg, C. H., & Berg, E. C. (2004). Landscape distribution of large hurricane-related canopy gaps in a southern Appalachian watershed. *Forest Ecology and Management*, 196, 435–447.
- Michaux, F. A. (1805). *Travels to the westward of the Allegheny Mountains, in the states of the Ohio, Kentucky, and Tennessee, in the year 1802*. Whitefish: Kessinger Legacy Reprints.
- Milner, G. R., & Chaplin, G. (2010). Eastern North American population at CAAD 1500. *American Antiquity*, 75, 707–726.
- Mosimann, J., & Martin, P. S. (1975). Simulating overkill by Paleoindians. *American Scientist*, 63, 304–313.
- Moss, E. D. (2001). *Distribution and reproductive success of native grassland birds in response to burning and field size at Fort Campbell Military reservation: Special focus on Henslow’s and grasshopper sparrows*. Thesis, University of Tennessee, Knoxville.
- Naiman, R. J., Johnston, C. A., & Kelley, J. C. (1988). Alteration of North American streams by beaver. *Bioscience*, 38, 753–762.
- Nesbitt, W. A., & Netboy, A. (1946). The history of settlement and land use in the Bent Creek forest. *Agricultural History*, 20, 121–127.
- Newbold, C. D. (1996). *The effects of tornado and clearcut disturbances on breeding birds in a Tennessee oak-hickory (Quercus-Carya spp.) forest*. Thesis, University of Tennessee, Knoxville.
- Nicholson, C. P. (1977). The red-cockaded woodpecker in Tennessee. *The Migration*, 48, 53–62.
- O’Gara, B. W., & Dundas, R. G. (2002). Distribution: Past and present. In D. E. Toweill & J. T. Ward (Eds.), *North American elk: Ecology and management* (pp. 67–119). Washington, DC: Smithsonian Institution Press.
- Partners in Flight Science Committee. (2013). *Population estimates database, version 2013*. <http://rmbo.org/pifpopestimates>. Accessed 29 Apr 2014.
- Peek, J. M. (2003). Wapiti, *Cervus elaphus*. In G. A. Feldhamer, B. C. Thompson, & J. A. Chapman (Eds.), *Wild mammals of North America: Biology, management, and conservation* (2nd ed., pp. 877–887). Baltimore: Johns Hopkins University.
- Perkins, K. A. (2006). *Cerulean warbler selection of forest canopy gaps*. Thesis, West Virginia University, Morgantown.
- Prather, J. W., & Smith, K. G. (2003). Effects of tornado damage on forest bird populations in the Arkansas Ozarks. *The Southwestern Naturalist*, 48, 292–297.
- Putnam, R. J. (1996). *Competition and resource partitioning in temperate ungulate assemblages*. London: Chapman and Hall.
- Rafferty, M. D. (1996). Introduction. In *Rude pursuits and rugged peaks: Schoolcraft’s Ozark journal 1818–1819* (pp. 1–15). Fayetteville: The University of Arkansas Press.
- Reynolds, H. W., Glaholt, R. D., & Hawley, A. W. L. (1982). Bison. In J. A. Chapman & G. A. Feldhamer (Eds.), *Wild mammals of North America: Biology, management and economics* (pp. 972–1007). Baltimore: The Johns Hopkins University Press.
- Rosell, F., Bozsér, O., Collen, P., & Parker, H. (2005). Ecological impact of beavers *Castor fiber* and *Castor canadensis* and their ability to modify ecosystems. *Mammal Review*, 35, 248–276.
- Rosenberg, K. V., Will, T., Buehler, D. A., Barker Swarthout, S., Thogmartin, W. E., & Chandler, R. (in press). *Historical and current distribution and population status of Golden-winged Warbler*. Studies in Avian Biology.

- Rostlund, E. (1960). The geographic range of the historic bison in the southeast. *Annals of the Association of American Geographers*, 50, 395–407.
- Sauer, J. R., Hines, J. E., Thomas, I., Fallon, J., & Gough, G. (2000). *The North American breeding bird survey, results and analysis 1966–1999, Version 98.1*. Laurel: USGS Patuxent Wildlife Research Center.
- Schoennagel, T., Veblen, T. T., & Romme, W. H. (2004). The interaction of fire, fuels, and climate across Rocky Mountain forests. *BioScience*, 54, 661–676.
- Schorger, A. W. (1955). *The passenger pigeon: Its natural history and extinction*. Madison: University of Wisconsin Press.
- Schreiner, E. G., Krueger, K. A., Kirsten, A., Happe, P. J., & Houston, D. B. (1996). Understory patch dynamics and ungulate herbivory in old-growth forests of Olympic National Park, Washington. *Canadian Journal of Forest Research*, 26, 255–265.
- Schroeder, M. J., & Buck, C. J. (1970). *Fire weather* (Agriculture handbook 360). Washington, DC: USDA Forest Service.
- Seton, E. T. (1929). *Lives of game animals*. Garden City: Doubleday, Doran.
- Shifley, S. R., & Thompson, F. R., III. (2011). Spatial and temporal patterns in the amount of young forests and implications for biodiversity. In C. H. Greenberg, B. S. Collins, & F. R. Thompson III (Eds.), *Sustaining young forest communities: Ecology and management of early successional habitats in the Central Hardwood Region, USA* (pp. 73–95). New York: Springer.
- Simmons, G. (1999). *The lost landscape of the Piedmont*. Salisbury. <http://www.learnnc.org/lp/pages/1683>
- Spetich, M. A., Perry, R. W., Harper, C. A., & Clark, S. L. (2011). Fire in eastern hardwood forests through 14,000 years. In C. H. Greenberg, B. S. Collins, & F. R. Thompson III (Eds.), *Sustaining young forest communities: Ecology and management of early successional habitats in the Central Hardwood Region, USA* (pp. 41–58). New York: Springer.
- Stoleson, S. H. (2013). Condition varies with habitat choice in postbreeding forest birds. *Auk*, 130, 417–428.
- Stottlemeyer, A. D., Shelburne, V. B., Waldrop, T. A., Rideout-Hanzak, S., & Bridges, W. C. (2006). Preliminary fuel characterization of the Chauga Ridges region of the southern Appalachian Mountains. In K. F. Connor (Ed.), *Proceedings of 13th biennial southern silvicultural research conference* (General technical report SRS 92, pp. 510–513). Asheville: USDA Forest Service Southern Research Station.
- Svenning, J. (2002). A review of natural vegetation openness in north-western Europe. *Biological Conservation*, 104, 133–148.
- Tesky, J. L. (1995). *Bos bison*. In *Fire effects information system*, [Online]. USDA Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory (Producer). <http://www.fs.fed.us/database/feis/>. Accessed 18 Nov 2014.
- Thompson, F. R., III, & Dessecker, D. R. (1997). *Management of early-successional communities in central hardwood forests with special emphasis on the ecology and management of oaks, ruffed grouse, and forest songbirds* (General technical report NC 195). St. Paul: USDA Forest Service North Central Research Station.
- US Fish and Wildlife Service. (2001). *Bog turtle (Clemmys muhlenbergii), northern population recovery plan*. <http://www.fws.gov/northeast/nyfo/es/bogturtle.pdf>. Accessed 22 Jan 2015.
- Van Doren, M. (1928). *Travels of William Bartram*. New York: Dover Publications Inc.
- Van Lear, D. H., & Waldrop, T. A. (1989). *History, uses, and effects of fire in the Appalachians* (General technical report SE 54). Asheville: USDA Forest Service Southeastern Forest Experiment Station.
- VDGIF. (2010). *Elk restoration and management options for southwest Virginia*. Virginia Department of Game and Inland Fisheries Publication. <http://www.dgif.virginia.gov/wildlife/elk/management-plan/>. Accessed 22 Jan 2015.
- Waldrop, T. A., Brudnak, L., & Rideout-Hanzak, S. (2007). Fuels of disturbed and undisturbed sites in the southern Appalachian Mountains, USA. *Canadian Journal of Forest Research*, 37, 1134–1141.

- Waldrop, T., Phillips, R. A., & Simon, D. A. (2010). Fuels and predicted fire behavior in the southern Appalachian Mountains after fire and fire surrogate treatments. *Forestry Sciences*, 56, 32–45.
- Walton, E. M. (2006). *Using remote sensing and geographical information science to predict and delineate critical habitat for the bog turtle, Glyptemys muhlenbergii*. Thesis, University of North Carolina, Greensboro.
- Warburton, G. S., Harper, C. A., & Weeks, K. (2011). Conservation of early successional habitats in the Appalachian Mountains: A manager's perspective. In C. H. Greenberg, B. S. Collins, & F. R. Thompson III (Eds.), *Sustaining young forest communities: Ecology and management of early successional habitats in the Central Hardwood Region, USA* (pp. 225–251). New York: Springer.
- Williams, M. (1989). *Americans and their forests: An historical geography*. New York: Cambridge University Press.
- Woodward, A., Schreiner, E. G., Houston, D. B., & Moorhead, B. B. (1994). Ungulate-forest relationships on the Olympic Peninsula: Retrospective exclosure studies. *Northwest Science*, 68, 97–110.
- Yarnell, S. L. (1998). *The southern Appalachians: A history of the landscape* (General technical report SRS 18). Asheville: USDA Forest Service Southern Research Station.
- Yeoman, B. (2014). *Why the passenger pigeon went extinct*. Audubon, May-June 2014.
- Zobel, D. B. (1969). Factors affecting the distribution of *Pinus pungens*, an Appalachian endemic. *Ecological Monographs*, 39, 304–333.