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

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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.

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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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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