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In My Opinion

Open Forest Management for Early Successional Birds

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ABSTRACT Wildlife biologists classify some bird species as early successional because of apparent dependence on early successional vegetation such as forbs, grasses, shrubs, and small trees. We propose that many "early successional" species were more often associated with open forests such as savannas and woodlands, which covered a much greater extent of the eastern United States under historical disturbance regimes than more ephemeral early successional forest. We draw on several lines of evidence, including knowledge of historical ecosystems and disturbance, landscape analyses, and general literature review to evaluate benefits of open forest ecosystems for early successional birds. Early successional forests covered 1–13% of forestlands in the eastern United States prior to Euro-American settlement, whereas open forests covered large extents of the United States. Many early successional songbirds reach great densities in open forests and potentially greater numbers in landscapes with historical amounts of open forest than in present-day landscapes and those under intensive even-aged forest management. Restoration and management of open forests has not been prioritized or well-articulated for management of early successional birds and other species. Although both early successional forests and open forests provide habitat for birds, we suggest the great reduction in the historical extent of open forests needs to be addressed through greater restoration and management of open forests if we want to better meet the needs of some early successional birds and other wildlife.

KEY WORDS fire, forest management, historical, savannas, wildlife, woodlands.

Species such as northern bobwhite (*Colinus virginianus*), blue-winged warbler (*Vermivora cyanoptera*), eastern towhee (*Pipilo erythrophthalmus*), prairie warbler (*Setophaga discolor*), white-eyed vireo (*Vireo griseus*), and yellow-breasted chat (*Icteria virens*) often are referred to as early successional birds because their habitat is created or maintained by disturbance. Most early successional species have undergone consistent declines during the past 50 years and are species of concern (Askins 2001, Hunter et al. 2001, Thompson and DeGraaf 2001, Sauer et al. 2017). During the past 25 years, wildlife biologists have stressed the importance of managing early successional habitat for these bird species (Litvaitis 1993, Greenberg et al. 2011, King and Schlossberg 2014).

"Early successional habitat" has been used as an umbrella term to capture grasslands, shrublands, savannas, woodlands, and regenerating forests that are successional. A common feature of these vegetation types is that they typically have a well-developed ground layer with grasses and forbs and varying amounts of shrubs and trees. Grasslands, shrublands, savannas, and woodlands generally persisted on the landscape because of historical disturbance regimes that included frequent fire and grazing or site conditions such as poor, thin, or wet soils. In contrast, early successional, or regenerating forest generally is ephemeral and succeeds to dense closed forest in 5–20 years, depending on forest type and site conditions, and subject to less frequent understory disturbance than savannas and woodlands (Thompson and DeGraaf 2001, Greenberg et al. 2011). Without additional disturbance, early successional forest quickly succeeds in structure and composition from herbaceous vegetation to trees, after which change in structure and tree species composition becomes a relatively slow process.

Early successional, regenerating forests provide habitat for bird species; nonetheless, many of the bird species associated with early successional forests historically may have occurred more frequently in open forests such as savannas and woodlands. Both open forests and early successional forests have decreased greatly in extent during the past century, concurrent with declines in early successional birds. Forest clearing and extensive, low-intensity agricultural land use increased early successional forests during Euro-American settlement (ca. 1620 to 1900) and perhaps up to 60% of forested land was early successional in many eastern states during the late 1800s and early 1900s (Lorimer 2001).

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However, prior to Euro-American settlement, early successional forests may have been <5% of forestlands (Lorimer 2001). Open forests of fire-tolerant pine and oak covered large extents of the United States for thousands of years that varied over time with changes in populations of indigenous people (Fig. 1; Delcourt and Delcourt 1987, Hanberry and Abrams 2018, Hanberry et al. 2018*a*). Forests of the southeastern United States were approximately 75% pine or oak–pine (*Quercus* spp., *Pinus* spp.) and 25% other forest types, whereas the central eastern United States was approximately 55% oak, with intermixing of other forest types, such as American beech (*Fagus grandifolia*; Hanberry and Nowacki 2016, Hanberry 2018). Therefore, "early successional" or "scrub-successional" guilds may be misnomers given the landscapes in which bird species evolved prior to European settlement.

Forest management and ecosystem restoration are advocated to create, restore, or sustain landscapes for early successional species (Thompson and DeGraaf 2001, King et al. 2011, Reidy et al. 2014). These practices affect large areas in North America and include both ecological and economic objectives. In regions of historically widespread open-forest ecosystems, birds associated with early successional forests historically may have relied on open forests, which share the herbaceous vegetation of early successional habitat, but with perpetual presence of overstory trees. Open forest management is not widely practiced or communicated as a forest management option for early successional species, but is considered for disturbance-dependent birds such as northern bobwhite and Bachman's sparrow (*Peucaea aestivalis*) and some open pine-forest obligates such as red-cockaded woodpecker (*Leuconotopicus borealis*) and brown-headed nuthatch (*Sitta pusilla;* e.g., Johnson and Hale 2002). Our objective was to evaluate the benefit of open forest management for many early successional bird species and compare the benefits of open forest management with more traditional forest regeneration practices for these species in eastern forests. We use birds as an example taxa that may benefit from such management because more information is available than for any other taxa. To accomplish this we 1) contrast early successional forests and open forests and clarify terminology, 2) describe historical ecosystems and disturbance in the eastern United States, 3) examine trends of early successional birds and vegetation in the eastern United States, 4) generally review effects of forestry practices on early successional birds, and 5) compare landscape-level abundances of some birds in managed forest landscapes to landscapes with historical amounts of open forests based on our studies in Missouri, USA.

Terminology

Terminology around early successional forest, open forests, and habitat can be variable (Greenberg et al. 2011), so we begin by clarifying some terms. We use habitat in the classical sense as the species-specific physical environmental factors that species require for survival and reproduction (Block and Brennan 1993, Hall et al. 1997). Therefore, the commonly used phrase early successional habitat is inaccurate and more accurately should be referred to as a vegetation type or state. The tendency to associate habitat with vegetation type also leads to confusion in describing a bird's habitat. A prairie warbler has likely been called all of the following: a shrubland bird, an early successional forest bird, a woodland bird, and a pine savanna bird. What actually

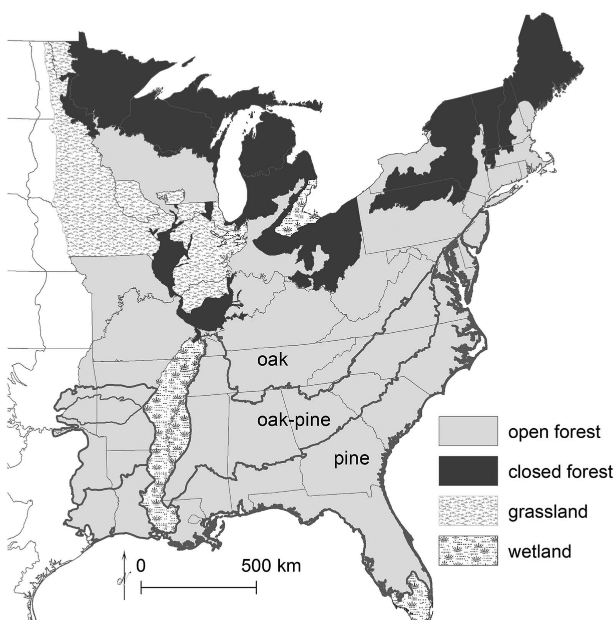

Figure 1. Estimated extent of open forests in the eastern United States during the 1800s (based on Hanberry and Nowacki 2016, Hanberry and Abrams 2018, Hanberry et al. 2018*a*). Finer scale variation within the open forest regions occurred based on features such as wetlands, rocky outcrops, and topography that provided protection from fire and resulted in some closed forest within these regions.

Figure 2. Open forest (on left) has few or no midstory trees and a low to moderate overstory density, which allows a dense and diverse herbaceous ground layer. Frequent low-severity fire controls woody vegetation and prevents tree entry into the midstory. Closed forest (on right) has understory, midstory, and overstory trees that prevent direct sunlight from reaching the ground. Photos courtesy of C. O. Kinkead.

accurately describes its breeding habitat or "niche gestalt" (i.e., James 1971) is the mix of open canopy, high grass and forb cover, and moderate low-woody cover that meets its needs for foraging, nesting, and brood-rearing, which could be found in any of the previously mentioned vegetation types.

We refer to forests as in closed or open states. Closed forest is what most people think of as forest—a vegetation state where trees fully capture the growing space. Conversely, open forests consist of savannas, open woodlands, and closed woodlands (Fig. 2). Closed forest develops through a series of successional or stand development stages following a major disturbance that removes most of the overstory: stand initiation, stem exclusion, understory re-initiation, and complex or old growth stage (Fig. 3; Oliver and Larson 1996, Johnson et al. 2009). The stand initiation stage and stem exclusion stages often are referred to as early successional forest and provide habitat for early successional wildlife (Greenberg et al. 2011). The mix of bare ground, herbs, shrubs, and young trees in the stand initiation stage provides habitat for many early successional birds because of its diverse composition and horizontal and vertical structure. In the absence of additional disturbance, this stage is ephemeral as conditions transition to a dense stand of young trees in the stem exclusion stage and these trees shade-out herbs and shrubs. Succession to a dense tree stage can happen as quickly as 5–20 years in eastern forests, depending on factors such as growing season length, site factors, and tree species (Thompson and DeGraaf 2001).

We consider savannas, open woodlands, and closed woodlands as different phases of open forests. Phases differ from successional or stand development stages in that they tend to capture spatial variation rather than temporal variation. Open forests typically have a well-developed herbaceous ground layer, a lack of midstory trees, and a low to moderate density of overstory trees that allows light and growing space in the forest floor, which is critical for grasses and forbs (Rogers et al. 2008). Low-severity fire historically was a widespread, frequent, anthropogenic disturbance that removed dense regenerating layers of fire-sensitive tree species and shrubs that otherwise would out-compete

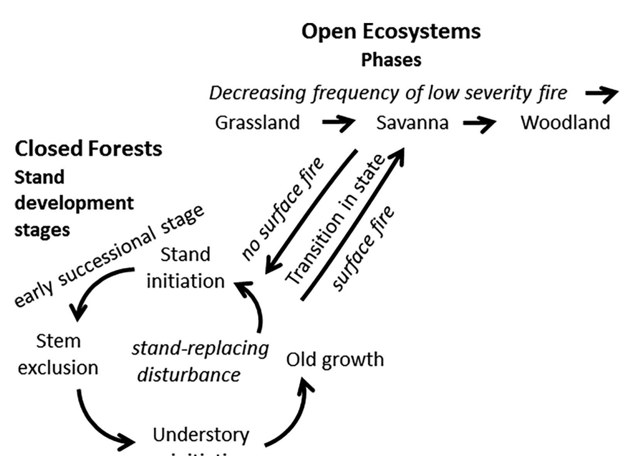

Figure 3. Conceptual model for the influences of disturbance and succession on open and closed forest ecosystems.

herbaceous plants for space and light. Sprouting trees and shrubs provided woody ground and understory cover when intervals between fires were long enough. Under historical disturbance regimes, frequent low-severity fire generally meant open forests were more stable spatially compared with the shifting mosaic of early successional forest that is created by less frequent stand removing disturbances (Fig. 3).

Open forest phases represent a continuum between prairie and closed forest. Definitions vary but typically savanna was described as 10–30% canopy closure and woodlands 30–80% canopy closure (Nelson 2005). Recent and more empirically derived definitions are based on the concept of growing space occupied by trees, as measured by percent stocking, and the functional implications of it (Hanberry et al. 2014, Dey et al. 2017). The structural threshold that separates temperate savannas from woodlands may occur at a maximum of 30% stocking (or growing space occupied) and 100 trees/ha of $\geq$12.7-cm diameter, with approximately 40–50% canopy closure (Hanberry et al. 2014). The threshold between open and closed woodlands is at approximately 55% stocking (including only larger diameter trees), or approximately 70% canopy closure; the threshold between closed woodland and forests is approximately 75% stocking, or approximately 80% canopy closure (Hanberry et al. 2014, Dey et al. 2017). Importantly, woodlands have relatively tree-free mid- and understories, while in closed forests understory and midstory trees fill the vertical profile.

Herbaceous ground cover is abundant in open forest and closed forest during the stand initiation stage. The combination of herbaceous ground cover and patchy regrowth of woody species benefits many early successional birds in open forests and early successional forests. Without disturbance, however, regenerating trees grow and take up the growing space, blocking much of the ground cover.

Historical Ecosystems and Disturbance

The overall percent of early successional forest has decreased over the past century and subsequent declines in early successional birds have been at least partly attributed to reduced area of early successional forest (Askins 2001, DeGraaf and Yamasaki 2003, Buffum et al. 2014, King and Schlossberg 2014). The amount of early successional forest reached a peak of up to 60% of forest cover in many eastern states during the early 1900s due to clearing for agriculture and wood products by Euro-American settlers. Early successional forests continued to decrease to approximately 15% in regions of the eastern United States by 2000 (trees of 1–15 yr; Lorimer 2001, Trani et al. 2001). Nonetheless, early successional forest still may be more abundant now than during pre–Euro-American settlement because natural mechanisms of widespread severe overstory disturbance occurred infrequently and typically produced more diffuse tree removal than clearcuts (Lorimer and White 2003). Moreover, current percentage of early successional forest represents only forestlands, and therefore does not include additional early successional vegetation resulting from clearings for various land uses.

Severe fires, winds from tornadoes and hurricanes, ice storms, drought, and tree removal by Indigenous peoples around settlements produced early successional forests on

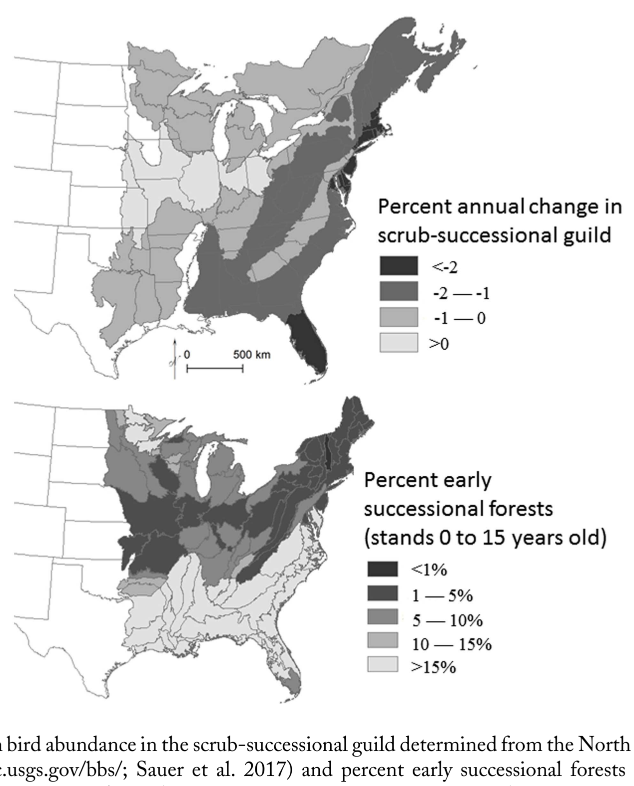

Figure 4. Mean percent annual change in bird abundance in the scrub-successional guild determined from the North American Breeding Bird Survey by region during 1966 to 2015 (https://www.pwrc.usgs.gov/bbs/; Sauer et al. 2017) and percent early successional forests (stands 0–15 yr old) during most recent inventories, which vary by state from 2002 to 2017 (USDA Forest Service, Forest Inventory and Analysis Evalidator; https://apps.fs.usda.gov/Evalidator/evalidator.jsp; Miles 2018).

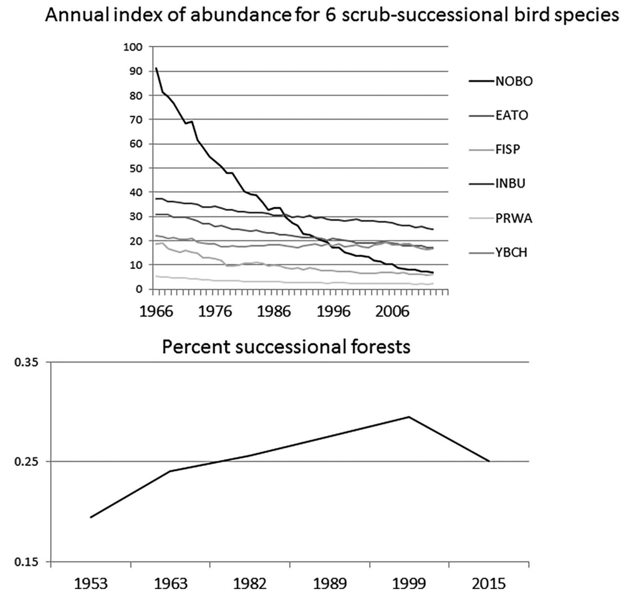

Figure 5. Trends for 6 species (NOBO = northern bobwhite, EATO = eastern towhee, FISP = field sparrow, INBU = indigo bunting, PRWA = prairie warbler, and YBCH = yellow-breasted chat) during 1966 to 2013 (https://www.pwrc.usgs.gov/bbs/; Sauer et al. 2017) and percent early successional forests (stands 0–15 yr old) during 1953 to 2015 in the southeastern United States (Conner and Hartsell 2002; USDA Forest Service, Forest Inventory and Analysis Evalidator; https://apps.fs.usda.gov/Evalidator/evalidator.jsp; Miles 2018).

approximately 1–13% of forestlands in the eastern United States prior to Euro-American settlement (Lorimer 2001, Lorimer and White 2003). Oak forests and northern hardwood forests (e.g., American beech) contained 1–3% young forests, whereas the greatest amount of early successional forests occurred in the northern Great Lake states, where stand-replacing disturbances occurred every 50–200 years (Fig. 1, Lorimer 2001, Lorimer and White 2003). Aside from the northern areas of the most northern states, stand-replacing disturbances occurred infrequently, particularly in open forests that are resistant to catastrophic fire. An average (but highly variable) fire frequency of $\leq$12 years for over half of the eastern United States led to a reduction of coarse fuel loads and resistance to severe, stand-replacing fires (Guyette et al. 2006). Intervals between stand-replacing disturbances may have ranged from 300 years to >9,000 years in eastern United States forests (Seymour et al. 2002, Elsner et al. 2008). Severe disturbances on less than a 100-year rotation produced gaps of <0.19 ha, whereas stand-replacing disturbances that created 2-ha openings occurred approximately every 190 years in the northeastern United States (Seymour et al. 2002). Historical stand-replacing events were rare relative to tree lifespans; so in most of the eastern United States forests were old growth. Long-lived oak and pine species formed old growth forests in which gap dynamics and recruitment of overstory species occurred after senescence of a canopy tree. Few tree species considered early successional, aside from oak and pine species, were present in historical forests and average diameters of historical forests generally were >1.5 times greater than trees of current forests (e.g., Hanberry et al. 2018*b*).

In contrast to the northeastern United States, landscapes in the central eastern and southeastern United States were predominantly open oak- or pine-forest ecosystems maintained by frequent, low-severity fires (Lorimer 2001, Hanberry and Nowacki 2016). Longleaf pine (*Pinus palustris*) forests dominated the Coastal Plain of the southeastern United States, open oak–pine forests occurred north of the Coastal Plain, and open oak forests occurred in the central eastern United States, reaching to the southern part of New England and the Great Lakes states (Hanberry and Nowacki 2016). Open forests usually were associated with humans and their use of fire (Komarek 1974, Pyne 1982, Nelson 2005). Indigenous people and early European settlers frequently set fires to increase forage, benefit wildlife, and for other objectives; fire frequencies averaged $\leq$12 years for much of the eastern United States based on fire scars and more frequent low-intensity fires occurred that did not scar trees (Guyette et al. 2006). However, as populations of European settlers and roads, railroads, settlements, and cultivation increased, the frequency of fire greatly decreased and open forest declined.

Few current forests are representative of historical forests in composition, structure, or age. Current forests are composed of a variety of tree species with varying drought and shade tolerance traits and closed in structure, with dense woody midstories and understories. Additionally, the age of most forests in the eastern United States is less than the lifespan of most tree species because of anthropogenic tree removal. Overall, early successional forests were rare historically because of the infrequent occurrence of stand-replacing disturbance, while open forests were abundant. Consequently, it may follow that many early successional bird species relied on open forests to supply a source of habitat that covered large extents of the eastern United States since glaciation.

Trends of Early Successional Birds and Forests in the Eastern United States

The U.S. Geological Survey North American Breeding Bird Survey (https://www.pwrc.usgs.gov/bbs/) groups 38 species into a scrub-successional guild in the eastern United States (species encountered on >14 routes; https://www.mbr-pwrc.usgs.gov/cgi-bin/guild15.pl; Sauer et al. 2017). This group excludes 89 species included in a woodland (i.e., primarily closed forest) guild and 18 species in a grassland guild in the eastern United States. During 1966–2015, 53% of species in the scrub-successional guild had a significant negative trend (−1.12%/yr for guild combined), while 83% of the grassland guild had a significant negative trend (−3.27%/yr for guild combined). In contrast, only 30% of species in the woodland (i.e., forest) guild had a significant negative trend, resulting in a slight positive trend of 0.14%/year for the guild combined, which is a similar trend to the 77 species in the wetland guild. Therefore, a greater percentage of species in the scrub-successional and grassland guilds are declining than in the woodland guild, although a greater absolute number of species are declining in the woodland guild because it includes more species.

The mean annual percent change in the scrub-successional bird guild from 1966 to 2015 was negative for each region except the eastern tallgrass prairie (Fig. 4). We summarized the percent of early successional forest by region (% stands 0–15 yr old; U.S. Department of Agriculture [USDA] Forest Service, Forest Inventory and Analysis Evalidator; https://apps.fs.usda.gov/Evalidator/evalidator.jsp; Miles 2018) and compared it with the mean annual percent change in the scrub-successional bird guild. Regions with lowest percentages of early successional forest do not appear to be associated with regions with greatest negative trends in scrub-successional birds (Fig. 4). For example, the eastern tallgrass prairie region is the only region where the trend in the scrub-successional bird guild is positive and early

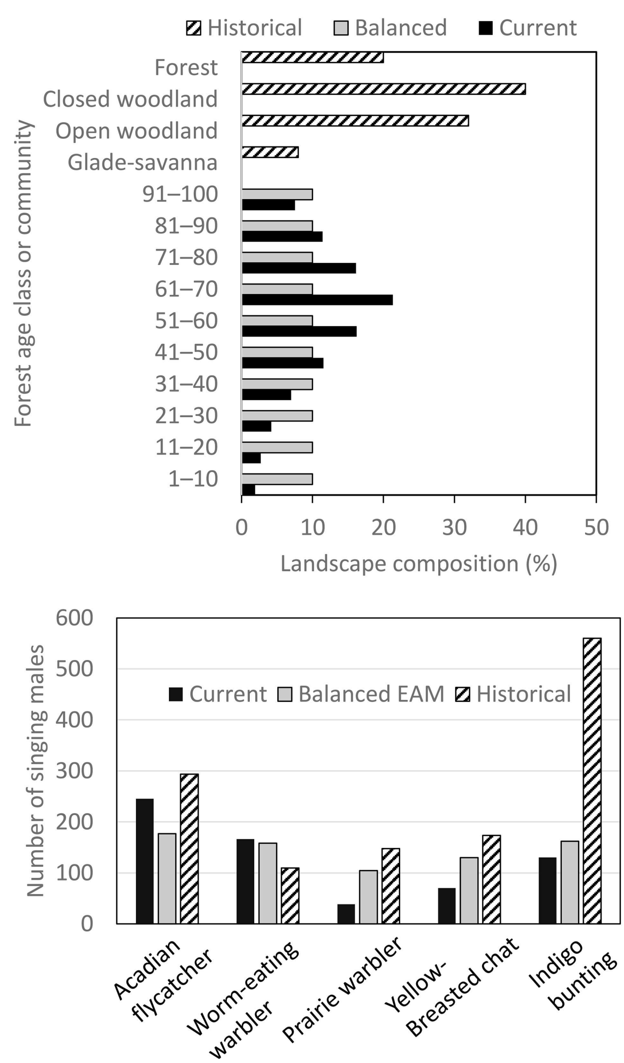

Figure 6. A historical landscape composed of 20% forest, 40% closed woodland, 32% open woodland, and 8% glade–savanna; a balanced even-aged management (EAM) forest landscape with 10% in each of 10, 10-year age classes from 1 to 100; and a current forest landscape with the same 10-year age classes but <3% in each of the 2 youngest age classes and 54% between 51 and 80 years old. Out of 5 bird species, including 2 species that are classified in the forest guild, the historical open-forest landscape supported a greater number of birds for 3 early successional species and 1 forest species than were supported by landscapes composed of even-aged stands of forest.

successional forests are only 1–5% of forests. The regions in the southeastern United States have the greatest percentages of early successional forest (15–33%) but also some of the greatest declines in scrub-successional birds. To illustrate trends over time (1966–2013) in the southeastern United States, 6 species in the scrub-successional guild steadily declined while percent young forest increased slightly and then decreased slightly (1953–2015; Fig. 5; Conner and Hartsell 2002; USDA Forest Service, Forest Inventory and Analysis Evalidator, http://apps.fs.fed.us/Evalidator/evalidator.jsp; Miles 2018).

The discrepancy between the large percentage of early successional forest and great declines in the scrub-successional bird guild in the southeastern United States is likely in part due the result of intensive short-rotation forestry. Intensive management of pine plantations on 20–25-year rotations rapidly pushes stands into the stem exclusion stage, which has limited value to open forest species. This region may demonstrate the low value of ephemeral early successional forest. Use of herbicides and mechanical treatments to suppress competition from herbaceous vegetation and hardwoods may have additional negative effects on early successional species. Note that open pine forests historically were dominant in the Southeast; the Coastal Plain was >75% pine, whereas the northern region of the Southeast was approximately 35–40% pine (Hanberry and Nowacki 2016; Hanberry et al. 2018*a*,*b*).

Birds associated with early successional habitat are declining except in the eastern tallgrass prairie ecoregion, where there is little early successional forest. The decreasing trend may be because populations were unprecedentedly high due to forest clearing and agriculture during settlement. However, birds associated with early successional habitat are declining in the southeastern United States, where early successional forest has been abundant (~25% of forests) during the past century or more of extensive logging, agricultural, and plantation land use, compared with historically when longleaf pine woodlands and shortleaf pine (*P. echinata*)–oak woodlands were dominant. There are many factors that may cause bird declines, but woodland (i.e., forest) and wetland guilds have slight increasing trends, unlike the scrub-successional and grassland guilds. Therefore, we suggest that widespread loss of open forests and grasslands in the eastern United States contributed to declines in these bird guilds.

Bird Response to Closed Versus Open Forest Management

Many studies have investigated effects of forest management on forest birds in the eastern United States and, in general, early successional birds respond positively to forest regeneration practices if sufficient canopy is removed to create the mixed herbaceous ground cover, shrubs, and young trees they prefer (reviewed by Dickson et al. 1993, Thompson et al. 1995, Sallabanks et al. 2000). However, somewhere along a gradient of low to high tree retention consisting of the clearcut, shelterwood, group selection, and single tree selection methods, too much canopy cover is retained for sufficient response by ground and understory vegetation, or patches are too small, to create habitat for these bird species (Annand and Thompson 1997). There is a lack of positive response by these bird species to partial cut practices when the objective is to regenerate fully stocked forests (Perry and Thill 2013, Kendrick et al. 2015). Species such as prairie warbler and yellow-breasted chat typically appear in these stands 1–2 years after harvest, peak in abundance in 4–8 years, and are gone in 10–15 years (Conner and Adkisson 1975, Schlossberg and King 2009). Species such as Kentucky warbler (*Geothlypis formosa*) and white-eyed vireo also use early successional forests. However, they historically may have used riparian zones and isolated wetlands and large extents of canebrakes that co-existed in wetlands of open forests (Platt et al. 2013).

Once a stand succeeds to the stem exclusion stage it provides habitat for young forest specialists such as ruffed grouse (*Bonasa umbellus*) and American woodcock (*Scolopax minor;* Dessecker and McAuley 2001) and forest songbirds such as worm-eating warbler (*Helmitheros vermivorum*) and wood thrush (*Hylocichla mustelina*) begin to appear (Thompson et al. 1992). This stage provides habitat for a smaller suite of young forest specialists and some mature forest birds begin to reappear. Early successional forest can exist as a shifting mosaic in space and time following repeated tree harvest or other substantial overstory tree disturbance in the landscape.

Our understanding of how birds respond to open forest management is in early stages compared with management of closed forests. Reasons for concerns about the benefits of open forest management for early successional birds stem from the observation that too much tree retention reduces the habitat quality of regenerating forests for early successional birds, and open forest typically have 30–90% canopy cover. This concern seems unfounded, however, because recent studies show open forest management has great promise for providing habitat for early successional birds. For example, oak and pine–oak woodland management in Missouri and Arkansas, USA, benefits many early successional birds (Reidy et al. 2014, Roach 2016). Abundance of field sparrow (*Spizella pusilla*), blue-winged warbler, eastern towhee, prairie warbler, white-eyed vireo, and yellow-breasted chat is positively related to management practices (prescribed fire, tree thinning) or the resulting vegetation structure (reduced canopy cover, tree density). Although abundance of most of these species was negatively related to canopy closure, abundances were still relatively high (0.1–0.4 males/ha) at 60% canopy cover. We believe this is because the combination of thinning and prescribed fire maintained moderate canopy cover, but virtually no midstory, a variable understory, and abundant ground cover. Spatial and temporal variation in occurrence or intensity of fire results in patches of resprouting shrubs and trees that are important for shrub-nesting birds such as prairie warbler and yellow-breasted chat. Furthermore, the management practices or changes in vegetation structure had neutral or positive effects on nesting success of early successional species (Brawn 2006, Reidy and Thompson 2018, Roach et al. 2018).

In terms of conventional forest-regeneration methods, harvesting that retains trees and approximates open forests generally provides habitat simultaneously for early successional (or open-forest) bird species and mature-forest bird species, unlike in early successional forests. Given enough tree removal, early successional birds may be at least as abundant in stands with tree retention as in clearcuts, while mature forest birds will be more abundant in stands with tree retention, albeit not be as abundant as in mature closed forests (Webb et al. 1977 in New York, USA; Freedman et al. 1981 in Nova Scotia, Canada; Merrill et al. 1998 in Minnesota, USA; King and DeGraaf 2000 in New Hampshire, USA; Rodewald and Yahner 2000 in Pennsylvania, USA; McDermott and Wood 2009 in West Virginia, USA; Hanberry et al. 2012*a,b*; 2013 in Mississippi, USA). For example, clearcuts with residual overstory trees and suppressed tree sprouts produced greater abundance of most species, including early successional species, than clearcuts with young small-diameter trees but no retained canopy trees during winter and spring in the southeastern United States (Hanberry et al. 2012*b*, 2013). Nonetheless, there were greater abundances of early successional birds in clearcuts 5–12 years after harvest than in shelterwoods in Arkansas, USA, but shelterwoods contained greater abundance of some species rare in clearcuts (Perry and Thill 2013).

Within the understory, some species may specifically select herbaceous or shrubby coverage without any small-diameter-tree coverage (particularly grassland or shrubland associates; Smetzer et al. 2014). Overstory tree presence may be more influential than particular understory vegetation coverage, at least in some locations (Hanberry et al. 2012*a*). However, particularly in the northern Great Lake states, where stand-replacing disturbances frequently terminated and originated forests, young trees alone may be important for some species, specifically ruffed grouse, which selects dense, small-diameter trees of early successional forests.

In contrast to early successional forest, succession in grasslands, shrublands, and open forests often is arrested by local site factors (e.g., high water table, shallow soil depth) or understory disturbance regimes, typically consisting of low-severity periodic fire. Therefore, under frequent fire regimes, grasslands, shrublands, and open forests were more stable on the landscape while early successional forest existed as a shifting mosaic that followed less frequent, but more severe disturbances. Schlossberg (2009:242) suggested "High site fidelity may have been adaptive in stable habitats of the past, but using such a strategy in more ephemeral habitats could be problematic ... High site fidelity of shrubland birds may, therefore, be a maladaptive relict of past times, but more research is needed to test this hypothesis." Ephemeral early successional forests may not provide conditions suitable for a single individual to reach its lifetime reproductive potential without needing to disperse.

Landscape Comparison of Open Forest versus Even-Aged Forest Management

We constructed a simple spreadsheet model to compare abundances of 3 early successional species (prairie warbler, yellow-breasted chat, indigo bunting [*Passerina cyanea*]), and 2 mature forest birds negatively affected by fire (Acadian flycatcher [*Empidonax virescens*], worm-eating warbler) to assess tradeoffs between management at a landscape scale in the Ozark highlands of Missouri. We defined 3 landscapes; a historical landscape composed of 20% forest, 40% closed woodland, 32% open woodland, and 8% glade–savanna; a balanced even-aged forest landscape with 10% in each of 10, 10-year age classes from 1 to 100; and a current forest landscape with the same 10-year age classes but <3% in each of the 2 youngest age classes and 54% between 51 and 80 years old (Fig. 6). We then assigned bird abundances to each of these land covers or age classes based on abundances from studies in the region for oak and pine–oak forest and woodlands (Thompson et al. 1992, Reidy et al. 2014, Kendrick et al. 2015, Roach 2016). The historical open-forest landscape supported a greater number of birds for 3 early successional species and one forest species than the landscapes with the balanced or current distribution of even-aged stands. Both the historical and balanced even-aged distribution supported more early successional species than the current landscape because of its low amount of early successional and open forest.

DISCUSSION

Closed forest management, including clearcut, shelterwood, group selection, and single tree selection, focuses on a cycle of tree regeneration and harvest. These methods customarily establish and grow trees to produce a fully stocked forest for economic, ecological, or other objectives. Early successional habitat created by these methods is ephemeral because it is a successional stage of stand development. Continued disturbance, such as prescribed fire, after overstory removal could maintain early successional vegetation, albeit that is not conventional forest management nor compatible with objectives for wood production.

Open forest management is not as well-formulated or often conveyed as an alternative to conventional forest management for early successional species. The science of open forest management is developing and it is increasingly being advocated for restoration, contributions to local and landscape diversity, forest health and resiliency, and wildlife (Dey et al. 2017). Mature overstory trees typically remain present at most times, producing old-growth open forests with gap dynamics resulting from natural tree mortality and spatial and temporal variation in fire. Alternatively open forests could be regenerated with even- or uneven-aged methods and progress through stages of stand development. This idea has not been actively discussed as part of restoration efforts but may be more applicable in commercial forest operations. As stocking increases with increasing tree diameters, trees can be thinned for forest products, providing there are suitable markets. Large-diameter trees are competitive for growing space and their presence helps reduce tree regeneration. Thinning and burning are necessary management treatments to control tree regeneration because too many small-diameter trees obstruct the desirable herbaceous plant component.

Early successional forests are currently more common in the southeastern United States because of commercial forestry in pine forest (Seymour et al. 2002, Lorimer and White 2003). Therefore, creation of more early successional forest for early successional birds may be difficult to justify in these places. One advantage of management for early successional forest is that it is often generated by commercial timber harvest and revenues from wood products offset the costs. However, management of open forests can generate revenue from timber harvest associated with thinning and have positive effects on local economies. Open forest management is not economically self-sustaining, but an upfront investment can have positive effects on local economies. For example, a US$20 million investment in pine–woodland restoration on the Mark Twain National Forest in Missouri is expected to support 138 jobs/year and generate an 8-year total of US$34 million in labor income as part of US$44 million in total value added (Song and Aguilar 2015). Public opposition to clearcuts may prevent landowners and governmental agencies from management for early successional wildlife by clearcutting (Buffum et al. 2014); whereas in contrast, open forests may produce more desirable aesthetics and historically natural landscapes, reducing negative public perceptions. However, landscape-scale prescribed burning associated with open forest restoration also has been criticized by the public and professionals for a variety of reasons (Thompson et al. 2018) and it can be logistically difficult to implement because of workforce and weather limitations.

Open forests are not only important for many birds, but additionally are important for insects and butterflies (Wood et al. 2011), herpetofauna (excluding *Plethodon* salamanders and litter-dwelling snakes; e.g., Means 2006), and mammals, including some bats but with exceptions including eastern spotted skunk (*Spilogale putorius*) and New England cottontail (*Sylvilagus transitionalis;* McShea et al. 2007, Starbuck et al. 2015). Loss of species dependent on open forests also is a relevant issue in western regions (dry pine forests and oak forests) and worldwide (e.g., Europe, Nilsson et al. 2008, Plue et al. 2013, Mölder et al. 2014).

CONCLUSION

Early successional birds are decreasing in the eastern United States despite varying amounts of early successional forests. We propose many early successional birds are declining in large part due to loss of historical open-forest ecosystems. It may be valuable to reframe many birds associated with early successional forests as open forest birds. Both early successional forests and open forests provide habitat for birds, but we suggest the great reduction in the historical extent of open forests needs to be addressed through greater restoration and management of open forests if we want to better meet the needs of early successional birds and other wildlife. Open forest management uses thinning and fire to maintain the desired structure, and does not preclude production of some forest products as well. Restoration and management of historical oak and pine woodlands has not been prioritized or well-articulated for management of early successional birds and other species. We suggest that greater emphasis be placed on the management of open forests for early successional birds and that more open forest management is needed in the eastern United States in addition to ongoing closed forest management if we want to have a positive effect on the declines in many early successional birds. We recommend future studies experimentally test the validity of this model of open forest management in comparison with the traditional early successional forest management as a tool to increasing populations of early successional bird species.

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