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Responses of early-successional songbirds to a two-stage shelterwood harvest for oak forest regeneration

Eric L. Margenau^{1,2*}, Yong Wang¹, Callie J. Schweitzer³ and Brandie K. Stringer¹

Abstract

Background: The early stage of forest succession following disturbance is characterized by a shift in songbird composition as well as increased avian richness due to increased herbaceous growth in the forest understory. However, regeneration of woody species eventually outcompetes the herbaceous understory, subsequently shifting vegetation communities and decreasing availability of vital foraging and nesting cover for disturbance-dependent birds, ultimately resulting in their displacement. These early stages following forest disturbance, which are declining throughout the eastern United States, are ephemeral in nature and birds depend on such disturbances for nesting and other purposes throughout their lives.

Methods: We investigated the use of a two-stage shelterwood method to manage long-term persistence of seven early successional songbirds over a 13-year period in an upland hardwood forest within the southern end of the mid-Cumberland Plateau in the eastern United States.

Results: Canopy and midstory gaps created after initial harvest were quickly exploited by tree growth and canopy cover returned to these areas, accelerating the displacement of early-successional species. Woody stem densities increased substantially following stage two harvest as advanced tree regeneration combined with the re-opening of the overstory layer increased resource competition for early-successional plants in the understory. Carolina Wren (*Thryothorus ludovicianus*), Eastern Towhee (*Pipilo erythrophthalmus*), Indigo Bunting (*Passerina cyanea*), and Yellow-breasted Chat (*Icteria virens*) were characterized by immediate increases following initial harvest in 2001; while the American Goldfinch (*Spinus tristis*), Prairie Warbler (*Setophaga discolor*), and White-eyed Vireo (*Vireo griseus*) did not show an immediate response. Stage two harvest in 2011 rejuvenated vegetation which benefitted focal species, with six of seven species showing increases in densities between 2010 and 2012.

Conclusion: The two-stage shelterwood method created conditions advantageous to early-successional birds by helping to re-establish understory vegetation through periodic disturbance to the canopy layer. This method provides evidence that early-successional species can be managed long-term (> 15 years) while using relatively small spatial disturbance through the two-stage shelterwood method.

Keywords: Early-successional forests, Mid-Cumberland Plateau, Silviculture, Shelterwood, Songbird community

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Background

Studies of songbird population fluctuations, as a function of timber management, are common (see Sallabanks et al. 2000; Brawn et al. 2001; Vanderwel et al. 2007) due to concerns of declining songbird populations as a result of decreasing total areas of natural habitats (e.g., forests, shrublands, savannas) in the eastern United States (US) (Hunter et al. 2001; Drummond and Loveland 2010; Sauer and Link 2011). Forest management practices can help alleviate habitat-related pressures felt by songbird species through the creation of heterogeneous vegetation structures (Thompson III et al. 1993; Perry and Thill 2013; Rankin and Perlut 2015). Forest management practices and songbird conservation may differ in their objectives (timber production versus maintaining rich ecological communities, respectively), but they both benefit by periodic forest disturbance. Land (or forest) managers are often interested in returning harvested stands to their former tree composition using various silvicultural practices. Through the implementation of these different silviculture techniques, tree harvest has also shown it can benefit songbird species characterized as early-successional obligates (Klaus et al. 2005; McDermott and Wood 2009). An important and often overlooked stage of forest succession occurs immediately following forest disturbances (i.e., tree harvest; Askins 2001; Swanson et al. 2011), where woody and non-woody plants in the understory are prominent vegetation features (Decocq et al. 2004). Until recently, the early-successional habitat (or young forest, shrubland; Litvaitis 2003) was thought to have low ecological importance (Swanson et al. 2011) and largely ignored (Askins 2001). However, many species of songbird rely on this stage of forest succession either for a portion of or for their entire life (Trani et al. 2001; Swanson et al. 2011; Oswalt et al. 2012). The early-successional habitat is critical for avifauna by provisioning essential functions during the nesting and post-nesting period including nesting cover (Confer and Pascoe 2003; Smetzer et al. 2014), cover from predators (Vitz and Rodewald 2006; Chandler et al. 2012), and foraging resources (Vega Rivera et al. 1998; McDermott and Wood 2010). Unfortunately, the distribution and total amount of early-successional habitat have recently declined throughout eastern US due to historical reasons (restrictions on logging, farm abandonment, or suppression of fire; Lorimer 2001; Trani et al. 2001), which are currently being compounded by land conversion (e.g., urban sprawl). Continued decreases in total area will likely have negative implications for songbird species associated with early-successional habitats (Dettmers 2003; King and Schlossberg 2014).

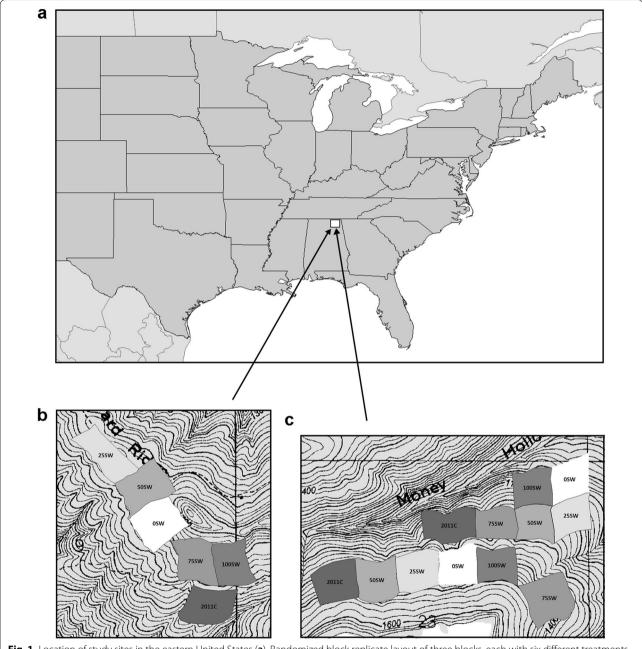
In recent decades, active management relating to ecosystem functions has facilitated greater understanding of forest use for timber production while sustaining ecosystem viability (Franklin et al. 1986; Franklin 1989; Hansen et al. 1991). The staged shelterwood method used to regenerate oak-dominated forests in the eastern US follows this framework as overstory trees are removed in one or two stages, promoting advanced regeneration of oak and other species in the understory under the protection of the remaining canopy (Loftis 1990). The shelterwood method can create varied temporal and spatial stand conditions suitable to a range of avian communities (Thompson III et al. 1995; Newell and Rodewald 2012), particularly bird species relying on early-successional forest habitats (Annand and Thompson III 1997; Goodale et al. 2009). However early-successional forest conditions are often transient, constrained by plant regeneration following canopy removal (DeGraaf and Yamasaki 2003; Schlossberg and King 2009; Schlossberg et al. 2010).

There are many scientific papers that have studied the relationships between bird communities and forest management practices (Baker and Lacki 1997; Campbell et al. 2007; Augenfeld et al. 2008). Although no study has ever examined the effects of the two-stage shelterwood method on the early-successional songbird community to test whether periodic disturbances can be a useful technique for early-successional songbird management. The objectives of this study were to provide a descriptive assessment (see "Statistical analyses" section for further explanation) of the vegetation and early-successional songbird community's responses to a two-stage shelterwood harvest and to test how varying tree basalarea retention harvests for oak forest regeneration might affect the habitat and bird community dynamics.

Methods

Study area

Study sites were located in northern Jackson County, Alabama, USA on the southern end of the mid-Cumberland Plateau (34°57'N, 86°08'E; Fig. 1a). To ensure proper replication, two sites within close proximity (11.7 km apart) with similar habitat characteristics were selected by the Forest Service (FS) of the US Department of Agriculture (USDA). Three block replications were implemented, one at Miller Mountain (Fig. 1b) and two at Jack Gap (Fig. 1c). Each block consisted of five stands implemented in 2001, with an additional control stand being added in 2011 (totaling 18 stands). Miller Mountain has a mean elevation of 500 m with a southwestern aspect and Jack Gap has elevations of 450 and 360 m with northern aspects; slopes at both sites range between 15 and 30% (Schweitzer 2004). The climate of this region is characterized by long and moderately hot summers, and short and mild winters (Smalley





1982). Forest stands at the study sites were mainly composed of oaks (*Quercus velutina*, *Q. rubra*, *Q. alba*, *Q. prinus*), yellow poplar (*Liriodendron tulipifera*), hickories (*Carya* spp.) and sugar maple (*Acer saccharum*) (Schweitzer 2004). For clarity, 'stage one' harvest refers to the initial tree harvest or herbicide treatment in 2001 and 'stage two' harvest refers to the canopy harvest in 2010.

Study design

Within each block, five stands each received one of five basal area retention treatments (0 [clearcut], 25, 50, 75, and 100 [control] percent retention). Stands were 4 ha in

size and roughly square in shape. During stage one, trees in the 0 (herein referred to as '0SW'), 25 (herein referred to as '25SW'), and 50 (herein referred to as '50SW') percent retention treatments were harvested by chain saw felling and grapple skidding. Stands with the 75 (herein referred to as '75SW') percent retention treatment had the midstory removed by stem injection using an herbicide (Arsenal[®], active ingredient imazapyr) (Schweitzer 2004). Stands receiving the 100 (herein referred to as '100SW') percent retention treatment were undisturbed. All fifteen stands were allowed to grow for 8 years, prior to final harvest (stage two removal) in 2010 (Schweitzer and Dey 2017). During stage two removal, remaining merchantable trees (≥ 14 cm diameter at breast height (DBH)) in the 25SW, 50SW, 75SW and 100SW were removed while the 0SW was left undisturbed. Three new control stands (one per block) were installed (see Schweitzer 2004 for further information). Consequently, five forest stand conditions were created in 2010: (1) 8-year old regeneration ('old clearcut', which consisted of 0SW stands), (2) released regeneration type 1, with more vertical structure due to the new sprouts from midstory and overstory trees and remaining or advanced growth of understory/midstory after the initial canopy removal in 2002 (consisted of 25SW and 50SW stands), (3) released regeneration type 2, with less vertical structure due to the killing of the midstory from herbicide during the initial treatment in 2002 which subdued resprouting (consisted of 75SW stands), (4) 'new clearcut' (the 'old control') (consisted of 100SW stands), and (5) mature or 'new control', forest stands that had not been disturbed for greater than 40 years (herein referred to as '2010C').

Habitat assessment

Five randomly generated 0.01 ha plots within each stand were used to measure habitat change over the study period. Percent overstory canopy cover was measured using a hand-held spherical densitometer at 1.4 m above the forest floor (Fiala et al. 2006; Korhonen et al. 2006). Woody stem data were enumerated from live trees measured, and classified into five diameter at breast height (DBH) categories ($\leq 2.5, \geq 2.6-5.0, \geq 5.1-7.5, \geq 7.6-10.0$, and ≥ 10.1 cm) (Schweitzer and Dey 2011) then divided by 4 to calculate stems/ha (stands were 4 ha in size). All woody stems measuring ≥ 10.1 cm DBH (canopy trees) were grouped into a single category since the focus of this study was on forest regeneration (small diameter trees). We averaged all collected data at the stand level and grouped those averages based on treatment type for each year collected. Stem measurements were taken during the 2001-03, 2009, 2011, and 2014 seasons and canopy measurements were taken during the 2002-06, 2009, 2011, and 2014 seasons.

Bird community surveys

The spot-mapping method (Ralph et al. 1993; Bibby et al. 2000) was used to determine territory density of selected songbirds during the peak of the breeding season (May 1-June 30) of the targeted species in 2002, 2003, 2010, 2012, 2013, and 2014. This technique was appropriate for this study because (1) stands were relatively small in size (4 ha) making accuracy feasible, (2) stands were all equal in area (which helps eliminate area-dependent variation), (3) all stands were roughly square in shape and had comparatively short total edge length (reducing the influence of edge effect on the bird community), and (4) because there were multiple surveyors, this technique reduces inter-observer bias as well as differences in experience of surveyors (McLaren and Cadman 1999). Each stand received 10 spot-mapping visits (\geq 3 days between visits) through the season in each year. Surveys started around 0500-0530 (CST) and lasted approximately 5 h each day, with each stand being surveyed for 45-60 min. Stands were surveyed by walking two parallel transects that evenly dissected each stand. Surveyors estimated locations of all bird species on a topographic map using pre-located markers along transect routes. Each stand visit was recorded on a separate data sheet, and all sheets were overlaid to delineate territories after all surveys were completed. Stand order and entrance were rotated to account for daily and temporal variation in songbird activities. Territory of an individual was determined by ≥ 3 detections over the 10 visits, with ≥ 2 of those detections occurring during non-simultaneous visits. Because stands were directly adjacent to one another, species that were recorded in two separate stands had their territory divided into 1/2 or 1/4 territories depending on location. About 17% (113 of 670 total species territories) were delineated and split between adjacent forest stands. Mean territory density of each species was calculated by dividing raw territory values for each stand by 4 (stands were 4 ha in size).

We selected bird species that were characterized as early-successional or disturbance-dependent (Blake and Karr 1987; Freemark and Collins 1992) with at least 10 territories 1 year during the 6-year study period. Species included in analyses were American Goldfinch (*Spinus tristis*), Carolina Wren (*Thryothorus ludovicianus*), Eastern Towhee (*Pipilo erythrophthalmus*), Indigo Bunting (*Passerina cyanea*), Prairie Warbler (*Setophaga discolor*), White-eyed Vireo (*Vireo griseus*), and Yellow-breasted Chat (*Icteria virens*). These songbird species were selected because they represented over 90% of territories from early-successional species group during the study, and selected species have been used in similar studies.

Statistical analyses

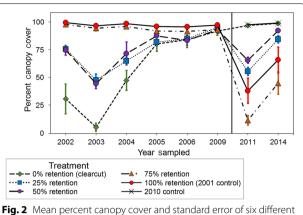
This study was first implemented as a silviculture study focusing on oak-hickory regeneration with avian community sampling added at a later date. Because avian sampling was not initially a priority in study design setup, statistical analyses relating the avian community to treatment type (0SW, 25SW, 50SW, 75SW, 100SW, and 2010C) were subject to some limitations. We were interested in determining whether basal retention treatments affected focal songbird densities, whether densities of focal songbirds changed over time (2002, 2003, 2010, and 2012-2014), while also investigating the interaction between treatments and years. We estimated the density of each focal species in each treatment (via ten replicated territory mapping visits each year) to produce a single density value for each treatment. This resulted in three replicated estimates of songbird density (one for each block replicate) for the six (five in 2002, 2003, and 2010) different treatment types each year. When using statistical models to predict relationship between predictor and response variables, small replication size increases the potential of overfitting models and limits predictive powers from our results (Babyak 2004). Due to the limited statistical power and the attempt to avoid erroneous conclusions based on our statistical analyses, we present descriptive results below. We assessed patterns of vegetation variables and songbird species' densities across treatment type, year, and within treatment types through years.

Results

Habitat

Canopy cover

Following stage one harvest, canopy cover in the 75SW and 100SW treatments remained high, while all other treatments (0SW, 25SW, and 50SW) showed a decrease during 2002 and 2003 (immediately following harvest in 2001). Canopy cover in the 0SW, 25SW, and 50SW treatments increased in 2004 (3 years following harvest) (Fig. 2). By 2005 (4 years after stage one harvest), canopy cover in 0SW, 25SW, and 50SW treatments reached relatively high levels (comparable to 75SW and 100SW treatments) until stage two harvest. Following stage two harvest in 2010, canopy cover declined in all treatments that received tree harvest (25SW, 50SW, 75SW, and 100SW). Canopy cover in 25SW, 50SW, 75SW, and 100SW treatments increased in 2014 (3 years after stage two harvest), which was similar to canopy responses following stage one harvest (in 0SW, 25SW, and 50SW treatments). Vegetation response was quicker following stage two harvest, with 1 year of reduced canopy in 2011 compared to 2 years of successive canopy decline in 2002



silviculture treatments during 2002–2006, 2009, 2011, and 2014. Solid black vertical line indicates when stage two harvest occurred (2010)

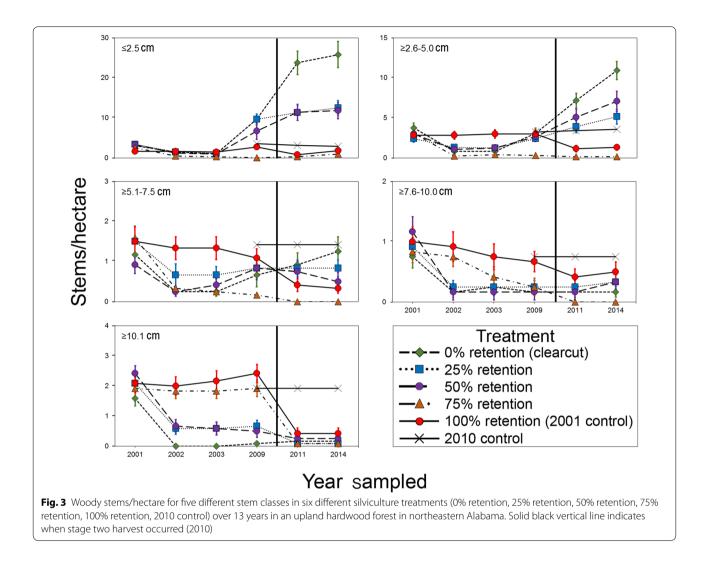
and 2003 (Fig. 2), possibly due to advanced regeneration already present in the midstory at the time of stage two harvest.

Stem classes

Stems/ha of 0–2.5 cm and \geq 2.6–5.0 cm DBH classes remained low during stage one, but increased prior to and following stage two harvest in treatments that received canopy removal during stage one (0SW, 25SW, and 50SW). Stems/ha of the \geq 10.1 cm DBH class decreased in treatments that received tree harvest in stage one (OSW, 25SW, and 50SW) and in stage two (75SW and 100SW stands; Fig. 3). Stems/ha of the \geq 5.1–7.5 cm DBH class were greater in 100SW compared to other treatments during stage one due to a lack of advanced regeneration in 0SW, 25SW, and 50SW stands coupled with midstory kill in 75SW stands following stage one harvest. Stems/ha of the > 7.6-10.0 cm DBH class were low (compared to other stem classes) through the entire study period, with the most evident reduction in density appearing immediately following stage one harvest (Fig. 3). Due to high competition during the regeneration stage (resources directed towards stem height rather than stem diameter), there was minimal response in the \geq 7.6–10.0 cm DBH class which resulted in little change over time.

Bird community

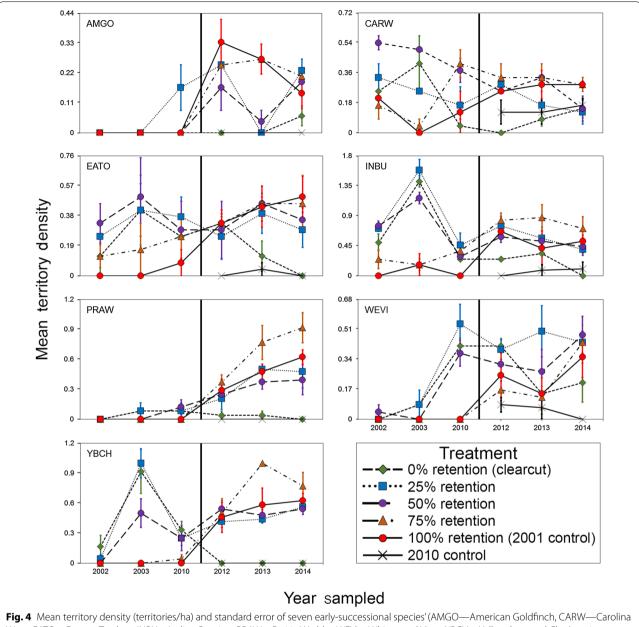
The use by American Goldfinch, Prairie Warbler, and White-eyed Vireo was delayed immediately following stage one tree harvest in OSW, 25SW, and 50SW treatments. American Goldfinch densities increased in treatments receiving any tree harvest during stage two (25SW, 50SW, 75SW, and 100SW), while densities in treatments receiving no harvest (0SW and 2010C) remained low. Prairie Warbler densities immediately increased in treatments that had tree harvest during stage two (25SW,

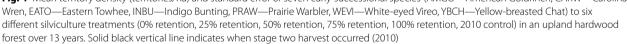


50SW, 75SW, and 100SW) and densities gradually increased in these treatments following stage two harvest (Fig. 4). Similar to the American Goldfinch, Prairie Warblers were not detected in treatments that were left undisturbed during stage two harvest (0SW and 2010C). White-eyed Vireo densities increased greatly between 2003 and 2010 (Fig. 4) in treatments receiving moderate to heavy tree harvest (0SW, 25SW, and 50SW) but remained low in minimally disturbed treatments (75SW and 100SW). Following stage two harvest, White-eyed Vireo densities increased in treatments that had drastic canopy change (75SW and 100SW, Fig. 2) and remained generally consistent in 25SW and 50SW stands while decreasing in 0SW stands.

Indigo Bunting and Yellow-breasted Chat densities increased immediately following stage one in treatments receiving tree harvest (0SW, 25SW, and 50SW). Between 2003 and 2010, Indigo Bunting densities declined but still remained at high levels (relative to other species' densities). Following stage two harvest, Indigo Bunting density increased in all but one treatment (0SW), and remained generally consistent following stage two harvest for all but 0SW, in which densities decreased. Yellow-breasted Chats shared a similar pattern as Indigo Buntings, with increased densities in all but 0SW stands following stage two harvest. Yellow-breasted Chat densities between 2010 and 2012 (immediately pre- and poststage two harvest) increased noticeably in the 75SW and 100SW stands, while densities in 25SW and 50SW stands remained consistent, similar to the Indigo Bunting (Fig. 4).

Carolina Wrens lacked a consistent pattern during stage one of the study but densities were generally higher in treatments with moderate to heavy tree harvest (0SW, 25SW, and 50SW). Following stage two harvest, densities were higher in treatments that received tree harvest (25SW, 50SW, 75SW, and 100SW) and remained stable following stage two tree harvest. This pattern was true





except for 25SW which showed 1 year of increased densities followed by 2 years of decreased densities. While Carolina Wren densities in treatments receiving no tree harvest during stage two (0SW and 2010C) had lower densities relative to other treatments, this difference was not as evident compared to other species (Prairie Warbler and Yellow-breasted Chat). Eastern Towhees had moderate to high densities in treatments receiving some forms of disturbance (tree harvest or herbicide treatment; 0SW, 25SW, 50SW, and 75SW) during stage one. Prior to stage two tree harvest, Eastern Towhee densities were similar in disturbed treatments, with the undisturbed treatment (100SW) also being occupied. Following stage two harvest, Eastern Towhee densities remained high with minor increases in treatments receiving tree harvest (25SW, 50SW, 75SW, and 100SW). Treatments that were left undisturbed during stage two (0SW and 2010C) had low

Common name	2002	2003	2010	2012	2013	2014
American Goldfinch	0	0	2	12	7	10
Carolina Wren	17	14	14	15	16	14
Eastern Towhee	10	18	15	20	23	19
Indigo Bunting	25	54	16	15	34	26
Prairie Warbler	0	2	4	14	26	29
White-eyed Vireo	0	2	16	20	16	23
Yellow-breasted Chat	2	29	11	20	30	30

Table 1 Observed territories of focal species for all sampling years

15 stands were sampled in 2002, 2003, and 2010, while 18 stands were sampled in 2012, 2013, and 2014

densities relative to other treatments. Observed territories of focal species are presented in Table 1.

Discussion

Bird species' responses varied with respect to treatment and time after the tree harvest, indicating a dynamic response across time and management by bird species. Treatments that were expected to provide habitat for early-successional bird species (e.g., OSW) did so, but given enough time, plant succession transitioned to a stem-exclusion stage, ultimately reducing usage by our focal bird species. This example highlights the importance of early-successional bird species oriented management for the long-term persistence of the earlysuccessional group of birds in forested regions of the eastern US. Our study showed that early-successional birds can be managed over a longer period of time (13 years) using a two-stage shelterwood harvest.

Following stage one harvest, Carolina Wrens, Eastern Towhees, Indigo Buntings, and Yellow-breasted Chats were recorded in high densities during the second year, showing marked increases from year one (Fig. 4). The delayed response for American Goldfinch, Prairie Warblers, and White-eyed Vireos (i.e., no increase in territory density from 2002 to 2003) was likely due to a delayed vegetation response (possibly due to dormant season harvesting, Keyser and Zarnoch 2014) in the understory (Conner and Adkisson 1975; Schweitzer and Dey 2011). Reaching treatment-minimum canopy levels in 2003 for 0SW, 25SW, and 50SW stands (Fig. 2) likely induced growth of the understory vegetation layer, driving early-successional bird species' presence in these treatments. Immediately following stage one harvest, Carolina Wrens and Eastern Towhees likely used tangles and undergrowth thickets (Brawn et al. 2001), and the presence of slash piles left behind from logging provided nesting habitat following 0SW tree harvest (McDermott and Wood 2009). Indigo Bunting and Yellow-breasted Chat occupancy in 0SW during stage one was likely in response to openings in the canopy (Strelke and Dickson 1980; Costello et al. 2000; Greenberg et al. 2014), creating dense layers of vegetation (e.g., *Rubus* spp., Ricketts and Ritchison 2000) for nesting cover. American Goldfinch's lack of immediate response to 0SW was likely due to their preference for semi-open areas with standing trees (Middleton and McGraw 2009), which 0SW stands did not provide. The delayed response of Prairie Warblers and White-eyed Vireos to 0SW stands in stage one may be due to location of treatments as these relatively small cuts were isolated within a primarily forested area (Morris et al. 2013), may be due to demographics (see Akresh et al. 2015 for Prairie Warbler example), or delayed vegetation response which limited nesting availability.

Stage-two harvest rejuvenated understory habitat for focal birds, as Indigo Buntings and Yellow-breasted Chats responded immediately to stage-two harvest (similar to phase one) with increased densities in all but 0SW and 2010C stands. Our sequential harvests (in 2002 and 2010) of 25SW and 50SW stands created freshly disturbed habitat for focal birds. Stage-two tree harvest in the 75SW and 100SW stands created even further disturbance for focal birds. Prairie Warblers' density continued to increase through 2012 and was the second most abundant bird species in 2014 (Table 1). American Goldfinch and Prairie Warblers intermediate response years (3-8 years post-harvest) were missed during phase one but showed positive responses to stage two harvest. Carolina Wrens, Eastern Towhees, and White-eyed Vireos all maintained abundant numbers during phase two. Increased focal bird density following stage two harvest was potentially due to increased structural complexity in these stands, as open canopy conditions facilitated herbaceous growth in the already semi-dense understory while fast-growing stump sprouts and non-merchantable residual midstory trees provided additional vertical structure.

Close proximity of stands may confound songbird usage or mislead songbird-treatment relationships (Hachè et al. 2013) as bird territories may encompass multiple stands. While stand sizes were not ideal, this study (along with others) demonstrates that small tree cuttings can support many individuals of the same species. Management for songbirds using smaller areas could become a popular practice in the future, due to private land ownership and parcelization throughout the eastern US (Fredericksen et al. 1999; Brooks 2003). Additionally, 4 ha is above thresholds for accommodating multiple territories of target species (> 0.6 ha, Askins et al. 2007; > 1.2 ha, Chandler et al. 2009; ≥ 0.23 ha, Roberts and King 2017). Also, territories of birds were estimated as individuals were not color-banded for re-sighting. To reconcile both of these limitations (close proximity of stands and lack of color-banded individuals), we used occurrence thresholds and divided territories into 1/2 and 1/4 depending on territory location. To identify unique individuals, individual territories were delineated only if observers recorded simultaneous songs between conspecifics. This reduced the possibility of double-recording or false-positives. Another limitation is that we did not survey the bird community during 2004-2009, but literature supports our expectations of temporal patterns exhibited by focal bird species in response to timber management in the eastern US (3-8 years post-harvest; Gram et al. 2003; Perry and Thill 2013; Akresh et al. 2015).

The comparison between both vegetation and bird responses in 2002 (following stage one) and 2011-12 (following stage two) should be noted. Stem counts in 2011 did not decrease to 2002 levels following tree harvest despite having all remaining canopies removed. While stage two harvest was 'prepared' prior to the final cut, stage one harvest had no site preparation; thus we would not expect to detect such immediate affects from tree cutting in stage one as in stage two. The presence of stump sprouts played an important role in maintaining early-successional birds in these treatments, as all bird species showed no major reduction in mean territory density in 2012. The second harvest extended species' presence beyond what similar studies have reported using a single harvest event approach. Early-successional vegetation is often short-lived, and management for birds is also shortlived reaching maximum bird abundances/densities 2-8 years post-harvest before populations begin to decline (Robinson and Robinson 1999; Keller et al. 2003; Twedt and Somershoe 2009). Over time bird densities return to pretreatment levels (Yahner 2003; Twedt and Somershoe 2009; Morris et al. 2013) once canopy gaps close and shade intolerant plants associated with disturbance die off. Our results reinforce what DeGraaf and Yamasaki (2003) and Twedt and Somershoe (2009) both recommended; that stands should be reevaluated 15 years after tree harvest to decide whether areas should be re-disturbed to recreate early-successional habitat conditions.

Conclusion

Compared with the clearcutting and other shelterwood methods of similar studies, the two-stage shelterwood method retained early-successional bird species longer. Though a shelterwood harvest is meant to regenerate trees, with the final harvest setting the stage for the next rotation, shelterwood cuts diminish in their capacity to provide early-successional habitat as stands eventually mature beyond the early-successional stage. Despite this, non-research entities are interested in the shelterwood method primarily to provide conditions conducive to regenerating oaks and hickories. Further use of the two-stage shelterwood method by land managers will likely benefit early-successional bird species. We suggest further investigation into the potential for two-stage shelterwood methods for the long-term management of early-successional or disturbancedependent breeding songbirds.

Authors' contributions

CJS designed the silviculture experiment. YW implemented the songbird component of the research. BKS and ELM collected the data. ELM finished the data analysis and wrote the first draft. CJS and YW supervised the research and provided multiple revisions in the early stages of writing. All authors read and approved the final manuscript.

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Competing interests

The authors declare they have no competing interests.

Consent for publication

Not applicable.

Ethics approval and consent to participate

The experiments comply with the current laws of the United States of America.

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