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ABSTRACT

Timber harvesting has been proposed as a management tool to enhance breeding habitat for the Cerulean Warbler (*Setophaga cerulea*), a declining Neotropical–Nearctic migratory songbird that nests in the canopy of mature eastern deciduous forests. To evaluate how this single-species management focus might fit within an ecologically based management approach for multiple forest birds, we performed a manipulative experiment using four treatments (three intensities of timber harvests and an unharvested control) at each of seven study areas within the core Cerulean Warbler breeding range. We collected pre-harvest (one year) and post-harvest (four years) data on the territory density of Cerulean Warblers and six additional focal species, avian community relative abundance, and several key habitat variables. We evaluated the avian and habitat responses across the 3–32 m² ha^{−1} residual basal area (RBA) range of the treatments. Cerulean Warbler territory density peaked with medium RBA (~16 m² ha^{−1}). In contrast, territory densities of the other focal species were negatively related to RBA (e.g., Hooded Warbler [*Setophaga citrina*]), were positively related to RBA (e.g., Ovenbird [*Seiurus aurocapilla*]), or were not sensitive to this measure (Scarlet Tanager [*Piranga olivacea*]). Some species (e.g., Hooded Warbler) increased with time post-treatment and were likely tied to a developing understory, whereas declines (e.g., Ovenbird) were immediate. Relative abundance responses of additional species were consistent with the territory density responses of the focal species. Across the RBA gradient, greatest separation in the avian community was between early successional forest species (e.g., Yellow-breasted Chat [*Icteria virens*]) and closed-canopy mature forest species (e.g., Ovenbird), with the Cerulean Warbler and other species located intermediate to these two extremes. Overall, our results suggest that harvests within 10–20 m² ha^{−1} RBA yield the largest increases in Cerulean Warblers, benefit additional disturbance-dependent species, and may retain closed-canopy species but at reduced levels. Harvests outside the optimum RBA range for Cerulean Warblers can support bird assemblages specifically associated with early or late (closed-canopy) successional stages.

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1. Introduction

Management focused on the critical needs of a single species (i.e., a “fine-filter” approach; Hunter, 2005) is warranted for species of high conservation concern. Focus on these species is

important for developing clear conservation targets and evaluating management outcomes (Villard and Jonsson, 2009). However, it is also important to consider positive and negative effects on other species. A focal species may be an “umbrella species” (*sensu* Roberge and Anglestam, 2004) if managing for it also benefits naturally co-occurring species. Knowledge of the effects on a wider range of species may also be valuable, particularly if obtained across multiple habitats included in an overall management approach. For example, while intensive management of breeding

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habitat for the endangered Kirtland's Warbler (*Setophaga kirtlandii*) may benefit other bird species associated with its primary habitat (5–23 year old jack pine [*Pinus banksiana*] plantations), other bird species assemblages are likely supported by the recent clearcuts and mature stands involved in this management (Corace et al., 2010). Corace et al. (2010) suggest a shift in Kirtland's Warbler management toward a more ecologically based approach for multiple bird species across jack pine habitat types.

Managing for the severely declining Cerulean Warbler (*Setophaga cerulea*) may have similar implications for avian associates and the broader forest bird community. The Cerulean Warbler is a Neotropical–Nearctic migratory songbird of mature deciduous forests in the eastern US. The majority of its population lies within the Appalachian Mountains region where a 3.2% year⁻¹ decline in abundance occurred during 1966–2011 (Sauer et al., 2012). Declines have been linked to land use changes on the breeding and wintering grounds as well as forest fragmentation and lack of appropriate forest structure on the breeding grounds (Bakermans and Rodewald, 2009). Timber harvesting has been proposed to increase Cerulean Warbler breeding populations, as they appear to respond positively to disturbances that create canopy gaps in even-aged forests (Boves et al., 2013; Hunter et al., 2001). Although studies have identified forest birds that may associate with Cerulean Warbler habitat (Carpenter et al., 2011; Jones et al., 2004), to our knowledge none have been in the direct context of timber harvesting in the core breeding range. Management strategies specifically intended to benefit Cerulean Warblers may be implemented across large areas in their core breeding range, and thus may have a large effect on the overall bird community. While studies within the core range of Cerulean Warblers have examined effects of specific timber harvest prescriptions on bird communities (e.g., Newell and Rodewald, 2012), knowledge of the effects of Cerulean Warbler management on a full range of early to late successional forest bird species is lacking.

Of the many studies that have addressed stand level, numeric responses of bird species to various harvest prescriptions (e.g., see review by Haulton, 2008), those that examine a wide range in the amount of timber removed (e.g., Annand and Thompson, 1997; Baker and Lacki, 1997; McDermott and Wood, 2009; Norris et al., 2009) clearly indicate a continuum of early to late successional forest bird responses along a harvest intensity gradient. At a much broader scale, Vanderwel et al. (2007) modeled this continuum in a meta-analysis of 42 North American studies of harvesting effects on birds. A number of forest birds had non-linear responses along the gradient, and species generally responded in a consistent way across their breeding ranges (Vanderwel et al., 2007). Thus a direct measure of harvest intensity may usefully quantify effects of forest management on the Cerulean Warbler and the avian community, and provide a basis for comparing species responses across a range of harvest intensities. Furthermore, identifying habitat alteration thresholds (e.g., density or volume of remaining trees) for species responses to harvesting provides quantitative targets for management of these species (Guenette and Villard, 2005).

We conducted a manipulative forest management experiment at seven study areas, across four states, in the Cerulean Warbler's core breeding range. In Boves et al. (2013) we focused exclusively on the Cerulean Warbler response in comparisons among silvicultural techniques that varied in harvest intensity. Here, we used the wide gradient in harvest intensity across our study plots to examine (1) how forest birds responded numerically to the harvest intensity range that was optimum for increases in Cerulean Warbler territory density; and (2) how the broader avian community responded numerically across the full range of harvest intensity. Specifically, we used the residual basal area (RBA) of our plots to analyze avian and key understory habitat responses measured from pre-harvest to four years post-harvest. We integrated our

results to identify species-specific optimal ranges of RBA, and suggest broader RBA ranges as ecologically based management approaches for multiple bird assemblages in actively managed, upland hardwood forests.

2. Methods

2.1. Study areas and region

We conducted this research during 2006–10 in mature forest stands at seven, widely spaced study areas within the Central Hardwoods mixed-mesophytic forest region (Fralish, 2003) of the central Appalachian Mountains (Fig. 1). This region generally corresponds with the core Cerulean Warbler breeding range as indicated by mapped relative abundance (Sauer et al., 2012). The study areas were: Royal Blue Wildlife Management Area, TN (RB), Sundquist Forest, TN (SQ), Raccoon Ecological Management Area, OH (RM), Daniel Boone National Forest, KY (DB), Lewis Wetzel Wildlife Management Area, WV (LW), Monongahela National Forest, WV (MF), and private lands in Wyoming Co., WV (WY). We selected study areas based on the presence of Cerulean Warbler breeding populations, potential to implement timber harvests, and absence of existing canopy disturbances. All study areas were within a matrix of mature forest; mean forest cover within 10 km of the geographic center of each study area was 84% (± 3 SE, range = 74–94%; 2006 National Land Cover Database [Fry et al., 2011]). Mean elevation was 550 m (± 80 SE, range = 250–850 m). Tree species composition differed somewhat among study areas (Table 1), but common overstory tree species included oaks (*Quercus rubra*, *Q. coccinea*, *Q. velutina*, *Q. alba*, *Q. montana*), hickories (*Carya* spp.), maples (*Acer rubrum*, *A. saccharum*), and yellow poplar (*Liriodendron tulipifera*).

2.2. Habitat manipulations

At each study area, four 20-ha plots were placed on ridgetops and north- or east-facing upper slopes, the predominant topographic location of the region's Cerulean Warbler populations (Buehler et al., 2006; Weakland and Wood, 2005; Wood et al., 2006). Plots were generally rectangular with the long axis parallel to the ridgetop or perpendicular to the general slope direction. We randomly assigned the four plots in each study area to the four study treatments. Three treatments were varying intensities of timber harvests that represented common silvicultural practices

Fig. 1. Location of the seven study areas in the central Appalachians. Inset: a ridgetop, 20-ha plot within a study area (LW) showing layout of the harvest and the unharvested buffers (2007 aerial photo of the shelterwood harvest treatment).

Table 1

Pre-treatment tree species composition of the seven study areas in the Central Appalachians. Percent basal area (mean $\pm$ standard error) of common tree species (red oaks and hickories grouped) of the four 20-ha plots per study area.

Study area (state)	Tree species						
	White Oak (<i>Quercus alba</i>)	Chestnut Oak (<i>Q. montana</i>)	Red Oaks (<i>Q. spp.</i>) ^a	Hickories (<i>Carya spp.</i>)	Red Maple (<i>Acer rubrum</i>)	Sugar Maple (<i>A. saccharum</i>)	Tulip Poplar (<i>Liriodendron tulipifera</i>)
DB (KY)	8.9 (0.9)	10.1 (2.7)	13.9 (2.2)	15.7 (1.9)	0.6 (0.1)	15.9 (2.2)	14.0 (3.0)
RM (OH)	25.9 (2.3)	6.4 (1.5)	16.3 (2.3)	12.2 (0.8)	5.9 (1.5)	7.1 (3.6)	11.6 (2.3)
RB (TN)	4.3 (1.6)	3.4 (1.9)	11.5 (1.9)	11.8 (1.5)	3.2 (1.2)	18.1 (2.3)	24.6 (6.8)
SQ (TN)	0.4 (0.3)	17.4 (3.2)	4.8 (0.8)	6.9 (1.8)	13.2 (1.8)	12.5 (3.0)	25.3 (2.3)
LW (WV)	2.3 (0.5)	15.0 (3.0)	9.8 (2.4)	5.9 (1.2)	6.7 (1.3)	24.9 (4.4)	13.2 (1.3)
MF (WV)	12.6 (0.8)	20.9 (1.9)	20.9 (2.8)	3.7 (1.4)	19.6 (0.2)	3.5 (0.6)	3.7 (1.2)
WY (WV)	2.5 (0.3)	16.4 (2.8)	15.0 (1.8)	16.7 (3.1)	12.9 (1.8)	0.4 (0.2)	18.1 (2.6)

^a *Quercus rubra*, *Q. coccinea*, and *Q. velutina*.

of the region, and the fourth treatment was an unharvested control. The harvest treatments and their RBA targets were a single-tree selection harvest (light; $\sim 18 \text{ m}^2 \text{ ha}^{-1}$ RBA), a shelterwood harvest (medium; $\sim 12 \text{ m}^2 \text{ ha}^{-1}$ RBA), and an even-aged harvest with residuals (heavy; $\sim 5 \text{ m}^2 \text{ ha}^{-1}$ RBA).

Harvest treatments were applied as evenly as possible within a 10-ha portion of the plot, with the remaining 10 ha left unharvested as a buffer (Fig. 1 inset). Buffers were part of the overall study design (see Boves et al., 2013); however, here we excluded buffer data (except for territory mapping; Section 2.3) to focus on 10 ha treatment effects. Harvests and unharvested controls were located $>200 \text{ m}$ apart within a study area to reduce the potential for another treatment to influence the avian response. Harvests were applied during winter 2006–07, with the exception of the heavy harvest at DB (late summer 2007). RBA varied in like-treatments among study areas (Table 2) due to differences in initial basal area and because landowners had discretion in harvest implementation. However, within each study area RBA was decreased in relation to the unharvested control basal area and on a gradient from the light to medium to heavy harvests. Tree composition remained similar following harvests (George, 2009). Across harvest intensities, mid- to large-diameter canopy dominants and co-dominants were retained, as were snags. We conducted avian surveys and vegetation sampling for one year pre-treatment (2006) and four years post-treatment (2007–10).

2.3. Avian surveys

Each year, we conducted avian surveys (territory mapping and point counts) during the breeding season (May and June) between local sunrise and 1030 on mornings without significant precipitation or sustained high winds. Surveys were conducted by observers trained in bird identification by sight and sound, and in distance estimation. Within study areas in a season, we rotated observers among the plots and varied start times and starting locations for the surveys.

We followed a standard territory mapping protocol (Bibby et al., 2000) to map territories of the Cerulean Warbler and six additional

focal species: Hooded Warbler, Kentucky Warbler, Ovenbird, Worm-eating Warbler, Scarlet Tanager, and Wood Thrush (scientific names for all birds in Appendix A). The additional focal species were selected for their conservation importance (USFWS Birds of Management Concern, Appendix A), because they were abundant on all study areas, and because they represented avian guilds of management interest (e.g., Hooded Warbler for shrub-associated species). The locations of singing males were mapped across each 20-ha plot on eight mornings each season (>4 days between visits), with special emphasis on identifying conspecific counter-singing males and noting other territorial activities (e.g., aggressive interactions and pairing behavior). At the end of each season, the eight survey maps were consolidated onto a single map (one per species per plot). To delineate a cluster of mapped locations as a territory, we used a minimum of two registrations mapped from different mornings (minimum required for ≤ 8 visits; Bibby et al., 2000). However, most territories were delineated based on clusters of registrations from >2 mornings, and counter-singing events often helped to differentiate territories.

Some territories contained registrations beyond the 20-ha plot boundaries; we considered these as full territories if $>1/2$ of registrations were within the plot boundary, and half territories if $\leq 1/2$ but $\geq 1/3$ of registrations were within the boundary. If a territory contained both harvest and buffer registrations, we assigned territory fractions (to the nearest $1/4$) to the harvest and buffer based on the proportion of the total territory registrations they contained. For harvest treatment plots, we calculated territory density (territories per 10 ha) by summing the whole and partial territories. For the unharvested control plots, we divided in half the total number of territories to express density as territories per 10 ha.

We systematically placed 1–2 avian point count stations in each 10-ha treatment plot to evenly cover the plot interior yet maximize distance between stations and to harvest edges. Due to plot configuration, we only placed one station in the DB and the SQ heavy harvests. For plots with two stations, we located them as far apart as possible (range 120–625 m, mean 230 m) given plot configuration. The stations were located 20–100 m from the plot boundaries (mean 60 m).

Table 2

Post-treatment residual basal area (RBA; $\text{m}^2 \text{ ha}^{-1}$) of the four treatments at the seven study areas in the Central Appalachians (RBA target listed for the harvest treatments). Value in parentheses is the RBA difference from the pre-treatment basal area.

Treatment	Study area (state)						
	DB (KY)	RM (OH)	RB (TN)	SQ (TN)	LW (WV)	MF (WV)	WY (WV)
Unharvested control	21.7	26.0	26.5	30.8	24.9	31.6	26.6
Light harvest $\sim 18 \text{ m}^2 \text{ ha}^{-1}$	19.4 (−3.7)	17.5 (−3.3)	24.4 (−1.6)	23.7 (−1.6)	19.2 (−8.6)	22.8 (−2.7)	22.0 (−8.2)
Medium harvest $\sim 12 \text{ m}^2 \text{ ha}^{-1}$	12.9 (−10.9)	12.2 (−13.0)	18.6 (−11.1)	15.9 (−6.6)	10.4 (−14.1)	12.1 (−11.1)	17.7 (−10.8)
Heavy harvest $\sim 5 \text{ m}^2 \text{ ha}^{-1}$	8.8 (−15.5)	3.9 (−15.9)	7.9 (−24.3)	10.1 (−16.2)	2.9 (−21.0)	7.5 (−20.9)	2.8 (−23.5)

We conducted 50 m fixed-radius point count surveys of the bird community during two visits to each station in each year. For each bird detected over a 10-min period, we recorded the species, detection type (singing, calling, or visual), and sex (if possible). We used a 50 m radius to ensure that recorded birds represented the treatment in which the station was located and were not likely to be counted at another station. We also assumed that between-treatment differences in detectability were negligible over this distance. Annual relative abundance per species was the maximum number of detections recorded over the two visits, species richness was the number of species detected over the two visits, and total abundance was the sum of all species' relative abundances.

2.4. Vegetation sampling

We measured the basal area of each plot using wedge prisms (10-factor English or 2.5-factor Metric) annually. We gridded each plot into 1-ha cells and randomly placed prism sampling points within each cell ($n = 8–11$). We revisited the same points each year at all study areas except RM, where random points were sampled annually. At each point, we tallied trees within the prism plot with dbh ≥ 10 cm (diameter at breast height [1.4 m]), and recorded each tree's dbh and species. In 2010, we tallied trees on 20–30 additional prism points within the treatments to check the accuracy of our post-harvest RBA estimates.

Within a 5-m radius of each prism point, we visually estimated the percent cover of shrubs (woody plants < 1.4 m in height) and saplings (≥ 1.4 m in height and < 10 cm dbh). We collected these understory variables because they respond strongly to tree canopy removal and are important to a variety of birds, particularly shrub nesting species.

2.5. Data analysis

We analyzed the post-treatment avian and understory responses to the RBA gradient of the 28 plots using mixed effects models to account for within-study area correlation and annually repeated measurements. We used each plot's post-treatment mean RBA (range $\sim 3–32$ m² ha⁻¹; Table 2) because of annual variation due to measurement error and some tree growth and mortality. For our analyses, we considered annual variation in RBA unimportant because it was small compared to the variation that resulted from the harvests. The more intensively sampled 2010 prism data confirmed the relative accuracy of the post-treatment mean RBA estimates (Pearson's $r = 0.97$; mean difference = 0.8 m² ha⁻¹). As fixed effects in the models along with RBA, we included year since treatment (YST; four growing seasons) as a factor variable in several ways to infer post-treatment changes in the response, and used the pre-treatment value as a covariate to control for pre-treatment differences among plots. We excluded the 2007 DB heavy harvest plot from all analyses due to the delay in treatment application, but included subsequent years because the avian and vegetation responses were not appreciably delayed. We used program R (version 2.15; R Development Core Team, 2012) and R packages (cited below) for all statistical analyses, and considered differences statistically significant at $\alpha = 0.05$.

Based on exploratory analysis, we determined that understory responses had linear fits to the RBA gradient. Therefore, we fitted linear mixed models using the lme4 package (Bates et al., 2012), with RBA, YST, the interaction of RBA and YST, and the pre-treatment covariate as explanatory variables. We included random intercepts for study area and plot. If the interaction was significant, we also fitted separate models by year (with RBA and the pre-treatment covariate as explanatory variables, and a random intercept for study area). We used likelihood ratio tests of nested models to evaluate the significance of the interaction term, and

report model parameter estimates and 95% confidence intervals. We used a Gaussian error structure (identity link) after inspecting model residuals for normality and variance homogeneity.

For the avian responses, we assumed no pre-specified functional form of response to the RBA gradient. Therefore, we fitted generalized additive mixed models (GAMMs) using the gamm4 package (Wood, 2012). The GAMMs included RBA as a smooth function ("smoother"). These functions do not assume a rigid form (i.e., may be linear or non-linear) and provide a non-parametric estimate of the response trend that is less variable than the response itself (Hastie and Tibshirani, 1990). We included random intercepts for study area and plot for territory density models, and study area and point count station for species richness and total abundance models. For relative abundance models we chose species judged sufficiently abundant to show a response (or lack of one) across the gradient, but only included a random intercept for point count station due to numerical issues (e.g., low means or frequent zeros). The models also included linear effects of YST and the pre-treatment covariate. The smoothers were estimated using cubic regression splines. The smoother estimated degrees of freedom, which determine the amount of smoothing (i.e., how closely the functions follow the response data), were estimated using Maximum Likelihood. We used a Poisson error structure (log link) due to non-normal response data and rounded territory density to the nearest whole territory.

We used the Akaike Information Criterion corrected for small sample sizes (AICc; Burnham and Anderson, 2002) to evaluate the importance of the RBA smoother and the additional linear effects for modeling the avian responses. We initially examined if including YST as a "by" factor variable in the RBA smoother (i.e., a replicated smoother; Wood, 2011) provided a better fit to the response. We only used this approach for Hooded Warbler density, however, because this was the only response with a replicated smoother model ranked higher than a non-replicated one ($\Delta AICc = 6.6$). We ranked the relative importance of the terms in each model set by summing for each term the AICc weights of the models containing that term (Burnham and Anderson, 2002), and evaluated model-averaged parameter estimates and 95% confidence intervals for the linear effects. We used the mgcv package (Wood, 2011) to visualize response curves using the best supported model containing a smoother in two ways. First we visualized the curve at the scale of the linear predictor to evaluate its general shape and 95% confidence band. To evaluate effect sizes, we then visualized the curve with the original response data (e.g., territory density), using the additional model terms to generate the curve (e.g., by year for models containing YST).

We used non-metric multidimensional scaling (NMDS) to visualize the avian community structure of each year using the metaMDS function in the vegan package (Oksanen et al., 2012). The NMDS was performed on the matrix of species' relative abundances for the 54 point count stations. We excluded species detected on < 3 study areas in each year's analysis to reduce clutter in the ordination diagrams. Based on exploratory analysis, this exclusion of "rare" species had little effect on the ordinations (see also McCune and Grace, 2002). We used the Bray-Curtis dissimilarity measure and performed ordinations using one to six dimensions to evaluate improvement in stress values.

To examine the relationship of environmental variables to the avian community structure in the ordination diagrams, we used the ordisurf and envfit vegan functions. NMDS is an unconstrained ordination technique, and these functions correlate environmental variables with the ordination scores in the space of the selected axes. Envfit finds the direction of maximum correlation for vectors and the correlation with the score averages for the levels of a factor, and ordisurf fits a smooth surface using generalized additive modeling (GAM) with thin plate splines (Oksanen et al., 2012;

Table 3

Annual linear mixed model analyses of post-treatment shrub and sapling percent cover relationships to residual basal area (RBA) and the pre-treatment covariate (Cov₀₆). The parameter estimates and 95% confidence intervals (CI) indicate, for example, that shrub cover became increasingly negatively related to RBA during 2008–2010.

Year	Parameter	Shrub cover		Sapling cover	
		Estimate	95% CI	Estimate	95% CI
2007	Intercept	5.574	(−1.922, 13.069)	−11.368	(−22.701, −0.035)
	RBA	0.149	(−0.131, 0.429)	1.179	(0.852, 1.506)
	Cov ₀₆	0.386	(0.172, 0.600)	0.295	(−0.002, 0.591)
2008	Intercept	34.270	(18.651, 49.889)	−0.464	(−13.621, 12.693)
	RBA	−0.926	(−1.563, −0.289)	0.817	(0.448, 1.187)
	Cov ₀₆	0.520	(0.096, 0.944)	0.285	(−0.058, 0.627)
2009	Intercept	48.354	(31.031, 65.677)	18.428	(1.731, 35.125)
	RBA	−1.281	(−1.864, −0.697)	0.295	(−0.106, 0.697)
	Cov ₀₆	0.316	(−0.182, 0.814)	0.205	(−0.172, 0.581)
2010	Intercept	49.417	(33.733, 65.102)	43.375	(26.674, 60.076)
	RBA	−1.413	(−1.868, −0.958)	−0.508	(−0.903, −0.113)
	Cov ₀₆	0.238	(−0.191, 0.668)	−0.088	(−0.459, 0.284)

function defaults used). For the pre-treatment (2006) ordination, we fit pre-treatment basal area, shrub cover, and sapling cover. For the post-treatment ordinations (2007–10), we fit mean RBA and annual post-treatment shrub and sapling cover. We fit study area as a factor to all ordinations. We evaluated the correlation (R^2) between the environmental variable and the ordination pattern, and the R^2 statistical significance. We used $n = 999$ permutations for the envfit permutation testing procedure.

3. Results

3.1. Shrub and sapling response

The RBA by YST interaction effect was significant for shrub cover ($X^2 = 20.01$, $P < 0.001$) and sapling cover ($X^2 = 30.86$, $P < 0.001$). Yearly analyses indicated that shrub cover was negatively related to RBA during 2008–10, but not in 2007 (Table 3; Fig. 2a). In contrast, sapling cover was positively related to RBA in 2007 and 2008, was not related to RBA in 2009, and was negatively related to RBA in 2010 (Table 3, Fig. 2b). Post-treatment shrub cover was positively related to its pre-treatment cover only in 2007 and 2008, while post-treatment sapling cover was not related to its pre-treatment cover (Table 3).

3.2. Model comparisons and avian responses

For the focal species territory density models (Table 4), relative importance of the RBA smoother was high (1.00) for Cerulean

Warbler, Hooded Warbler, Kentucky Warbler, Ovenbird, and Wood Thrush. Relative importance of the RBA smoother was moderate for Scarlet Tanager (0.51) and Worm-eating Warbler (0.63). Hooded Warbler density (Fig. 3a) had little response in the first year, but by the fourth year post-treatment was negatively related to RBA with a plateau at $\sim 13 \text{ m}^2 \text{ ha}^{-1}$ RBA. Cerulean Warbler density (Fig. 3b) peaked in the middle of the gradient at $\sim 16 \text{ m}^2 \text{ ha}^{-1}$ RBA. Ovenbird density (Fig. 3c) was positively related to RBA, plateauing at $\sim 25 \text{ m}^2 \text{ ha}^{-1}$ RBA. Relative importance of YST was higher for Cerulean Warbler (0.94) than for Ovenbird (0.31). To infer the YST effect on these and the remainder of the responses that were not modeled with an annually replicated smoother, we examined the YST model-averaged estimates and 95% confidence intervals as well as the annual response-scale curves if YST was included in the best supported model (Fig. 3 insets, Fig. 4, Supplementary online data). For example, these results indicated that the Cerulean Warbler (Fig. 3b inset, Fig. 4c) increased during the post-treatment period while the Ovenbird decline (Fig. 3c inset) was immediate.

Scarlet Tanager density (Fig. 3d) peaked at $\sim 20 \text{ m}^2 \text{ ha}^{-1}$ RBA; however, the 95% confidence band was particularly wide in relation to the curve's overall variation, indicating relatively large uncertainty in the response. Relative importance of YST was low (0.09) for Scarlet Tanager, with no YST effect apparent. Similar to the Hooded Warbler response, Kentucky Warbler density (Fig. 3e) was negatively related to RBA, but with a plateau at $\sim 10 \text{ m}^2 \text{ ha}^{-1}$. For Kentucky Warbler, relative importance of YST was 1.0 and density increased post-treatment. Similar to the

Fig. 2. The post-treatment shrub (a) and sapling (b) cover relationships with the residual basal area (RBA) gradient of the 28 plots (circles = harvest, triangles = no-harvest) from the seven study areas in the central Appalachians. Slopes obtained from results of annual linear mixed models (Table 3).

Table 4

Alternative generalized additive mixed models for avian post-treatment responses. The full model set is shown for Cerulean Warbler, for the remaining sets only models with AIC_c weight (*w*) summing to ≥ 0.80 are shown. Relative importance values are provided for the model terms in each set and indicate relative support for a response to residual basal area (RBA), an effect of year since treatment (YST), and an effect of the pre-treatment covariate (Cov₀₆).

Response	Model ^a	<i>k</i>	LL	ΔAIC _c	<i>w</i>	RBA	YST	Cov ₀₆
<i>Territory density</i>								
Cerulean Warbler	s(RBA), YST, Tden ₀₆	9	−77.88	0.00	0.75	0.80	0.94	1.00
	YST, Tden ₀₆	7	−81.61	2.77	0.19			
	s(RBA), Tden ₀₆	6	−84.05	5.37	0.05			
	Tden ₀₆	4	−87.84	8.51	0.01			
	s(RBA), YST	8	−84.92	11.71	0.00			
	YST	6	−89.73	16.72	0.00			
	s(RBA)	5	−91.05	17.13	0.00			
	null	3	−95.93	22.53	0.00			
Hooded Warbler	s(RBA:YST), YST, Tden ₀₆	15	−62.16	0.00	0.65	1.00	0.89	0.73
	s(RBA:YST), YST	14	−64.47	1.93	0.25			
Kentucky Warbler ^b	s(RBA), YST, Tden ₀₆	9	−37.43	0.00	0.84	1.00	1.00	0.84
Ovenbird	s(RBA), Tden ₀₆	6	−69.25	0.00	0.69	1.00	0.31	1.00
	s(RBA), YST, Tden ₀₆	9	−66.58	1.63	0.31			
Scarlet Tanager	s(RBA)	5	−42.46	0.00	0.35	0.51	0.09	0.25
	null	3	−44.69	0.11	0.33			
	s(RBA), Tden ₀₆	6	−42.46	2.24	0.11			
Wood Thrush	s(RBA), Tden ₀₆	6	−59.75	0.00	0.73	1.00	0.26	0.98
	s(RBA), YST, Tden ₀₆	9	−57.33	2.14	0.25			
Worm-eating Warbler ^b	s(RBA)	5	−43.70	0.00	0.27	0.63	0.18	0.42
	s(RBA), Tden ₀₆	6	−42.66	0.19	0.25			
	null	3	−46.20	0.59	0.20			
	Tden ₀₆	4	−45.90	2.18	0.09			
<i>Relative abundance</i>								
American Redstart	s(RBA), YST, Abun ₀₆	8	−90.23	0.00	0.85	0.86	1.00	0.99
Black-and-white Warbler	s(RBA), Abun ₀₆	5	−85.03	0.00	0.22	0.49	0.20	0.54
	Tden ₀₆	3	−87.16	0.08	0.21			
	null	2	−88.27	0.25	0.20			
	s(RBA)	4	−86.35	0.53	0.17			
Black-throated Green Warbler	s(RBA), Abun ₀₆	5	−72.20	0.00	0.92	1.00	0.08	1.00
Blue-grey Gnatcatcher ^c	s(RBA)	4	−79.99	0.00	0.89	0.96	0.07	n/a
Eastern Towhee ^c	s(RBA), YST	7	−81.80	0.00	0.94	1.00	0.94	n/a
Indigo bunting	s(RBA), YST	7	−86.68	0.00	0.69	1.00	0.98	0.30
	s(RBA), YST, Abun ₀₆	8	−86.45	1.70	0.29			
Red-eyed Vireo	Abun ₀₆	3	−94.50	0.00	0.52	0.29	0.18	0.89
	s(RBA), Abun ₀₆	5	−93.29	1.75	0.22			
	YST, Abun ₀₆	6	−92.86	3.01	0.11			
White-breasted Nuthatch ^c	null	2	−94.56	0.00	0.38	0.26	0.48	n/a
	YST	5	−91.51	0.13	0.36			
	s(RBA)	4	−93.51	2.05	0.14			
<i>Community measure</i>								
Species richness	s(RBA), YST, Rich ₀₆	9	−85.76	0.00	0.65	1.00	1.00	0.65
	s(RBA), YST	8	−87.46	1.20	0.35			
Total abundance	s(RBA), YST, Abun ₀₆	9	−139.03	0.00	0.87	1.00	1.00	0.87

^a s(RBA) = RBA smoother, YST = year since treatment, s(RBA:YST) = RBA smoother replicated by YST, Tden₀₆ = species pre-treatment territory density, Rich₀₆ = pre-treatment species richness, Abun₀₆ = pre-treatment abundance.

^b Due to study area absences, Kentucky Warbler analyzed excluding RB and MF, and Worm-eating Warbler analyzed excluding MF.

^c Species model set did not contain Abun₀₆ since this was ≈ 0 .

Ovenbird response, Wood Thrush (Fig. 3f) and Worm-eating Warbler (Fig. 3g) densities were positively related to RBA but exhibited less definitive plateaus. Relative importance of YST was low for Wood Thrush (0.26) and Worm-eating Warbler (0.18), and their declines were immediate.

The size of a species response along the RBA gradient and in relation to its pre-treatment density (Fig. 4; Supplementary online data) provided additional insights of management interest. For example, Ovenbird (Fig. 4a) mean pre-treatment density was relatively high (8.6 territories/10 ha). While the Ovenbird declined to near absence at low RBA, it remained at moderate densities at $\sim 20\text{--}25\text{ m}^2\text{ ha}^{-1}$ RBA. Hooded Warbler (Fig. 4b) mean pre-treatment density was relatively low (3.8 territories/10 ha). Hooded

Warbler had the largest increases at low RBA, but increases at $\sim 15\text{--}20\text{ m}^2\text{ ha}^{-1}$ were also substantial. The maximum height of the Cerulean Warbler response curve (Fig. 4c) in relation to its mean pre-treatment density (4.6 territories/10 ha) was rather low ($<1\times$ higher) in comparison to this characteristic for the Hooded Warbler response curve ($>2\times$ higher), despite high post-treatment plot densities (>15 territories/10 ha) for both species. Based on territory maps, some plots may have been fully occupied by these two species post-treatment. Cerulean Warbler pre-treatment densities were high for some medium RBA plots, and increases there may have been constrained by little space for additional territories. In contrast, Hooded Warbler pre-treatment densities were uniformly low across the plots, which may have

Fig. 3. Smoothers and 95% confidence bands (shaded area) for the post-treatment relationship between residual basal area (RBA) and focal species' territory densities (a–g), American Redstart relative abundance (h) and species richness (i). Smoothers were generated for the best supported model with a smoother in Table 4. For Hooded Warbler (a) smoothers were replicated for each year since treatment (YST). Y-axis labels provide estimated degrees of freedom of the smoothers. Tick marks above the x-axis indicate RBA for each of the 28 plots. Partial effects plots with model-averaged estimates and 95% confidence intervals for the YST effect were added (b–i) to evaluate post-treatment changes in the response.

allowed for more large increases. The Scarlet Tanager response (Fig. 4d) was relatively minimal in relation to its pre-treatment density (3.4 territories/10 ha). The Worm-eating Warbler decline was less steep across the gradient than that of the Ovenbird and Wood Thrush; however, it had the lowest mean pre-treatment density of the focal species (1.4 territories/10 ha), and its decline led to near absence at low RBA.

For the focal species, relative abundance and territory density model results were similar (Supplementary online data). Relative importance of the RBA smoother was high (0.96–1.00) for five additional species and inspection of the relative abundance curves indicated that these species had RBA responses (and YST effects) similar to those of the focal species (Table 4, Fig. 3, Supplementary online data). American Redstart (Fig. 3h) had a response peak in the middle of the gradient ($\sim 19 \text{ m}^2 \text{ ha}^{-1}$). Black-throated Green Warbler was positively related to RBA while Blue-gray Gnatcatcher, Eastern Towhee, and Indigo Bunting were negatively related to RBA. Relative importance of YST was 1.0 for American Redstart, Eastern Towhee, and Indigo Bunting; these species had post-treatment increases. Relative importance of YST was low for Blue-gray Gnatcatcher (0.26) and Black-throated Green Warbler

(0.18), and their responses were immediate. Relative importance of the RBA smoother was low (0.26–0.49) for Black-and-white Warbler, Red-eyed Vireo, and White-breasted Nuthatch; inspection of the curves indicated that these species had little response to RBA. Relative importance of the RBA smoother and YST was 1.0 for species richness (Fig. 3i) and total abundance (Table 4). Both measures were negatively related to RBA, exhibited plateaus (~ 10 – $15 \text{ m}^2 \text{ ha}^{-1}$), and had post-treatment increases. Species richness and total abundance responses were of similar magnitude; by 2009 and 2010 the species richness plateau was approximately 2 $\times$ the pre-treatment mean of 5.7 species/station.

3.3. Pre- to post-treatment avian community ordination

A three-dimensional solution was required to achieve stress <0.2 for all NMDS ordinations, and scree plots indicated that >3 dimensions only minimally improved stress. Therefore, we concluded that three dimensions sufficiently characterized the avian community structure. Of the four variables tested, study area had the strongest fit to the 2006–07 ordinations while RBA had the strongest fit to the 2008–10 ordinations (Table 5). The

avian community changes in response to RBA developed over the four post-treatment years. RBA surface and vector fits were poor and not significant in 2006 and 2007, but became significant in 2008–10 with relatively high R^2 values (~ 0.70) in 2009 and 2010. While the effect of RBA became dominant, some influence of study area on the avian community remained, as the fit of study areas (0.20 – $0.47 R^2$) was significant for all years. The surface fits and their respective vectors had generally similar R^2 values; thus, we found only linear relationships between the environmental variables and the avian community.

We plotted ordinations for all years and overlaid the fit of the significant environmental variables (Fig. 5; Supplementary online data). We plotted NMDS axes 1 and 2 because this ordination pattern had the highest RBA fit and ordinations using other axis combinations did not provide new information on the avian community–environmental variable relationships. The 2006 pre-treatment ordination had species mostly clustered around the center, with little spread along either axis. The 2007 ordination bore little resemblance to the pre-treatment or the subsequent post-treatment ordinations, likely due to the immediacy of the timber harvests. The 2008 ordination showed an avian community structure in transition between 2006 pre-treatment and 2009–10 post-treatment. Some avian community differentiation among the study areas was revealed by the somewhat separate clusters of study area point count stations in the ordinations. Species differed in abundance and occurrence among the study areas (Supplementary online data), and the study areas were generally arranged in the ordinations from the Tennessee sites (RB and SQ) to the more northerly sites.

The 2010 post-treatment ordination had the species distributed primarily along axis 1 as RBA increased from left to right (Fig. 5).

The shrub cover and RBA vectors were nearly opposite, reflecting the negative relationship between these variables (Fig. 2a). Open woodland/shrubland species such as Blue-winged Warbler (BWWA), Chestnut-sided Warbler (CSWA), Chipping Sparrow (CHSP), Mourning Dove (MODO), Northern Cardinal (NOCA), and Yellow-breasted Chat (YBCH) were located at low RBA. Forest area-sensitive species associated with closed-canopy forests such as Acadian Flycatcher (ACFL), Black-throated Green Warbler (BTNW), Blue-headed Vireo (BHVI), Ovenbird (OVEN), and Wood Thrush (WOTH) were located at high RBA. Species located in the middle of the RBA gradient included those with peak responses at medium RBA (Cerulean Warbler [CERW] and American Redstart [AMRE]), and those with little sensitivity to RBA (Scarlet Tanager [SCTA] and White-breasted Nuthatch [WBNU]).

4. Discussion

We found that wide variation in harvest intensity as measured by RBA led to strong, and often greatly contrasting, responses of forest birds. Avian responses also were dynamic in that some species took time to increase following harvesting. For example, increases in shrub nesting species closely coincided with shrub cover increases. Declines were immediate for closed canopy species. Avian community differentiation across the RBA gradient became most apparent by the end of the relatively short term (four years post-treatment) of our study. Avian responses were often non-linear, and in particular for Cerulean Warbler, Hooded Warbler, and Ovenbird, indicated differences in how species might generally respond to a wide RBA gradient. These differences suggest a variety of harvest intensity thresholds that may be useful

Fig. 4. Annual post-treatment territory densities of Ovenbird (a), Hooded Warbler (b), Cerulean Warbler (c), and Scarlet Tanager (d) along the residual basal area (RBA) gradient of the 28 plots (circles = harvest, triangles = unharvested control) from the seven study areas in the central Appalachians. Curves are the estimated response trend (single 2007–10 for graphs a and d, annual 2007–10 for graphs b and c) generated for the best supported model with a smoother in Table 4, and indicate response effect sizes across the gradient. The value indicated by the horizontal grey line is the mean pre-treatment density. A small amount of jitter was added to the points to reduce overlap.

Table 5

Fits of residual basal area (RBA), shrub cover, sapling cover, and study area to the pre-treatment 2006 and post-treatment 2007–10 NMDS (non-metric multidimensional scaling) ordinations (axis 1 and 2). The effect of RBA on the structure of the avian community became increasingly strong during the post-treatment period, but some effect of study area remained.

Year	RBA ^a				Shrub cover				Sapling cover				Study area	
	Surface		Vector		Surface		Vector		Surface		Vector		Centroid ^b	
	R ²	P	R ²	P	R ²	P	R ²	P	R ²	P	R ²	P	R ²	P
2006	0.13	0.274	0.03	0.423	0.10	0.282	0.04	0.336	0.04	0.512	0.04	0.353	0.33	0.001
2007	0.19	0.109	0.05	0.295	0.00	0.369	0.03	0.411	0.21	0.062	0.17	0.013	0.47	0.001
2008	0.55	0.001	0.57	0.001	0.08	0.050	0.11	0.057	0.28	0.001	0.31	0.001	0.22	0.024
2009	0.72	0.001	0.67	0.001	0.23	0.001	0.26	0.003	0.08	0.049	0.11	0.058	0.27	0.002
2010	0.71	0.001	0.68	0.001	0.34	0.001	0.32	0.001	0.07	0.467	0.03	0.502	0.20	0.039

^a Pre-treatment basal area was used for the 2006 ordination and mean post-harvest RBA for the 2007–10 ordinations.

^b The average of the site (point count station) scores per study area.

as quantitative targets for the management of these and similar species in upland hardwood forests.

Patterns of species responses to harvesting showed remarkable consistency across our widely separated study areas, which is similar to findings of Vanderwel et al. (2007). Species responses also generally matched their known habitat needs or preferences. Given this apparent predictability, we report optimal ranges of RBA for the focal species and additional species that we examined (Fig. 6). Although these targets may require modification based on specific regions or other forest types, we believe the proposed ranges are useful starting points for management of single species in second-growth upland hardwood forests. We also consider the species responses within broader RBA ranges (Sections 4.1 and 4.2) to provide more ecologically based approaches to management of assemblages of these forest birds. We recognize that we base management targets and approaches on numeric responses (e.g., territory density, number of singing males). While some studies (e.g., Boves et al., 2013; Leblanc et al., 2011) have examined the effects of harvesting on other demographic parameters such as pairing or nesting success, more are needed. Furthermore, some species requirements (e.g., snags) may not be met unless explicitly addressed in the management.

4.1. Medium RBA forest bird management

We begin with the likely optimal range for increasing the number of Cerulean Warblers due to the high conservation priority of this species. Based on our results, Cerulean Warbler increases were most reliably obtained for $\sim 10\text{--}20\text{ m}^2\text{ ha}^{-1}$ RBA, and this range encompassed the increases or retention of a variety of forest gap and canopy-dependent species (Fig. 6). When largest increases in the numbers of Cerulean Warblers is the management goal, a target RBA of $\sim 16\text{ m}^2\text{ ha}^{-1}$ is most effective based on the peak response we detected. Avian management at medium RBA may retain species that did not respond positively to the management. For example, Ovenbird and Wood Thrush were retained in reduced numbers, albeit with greatest retention at the upper end of the range. If RBA at the low end of the range is achieved with management, we expect near or complete elimination of these species. Species that are generally tolerant of moderate harvesting (e.g., Scarlet Tanager, Red-eyed Vireo) will also contribute to avian diversity at medium RBA.

Identifying some of the likely proximate factors behind the species associations at medium RBA is necessary to provide an ecological basis for this management. The Cerulean Warbler response is consistent with much of what is known about its habitat preferences, particularly the association with canopy gaps (Hamel, 2000; Perkins, 2006). The American Redstart and Blue-gray Gnatcatcher responses probably reflect a general preference for forest with openings (Kershner and Ellison, 2012; Sherry and Holmes,

1997). Other species responding to the understory development in the canopy gaps included the shrub- or dense understory-associated Hooded Warbler (Chiver et al., 2011), Kentucky Warbler (McDonald, 1998), Indigo Bunting (Payne, 2006), and Eastern Towhee (Greenlaw, 1996). However, these species continued to increase (and sometimes plateau) below $10\text{ m}^2\text{ ha}^{-1}$ RBA, indicating that they are adapted to a wide range of disturbance intensities that create forests with a moderately to mostly open canopy. Species such as these may make an important contribution to the avian diversity of medium RBA harvests, provided sufficient canopy gaps with appropriate understory development (e.g., shrubs for nesting) are created. We did not quantify the response of the residual trees to the increased canopy openness at medium (and lower) RBA, although qualitatively the tree foliage increases were visually obvious. The tree and understory responses occurred in tandem, and increases in habitat features (e.g., nesting cover, foliage for arthropod prey) across multiple forest layers were likely valuable for supporting a wide variety of forest birds.

Reduced levels of timber harvesting on many ownerships, even-aged forestry practices, and fire suppression have resulted in a closed canopy for much of the mature eastern deciduous forest. Historically, stand senescence and canopy disturbances such as moderate-intensity fires or wind-throw likely led to extensive

Fig. 5. The 2010 post-treatment NMDS species ordination. The ordination shows Alpha codes (Appendix A) for species occurring at >2 study areas in 2010, and the significant 2010 fits (Table 5) of the residual basal area (RBA) surface gradient (dashed vertical lines, $\text{m}^2\text{ ha}^{-1}$) and the vectors for RBA and shrub cover (arrows).

Fig. 6. Estimated canopy tree basal area targets for birds of mature, Appalachian upland oak hardwood forest based on the analyses. Thick lines indicate the range with peak increases/highest numbers retained and thin lines indicate where species may be present for management consideration (e.g., $\geq 1/2$ peak increase/highest retention or general tolerance across basal area).

areas with a structure similar to that created by medium RBA harvests. Moderate intensity timber harvests appear to provide surrogate habitat for species adapted to mature forest impacted by natural, medium-intensity disturbances or old-growth forest with abundant gaps (this study; Bakermans and Rodewald, 2009). However, harvests may lack key habitat components (e.g., snags) present due to natural disturbances or in old growth, so the specific requirements of species remain an important consideration and sometimes a research need (Villard and Jonsson, 2009). Furthermore, in contrast to the likely more stable associations in structurally complex old growth stands, species associations in second-growth, actively managed forests that are due to harvesting (e.g., in response to initial understory development) may be more ephemeral.

Shelterwood harvests are one way to create adequate canopy disturbance, and to achieve medium RBA, while still providing large canopy trees to benefit Cerulean Warblers. Additionally, shelterwood harvests can benefit forest-dwelling bats (Dodd et al., 2012) and wildlife that forage on hard and soft mast (Greenberg et al., 2007; Perry and Thill, 2003). The shelterwood harvesting sequence may include a variety of initial practices that retain canopy trees and establish or improve regeneration of oaks or other tree species of value (see Brose et al., 2008). How long conditions remain favorable during the sequence for the Cerulean Warbler

and its associates requires further study. Removing the residual canopy in stages, as is sometimes done, perhaps may extend the benefits for canopy-dependent birds. However, the benefits for these species will eventually end due to often complete overstory removal later in the cutting cycle (Newell and Rodewald, 2012). Further, as these stands age the understory will eventually become unsuitable for some gap-dependent species. A sustainable approach for management of both canopy-dependent and gap-dependent avian species may be to retain the residual canopy of a shelterwood harvest as long as possible (given economic and regeneration considerations), and prior to the overstory removal, enhance adjacent habitat with shelterwood harvests or other silvicultural harvests that achieve $10\text{--}20 \text{ m}^2 \text{ha}^{-1}$ RBA. While retention of a shelterwood harvest's residual canopy over a longer period of time may result in the canopy closing somewhat, overall structural heterogeneity will remain high and may continue to benefit some bird species.

4.2. Low and high RBA forest bird management

Managing for forest birds using levels of RBA outside the medium range may be desirable when response of the Cerulean Warbler or its associates is not of primary management interest. Low or high RBA may be needed to manage for a wider array of

forest birds, or for economic or silvicultural reasons. Interestingly, we found Cerulean Warblers to be remarkably tolerant of a wide range in harvest intensity, even when initial populations were large. Cerulean Warbler abundance was similar between 15–18 year old, regenerated, two-aged harvests and unharvested controls in West Virginia (Wood et al., 2005), and between group or single-tree selection harvests and unharvested controls in Indiana (Register and Islam, 2008). These findings imply flexibility in forest management for other bird species at least in terms of not leading to declines in Cerulean Warbler numbers. However, while lower-RBA harvests may retain some canopy trees, at some level of harvesting intensity the stand will likely lack adequate suitable trees to support Cerulean Warbler nests and territories, and in some cases, reproductive success may be depressed (Boves et al., 2013).

Species such as Chestnut-sided Warbler and Yellow-breasted Chat, which are often found in regenerating central hardwoods clearcuts (Eckerle and Thompson, 2001; McDermott and Wood, 2009; Richardson and Brauning, 2013), increased at the low end of the RBA gradient. Harvests achieving low levels of RBA (e.g., $\sim 5 \text{ m}^2 \text{ ha}^{-1}$) may be an appropriate option when the primary goal is to increase populations of early successional species, many of which are experiencing population declines (Sauer et al., 2012). Low RBA management also will benefit species exhibiting a wide response from low to medium RBA (e.g., Hooded Warbler). Historically, severe fires were likely important for creation of early successional habitat for birds in eastern deciduous forests, and fire reestablishment has been recommended (e.g., Klaus et al., 2010; Rush et al., 2012). High intensity harvests may provide a useful surrogate for severe fires, particularly when use of fire as a management tool is impractical.

A number of species peaked at the upper end of the RBA gradient within unharvested plots. Acadian Flycatcher (Whitehead and Taylor, 2002), Black-throated Green Warbler (Morse and Poole, 2005), Blue-headed Vireo (James, 1998), Ovenbird (Porneluzi et al., 2011), and Wood Thrush (Evans et al., 2011) prefer relatively undisturbed mature forests. The $>20 \text{ m}^2 \text{ ha}^{-1}$ RBA harvests appeared to retain some habitat for a number of these species (e.g., Ovenbird and Wood Thrush). While species negatively responding to this level of harvesting may recover given sufficient time before additional harvesting, leaving a proportion of forest unharvested is the best approach if the management focus is on late successional but closed-canopy forest birds. On the other hand, selection harvests may mimic natural disturbances (e.g., wind-throw, tree senescence) to some extent (Villard et al., 2012), and create habitat for species able to inhabit small forest gaps (e.g., Hooded Warbler, Kentucky Warbler). In our study, however, the minimal level of canopy disturbance in harvests with $>20 \text{ m}^2 \text{ ha}^{-1}$ RBA resulted in comparatively little increase for these species and for Cerulean Warblers. Additionally, Cerulean Warblers had lower nesting success in these harvests (Boves et al., 2013).

4.3. Other management considerations

Knowledge of the regional species pool and other site factors (e.g., elevation) will assist management application and prediction of outcomes. While our widespread study areas had consistent community-level responses to RBA, different species could be involved depending on the study area. For example, Chestnut-sided Warblers and Yellow-breasted Chats were absent from all study areas pre-treatment, and appeared in low RBA harvest plots by the fourth year post-treatment. However, Chestnut-sided Warblers appeared only at MF, RB, and SQ, the study areas at highest elevation (range 636–829 m), while Yellow-breasted Chats were absent only from MF. The Yellow-breasted Chat is fairly ubiquitous within the Central Appalachians, while the Chestnut-sided Warbler is primarily found at higher elevations.

For Cerulean Warbler management, medium-RBA harvests may have the greatest benefit when the population in a stand is low (e.g., <5 territories per 10 ha). Upper limits on territory density may make proportionally larger increases more likely to occur for initially low populations. High pre-harvest density suggests that habitat structure is already suitable, so no habitat enhancement is needed. Further, Cerulean Warbler per capita productivity can be reduced in some harvested stands (Boves et al., 2013), and negative effects from harvesting may have greater consequences for larger initial populations. For initially low populations, while declines in productivity as noted above for high and low RBA harvests may also occur in medium RBA harvests, there may be a net population benefit in landscapes where Cerulean Warbler density is suppressed due to an over-abundance of sub-optimal closed canopy forests (Boves et al., 2013). Of greater concern would be situations where medium RBA harvests pull Cerulean Warblers out of optimal habitat nearby where they would have had higher productivity. The effects of harvesting on Cerulean Warbler productivity, and the consequences of this for the species' population viability in different forest management scenarios, require further study.

Tree removal across our harvest treatments was spatially uniform, and the harvests were roughly square to broadly rectangular and 10 ha in size. Harvests that do not conform to this description may have different effects. While the generally small openings (1–2 ha or less) that result from group selection harvests do not negatively affect abundances of most forest birds (Campbell et al., 2007; Forsman et al., 2010), early-successional species may not benefit from this technique due to minimum area requirements. For example, Shake et al. (2012) found that Yellow-breasted Chat and two other shrubland birds had minimum area requirements as well as higher occupancy probability in early successional habitat patches >5.5 ha in size. Harvests too large, on the other hand, may negatively impact forest interior species avoiding the edges of adjacent patches of unharvested forest (e.g., Ovenbird and Acadian Flycatcher: Kroodsma, 1984) or result in unharvested forest patches too small to meet their area needs (Robbins et al., 1989; Whitcomb et al., 1981). Managing for forest birds with minimum area requirements but contrasting habitat requirements in an intensively managed forest is undoubtedly difficult, and a decision to focus on one group of species over another (e.g., early successional vs. mature forest specialists) in the short term may be necessary. Over the longer term and at larger (e.g., landscape) scales, balance between the management of species with competing needs may be more achievable (e.g., via a spatially and temporally dynamic “shifting mosaic” approach; Harris, 1984).

Harvesting will seldom be used as an end point for management of forest birds. Here, we focused on the initial and subsequent short-term responses of species, albeit across a wide range of harvest intensity. Some species and community responses occurred immediately while others developed over four breeding seasons (e.g., those likely related to understory development). Thus, several years of post-harvest assessment may be needed to fully evaluate management success. However, our four years of post-harvest study is also short-term as the stands will continue to change due to succession. By 15 years post-harvest, even-aged stands likely will not provide suitable breeding habitat for most early-successional birds (McDermott et al., 2011).

Finally, our study areas were located in heavily forested landscapes (74–94% forest cover), generally in oak-dominated upland forest, and plots were placed on ridgetops and associated sideslopes where Cerulean Warblers tend to be most dense. Additional study is required to see if timber harvesting can produce similar results in more patchily forested landscapes, in other forest types, or in other topographic situations.

5. Conclusions

Within the range of the Cerulean Warbler, forestry is a common land use that provides economic incentives for landowners to keep land in forest cover, and it is important to understand bird-forestry relationships if managed forests are to provide forest products as well as habitat for diverse avian communities (Sallabanks and Arnett, 2005). Our study found that use of forest management practices to achieve medium levels of RBA ($\sim 10\text{--}20\text{ m}^2\text{ ha}^{-1}$ RBA) in second-growth, actively managed Appalachian oak-dominated forests enhanced Cerulean Warbler habitat and also benefited a wide range of other forest birds, including those that were under-story-dependent. Stands managed for Cerulean Warbler increases are likely to have high overall avian diversity, which includes species at least partially retained, or relatively unaffected, by this harvesting. Indeed, we found that species richness increases, which were large and in the direction of lower RBA, began to level off within this medium range of RBA. The Cerulean Warbler appears to be a valuable umbrella species whose conservation needs may spur forest management that enhances avian diversity, particularly where forest areas are judged to be overly dominated by a mature, closed canopy.

While increasing avian diversity may be a viable goal within a single forest stand, the full range of responses we documented across our harvest intensity gradient suggests that a more regional and comprehensive ecosystem management approach is warranted. Primary focus on the Cerulean Warbler is needed to reverse, or at least slow, its decline. However, in a managed forest of many stands, it may be possible to also manage for species assemblages associated with specific successional stages. Our heavier harvest treatments, which retained at least some mature residual trees, supported an assemblage of area-sensitive, early successional species. Retaining sufficient unharvested or lightly harvested stands as part of a rotation strategy until even-aged stands reach maturity may effectively conserve harvest-intolerant species. Ideally, the best approach may be to employ multiple harvesting strategies at the landscape scale to support an array

of forest bird species adapted to different intensities of harvest-based disturbance. To achieve this, coordination among multiple stakeholders will be required.

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Appendix A

Common names, scientific names, American Ornithologists' Union Alpha codes, detection type(s) used for analysis, and nesting guilds of bird species effectively surveyed by the point count method and included in analyses.

Common name ^a	Scientific name	Alpha code	Detection type(s)	Nesting guild ^b
Acadian Flycatcher	<i>Empidonax virens</i>	ACFL	Song	SC
American Redstart	<i>Setophaga ruticilla</i>	AMRE	Song	SC
American Robin	<i>Turdus migratorius</i>	AMRO	Song + call	SC
Black-and-white Warbler	<i>Mniotilta varia</i>	BAWW	Song	GG
Blackburnian Warbler	<i>Setophaga fusca</i>	BLBW	Song	CA
Black-throated Green Warbler	<i>Setophaga virens</i>	BTNW	Song	CA
Blue-grey Gnatcatcher	<i>Poliophtila caerulea</i>	BGGN	Song + call	SC
Blue-headed Vireo	<i>Vireo solitarius</i>	BHVI	Song	SC
Blue-winged Warbler	<i>Vermivora cyanoptera</i>	BWWA	Song	GG
Carolina Chickadee	<i>Poecile carolinensis</i>	CACH	Song + call	HH
Carolina Wren	<i>Thryothorus ludovicianus</i>	CARW	Song	HH
Cerulean Warbler	<i>Setophaga cerulea</i>	CERW	Song	CA
Chestnut-sided Warbler	<i>Setophaga pensylvanica</i>	CSWA	Song	SH
Chipping Sparrow	<i>Spizella passerina</i>	CHSP	Song	SH
Downy Woodpecker	<i>Picoides pubescens</i>	DOWO	Call + visual	HH
Eastern Towhee	<i>Pipilo erythrophthalmus</i>	EATO	Song + call	GG
Eastern Wood-Pewee	<i>Contopus virens</i>	EAWP	Song	CA

Appendix A (continued)

Common name ^a	Scientific name	Alpha code	Detection type(s)	Nesting guild ^b
Hairy Woodpecker	<i>Picoides villosus</i>	HAWO	Call + visual	HH
Hooded Warbler	<i>Setophaga citrina</i>	HOWA	Song	SH
Indigo Bunting	<i>Passerina cyanea</i>	INBU	Song	SH
Kentucky Warbler	<i>Geothlypis formosus</i>	KEWA	Song	GG
Mourning Dove	<i>Zenaidura macroura</i>	MODO	Song	SH
Northern Cardinal	<i>Cardinalis cardinalis</i>	NOCA	Song	SH
Ovenbird	<i>Seiurus aurocapilla</i>	OVEN	Song	GG
Pileated Woodpecker	<i>Dryocopus pileatus</i>	PIWO	Call + visual	HH
Red-bellied Woodpecker	<i>Melanerpes carolinus</i>	RBWO	Call + visual	HH
Red-eyed Vireo	<i>Vireo olivaceus</i>	REVI	Song	SC
Rose-breasted Grosbeak	<i>Pheucticus ludovicianus</i>	RBGR	Song	SC
Scarlet Tanager	<i>Piranga olivacea</i>	SCTA	Song	CA
Tufted Titmouse	<i>Baeolophus bicolor</i>	ETTI	Song + call	HH
White-breasted Nuthatch	<i>Sitta carolinensis</i>	WBNU	call	HH
Wood Thrush	<i>Hylocichla mustelina</i>	WOTH	Song	SC
Worm-eating Warbler	<i>Helmitheros vermivorum</i>	WEWA	Song	GG
Yellow-billed Cuckoo	<i>Coccyzus americanus</i>	YBCU	Call	SC
Yellow-breasted Chat	<i>Icteria virens</i>	YBCH	Song	SH
Yellow-throated Vireo	<i>Vireo flavifrons</i>	YTVI	Song	CA

^a Species in bold are U.S. fish and wildlife service birds of management concern.

^b Nesting guilds: GG = ground, SH = shrub, HH = cavity, SC = sub-canopy, CA = canopy.

Appendix B. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.foreco.2013.07.037>.

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