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Identifying coarse- and fine-scale drivers of avian abundance following prescribed fires

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ABSTRACT

Suppression of historic fire regimes in North America has altered successional stages and shifted vegetation communities, negatively impacting wildlife diversity in forests. Prescribed fire is often used to increase habitat for wildlife populations and diversity but monitoring of responses does not always capture nuanced differences in habitat that influence wildlife communities over a range of ecological conditions and processes. We matched avian point count data with extensive vegetation sampling of unburned plots and plots that burned 12–16 months prior to evaluate the effects of coarse- and fine-scale habitat variables on the abundance of a suite of avian indicator species and nesting guilds. We estimated abundance conditional on detection probability based on repeated sampling over time intervals using N-mixture models and assessed support for coarse- and fine-scale habitat variables using multimodel inference and AIC. Six of 10 species demonstrated different abundances on burned and unburned plots. Abundances of three species were influenced solely by coarse variables, one species by fine-scale vegetation, and five species were dependent on a mix of coarse- and fine-scale variables. Even fine-scale vegetation characteristics did not fully capture the ecological processes stimulated by fire and compensatory community differences including interactions among species such as competition and predator avoidance should be considered in predicting species responses to prescribed fire. Shrub nester abundance was much higher on plots that burned the year prior, but the effect sizes of other variables were small for ground, tree, and cavity nesters, even though there were strong differences in abundances of individual species within those guilds. Detection probability was most often affected by conditions during the count including start time, temperature and wind, but also burn status and observer, suggesting potential bias in findings that do not account for heterogeneity in detection probability. We suggest variable responses of individual species within nesting guilds may obscure identification of responses in the avian community and inhibit assessment of management and restoration actions. Understanding species-specific responses to fine-scale habitat variables in the context of coarse ecological typology and the associated vegetative and wildlife community will provide the greatest insight to how prescribed fire characteristics interact to produce wildlife responses, and thus enhance its use as a restoration tool.

1. Introduction

Suppression of disturbance events such as fires have fundamentally altered landscapes and reliant wildlife communities (Parsons and DeBenedetti, 1979, Pyne et al., 1996, Pasch and Koprowski, 2011, Harper et al., 2016). Disturbance is a critical process in ecosystems (Pickett and White, 2013, White and Jentsch, 2001) generating spatial and temporal heterogeneity in vegetation communities and credited with increasing biodiversity (Martin and Sapsis, 1992). Through immediate redistribution of resources, disturbances alter competition dynamics among species and disturbances at various trophic levels can cascade through the ecosystem producing variable outcomes (Bowman

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et al., 2016, Lugo, 2020).

Prescribed fire is often implemented with the intent to create conditions that will support an increase in wildlife populations or diversity (Leopold, 1933), but changes in habitat and wildlife community responses are nuanced and vary over a range of site conditions and ecological processes such as competition and predation (Bowman et al., 2016, Harper et al., 2016). The frequency and intensity of prescribed fire regimes is expected to generate different wildlife responses and capacity to sustain early successional dependent species (Falk et al., 2011; Greenberg et al., 2013, Harper et al., 2016). Further, the spatial scale of habitat management and prescribed fire parameters and regimes are often constrained by land ownership and different objectives for use and stewardship resulting in inconstant wildlife responses under different conditions (Pitt et al., 2014). But ultimately, the recruitment of wildlife is not dependent on the fire or fire characteristics alone, but the vegetation and habitat characteristics produced (Rose and Simons, 2016). Understanding how spatial scale, frequency, and severity interact to create different vegetation and habitat characteristics will aid land managers in determining appropriate fire prescriptions to recruit and maintain desired wildlife communities across the landscape (Parr and Andersen, 2006).

Suppression of historic fire regimes in North America have resulted in vegetation community shifts, including a "mesophication" and homogenization of the forested landscape in the Ridge and Valley Province of the central Appalachians over the last 100 years (Nowacki and Abrams, 2008). Stand-level tree and shrub species richness are declining as closed canopy forests composed of mesophytic fire-sensitive species now dominate the landscape (Lafon et al., 2017). As the vegetation community has changed, wildlife species adapted to persistent early successional seral stages associated with previously frequent fire intervals have declined (Harper et al., 2016). With documented changes in communities and overall diversity, the use of prescribed fire to mimic previous disturbance regimes has increased as a restoration tool in this region (Pitt et al., 2014, Ford et al., 2010).

Avian species or communities are a common focus for studies on the effects of prescribed fire (Pitt et al., 2014) due to their high detectability and relatively easy sampling method (point counts), rapid reaction to changes in habitat, and broad diversity of guilds with different expected responses to fire treatments (Blake, 2005, Rush et al., 2012). However, studies of prescribed fire effects have demonstrated conflicting results with some describing an increase in diversity (Greenberg et al., 2018) or focal species (Percy, 2012) with introduction of fire, while others demonstrated no strong or long-lasting effects for many species (Blake, 2005, Rush et al., 2012). These discrepancies in findings illustrate the importance of understanding how fire characteristics translate to vegetation community characteristics (Pitt et al., 2014) if prescribed fire is to be used to effectively create habitat to restore historical avian communities.

We used a subset of a point count data set collected over a 74 km^2 project area managed in units with varying prescribed fire regimes to evaluate the effects of coarse- and fine-scale habitat variables on avian species and nesting guild abundance on unburned plots compared to plots the year following the first prescribed fire. We expected to find differences in abundance among species with differences in vegetation structure and preferred nesting habitat, including lower abundances of forest-interior ground-nesters on plots that had experienced a fire the year prior and higher abundance of early successional species and shrub-nesters with greater canopy openings and understory and midstory vegetation density. We predicted differences in cavity nester abundance would be better described by coarse variables such as burn status or ecological zone that likely correlate with higher overall snag density for nesting. Conversely, we predicted differences in early successional species' abundances would be better described by more nuanced fine-scale vegetation features representing nesting and foraging habitat for these species that vary with localized fire characteristics across burned plots. We compiled the results across 1) a suite of avian species identified as Management Indicator Species or High Conservation Value and 2) by nesting guilds to assess the value of indicator species and guilds as monitoring tools. The results provide insight to how prescribed fire and forest restoration can be used to manage for diverse avian communities.

2. Methods and materials

2.1. Study area

The study area is located in Bath County, Virginia, USA, in the Ridge and Valley Province of the Central Appalachian Mountains (Fig. 1) and is the site of the Warm Springs Mountain Restoration Project (WSMRP). The WSMRP spans 1,491 ha of the Warm Springs Mountain Preserve, owned by The Nature Conservancy, and over 5,938 ha of the adjacent George Washington and Jefferson National Forest (GWJNF). Elevations range from 580 m above sea level in the northeastern portion of the site to 1287 m at the highest elevation. The project area is typical of the region and characterized by linear ridges with continuous valleys. Central Appalachian Dry Oak-Pine Forest, Southern Appalachian Oak Forest, and Northeastern Interior Dry-Mesic Oak Forest are the dominant ecological systems in the study site (Simon, 2011).

The WSMRP is a collaborative restoration project developed by partners in the Central Appalachians Fire Learning Network (FLN), who are working to restore the role of fire to Appalachian pine-oak forests and woodlands. Since 2008, FLN partners have conducted controlled burns on 2,639 ha divided into 11 burn units across the project area. Burn unit size ranged from 60 to 2,023 ha. Six units were not burned and served as baseline controls (Fig. 1 and Appendix A). Prescribed burns were conducted throughout the late dormant to early growing season from March-May under a range of weather conditions. One unit was burned by a wildfire that was then managed as a prescribed fire (unit 5; 356 ha). The main ignition techniques used for prescribed burns included firing with drip torches and incendiary devices and helicopter ignitions with a plastic sphere dispenser. The primary fuels were broadleaf litter and pine needles interspersed with patches of mountain laurel (*Kalmia latifolia*). Firing patterns included a combination of ridge and contour firing once blacklines were established along fire control lines. Burn severities ranged from unburned to high producing high levels of heterogeneity in vegetation characteristics on burned units compared to unburned units (Fig. 2; detailed analysis in Lorber et al., 2018). Approximately 14% of burned acreage experienced higher burn severities, hot enough to cause significant tree mortality and convert the closed-canopy forest to open-canopy or early-successional conditions. This level of effects is slightly above average for prescribed burns on the GWJNF (Lorber et al., 2018). Overall impacts to duff layers were low to moderate and impacts on soil were low. Prescribed fire characteristics and additional example photo point monitoring pictures are included in Appendix A.

2.2. Study design

We established a total of 108 permanent monitoring plots across the 11 units (5 burned and 6 unburned) as part of the WSMRP to monitor changes in forest structure and composition and breeding bird populations in response to controlled burning. We randomly stratified the study area by ecological system type using an ecological zones model (Simon, 2011, described in Section 2.3. Vegetation and forest structure sampling, below) created for GWJNF to select plots. We generated plot centers in ArcGIS using Hawth Tools requiring plots to be $\geq$ 30 m from a road or trail, and $\geq$ 250 m apart to avoid duplicate sampling. Plot centers were georeferenced in the field with a handheld global positioning system (GPS) unit and marked with steel rebar. The center points served as the plot center for forest structure and composition monitoring, avian point counts and photo monitoring points. Two units were removed from the analysis due to a change in point count methodology early in the implementation of monitoring. For this study, we further

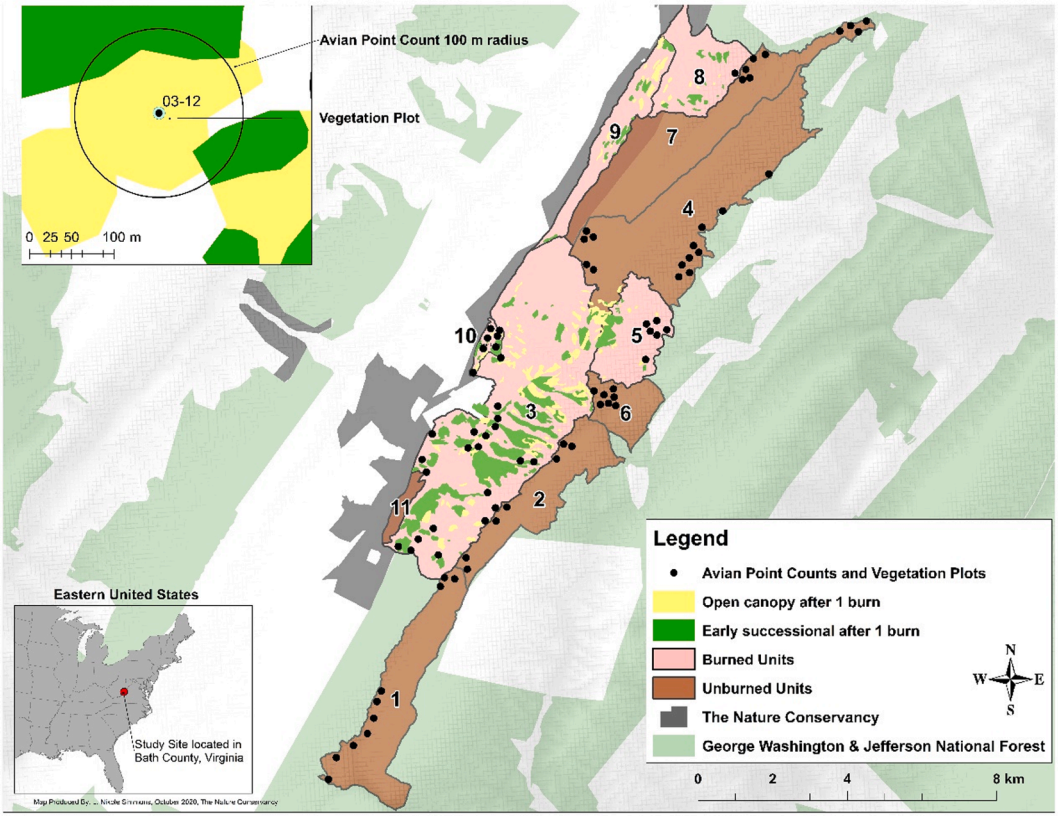

Fig. 1. Study area for avian community and forest structure and composition monitoring for the Warm Springs Mountain Restoration Project, Bath County, Virginia, USA. Burn units are labeled 1–11. Unit 5 initiated as a wildfire that was then managed in the same manner as the prescribed fires in units 3, 8, 9, and 10. Remaining units serve as unburned controls. Upper right inset shows one of the avian and vegetation monitoring plots (03–12) with open canopy following a single burn in unit 3.

subsampled the monitoring data set to allow for direct comparisons of avian communities and the role of vegetation and habitat on plots that had not burned in recent history compared to plots 1 year (12–16 months) following the first fire in recent history (>50 years). We selected plots with both avian and vegetation sampling in the year following the first fire (34 plots across 5 units) and compared them to plots in unburned units (47 plots across 4 units). The subsampling resulted in a total of 81 plots across 8 units in the study area, each of which were sampled once from 2012 to 2015 either the year following the first fire or in an unburned state.

2.3. Vegetation and forest structure sampling

2.3.1. Fine-scale features

Vegetation sampling was designed to measure fine-scale differences in understory, midstory, and overstory habitat (Table 1). We used a nested plot design for sampling and followed a standardized vegetation monitoring protocol adapted from Elzinga et al. (1998) and NPS Fire Monitoring Handbook (2003) by partners in the FLN. We measured two variables along the forest floor (extent of nonwoody vegetation and total seedling density) and two understory variables (live stem density and dead stem density). Forest Floor nonwoody vegetation and forest floor seedling density were measured at four 1 m^2 quadrats located 3.59 m from plot center in four cardinal directions. Forest floor nonwoody vegetation was measured as the percent aerial cover of graminoids and forbs species using the Daubenmire scale and averaged for a plot mean. Forest floor seedling density included all woody stems 15 cm to 1 m in height. Total count of stems in quadrats were averaged for each plot and extrapolated to stems ha^{-1}.

For understory and midstory variables, we counted all woody tree and shrub stems > 1 m tall within a 3.59 m radius (0.004 ha, extrapolated to stems ha^{-1}) measured dbh, and identified stems as live or dead. We estimated understory dead stem density as the count of dead stems > 1 m tall and < 2.5 cm dbh, and understory live stem density by summing the count of tree and shrub stems > 1 m tall and < 2.5 cm in dbh. We separated out tree, shrub, and dead stems > 1 m tall with 2.5–10 cm dbh to estimate midstory tree density, midstory shrub density, and midstory dead stem density. We used a Geographic Resource Solution (Arcata, CA) densitometer to estimate overstory canopy cover recording data at five points (0.72 m spacing) along each of four 3.59 m transects (20 points total) radiating in the cardinal directions from plot center and averaged the measures at each point to represent the plot (Appendix A).

2.3.2. Coarse-scale features

We used burn history and geographical information systems (GIS) to describe coarse-scale variables at each plot. Each plot was recorded as either unburned or burned the year prior when sampling occurred (burn status). We created a 100 m buffer around each plot center point and digitized the canopy with the resulting area as closed, open, or early successional. As the three categories summed to 1 and were highly correlated, we only used % canopy closure as a coarse-scale variable in our candidate model set.

To describe coarse-scale ecological differences as a continuous variable we developed an index representing fire-adapted community dominance for the 100 m around each point. The presence of fire-adapted communities was represented by an ecological classification model (Simon, 2011) developed for the region similar to LANDFIRE's Biophysical Settings (LANDFIRE, 2008). An "ecozone" in this model is defined as a unit of land that can support a specific plant community or

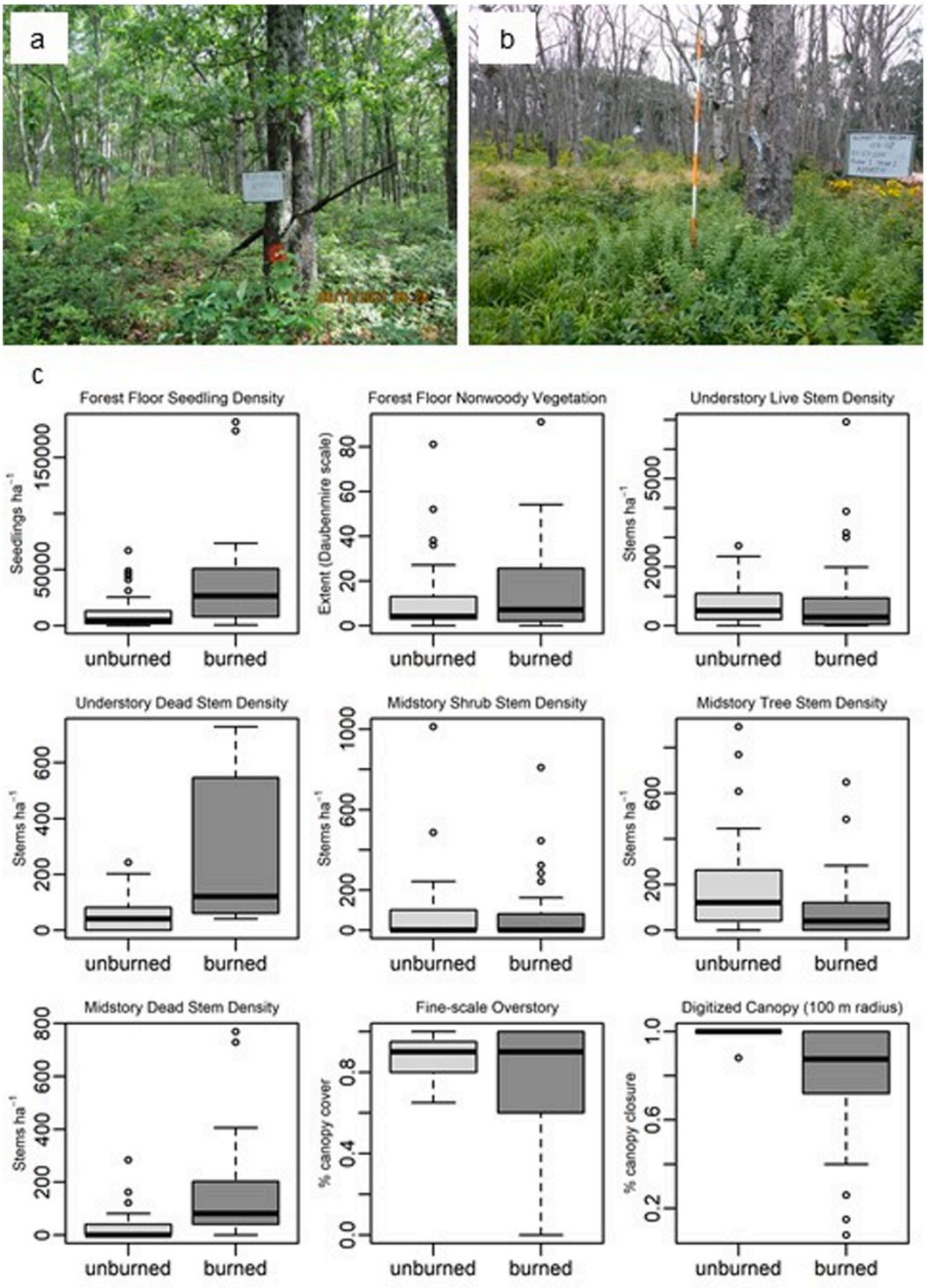

Fig. 2. Example of fire severity created by prescribed fire in burn unit 3. The baseline reference photo (a) in shows conditions plot 03–02 prior to a prescribed fire compared to the photo of the same plot 1 year following a prescribed fire (b). Each photo was taken at plot center facing north. Box plots (c) of vegetation characteristics across all plots (y-axis) show variable differences in vegetation structure between unburned plots (light gray) and plots that had burned 1 year prior (dark gray).

plant community group based upon environmental factors such as temperature, moisture, fertility, and solar radiation. The defined ecozone unit may or may not represent existing vegetation, but instead, the vegetation that could occur on a site with historical disturbance regimes. Ecozones in this landscape were modeled from intensive field data and by applying logistic regression coefficients to digital terrain models using GIS and mapped at a scale of 30 m by 30 m pixels. Each of the > 20 ecozones was assigned a rating representing degree of fire-adaptation based on the expertise of a working group of the FLN and GWNF staff. Fire-adapted index (FAI) scores ranged from 0 to 5, with the most fire-adapted ecozones (e.g. pine-oak heath) receiving the highest score. To estimate the coarse-scale FAI for a plot, we extracted all ecozone pixels within 100 m of a monitoring point (3.14 ha) and calculated the area for each ecozone polygon. We multiplied the area of each relevant ecozone

Table 1
Coarse- and fine-scale covariates hypothesized to influence differences in avian species abundances on unburned plots compare to plots that had experienced a prescribed fire one year prior in the Ridge and Valley Province of the central Appalachian Mountains, USA. Summary statistics (mean, median, and range) of each continuous variable for the subsampled plots are shown in the last 3 columns for all plots (N = 81), unburned plots (N = 34), and plots 1-year following a fire (burned; N = 47).

Scale	Level	Covariate	Measurement	All plots (mean median range)	Unburned plots (mean median range)	Burned plots (mean median range)
Fine	Forest floor	Seedling density	Total woody stems ha^{-1}, 15 cm −1m in height	22,193 8,727 0–181,521	11,475 4,507 0–66,790	37,010 26,429 410–181,521
Fine	Forest floor	Nonwoody vegetation	Daubenmire: grasses and forbs	13.43 6 0–91	11.07 4 0–81	17.37 7 0–91
Fine	Understory	Live stem density	Live tree and shrub stems ha^{-1}, <2.5 cm dbh, >1m tall	792 365 0–6,926	752 506 0–2,714	846 284, 0–6,926
Fine	Understory	Dead stem density	Dead stems < 2.5 cm dbh, >1m tall ha^{-1}	103 41 0–729	64 41 0–243	278 122 41–729
Fine	Midstory	Shrub density	Shrub stems 2.5–10 cm dbh, >1m tall ha^{-1}	81 0 0–1,013	81 0 0–1,013	81 0 0–810
Fine	Midstory	Tree density	Tree stems 2.5–10 cm dbh, >1m tall ha^{-1}	150 41 0–891	195 122 0–891	87 41 0–648
Fine	Midstory	Dead stem density	Dead stems 2.5–10 cm dbh, >1m tall ha^{-1}	88 41 0–770	34 0 0–284	162 81 0–770
Fine	Overstory	% canopy cover	Daubenmire scale	81.46% 90.00% 0–100%	87.00% 90.00% 65–100%	74.12% 90.00% 0–100%
Coarse		Fire-adapted index (FAI)	Weighted mean of fire-adapted index score within 100 m buffer	31.90 34.00 1.00–86.0	31.23 33.00 1.00–86.00	32.82 35.50 6.00–50.00
Coarse		Canopy closure	% digitized closed canopy within 100 m buffer	91.60% 100% 8.00%–100%	99.74% 100% 88.00–100%	80.35% 87.50% 8.00–100%
Coarse		Burn status	Burned or no burn			

polygon by its FAI rating and summed to get a weighted average representing the FAI for each plot. The FAI values could range from 0 for the most mesophytic, fire-sensitive plots to 38.75 for the most fire-adapted plots.

2.4. Avian sampling

We conducted point counts in the same year as vegetation sampling at each plot. We used an observational capture-recapture method and recorded detections of each individual bird at a 100 m fixed radius for 1-minute intervals over 10 min. Individual birds were identified by ocular and/or acoustical characteristics. Sampling points were visited 1 time between mid-May and mid-June, during the height of avian breeding. Each point was visited between the times of 1/2 h after official sunrise to 1030, during fair to good weather (winds $\leq$ 8 mph and no precipitation) to improve detection probabilities. Points were visited in teams of two, with one person designated as an observer and one as a recorder. Over the years there were 4–6 primary observers, with additional observers who received training on common bird songs in the study area and served as recorder until they felt confident in the protocol and identification. Upon arrival to each plot we recorded start time, temperature, cloud cover and wind speed using a Kestrel weather meter.

2.5. Statistical methods

2.5.1. Selection of avian species and guilds for analysis

Forest bird communities can be diverse and responses to prescribed fire and other disturbances are frequently described by selecting a suite of representative species (USFS, 2014) or by grouping species with similar characteristics expected to drive responses of breeding birds such as nesting guilds (Greenberg et al., 2018). We chose to evaluate both approaches, estimating abundance of a selection of "Management Indicator Species" (MIS) and "High Conservation Value" (HCV) species, and then estimating abundance of four nesting guilds (cavity-, shrub-, tree-, and ground-nesting species). The USFS uses MIS as a planning tool and species are selected based on representations of different preferred habitat types (USFS, 2014). For breeding birds in the study area, we selected eight MIS bird species identified in the GWNF Management Plan (USFS, 2014) representing different habitat preferences and indicator value including scarlet tanager (*Piranga olivacea*), eastern towhee, (*Pipilo erythrophthalmus*), ovenbird (*Seiurus aurocapilla*), worm-eating warbler (*Helmitheros vermivorum*), Acadian flycatcher (*Empidonax virescens*), hooded warbler (*Setophaga citrina*), chestnut-sided warbler (*Setophaga pensylvanica*), and pileated woodpecker (*Dryocopus pileatus*); Table 2). We also selected a suite of designated HCV species that range from common to uncommon in the region but have experienced population declines including cerulean warbler (*Setophaga cerulea*), wood thrush (*Hylocichla mustelina*), Canada warbler (*Cardellina canadensis*), black-and-white warbler (*Mniotilta varia*), and eastern wood pewee (*Contopus virens*). Finally, we grouped detected species based on nesting habitat requirements as a simple proxy assumed to represent many single species responses (Appendix B).

2.5.2. Abundance estimation and model selection

We estimated species and guild abundance using the pcount() function in the unmarked package (Fiske and Chandler, 2011) in R (R Core Team, 2020) and selected from models within the candidate set using Akaike's Information Criterion (AIC). Avian species abundances may be driven by coarse-scale landscape features in the vicinity of a point count (i.e., FAI, % canopy closure within 100 m, or burn status), but also by specific or fine-scale vegetation differences influencing habitat structure and forage availability (overstory, midstory, and

Table 2
Bird management indicator species (MIS) and high conservation value species (HCV) selected for evaluating drivers of abundance on unburned plots compared to plots the year following a fire (burned) in the Ridge and Valley Province of the central Appalachians, USA. Bird MIS species were selected to represent differences in habitat preferences and to answer specific questions posed by the George Washington-Jefferson National Forest Management Plan (USFS, 2004) to assess impacts of management actions.

Species (classification)	Habitat preference	Reason for inclusion	Expected difference in abundance
Eastern towhee (MIS)	Early successional forest	Presence and abundance indicate key successional stages are available	Higher on burned plots
Chestnut-sided warbler (MIS)	High elevation early successional habitat	Presence and abundance indicate key successional stages are available	Higher on burned plots
Ovenbird (MIS)	Mature deciduous, interior forest	Presence and abundance indicate key successional stages are available	Lower on burned plots
Acadian flycatcher (MIS)	Mature riparian	Presence and abundance indicate key successional stages are available	Lower on burned plots
Hooded warbler (MIS)	Mature mesic deciduous forests	Presence and abundance indicate key successional stages are available	Lower on burned plots
Scarlet tanager (MIS)	Mid- to late-successional oak and oak-pine forests	Presence and abundance expected to indicate a desirable range of variability in landscape and stand-level composition	Higher on burned plots
Pileated woodpecker (MIS)	Abundance of snags	Presence and abundance indicate key terrestrial habitat features are provided	Higher on burned plots
Cerulean warbler (HCV)	Older deciduous forest with tall trees and gaps in canopy	Populations in decline	Higher on burned plots
Wood thrush (HCV)	Mature deciduous and mixed forests, requires complex habitat but sensitive to fragmentation	Populations in decline	No difference or slightly lower on burned plots
Canada warbler (HCV)	Dense understory	Populations in decline	Higher on burned plots
Black-and-white warbler (HCV)	Intact forest interior	Populations in decline	Lower on burned plots
Worm-eating warbler (HCV)	Mature deciduous, interior forest	Presence and abundance indicate key successional stages are available	Lower on burned plots
Eastern wood pewee (HCV)	Edges and multi-successional stages	Populations in decline	Higher on burned plots

understory features). To parse apart these effects, we created two candidate model sets (Table 1) based on a priori hypotheses describing possible population differences for each species (coarse-scale and fine-scale candidate sets, hereafter). We used a sequential workflow to fit models within and among candidate sets, first creating secondary candidate model sets and then selecting variables to carry forward to final candidate sets based on a liberal ΔAIC threshold (≤5 ΔAIC) to assess support for variables and estimate abundance (Morin et al., 2020; see below for description of progression). Although multiple plots occur within each unit, we were unable to include unit as a factor or random effect due to insufficient data. Thus, we acknowledge there is likely some correlation among variables for plots within the same unit, but the spacing of plots is large enough to expect independence for point counts.

We compared models with single covariates and combinations of covariates within each candidate set. All continuous variables were scaled and centered on 0 to allow for relative comparisons of effect sizes in the avian abundance models. For the coarse-scale candidate set, we first considered the relative support for FAI (calculated at 100 m buffer), % canopy closure within 100 m, and burn status. For the fine-scale candidate model set, we fit models with combinations of up to three covariates within each subclass of covariates first (overstory, midstory, or understory and forest floor covariates). Next, we combined abundance submodels with support (ΔAIC $\leq$ 5) and without uninformative parameters (Arnold, 2010) from both initial candidate sets to create a secondary candidate set, and then combined all results to create a final candidate set. We included all detection probability submodels (~1, ~temperature, ~start time, ~wind, ~temperature + start time + wind, ~observer, ~burn status) in the coarse- and fine-scale candidate sets and carried forward detection probability submodels within 5 ΔAIC that were not associated with uninformative parameters to the secondary candidate set. We assessed relative support for coarse- and fine-scale scale features based on all models in the final candidate set within 5 ΔAIC of the top-ranked model after uninformative parameters were removed. We estimated abundance for each species and guild and compared effect sizes of supported covariates based on the top-ranked model.

3. Results

The abundances of three species were influenced solely by coarse-scale variables (eastern towhee and worm-eating warbler: % canopy closure at 100 m radius and burn status; black-and-white warbler: burn status) while one species was influenced by only fine-scale variables (hooded warbler: understory variables; Fig. 3). Abundance estimates of five species were influenced by a combination of both coarse- and fine-scale variables (scarlet tanager: FAI, midstory variables, and burn status; ovenbird: FAI and understory variables; Acadian flycatcher: burn status, FAI and understory variables; piliated woodpecker: % canopy closure at 100 m, understory and midstory variables; and eastern wood pewee: burn status and understory variables). Detection probability was most often affected by conditions during the count (start time, temperature and wind), and observer, but also burn status. Model selection tables are presented in Appendix C and species-specific and guild results are detailed below.

3.1. Management indicator species

Scarlet tanagers were detected at 61% of plots (1–2 individuals detected) and detection probabilities ranged from 0.32 (95% CI = 0.16–0.48) to 0.78 (95% CI = 0.64–0.98) by observer. Mean scarlet tanager abundance ($\widehat{N}$) was higher at unburned plots (0.86 individuals, 95% CI = 0.53–1.18) compared to plots that burned the year previously (0.53 individuals, 95% CI = 0.27–0.78; Fig. 4), was higher with increasing FAI values (β = 0.30, SE = 0.12) and lower on plots with greater midstory shrub density (β = −0.66, SE = 0.36). Predicted potential abundance (at minimum and maximum values of included covariates) ranged from 0.02 individuals (95% CI = 0–0.08) to 3.03 individuals (95% CI = 0.78–5.28). There was greatest support for inclusion of the FAI in estimating abundance (included in all models within ΔAIC = 5; Appendix C).

Eastern towhees were detected at 34% of plots (1–3 individuals) and detection probabilities ranged from 0.32 (0.14–0.62) to 0.73 (0.52–0.95) by observer. Eastern towhee abundance was higher on plots that burned the year prior (β = 1.89, SE = 0.47) and with lower % canopy closure within 100 m (β = −0.91, SE = 0.56). Mean eastern towhee abundance was 0.34 individuals (0–0.81) at unburned plots and

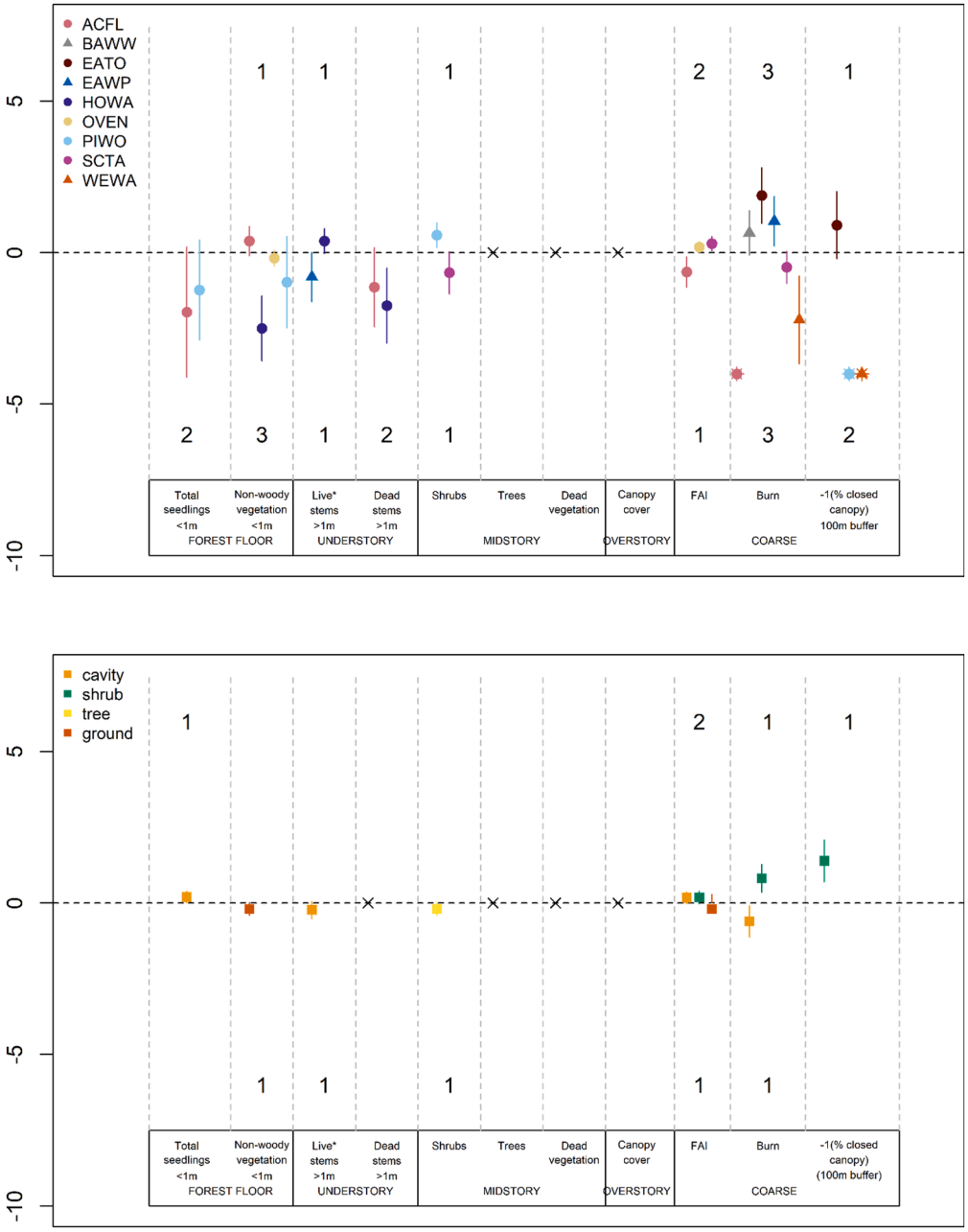

Fig. 3. Effect sizes of beta coefficients for top-ranked models for (top) management indicator species (circles; ACFL: Acadian flycatcher, EATO: eastern towhee, HOWA: hooded warbler, OVEN: ovenbird, PIWO: pileated woodpecker, SCTA: scarlet tanager) and high conservation value species (triangles; BWWA: black-and-white warbler, EAWP: eastern wood pewee, WEWA: worm-eating warbler) and (bottom) by nesting guild (squares). Asterisks indicate a species was only found under that condition and "x" indicates no species demonstrated differences in abundance in response to that variable. Number at the top and bottom of each column summarize the total number of species or guilds that were affected by the corresponding variable. Error bars represent 95% confidence intervals and effects are grouped by fine-scale features describing understory, midstory, and overstory conditions, and coarse-scale variables.

2.28 individuals (0.28–4.28) individuals at plots that burned the year prior. Predicted potential abundance ranged from 0.14 (95% CI = 0.02–0.26) to 2.12 (95% CI = 0.41–3.83).

Ovenbirds were detected at 77% of plots (1–4 individuals detected). Expected detection probability was 0.54 (95% CI = 0.50–0.58) and varied with conditions during the count including start time ($\beta = -0.20$, SE = 0.10), and temperature ($\beta = 0.38$, SE = 0.12), but wind had little effect ($\beta = -0.004$, SE = 0.11). Mean abundance was 1.38 individuals (1.09–1.67) and was higher at plots with high FAI values ($\beta = 0.19$, SE = 0.09) and with less forest floor nonwoody vegetation ($\beta = -0.18$, SE = 0.13). Predicted potential abundances ranged from 0.50 (95% CI = 0–1.03) to 2.98 (95% CI = 1.18–4.78) across observed values of FAI and forest floor nonwoody vegetation.

Acadian flycatchers were detected at 24% of plots (1–2 individuals) and were only detected on unburned plots. The absence of any detections on burned plots and the resulting distribution of potential detections by different observers prohibited estimation of abundance or detection probability when either variable was included. Thus, we removed models with either variable from the candidate set with the acknowledgement that there was an overwhelming negative effect of burn status on Acadian flycatchers. When observer was removed there was greatest support for an effect of survey conditions on detection probability including start time ($\beta = 0.39$, SE = 0.21), wind ($\beta = -0.98$, SE = 0.365), and temperature ($\beta = -0.77$, SE = 0.29). Mean abundance was low (0.06 individuals, 95% CI = 0.53–0.71) and lower on plots with greater forest floor seedling density ($\beta = -1.96$, SE = 1.10) and understory dead stem density (−1.14, SE = 0.67), and higher FAI values ($\beta = -0.64$, SE = 0.25). Acadian flycatcher abundance was also higher on plots with greater nonwoody vegetation ($\beta = 0.38$, SE = 0.25). Predicted abundances across supported variables ranged from 0 to 0.35 (95% CI = 0.25–0.45).

Chestnut-sided warblers were detected at only 10% of plots (1–2 individuals) and there was no support for any variables changing abundance (intercept-only abundance model received greatest support).

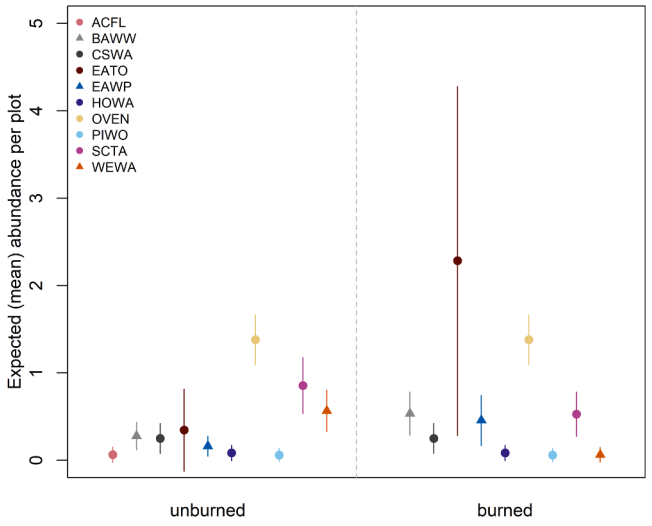

Fig. 4. Predicted abundance of management indicator species (circles; ACFL: Acadian flycatcher, EATO: eastern towhee, HOWA: hooded warbler, OVEN: ovenbird, PIWO: pileated woodpecker, SCTA: scarlet tanager) and high conservation value species (triangles; BWWA: black-and-white warbler, EAWP: eastern wood pewee, WEWA: worm-eating warbler) by burn status. Expected abundance is estimated based on point count data collect on unburned plots and plots 1-year post-fire in the Warm Springs Mountain Restoration Project study area in Bath County, Virginia, USA.

Chestnut-sided warbler abundance was estimated to be low and constant across plots (0.25 individuals, 95% CI = 0.08–0.42), but detection probability (p) was affected by burn status with lower detection probability at unburned plots (p = 0.01, 95% CI = 0–0.03) compared to burned plots (p = 0.46, 95% CI = 0.33–0.59). There was not competing support for the top-ranked model that included a burn status effect on abundance (ΔAIC = 3.43) compared to the intercept-only abundance model indicating it was likely a detection probability effect, and not an abundance effect.

Hooded warblers were detected at 22% of plots (1–2 individuals) and detection probability was most influenced by temperature at the time of the survey (β = 0.80, SE = 0.24). Mean abundance was 0.08 individuals at a plot (95% CI = 0–0.17) and was higher on plots with greater understory live stem density (β = 0.39, SE = 0.21), while lower on plots with greater forest floor nonwoody vegetation (β = −1.53, SE = 0.67) and understory dead stem density (β = −1.75, SE = 0.63). Predicted abundances ranged from 0 to 10.52 (95% CI = 0–36.22) across the range of supported fine-scale covariates.

Pileated woodpeckers were detected at 11% of plots (1–2 individuals) and were only detected at plots with 100% canopy closure at 100 m, causing models with that variable included to fail to converge. We acknowledged the positive effect of coarse-scale canopy closure on pileated woodpeckers and removed models with that variable from the candidate set. When coarse-scale canopy closure was removed mean abundance was 0.06 individuals at a plot (95% CI = 0–0.13) and was generally low (predicted abundances ranged from 0 to 0.27, 95% CI = 0–0.56) but higher on plots with greater with greater midstory shrub density (β = 0.58, SE = 0.21), fewer forest floor seedlings < 1 m (β = −1.23, SE = 0.84) and less nonwoody vegetation (β = −0.97, SE = 0.77). However, multimodel inference and statistical interpretation for this species with limited data (low abundances on a small number of plots) and likely dependent on 100% closed canopy should be interpreted with caution.

3.2. High conservation value species

Only three of six HCV species had enough detections to fit abundance models describing responses to coarse-and fine-scale variables (black and white warbler, eastern wood pewee, and worm-eating warbler). Cerulean warblers were only detected at one plot during the time frame used for this comparison (one individual at one plot with 89% canopy closure and a fire the previous year), while three wood thrush were detected at three plots (two unburned with 100% canopy closure and one with a fire the previous year and 85% canopy closure). Canada warblers (four individuals) were detected at four plots with canopy closure ranging from 15% to 100% and all having experienced a fire the previous year.

Black-and-white warblers were detected at 35% of plots (1–2 individuals) and detection probability was higher on plots that had burned (0.61, 95% CI = 0.54–0.69) compared to plots that had not (0.32, 95% CI = 0.22–0.42). Black-and-white warbler abundance was also higher at plots that had burned the year before (0.53 individuals, 95% CI = 0.29–0.78) compared to plots that did not (0.28 individuals, 95% CI = 0.12–0.44).

Eastern wood pewees were detected at 31% of plots (1–2 individuals) and detection probability varied by observer ranging from 0.38 (95% CI = 0.19–0.57) to 0.79 (95% CI = 0.60–0.98). Mean abundance was higher at plots that had burned the year prior (0.46 individuals, 95% CI = 0.17–0.74) compared to plots that had not burned (0.16 individuals, 95% CI = 0.05–0.28), and lower on plots with greater understory live stem density > 1 m in height (β = -0.80, SE = 0.41). Predicted abundances ranged from 0 (95% CI = 0–0.02) to 0.86 (95% CI = 0.39–1.33) across observed values of understory live stem density.

Worm-eating warblers were detected at 24% of plots (1–3 individuals). Mean detection probability was 0.72 (95% CI = 0.59–0.85), higher with wind (β = 2.42, SE = 0.60), and lower with start time (β = −0.23, SE = 0.16) and temperature (β = −0.82, SE = 0.33). Abundance was lower on plots that burned the previous year (0.06 individuals, 95% CI = 0–0.15) compared to plots that did not burn (0.56 individuals, 95% CI = 0.33–0.80).

3.3. Nesting guilds

Cavity nester abundance was most influenced by both coarse- (burn status and FAI) and fine-scale (understory) variables, but effect sizes were small (Fig. 3). Mean cavity nester abundance was higher at unburned plots (1.76 individuals, 95% CI = 1.25–2.27) compared to burned plots (0.96 individuals, 95% CI = 0.50–1.43; Fig. 5) and higher

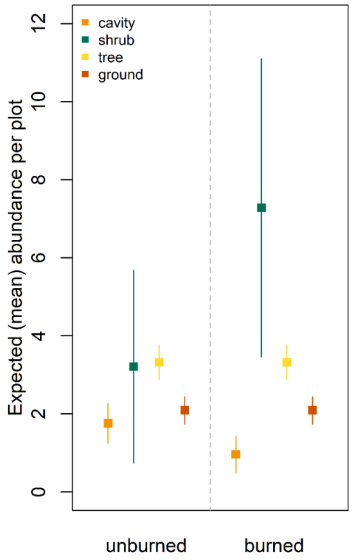

Fig. 5. Predicted abundance of birds grouped by nesting guilds by burn status. Expected abundance is estimated based on point count data collect on unburned plots and plots 1-year post-fire in the Warm Springs Mountain Restoration Project study area in Bath County, Virginia, USA.

with greater forest floor seedling density (β = 0.20, SE = 0.10) and FAI values (β = 0.18, SE = 0.10), while lower with greater live understory stem density (β = −0.23, SE = 0.15). Predicted abundances ranged from 0.34 (95% CI = 0–10.80) to 5.37 (95% CI = 0–0.91). Mean detection probability was 0.26 (95% CI = 0.18–0.33) and conditions during the counts most affected detection probability including start time (β = 0.09, SE = 0.11), wind (β = −0.38, SE = 0.24), and temperature (β = 0.34, SE = 0.15).

Shrub nester abundance was only affected by coarse variables (FAI, burn status, and % closed canopy). Mean shrub nester abundance was higher at plots that had burned the previous year (7.28 individuals, 95% CI = 3.46–11.10) compared to those that had not burned (3.21 individuals, 95% CI = 0.74–5.68), was higher with higher FAI values (β = 0.19, SE = 0.11) and lower on plots with greater % canopy closure at 100 m (β = −1.39, SE = 0.35). Predicted abundances ranged from 0.56 (95% CI = 0.25–0.87) to 11.94 (95% CI = 2.83–21.05) across observed values for supported covariates. Mean detection probability was 0.43 (95% CI = 0.38–0.48) and was affected by conditions during the point counts including wind (β = 0.24, SE = 0.07) and temperature (β = −0.46, SE = 0.10), but not start time (β < 0.001, SE = 0.09).

Mean tree nester abundance was 3.32 individuals (95% CI = 2.87–3.77) and only differed by a small negative effect of midstory shrub density (β = −0.20, SE = 0.11). Detection probability varied by observer and ranged from 0.51 (95% CI = 0.45–0.57) to 0.63 (95% CI = 0.56–0.70). Mean ground nester abundance (2.09, 95% CI = 1.74–2.44) was higher on plots with higher FAI values (β = 0.14, SE = 0.07) and lower on plots with greater forest floor nonwoody vegetation (β = −0.20, SE = 0.1076), although effect sizes were small. Detection probability of ground nesters was higher at plots that had burned the year prior (0.62, 95% CI = 0.57–0.67) compared to unburned plots (0.52, 95% CI = 0.47–0.57).

4. Discussion

Our results demonstrate prescribed fire can be an effective tool to manage habitat conditions for bird communities in eastern hardwood forests of the central Appalachian Mountains. Six of the 10 species in our study showed a difference in abundance on burned plots compared to unburned plots including three high conservation value (HCV) species. Holding time since fire constant by only assessing population differences on unburned plots compared to plots one-year post-burn allowed us to assess direct impacts of vegetation differences in the absence of temporal effects. Multiple species were influenced by combinations of coarse-scale variables (primarily burn status) and fine-scale vegetation differences. However, while we documented greater abundance in shrub nesters on burned plots, many fine- and coarse-scale variable differences were muted in the nesting guild results, even when there was a difference detected for individual species within the guild (e.g., tree-nesting Acadian flycatcher and eastern wood pewee, or ground-nesting black and white warbler; Fig. 4). Finally, % closed canopy cover (expected to be inversely related to burn severity) was not a strong predictor for most species at the 1-year time scale and several species did not show differences based on variables as expected based on assumed habitat preferences (e.g., ovenbird abundance did not vary with burn status). While some of these expected differences may develop with increased time since fire and additional fires, it is also likely factors such as predation, competition, and other compensatory community changes may influence or even counteract direct changes due to vegetation and fine-scale habitat.

In contrast to recent studies in eastern forests suggesting little overall avian community response to prescribed fire (Pitt et al., 2014, Greenberg et al., 2019), we found differences in abundances among species corresponding to burn status vegetation characteristics that could translate to broadscale community changes (Fig. 3). More species showed positive response to burn status than any other variable and effect sizes were generally larger for coarse-scale variables compared to fine-scale variables. One possible explanation for the dominant effect of coarse variables could be the scale of sampling: coarse variables were measured within 100 m of the plot center while fine-scale vegetation sampling occurred at the plot center within < 8 m. It is possible that more extensive vegetation sampling throughout the plot would have captured more heterogeneity in the variables and resulted in greater detection of effects and size of differences.

Regardless, the strong effect of burn status and lower canopy closure on abundance of several species support hypothesized benefits of prescribed fire in the region. The findings are likely due to localized variability in burn severity within management units, and even over 3.14 ha plots (Figs. 1 and 2, Appendix A). Single prescribed fires in previous studies often resulted in only small changes to forest structure (Greenberg et al., 2019, Rush et al., 2012), especially at low and moderate fire intensities. Nevertheless, we only evaluated bird abundances the year following the first fire in a burn unit but still demonstrated differences based on coarse- and fine-scale variables related to the fires. Burning in large blocks (60–2,023 ha) in the study area over elevational and xeric-mesic gradients produced heterogeneity in fire severity (Fig. 2, Appendix A), which can open the mature deciduous canopy that dominates the region (Lorber et al., 2018) allowing sunlight to reach the forest floor and stimulate growth of understory vegetation while reducing accumulating leaf litter and dead shrubs and trees (Harper et al., 2016). Shrub-nesting species abundances such as eastern towhee were higher on burned plots and with greater canopy openings. But other shrub-nesting species such as hooded warbler responded to vegetation variables related to increased nesting habitat structure (Fig. 3). These results along with a landscape analysis of the study area (Lorber et al., 2018) suggest the fires implemented during the project area produced more profound changes to mature forest canopy which should extend the duration of vegetation effects, and hopefully will produce longer-term benefits to many avian populations.

Management objectives for prescribed fire in eastern forests commonly focus on increasing open canopy. In our evaluation only one species (eastern towhee) exhibited greater densities with increased canopy openness relative to other variables, but this is not surprising as open canopy is not expected to dramatically change following single prescribed fires (Greenberg et al., 2019, Rush et al., 2012). Alternatively, five out of 10 species showed responses to coarse- and fine-scale variables demonstrating the importance of differences forest structure. Thus, our findings support previous studies suggesting substantial changes to the overstory and midstory resulting from high intensity and repeated fires are required to functionally change habitat for birds (Comer et al., 2011).

Even fine-scale vegetation characteristics may not fully capture the ecological processes stimulated by fire and compensatory community changes (interactions among species) should be considered (Bowman et al., 2016, Harper et al., 2016). For example, previous studies found ground-nesting ovenbird densities were lower on sites recently treated with prescribed fire (Rush et al., 2012), but we found no differences on burned plots compared to unburned plots (we also did not find a difference for ground nesters as a guild). Ovenbirds were common on plots (77% of plots had detections) despite large-scale burns across the project area and abundance was instead most influenced by nonwoody vegetation (lower abundances on plots with higher amounts of grasses and forbs) and FAI (abundance was higher on plots that were more xeric and historically adapted to fires). Greenberg et al. (2019) found reduction of leaf litter following both growing season and dormant season fires was fleeting and fine-scale overstory canopy cover in our study was not substantially correlated with nonwoody vegetation (Pearson's r = −0.27, unburned and burned plots combined). It is possible live grasses and forbs inhibit accumulation of leaf litter, even when there is some deciduous canopy remaining. However, individual adaptation among ovenbirds to other wildlife populations is a more likely explanation.

While ovenbirds are considered a forest interior species, a study in northwestern Pennsylvania (Morton 2005) found they nested in early

successional forest edge more and suggested habitat selection resulted from avoidance of predation on eggs, nestlings, and fledglings by chipmunks (*Tamias striatus*) as opposed to direct vegetation characteristics such as amount of leaf litter (correlated with invertebrate prey availability). Furthermore, stomach content and stable isotope analyses revealed ovenbird diet could change with availability including invertebrates such as caterpillars and snails (Streby et al., 2013) that may be more available with increased understory shrub and tree regeneration. Thus, if threat of predation by chipmunks is the primary consideration in ovenbird selection of nesting territories in the region and alternative diet items increase in availability, species including ovenbirds could indeed benefit from early successional habitat along edges and resulting from fires, even when traditional prey availability declines with reduced leaf litter (assuming reproduction is positively correlated with density, as found by Perot and Vallard, 2009).

Our results also provide insight to best practices in monitoring and assessing impacts of prescribed fire in eastern forests. Guilds are commonly used as a grouping mechanism to describe general responses of many species with different amounts of data within a single analysis (Blake, 2005, Greenberg et al., 2019), but in our study grouping by guilds obscured both coarse-scale and fine-scale responses (Fig. 3). Multiple single species models indicated understory vegetation influenced abundance on a plot. But few fine-scale variables received support in the guild abundance models and for those that did, effect sizes were nearly negligible (Fig. 3). For example, tree-nesting species diverged in response to burn status with eastern wood pewee abundance higher on burned plots, scarlet tanager abundance lower, and Acadian flycatcher only detected on unburned plots (Fig. 4). Yet the tree-nesting guild showed no differences based on burn status (Fig. 5). Similarly, cavity-nesting pileated woodpeckers were not even detected on plots with < 100% canopy closure but there was no model support for a canopy closure effect on cavity nesters. These results call into question the practice of grouping by guilds for monitoring purposes. Species-specific responses are complex and inherently dependent on interactions with not just the vegetation structure, but other species' responses including intraguild competition. Furthermore, the increased variance associated with grouping potentially disparate responses reduces the usefulness of guilds as a monitoring tool as precision is reduced and there is little statistical power to detect differences among sites or over time (Gitzen et al., 2012).

Our results also highlight the importance of indicator species selection within the context of specific objectives. Only four of nine selected species demonstrated the expected differences in abundance based on burn status (two MIS and two HCV; Table 3) and only three HCV species had sufficient data to fit abundance models to allow for monitoring of responses or trends over time. However, the reason for inclusion of most species in the MIS set was to indicate if key successional stages are present within the forest. While early successional species may be expected to benefit from creation of this habitat within the forest, the selection of indicator species overall was not necessarily made with the objective of monitoring changes resulting from prescribed fires.

Monitoring programs frequently favor efficiency over effectiveness in the selection of indicator species (Bal et al., 2018). But the discrepancy of or lack of expected differences demonstrated in our analysis suggests empirical validation is required for indicator species to be useful as the basis of management decisions. We recommend indicator species should be selected considering quantifiable expected trends based on data from the region (Carignan and Villard, 2002) and revaluated frequently to be sure information obtained can be used to guide management. It is also possible to use beta coefficient estimates from existing or pilot data to conduct power analyses and assess the ability of each species to indicate meaningful changes (Green, 1989, Guillera-Arroita and Lahz-Monfort, 2012). Formalizing selection of indicator species within a structured decision-making framework (Lyons et al., 2008) can maximize effectiveness to meet objectives and achieve desired outcomes within the constraints of effort and budgets (Bal et al., 2018). Alternatively, shifting monitoring focus from individual or a set of species to community metrics including richness and diversity would more broadly represent the full community response. New developments in hierarchical community models including multispecies abundance models will improve our ability to fully assess community responses over time if appropriate sampling protocols are implemented (Royle and Dorazio, 2008, Yamaura et al., 2012, Iknayan et al., 2014). An additional advantage to these approaches is the ability to incorporate imperfect detection which we found to vary by observer, sampling conditions, and burn status, potentially confounding uncorrected counts.

Table 3
Predicted and observed differences in abundance of indicators on unburned plots compared to plots that experienced a prescribed fire the year prior. Bolded rows indicate species with concurring predicted and observed differences. Species with no observed difference reported did not have sufficient data for comparisons.

Species (classification)	Predicted difference in abundance	Observed differences in abundance
Eastern towhee (MIS)	**higher on burned plots**	**higher on burned plots**
Chestnut-sided warbler (MIS)	higher on burned plots	
Ovenbird (MIS)	lower on burned plots	no difference
Acadian flycatcher (MIS)	**lower on burned plots**	**lower on burned plots**
Hooded warbler (MIS)	lower on burned plots	no difference
Scarlet tanager (MIS)	higher on burned plots	lower on burned plots
Pileated woodpecker (MIS)	higher on burned plots	no difference
Cerulean warbler (HCV)	higher on burned plots	
Wood thrush (HCV)	no difference or slightly lower on burned plots	
Canada warbler (HCV)	higher on burned plots	
Black-and-white warbler (HCV)	lower on burned plots	higher on burned plots
Worm-eating warbler (HCV)	**lower on burned plots**	**lower on burned plots**
Eastern wood pewee (HCV)	**higher on burned plots**	**higher on burned plots**

5. Conclusions

This study used avian and vegetation monitoring data collected at the plot level as part of an operational landscape-scale restoration project. Avian populations responded to both coarse- and fine-scale habitat variables in the year following prescribed fire demonstrating the potential of large-scale fire as a management tool in the eastern hardwood forests of North America. In short-term studies in the years shortly following a fire treatment, the ability to link avian abundances with specific coarse- and fine- habitat variables at the plot level is critical to understand observed differences and evaluate future management actions on the site. Advancements in methods to analyze point count data, estimating abundance at each plot while accounting for biased detection probability, aided in identifying nuanced differences for individual species on plots treated with prescribed fire by relating differences directly to the conditions on the plot and increasing sample size. While manipulated experiments may be more appropriate for determining causal effects, they are difficult to implement at spatial scales and samples sizes necessary to achieve statistical power to detect differences in treatments and describe responses. Finally, we suggest managers re-examine and validate species classified as MIS to directly inform management decisions, and we discourage the use of broad categorization in guilds based on single habitat requirements.

CRediT authorship contribution statement

Dana J. Morin: Conceptualization, Methodology, Formal analysis, Data curation, Writing - original draft, Visualization. **Laurel Schablein:** Conceptualization, Methodology, Writing - review & editing. **L. Nikole Simmons:** Conceptualization, Methodology, Data curation, Writing - review & editing, Visualization. **Jean H. Lorber:** Conceptualization, Methodology, Data curation, Writing - review & editing. **Marek K. Smith:** Supervision, Writing - review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2021.118940.

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