Forest Ecology and Management 324 (2014) 186–195

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Synthesis of the conservation value of the early-successional stage in forests of eastern North America

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ARTICLE INFO

Article history:
Available online 28 December 2013

Keywords:
Bird
Conservation
Habitat
Management
Shrubland
Succession

ABSTRACT

As a result of changes in natural and anthropogenic disturbance regimes, the extent of early-successional forest across much of eastern North American is near historic lows, and continues to decline. This has caused many scientists to identify the conservation of early-successional species as a high priority. In this synthesis, we discuss the conservation implications of this loss of early-successional habitats using examples from the literature on songbirds. Early-successional "shrubland" bird species require conditions and resources present in recently disturbed sites. These conditions are ephemeral and change rapidly over time as sites become dominated by later-seral species. Historical disturbance regimes such as windthrow, fire and flooding have been altered or suppressed in eastern forests through human activity such as conversion of forests to younger aged stands more resistant to wind, fire suppression and mesophication of fire-adapted communities, and suppression of beaver activity and flooding. Furthermore, anthropogenic disturbance has shifted over much of the region to types of land use that provide less shrubland habitat of lower quality than historically. Despite scientific evidence in support of this concern, there is still misunderstanding about the role of disturbance in maintaining biodiversity, and public opposition to management remains a challenge to conserving these communities. Contemporary approaches use natural disturbance regimes to inform management practices that employ historical agents where possible or surrogates when necessary to achieve desired future conditions defined on the basis of regional population or community status. Conservation of early-successional communities occurs within the context of other potentially conflicting ecological values, such as the conservation and enhancement of biologically mature forest. Recent findings, however, show shrubland habitat can augment diversity in forested landscapes by providing seasonal resources for mature-forest species, such as food or predator-free space for juvenile forest songbirds that seek out early-successional habitats during the transition to independence. Balancing the conservation of early-successional shrubland species with other, sometimes conflicting values is an active area of current conservation research. In some cases the conservation of shrubland birds can be coordinated with commercial activities like silviculture or maintenance of infrastructure (e.g. powerline corridors), although our work indicates that deliberate efforts expressly directed at conservation of early-successional shrubland species are more effective.

1. Geographic, taxonomic and conceptual scope

For the purpose of this synthesis we consider the forested regions of North America east of 95° approximately longitude. This is an ecologically cohesive area bounded to the west by the Great Plains and corresponding roughly to the eastern forested area described by Braun (1950). This region encompasses a diversity of forest types, including spruce-fir, northern hardwoods, central hardwoods, southeastern evergreen etc., all of which are subject to natural or anthropogenic disturbances that create open-canopy conditions (Runkle, 1985; Brawn et al., 2001; Lorimer, 2001) and support species particular to various stages of stand development (Titterington et al., 1979; Crawford et al., 1981; DeGraaf, 1991). Many of the issues characteristic of eastern forests are common to western forests, in that recently disturbed stands differ in structure and/or species composition from older stands (Swanson et al., 2010); however, western systems differ in fundamental aspects including topographical relief, species composition and geological history (King et al., 2011a) and have also received detailed attention elsewhere (Swanson et al., 2010; Ellis and Betts, 2011). In contrast the commonalities in species, communities and ecosystem characteristics within the eastern region make it a logical subject for this discussion.

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0378-1127/$ - see front matter Published by Elsevier B.V.
http://dx.doi.org/10.1016/j.foreco.2013.12.001

We focus primarily on birds in our discussion of the conservation value of the early-successional stage of eastern North American forests for several reasons. First, the class Aves encompasses numerous species that are restricted to particular stages of stand development (DeGraaf, 1991; Schlossberg and King, 2009). Furthermore, a substantial proportion of bird species (13%) are considered vulnerable to extinction worldwide according to the IUCN 2012 Red List of Threatened Species (BirdLife International, 2013). Finally, although there are a myriad of plant and animal species that exhibit responses and specificity to disturbance and successional development, the patterns birds reflect are common to other less well-studied taxa, including plants (Elliott et al., 2011), insects (Wagner et al., 2003), and mammals (Litvaitis, 2001). Because birds exhibit sensitivity to and dependence on disturbance, are of broad conservation interest, are a group for which there is a wealth of information, and exhibit patterns of abundance that illustrate general patterns of responses of organisms to disturbance in general, we propose birds as a suitable subject for this synthesis.

Early-successional habitats in eastern North America can be divided into two categories based on how they originate and their structure and species composition. "Early successional" habitats are those that are dominated by shade-intolerant pioneer plant species, whereas, "young forest" describes stands that are recovering from disturbance largely through the recruitment of canopy species from advanced regeneration (Lorimer, 2001). Although bird species that occupy disturbed sites may differ in terms of their association with early-successional versus young-forest habitat (e.g. King et al., 2009a), all of these species are absent or scarce in the closed canopy stands that develop following disturbance, and thus share common conservation and management challenges. Hence except where informative we ignore the distinction between "early-successional" and "young forest", and refer to them collectively as "early-successional" or "shrubland" communities, habitats and species (*sensu* Askins, 2001). Furthermore, we also ignore grassland birds, which although disturbance-dependent, do not necessarily represent a stage in forest succession or stand development, and do not occur in forested regions except in exceptional circumstances. Nor do we concern ourselves with disturbance-dependent bird species that also occur in closed-canopy forests, yet are more abundant in gaps (e.g. Hooded warbler [*Wilsonia citrina*]; Hunter et al., 2001), because they face very different conservation issues and challenges than species that do not occupy mature forest. Instead, we focus on bird species that occupy open-canopy habitats characterized by a dense understory of shrubs, saplings and herbaceous vegetation with little or no mature tree cover (Thompson and DeGraaf, 2001; Greenberg et al., 2011a).

1.1. Early-successional habitats

In eastern forests naturally occurring early-successional habitats include glades, barrens, beaver (*Castor canadensis*) meadows, floodplains, xeric scrublands, oak woodlands, tree fall gaps and burns and blowdowns in closed canopy forest (Thompson and DeGraaf, 2001; Hunter et al., 2001). The natural disturbance agents (those that occur in the absence of direct human intervention) that create shrubland habitat include edaphic factors like moisture or nutrient limitation that inhibit succession (Brawn et al., 2001) as well as the mortality or damage to stands of trees from disease, insect damage (Oliveri, 1993) or weather events such as ice storms (Faccio, 2003) to larger-scale events like blowdowns (Burris and Haney, 2005), wildfire (Pyne, 1982; Haney et al., 2008), or flooding by beaver (Chandler et al., 2009a). Human-created shrublands include regenerating clearcuts, old fields, powerline corridors and reclaimed surface mines (Thompson and DeGraaf, 2001; Hunter et al., 2001).

The key to understanding the response of shrubland birds to disturbance is the extent to which disturbance agents change conditions in the stand with respect to the features with which shrubland species abundance is associated. In general, habitat structure is considered the most important habitat feature influencing suitability for birds (Niemi and Hanowski, 1984; Hagan and Meehan, 2002) and shrubland species in particular (Schlossberg et al., 2010). Structural characteristics known to be important include the height of the vegetation, its vertical profile, horizontal patchiness, the diameter and density of stems, and the proportion of coverage by woody versus herbaceous plants. Plant species composition is less important than structure to vertebrates inhabiting eastern shrublands, although the presence of fruiting species can be important (Greenberg et al., 2011b).

Finally, for many shrubland birds, there exists a threshold patch size under which they will not occupy a site (Kerpez, 1994; Annand and Thompson, 1997; Robinson and Robinson, 1999; Costello et al., 2000; Moorman and Guynn, 2001; Rodewald and Vitz, 2005). Schlossberg and King (2007) compiled all published studies comparing the abundance of shrubland birds between small (0.12–1.1 ha) and large (4.9–12 ha) patches and of 37 individual comparisons of 21 species, 36 of these comparisons indicated a positive association with patch size. Thus, patch size represents another way in which habitat suitability for shrubland species varies with the type and intensity of disturbance.

Damage to forest stands from wind, ice storms, insects and disease can cause the death of individual or groups of trees or can have dramatic effects on stand structure by knocking over or snapping the trunks of canopy trees (Lorimer, 2001; White et al., 2011). Studies of birds in eastern forests subject to disturbance illustrate how the response of shrubland birds varies with disturbance intensity, particularly the reduction of forest canopy. For example, an ice storm in 1998 that impacted nearly 7 million ha of forest land in the northeastern US and Canada caused extensive damage to individual trees within stands, but did not open up the forest canopy enough to accommodate shrubland birds (Faccio, 2003). In contrast, a number of shrubland specialists, including chestnut-sided warblers (*Setophaga pensylvanica*) and mourning warblers (*S. philadelphia*) as well as white-throated sparrows (*Zonotrichia albicollis*) were more abundant in late-successional spruce-fir forest (*Picea mariana-Abies balsamea*) in which 80% of the canopy had been removed by a straight line microburst in northern Minnesota relative to undisturbed areas (Burris and Haney, 2005). Similarly, Oliveri (1993) reported increases in these same shrubland bird species in spruce-fir forests in northern Maine in which all fir trees and most spruces had been killed by a spruce budworm (*Choristoneura fumiferana*) outbreak, as did Haney et al. (2008) in a jack pine-black spruce forest in Minnesota that suffered complete mortality as the result of a catastrophic wildfire.

The impacts of disturbance on shrubland birds are also affected by the spatial extent of the disturbance. For instance, Greenberg and Lanham (2001) reported that a hurricane in the southern Appalachians of North Carolina created canopy gaps up to 1.2 ha in size, which was sufficient to support several species of shrubland birds, including indigo bunting (*Passerina cyanea*) and eastern towhee (*Piplio erythropthalmus*), but several other shrubland specialists known to be "area-sensitive" from other studies (e.g. prairie warblers [*S. discolor*] and yellow-breasted chats [*Icteria virens*]) were not encountered in these gaps. Although the wind-created openings studied by Greenberg and Lanham (2001) were too small for some shrubland birds, there are numerous historical accounts of blowdowns on the scale of 100s or 1000s of hectares (Lorimer, 2001), particularly near the Atlantic coast, with return intervals for disturbances of all sizes on the order of 50–200 years (Runkle, 1985; Boose et al., 2001; Lorimer, 2001), so clearly wind events are capable of creating openings sufficiently large to support even the most area-sensitive shrubland birds. This is supported by bird survey data from a forested area in central Massachusetts where a tornado strike in 2011 created an opening of approximately 450 ha that now supports breeding prairie warblers as well as nearly every other shrubland bird species occurring in the area (Vitz et al., unpublished data).

Beaver create early-successional habitat partially through their foraging activities that involve stripping bark from the trunks of live trees, but more importantly through their creation of temporary impoundments that revert to meadows once the beavers deplete the local food resource and abandon the site (Naiman et al., 1988). Although beaver meadows create early-successional shrubland habitat, sites selected by beaver are often resistant to succession because of their wet soils and vulnerability to flooding (Rosell et al., 2005). Thus, even long-abandoned sites in Minnesota were characterized as bogs and seasonally flooded meadows by Naiman et al. (1988), and McMaster and McMaster (2000) reported that even the driest sites within beaver meadows that had been abandoned for up to 40 years in Massachusetts were dominated by wetland associated plant species such as sedges, rushed, cattails and alders. Finally, the return interval is relatively short, 10–30 years in the Adirondacks of New York (Remillard et al., 1987). Therefore, a site is likely to be re-flooded before plant succession can proceed beyond the earlier stages characterized by hydrophytic plants (McMaster and McMaster, 2000). The distinctive habitat structure and composition within beaver meadows is reflected in their avifauna. For example, Chandler et al. (2009a) encountered several shrubland bird species in beaver meadows that were also common to upland shrublands such as gray catbird (*Dumetella carolinensis*), chestnut-sided warbler and white-throated sparrow, but not several species evidently restricted to upland sites, such as prairie warbler and field sparrow (*Spizella pusilla*). Some species characteristic of upland sites were present in beaver meadows in south-central New York (e.g. prairie warbler and indigo bunting); however, these species were very scarce even in abandoned beaver meadows, occupying <5% of sites (Grover and Baldassarre, 1995). Conversely, shrubland species abundant in beaver meadows (e.g. yellow warbler [*S. petechia*], alder flycatcher [*Empidonax alnorum*]) are scarce or absent in upland shrublands (King et al., 2009a).

As with other disturbance agents, patch size is an important influence on shrubland birds within beaver meadows. Beaver meadows in central Massachusetts averaged 8.3 ha in area, ranging from 1.1–22.4 ha, which is within the range of patch sizes required by area-sensitive shrubland bird species (Schlossberg and King, 2007). Chandler et al. (2009a) reported positive relationships between bird abundance and the area of beaver meadows for several shrubland species, as did Grover and Baldassarre (1995). This further suggests that the absence of area-sensitive shrubland birds from beaver meadows in central Massachusetts was not because habitat patches were too small, but rather because the structure and composition of the vegetation was not suitable.

The principal anthropogenic sources of early-successional habitat in eastern forests today include forest regeneration from silviculture, powerline corridors, abandoned agricultural land and reclaimed surface mines. Depending on the silvicultural system prescribed, forestry can create early-successional habitat through the removal of overstory trees during harvest, which increases light level to the ground and stimulates the development of a dense layer of shrubs and samplings (DeGraaf and Yamasaki, 2003; Tozer et al., 2010; Haché et al., 2013). Generally, even-aged systems are more effective for managing shrubland birds because many of these species are negatively associated with canopy closure (Smetzer et al., in press). Also, the size of the resulting habitat patches is large enough to accommodate area-sensitive bird species (Annand and Thompson, 1997; Costello et al., 2000; King and DeGraaf, 2000).

Powerline corridors are maintained by electric utility companies with mowing or herbicide application to prevent interference by trees with transmission lines, and in many cases, these practices provide suitable habitat for shrubland birds (Askins, 1994; Confer and Pascoe, 2003; King et al., 2009b; Askins et al., 2012). Shrubland specialists like prairie warbler and field sparrow are only present in corridors >45 m wide (King et al., 2009b), however, a situation analogous to the absence or scarcity of shrubland specialists from smaller openings (but see Askins et al., 2007). Because not all corridors are managed in a way that permits the development of suitable shrubland habitat, and shrubland specialists are scarce or absent in corridors <45 m wide, the contribution of powerline corridors to shrubland bird conservation is reduced, accounting for only 10% or so of shrubland habitat in Massachusetts (King and Schlossberg, 2012).

Abandoned agricultural land is another type of habitat that supports shrubland birds as it becomes colonized with forb, shrub and tree species (Hunter et al., 2001). Formerly common in eastern forests, the amount of post-agricultural habitat has decreased to a small fraction of its former extent (Litvaitis, 1993). In some cases, efforts are made by conservationists to arrest plant succession through periodic mowing or burning, often to support game species. Hence these openings, when maintained, are referred to as "wildlife openings" (Chandler et al., 2009b). Because of the cost of their maintenance, which can exceed \$450 ha^{-1}, and the limited budgets of natural resource agencies, old fields managed as wildlife openings comprise a small percentage (~2% for Massachusetts) of regional shrubland habitat (Oehler, 2003; King and Schlossberg, 2012).

Surface mines are reclaimed after mining operations are complete, and in some cases reclaimed mines provide high-quality habitat for early-successional birds (e.g. Bulluck and Buehler, 2006). Because of their poor soils, the resulting shrublands tend to be persistent, and as with powerline corridors, the cost of creation is born by rate payers, and not directly by natural resource agencies. Shrubland habitat created by mining is restricted geographically to areas where subsurface minerals are present in commercially exploitable quantities; however in some regions mining makes a substantial contribution to the creation of this type of habitat. In one study of several central Appalachian watersheds, reclaimed surface mines comprised nearly 5% of the land area (Townsend et al., 2009).

Although both support disturbance-dependent bird species absent from mature forest, there are important contrasts between successional habitats found within powerline corridors, old fields and reclaimed surface mines, and young forest habitats created by silviculture or wind damage (Lorimer, 2001). Successional habitats typically have a greater representation of herbaceous vegetation as well as more exotic invasive plant species compared to young forest habitats created by silviculture (Bulluck and Buehler, 2006; King et al., 2009a; Elliott et al., 2011). These differences in habitat conditions are reflected in the abundance of the shrubland bird species occupying these sites. Densities of most shrubland bird species differ between successional and young forest habitats, and some species are largely restricted to one or the other (Askins, 2001; Bulluck and Buehler, 2006; Kubel and Yahner, 2008; King et al., 2009a).

1.2. Early-successional species

There is general consensus on which species should be termed shrubland birds, despite the fact that most lists that have been compiled do not use any quantitative basis for this assignment, and the degree of association of shrubland species with these habitats also varies, with some species exhibiting an obligate association and others able to occupy other habitats. For the purposes of this review, we use the list of 41 species developed by Schlossberg and King (2007), which is based on a meta-analysis of studies of bird distribution between forest and shrubland habitat that yielded a numerical score ranging from 0 to 1 indicating the degree of association between a species and shrubland habitat. This was complimented by reference to published lists by previous authors. This "Early-successional Index" (ESI) identified some species as nearly obligate associates with shrubland habitat (e.g. prairie warblers, ESA = 0.95), whereas other species were more facultatively associated with shrublands (e.g. black-and-white warblers [*Mniotilta varia*], ESA = 0.64), occurring both in shrubland openings caused by disturbance, yet also in closed canopy forest in some situations (King and DeGraaf, 2000). Almost all species identified as shrubland birds on expert lists had ESI values of >0.5. Most species are songbirds (Passeriformes), reflecting the numerical dominance of this taxon.

1.3. Trends in shrubland habitats and species

A conspicuous feature of shrublands is they are ephemeral, changing over the course of a decade or so from an open-canopy condition in which grassy and herbaceous cover is well represented to a closed-canopy condition dominated by saplings (Keller et al., 2003; Loftis et al., 2011). These changes in plant succession are reflected in changes in the fauna. For example, studies show some early-successional birds, particularly seed-eaters such as dark-eyed juncos (*Junco hymalis*) and white-throated sparrows, are most abundant directly after disturbance (DeGraaf, 1991; Keller et al., 2003; Schlossberg and King, 2009; Smetzer et al., in press). In contrast, other species like chestnut-sided and prairie warblers colonize disturbed sites within a few years after disturbance but only reach their greatest abundance five or more years after disturbance as shrub and young tree species dominate the site. Most early-successional species disappear from disturbed sites once the canopy closes, typically 15–20 years post-disturbance, presumably due to decrease in food or suitable nests sites (Keller et al., 2003; Schlossberg and King, 2009). The rapidity with which shrubland habitat changes from suitable to unsuitable poses a challenge to conservationists concerned with managing these populations, since a population within an area of concern can become locally extirpated within a decade in the absence of habitat manipulation, or over greater areas in the event that restrictions on active management are imposed based on concerns about late-seral species, for example.

The most widely available data on the extent of early-successional forest come from the US Forest Service Forest Inventory and Analysis (FIA) program, which consists of permanent plots on which measurements of forest structure and composition are made every 5–10 years (Smith et al., 2004). From the standpoint of habitat structure potentially suitable for shrubland birds and other wildlife, the relevant measurement is the proportion of forest area in the seedling/sapling stage, which is defined as trees as large as 12.7 cm dbh. Two recent summaries have been undertaken of the FIA data with regards to habitat needs of shrubland wildlife. Schlossberg and King (2007) used these data to summarize the age class distribution for forests in the six New England States (Maine, New Hampshire, Vermont, Massachusetts, Connecticut and Rhode Island). They found that on average 14.9% of New England forests were in the seedling/sapling stage as of 2006, and the amount of shrubland habitat within the region had only declined by a few percent since 1950. The majority of current shrubland habitat in 2006 was located in Maine, however, and the average over the other five states at that point in time was 5.9% of forest area. This is important from the standpoint of shrubland birds because the habitat created by forestry in northern Maine does not benefit most of the early-successional species of conservation concern (e.g. prairie warbler, golden-winged warbler [*Vermivora chrysoptera*]) because their ranges do not extend that far north (Dettmers, 2003; Schlossberg and King, 2007). Furthermore, the apparent stability in the amount of shrubland habitat in New England was the result of extensive industrial logging operations in Maine; the loss of shrubland habitat for the New England states excluding Maine was approximately 66% since 1950. In another study, Shifley and Thompson (2011) summarized FIA data for 10 states that cover much of the Central Hardwoods region (Arkansas, Illinois, Kentucky, Michigan, Missouri, Ohio, Pennsylvania, Tennessee, and West Virginia) and reported similar trends. The proportion of forest in the seedling/sapling age class had declined in this region to 5.5% of its original extent since the 1950s. Finally, we summarized the FIA data for 31 US states within the North American Breeding Bird Survey Eastern region, which corresponds generally with the geographic scope of this paper, and found again that the amount of early-successional (0–19 years old) forest varied geographically, from 6% in the northeastern US to 24% in the southeast (Table 1). Notably the percent change over the past decade is negative for 71% of these states, and all three regions, averaging a 3% per year decline in seedling sapling habitat (Table 1).

The fact that the amount of early successional shrubland habitat in eastern forests has declined substantially in just a few decades has caused alarm among conservationists. It is likely, however, that the actual situation is even more serious than the FIA data suggest.

Table 1
Percent of forest in the seedling-sapling stage of succession (0–19 years post harvest) for states within the Eastern Region of the North American Breeding Bird Survey calculated using Forest Inventory and Analysis data for the most recent survey years (2005–2008), and divided into geographic regions. Also shown are short-term changes for the previous decade of survey data, the period for which data were consistently available, expressed in percent change. Data shown are for productive timberlands only. *Source:* US Forest Service (2006).

Northeast region	Current estimate	Trend (%/year)
Connecticut	2.46	−6.30
Delaware	11.2	3.05
Massachusetts	1.78	−7.14
Maryland	8.40	1.50
Maine	4.72	−6.03
New Hampshire	5.73	−0.92
New Jersey	4.62	0.33
New York	3.99	−6.51
Pennsylvania	5.91	−2.67
Rhode Island	1.50	−6.94
Virginia	20.1	−0.96
Vermont	2.79	−4.99
West Virginia	5.00	6.59
Region average	6.01	−2.38
Southeast region		
Alabama	39.1	−0.38
Arkansas	20.3	0.83
Florida	29.8	−2.45
Georgia	33.9	−1.89
Kentucky	4.44	−5.75
Louisiana	5.99	−16.7
Mississippi	38.1	−1.22
North Carolina	25.5	−2.45
South Carolina	32.3	−2.19
Tennessee	14.1	0.34
Region average	24.3	−3.19
Midwest region		
Iowa	4.44	−4.57
Illinois	5.99	−3.51
Indiana	5.30	−2.65
Michigan	9.11	2.14
Minnesota	16.7	0.71
Missouri	3.96	−4.60
Ohio	8.12	−1.53
Wisconsin	11.0	0.49
Average	8.08	−1.69

The seedling/sapling age class as defined by FIA overestimates the amount of shrubland habitat available, because its upper dbh limit, 12.7 cm, represents a stand that is in the self-thinning stage, and thus has matured far past the stage where it is usable by most shrubland-specialist birds (DeGraaf, 1991; Keller et al., 2003). To illustrate this, Schlossberg and King (2009) conducted a meta-analyses of studies documenting the change in bird abundance as a function of stand age and used the area under the abundance–time regression curves to estimate the proportion of regenerating forest effectively used by each bird species expressed as the proportion of their maximal abundance. Based on these results, they concluded that over the period from stand initiation to the point at which shrubland birds become locally extirpated the realized abundance of shrubland birds is on average 53% of their maximum abundance, demonstrating that current estimates of habitat capacity for shrubland birds may be inflated by a factor of 2 (Schlossberg and King 2009).

Analyses of data sources other than the FIA program also indicate that the actual amount of available habitat is far less than indicated by estimates of seedling/sapling habitat from FIA. For example, King and Schlossberg (2012) surveyed early-successional habitats in Massachusetts using a combination of landowner queries, GIS and review of timber harvest plans, and on the basis of this analysis concluded that early-successional shrublands cover approximately 5.7% of the state, which is the same as estimated by FIA, but 55% of these shrublands consisted of wetlands that do not support priority shrubland birds (Chandler et al., 2009a). If only upland shrublands that would support these priority species are considered, they estimated 2.8% of the state's area was shrubland habitat, which is approximately half of the amount of shrubland habitat estimated from the FIA data (5.7%). In contrast, a similar study in nearby Rhode Island indicated 2.5% of the area of that state consisted of upland shrubland (Buffum et al., 2011), which is higher than the most recent FIA estimate for that state (1.5%; Table 1).

Declines in early-successional habitats are the result of a combination of the disruption of natural disturbance regimes, outright conversion of disturbance-prone forest types to non-forest or a condition less prone to disturbance, or in some cases, interactions between them. Suppression of fire and flooding are two clear examples of how the influence of disturbance agents have been reduced through direct interference. Fire suppression efforts were initiated in the early 20th century, and have increased in effectiveness to the point where the rate of ignition and spatial scale of impact have decreased to a fraction of their historical levels in fire prone regions, such as the Central Hardwoods, limiting fire from its historic role as an agent of forest regeneration and causing shifts in forest structure and species composition (Spetich et al., 2011).

The effect of fire suppression is exacerbated by the conversion of forest to less fire-prone forest types or non-forest. Fire-adapted ecosystems such as coastal pitch pine-scrub oak were historically widespread, although whether they are artifacts of European agriculture or were present earlier is debated (e.g. Foster and Motzkin, 2003). In any case, pitch pine-scrub oak barrens were also subject to frequent disturbances by fire, with as much as 10–31% of this cover type consisting of shrubland habitat pre- settlement (Lorimer, 2001; Lorimer and White 2003). This forest type supports priority disturbance-dependent species that are scarce in other habitats such as whippoorwill (*Antrostomus vociferus*) and prairie warbler when fire is allowed to occur, or surrogates like thinning are employed (King et al., 2011b). Fire suppression may also reduce the susceptibility of sites to future disturbance by fire through the process of "mesophycation", whereby fire suppression encourages the dominance of fire-intolerant species that in turn reduce the flammability of the system and thus its susceptibility to future disturbance (Brose et al. 2001; Nowacki and Abrams, 2008).

The role of beaver in creating early-successional habitat has also changed in recent history (DeGraaf and Yamasaki, 2003). For example, beaver-associated habitats formerly occupied 3.5% of the land area of New York State, which has since been reduced by over 65% (Gotie and Jenks, 1982). Beaver were extirpated from much of the east during the 18th and 19th centuries through trapping and human development (DeStefano and Deblinger, 2005), and although widespread, their impacts on contemporary landscapes provide another example of how the effect of a disturbance agent is lessened through displacement to an area where it is less potent. During the period of their absence, humans developed the lower reaches of many watersheds that would have been impacted by beaver flooding. Hence, although beaver populations have been recovering over much of the region they are prevented from establishing dams that would threaten transportation infrastructure, and thus are more often confined to the upper reaches of watersheds where topography restricts the extent of their impoundments, and thus also the extent of early-successional habitat they create (Naiman et al., 1988; S. DeStefano, pers. com.).

Another example of how a disturbance agent remains in force but the substrate it affects has been altered is the decreased vulnerability of younger forests windthrow (Foster and Boose, 1992; Leak et al., 1994). The effects of blowdowns are further reduced by the conversion of forest within the zones where disturbance has been most pronounced to non-forested habitat. The severity and rate of return of wind storms has historically been higher in coastal areas, with the return interval of storms to an individual site ranging from 85 years on average near the coast to >300 years in interior forests (Boose et al., 2001). Forests in coastal areas, however, have been impacted by extensive urban and commercial development (Litvaitis, 2003), reducing the area of forest available to serve as substrate for wind impacts that could create early-successional habitat for species that need it in the regions where it was historically most abundant.

The nature anthropogenic disturbance has shifted over much of the region to types of land use that provide less and lower quality shrubland habitat. These changes include both the types of anthropogenic disturbance as well as the intensity. During Colonial times through the Industrial Revolution, agricultural clearing and the consumption of fuelwood created extensive areas of disturbed forest that provided early-successional habitat during fallow periods in the case of agriculture or between harvests in the case of woodlots (DeGraaf and Miller, 1996). This period was followed by one of westward migration and the adoption of alternative fuel sources that reduced the level of agricultural and forestry activities. Subsequently eastern forests were subject to silvicultural management; however, economic factors related to regional and global shifts in wood supply and demand again caused a decline in the level of forestry that continues to the present. This, combined with increased parcelization of eastern forests has reduced the amount of anthropogenically created shrubland to a fraction of its earlier extent (Trani et al., 2001). The decline in industrial-scale forestry has been compounded by a shift from even-aged management to uneven aged systems that do not create patches of shrubland habitat of sufficient size for some shrubland bird species.

The regional declines in early-successional forest are reflected in population trends of species that depend on them. For example, declines in early-successional bird species are reflected in data from the BBS, a long-term, continental-scale monitoring program that uses standardized counts of singing birds on roadside transects to track their populations. Analyses of these data reveal long term declines for 71% of early-successional bird species over the

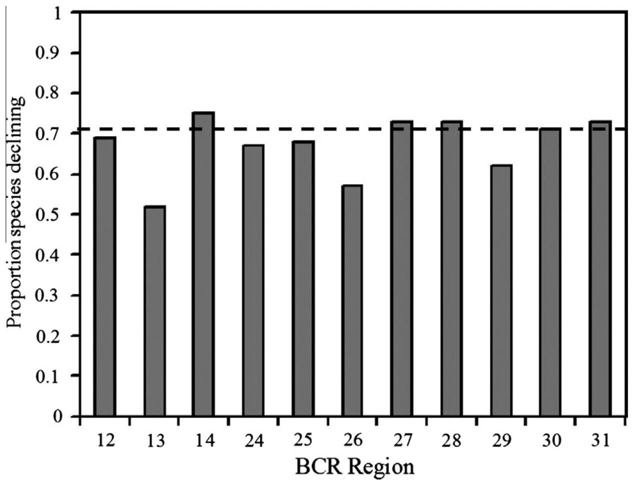

Fig. 1. Proportion of shrubland species observed on the North American Breeding Bird Survey exhibiting declines from 1966–2011 for all forested eastern Bird Conservation Regions (BCRs) of North America (<http://www.nabci-us.org/map.html>; 12. Boreal hardwood transition, 13. Lower Great Lakes/St. Lawrence Plain, 14. Atlantic northern forest, 24. Central hardwoods, 25. Western Gulf coastal plain/Ouachitas, 26. Mississippi alluvial valley, 27. southeastern coastal plain, 28. Appalachian mountains, 29. Piedmont, 30. New England/mid-Atlantic coast, 31. Peninsular Florida). The proportion declining across the entire eastern BBS region is indicated by the dashed line. All trends are considered regardless of statistical significance, although the pattern is the same if the analyses are restricted to significant trends. *Source:* Sauer et al. (2012).

period between 1966, the year the BBS was initiated, and 2011 (Fig. 1). Notably, more species are declining than increasing in all Bird Conservation Regions (geographic subunits for bird conservation planning; http://www.nabci-us.org/map.html) within the Eastern BBS region.

Other evidence for long-term declines in shrubland species include data from counts of migrating birds. Hill and Hagan (1991) analyzed 53 years of birdwatching trip lists from eastern Massachusetts and reported that 70% of shrubland birds observed on these trips exhibited significant declines over this period, a proportion similar to that reported from the BBS. Hussell et al. (1992) calculated trends from bird captures at a site in Ontario and reported that 92% of shrubland birds exhibited significant declines from 1967–1997. Hagan et al. (1992) reported trends calculated from 19 years of constant effort mistnetting at two sites, one in coastal Massachusetts and the other in eastern Pennsylvania, and found that 81% of shrubland birds exhibited significant declines at the Massachusetts site and 50% at the Pennsylvania site. These declines are not surprising, indeed it would be unexpected if populations were not decreasing given the evidence of habitat declines and the close association between shrubland birds and early-successional habitat.

1.4. Concern about shrubland species

As a result of this evidence of declining populations, conservationists have identified early-successional shrubland birds as species of particular conservation concern. This is reflected in a number of ways. Partners in Flight, an international consortium of state and federal agencies and NGOs concerned with bird conservation has assigned each North American bird species a composite conservation rank based on 6 individual measures of its vulnerability, including total population size and trends, etc. (Partners in Flight Science Committee, 2012). Early-successional species rank highly by these measures; six of the 10 top-ranked species are shrubland species (Gunnison sage-grouse [*Centrocercus minimus*], Florida scrub-jay [*Aphelocoma coerulescens*], Bachman's warbler [*Vermivora bachmanii*], Kirtland's warbler [*S. kirtlandii*], lesser prairie chicken [*Tympanuchus pallidicinctus*] and black-capped vireo [*Vireo atricapillus*]). Similarly, bird species in the US are ranked in terms of their conservation importance in State Wildlife Action Plans, which are prepared under a federally mandated program as a condition for Federal Aid. On average, a higher proportion (49%) of shrubland species were listed as "species of greatest conservation need" by 12 eastern states and the District of Columbia than mature forest species (39%). Finally, a large proportion (43%) of shrubland bird are identified as high-priorities for conservation by the Canadian Wildlife Service (Dunn et al., 1999).

Conservation concern is also elevated for non-avian shrubland species, including the Karner blue butterfly (*Lycaeides melissa samuelis*) and the New England cottontail rabbit (*Sylvilagus transitionalis*), eastern shrubland species that are either listed or are candidates for listing under the US Endangered Species Act as a result of the steepness and extent of recent population declines. Thirteen of 19 tiger beetle species (*Cicindela* spp.) in New England are listed as "critically imperiled" in at least one state in the region (Litvaitis et al., 1999); all but one of these species require early-successional habitats. Similarly, two-thirds of the state-listed species of moths and butterflies in Massachusetts are early-successional species (Litvaitis et al., 1999), and 23% of Connecticut's state-listed lepidopterans are associated with shrublands (Wagner et al., 2003).

There is substantial evidence that the focus of research and conservation has shifted over the past decade from mature to early-successional forests. For example, a Web of Science search on "early, succession, and conservation; or early, seral, and conservation; or early, succession, and ecosystem" returned 416 citations published between 2001 and 2010. In contrast, this same search with "late" substituted for "early" returned only 254 references. Furthermore, the annual number of publications on this topic has increased ~300% over the past decade (King et al., 2011a).

1.5. Controversy

Despite the preponderance of scientific evidence indicating that natural disturbance regimes have been disrupted and that shrubland birds have sustained large population declines or even extirpations, there is still skepticism about the importance of management of early-successional habitats for maintaining biodiversity and the means, if any, by which this should be accomplished, and public opposition remains a challenge to conserving these communities (Litvaitis et al., 1999; Askins, 2001; Gobster, 2001). Creating and maintaining shrublands requires inherently destructive methods. The early conservation movement in North America was in part a reaction to unregulated logging, and thus cutting trees and clearing forest has long been viewed by many as necessarily harmful to the environment (Askins, 2001).

Arguments against shrubland management typically consist of variants of the following: 1. Shrubland birds were not a natural component of the eastern avifauna, and 2. Shrubland species are generalist, "weedy" species that can use habitats created incidentally via human activities. Accounts by colonists of large tracts of unbroken forest form the basis for much of the popular impression that this condition was eastern forests in their "natural state". Investigations based on historical records, ecological treatises and paleoecological reconstructions indicate that shrubland habitats have been present within the eastern forest region in historical times as well as within a longer timescale encompassing the evolution of extant species of shrubland birds (DeGraaf and Miller, 1996; Askins, 2000). Accounts of habitat conditions from Colonial times likely underestimated the extent of early-successional habitats since they reflected forest conditions after over a century of regeneration following the displacement or extirpation of Native

Americans from coastal areas by warfare with colonists or diseases derived from them (Denevan, 1992; Whitney, 1994). Native Americans practiced used fire and other means for agricultural purposes and to encourage the growth of food plants for game for millennia before Europeans arrived (Whitney, 1994; Askins, 2000; Lorimer 2001). Nevertheless, surveys from the late 1700s in central New York still reported that 2.6% of the forest consisted of burned areas, windfalls or shrubby wetlands (Marks and Gardescu, 1992). Government land surveys of northern hardwood forest from Maine, New York, Michigan and Wisconsin indicated that on average 5.3% of the region consisted of blowdowns and barrens during the late 18th and early 19th centuries, and estimates ranged as high as 13% (Lorimer, 2001). Estimates of the pre-settlement proportion of prairie and oak savannah in the upper Midwest range as high as 65% (Whitney, 1994). Runkle (1985) estimated that annual disturbance rates in mesic eastern forests averaged 0.5–2%, yielding an average return interval of 50–200 years. In many regions the average gap size were too small (0.01 ha) to be used by many early-successional species (Schlossberg and King, 2007); however Lorimer (2001) cites blowdowns of 1000s of hectares, so clearly some larger openings were present. Contemporary studies suggest the presence of shrubland habitat in pre-settlement landscapes as well. In New Hampshire, old growth spruce-fir forests are extensively disturbed by wind and disease, with 10–50% of forest area consisting of canopy gaps (Worrall and Harrington, 1988).

Considering the time-scale on which disturbance dependent species evolved in eastern forests, which is several millennia for songbird species of greatest conservation need like the prairie warbler, extensive early-successional habitats were available resulting from the effects of drought, glaciation and grazing by Pleistocene megafauna that created and maintained a region of grassy savannah and parkland that extended from the Atlantic ocean to the Great Plains (Askins, 1998, 2000). This view is supported by pollen records, as well as the discovery of bones of bird and mammal species typical of grasslands and plains in sinkholes and owl pellets deposited in caves (Askins, 2000), and eighteenth century accounts of bison (*Bison bison*), a prairie and savannah species, in the southeast and mid-Atlantic states (Rostlund, 1960). Although this argument may seem specious to some, isolation of ancestral populations by glaciers is thought to have been a major influence in the evolution of the American bird fauna, so the assertion that disturbance was absent from the Northeast based on accounts of pre-Columbian forests by early explorers does not reflect the same time-scale as the biological processes that created the bird fauna of the region.

Another reason why early-successional species receive less popular concern than forest species is the view that these species are generalists that can persist today in the absence of deliberate conservation attention. Shrubland birds require disturbance to persist, and humans routinely create disturbance as the result of industrial, agricultural and commercial activities. Thus, one could conclude that this chronic and increasing level of disturbance could be sufficient to maintain shrubland birds. The perception that shrubland birds are generalists is further is reinforced by the fact that humans live in areas where early-successional habitats occur disproportionately in the form of road and field margins etc. Habitats such as field edges and road margins do not appear to provide sufficient area for shrubland birds to attract a mate or successfully fledge young, however, as indicated by the work of Fink et al. (2006). They reported that some shrubland birds, including species of the high conservation concern such as the prairie warbler and yellow-breasted chat, were present in field forest ecotones, which might have led the researchers to conclude these species were flexible in their habitat use, but further examination showed these species were unable to reproduce successfully in edges. Thus, the sporadic occurrence of shrubland birds on roadsides or edges probably does not represent a viable population that can sustain itself. Additional evidence for this comes from the North American Breeding Bird Survey (BBS), which is conducted on roadsides, and which shows that shrubland birds in these roadside habitats are declining precipitously, suggesting they are marginal habitats that are not sufficient to support shrubland bird populations. The narrow range of age and habitat conditions tolerated by shrubland birds, some of which are only present a few years after disturbance, argue against the contention that these species are generalists, and also effectively reduces the capacity of available habitat for these species (Schlossberg and King, 2009; King and Schlossberg, 2012).

1.6. Balancing early-successional forest with other values

Conservation of early-successional communities occurs within the context of other potentially conflicting ecological values, such as the conservation and enhancement of biologically mature forest. Because creation of shrubland habitat results in a nearly complete turnover of the bird fauna (e.g. King and DeGraaf, 2000), it is not possible to manage for all species at a given site. It is possible to maintain both mature-forest and shrubland birds in the same landscape, however. Thompson et al. (1992) and Welsh and Healy (1993) showed that forested landscapes in New Hampshire and Missouri with 18% and 20% of their area in regenerating clearcuts, respectively, had more species than landscapes without clearcuts, and all of the species present in the unmanaged landscapes were present in the managed landscapes. The presence of agricultural and residential development within the landscape can negatively affect birds through nest predation and parasitism (Robinson et al., 1995); however these threats are not typical of extensively forested (~70%) landscapes (Hunter et al., 2001).

Also, regenerating clearcuts are used extensively by mature-forest birds during the vulnerable postfledging period (Vega Rivera et al., 1998; Marshall et al., 2003; Vitz and Rodewald, 2006; Stoleson, 2013) and in some situations are selected over mature forest (Chandler et al., 2012). This switch in habitat preferences during the postfledging period probably occurs because regenerating clearcuts have greater fruit and insect resources, or offer better protection from predators (Vitz and Rodewald, 2007). Postfledging habitat can be as important for population viability as nesting habitat (King et al. 2006). These findings suggest early-successional communities can augment diversity in forested landscapes by providing resources for mature-forest species, such as food or predator-free space for juvenile forest songbirds that seek out early-successional habitats during the transition to independence.

Research findings indicating that even-aged management applied under sustainable best management practices does not exclude any mature-forest bird species from extensively forested landscapes, and that it may actually enhance habitat for these species during the postfledging period, suggests that management for shrubland and mature-forest species is feasible at the landscape scale, a notion that has been confirmed through landscape-based population viability models (Bonnot et al., 2013). The converse is not necessarily true, however. Approximately 5% of the land area of the US is designated as wilderness where management for early-successional habitat is not permitted, and in these areas the development of mature-forest conditions will take place. While this is clearly beneficial from the standpoint of the conservation of species that depend on mature forest, it also highlights that fact that early-successional shrubland habitats and species have no such assurance.

1.7. Conservation of early successional species

It is clear from the preceding that the extent of early-successional shrubland habitat within much the eastern forest region has declined from levels that have characterized eastern forests for millennia, and that it is still decreasing. Furthermore, the area of forest available to be converted into shrubland habitat, although higher than its historical lows of 150 years ago, is reduced from its pre-historical maxima by extensive urban and commercial development, particularly in coastal areas and forest types that historically would have hosted the greatest amount of shrubland habitat. Within the remaining forested areas, natural and anthropogenic processes that create habitats suitable for shrubland birds and other species have been reduced or suppressed. As a consequence, obligate shrubland species have declined at rapid rates, sometimes to the point of threatened or endangered status, or to the point of conservation concern that regional or continental conservation plans are being developed. Because most eastern shrubland habitats are ephemeral, changing continually with succession such that it is suitable for perhaps 10–20 years for most species and systems, this habitat type and the species that use it are subject to annual losses of 5–10% that must be replenished via natural or anthropogenic disturbance to arrest population declines, and the local extirpation of species at any given site is certain in the absence of human or natural intervention.

There has been extensive debate regarding whether these declines in eastern forests are in fact populations returning from elevated levels caused by European agriculture to more natural conditions, and thus, whether conservation concern or management response is indicated. Because the regional extent of shrubland habitats and disturbance regimes has varied so much over the timescale in which species and ecosystems have evolved, it is not clear to what extent historical conditions can be used as a guide to the optimum level of early-successional habitat in the landscape (Lorimer, 2001). For example, by one interpretation, northeastern coastal barrens that currently support some of the most endangered invertebrate species in the region were formerly forested, and current conditions that support these species are artifacts of European agriculture (Foster and Motzkin, 2003), yet it would be hard to advocate for allowing these species to become globally extinct on the basis that they were not historically present at that locality.

This begs the question of what habitat and population goals are appropriate? The decision to manage shrubland species is a forgone conclusion for most agencies and many NGOs because their conservation status and trends described above identify them as species in need of protection by statute, which is a simpler justification for managing habitat for them than the selection of an arbitrarily selected historical baseline condition for restoration (Lorimer, 2001). Managers typically gauge their activities relative to population targets, but a rigorous means for establishing the desired populations of shrubland birds in general, and thus the amount of shrubland habitat, has not yet been developed. One suggestion is to increase populations to levels in 1966, the year the BBS was initiated for species that have declined by more than 50% since that time (Rich et al., 2004), which describes populations of most shrubland bird species in the East. Since it is beyond the scope of most agencies or NGOs to create the amount of habitat needed to accomplish this, which would involve doubling the amount of shrubland habitat in the region, the scale of management efforts nearly always consists of a fraction of the amount of habitat specified by the management goals (Litvaitis et al., 1999; Oehler, 2003).

Alternatively, management targets have been suggested based on levels that would result in a balance of conditions across a managed landscape that would support all native species, exclusive of those requiring old-growth or other specialized habitats, which would be provided in reserves or other areas outside of management zones. For managed lands, ten percent of forest in early-successional shrubland has been suggested as a level that would support regional populations of shrubland birds and other wildlife but also provide sufficient cover of older forests to support mature-forest species (DeGraaf et al., 1992; Dettmers, 2003). Anthropogenic habitat created during the course of commercial activities like logging or the maintenance of power transmission corridors provides additional habitat, but in general management activities directed at creating habitat for shrubland birds and other wildlife are more effective, creating larger habitat patches with less tree cover, and consequently, making a disproportionate contribution to regional populations. For example, in Massachusetts management activities directed specifically at creating and managing habitat for shrubland wildlife comprise only 20% of shrubland habitat but support over 40% of several priority shrubland bird species because these patches tend to be larger and have less tree cover (King and Schlossberg, 2012).

1.8. Conclusion

Early-successional shrubland habitats over much of the eastern forest region have declined precipitously and continue to decline, and as a result, most species that depend on them have also declined, and this group makes up a disproportionate number of threatened or endangered species. This decline is the result of the disruption of natural disturbance regimes, changes in anthropogenic land use, and conversion of forest ecosystems to non-forest habitat such as urban, commercial or agricultural uses. Early-successional habitats currently comprise a small fraction of forested area, a percentage in the single-digits over much of the region, and the amount continues to decrease.

Skepticism about the importance of conserving these habitats is often based on the assumption that shrublands and shrubland species were not present in the eastern forest region historically. However, open and shrubland habitat have been extensive in the East during previous periods within the evolutionary time scale of extant species and communities, including within areas that are now dense forest. Many of the specific areas where shrublands were formerly present have been converted by human activities, however, so activities to conserve these species must take place at sites where disturbance was historically less prevalent. Furthermore, since only a fraction of the landscape formerly available as a substrate for disturbance is available for natural or anthropogenic disturbances to occur, the proportion of managed lands maintained as shrubland will have to be greater than the historical norm in order to achieve an amount of shrubland habitat comparable to historical levels at the regional scale.

Management for shrubland species must be conducted in such a way as to conserve other ecological values, such as the persistence of mature-forest species, and although it is not possible to manage for both at the same site, the conservation of shrubland and mature-forest species can be accomplished within the same landscape. The presence of some shrubland habitat within the landscape appears to augment habitat quality for many mature-forest birds by providing resources for fledglings and adults during the post-fledging period. Incidental commercial activities such as logging and maintenance of power transmission corridors can support shrubland birds; however these habitats are generally of lower quality than habitat created expressly for shrubland birds. Effective conservation of shrubland species should include maintaining or restoring disturbance-dependent communities like barrens and tailoring commercial activities to provide the maximum benefit for shrubland-dependent birds and other species. In many cases, however, these disturbance agents will not provide sufficient habitat to arrest population declines, and thus it will be necessary to supplement these efforts with management specifically directed at the conservation of these species.

Acknowledgements

We thank the National Resources Conservation Service Resource Inventory and Assessment Division for supporting this research, and R. DeGraaf, J. Scanlon, C. Costello and two anonymous reviewers for helpful comments on earlier versions of this manuscript.

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