Research Article

Avian response to fire in pine–oak forests of Great Smoky Mountains National Park following decades of fire suppression

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ABSTRACT

Fire suppression in southern Appalachian pine–oak forests during the past century dramatically altered the bird community. Fire return intervals decreased, resulting in local extirpation or population declines of many bird species adapted to post-fire plant communities. Within Great Smoky Mountains National Park, declines have been strongest for birds inhabiting xeric pine–oak forests that depend on frequent fire. The buildup of fuels after decades of fire suppression led to changes in the 1996 Great Smoky Mountains Fire Management Plan. Although fire return intervals remain well below historic levels, management changes have helped increase the amount of fire within the park over the past 20 years, providing an opportunity to study patterns of fire severity, time since burn, and bird occurrence. We combined avian point counts in burned and unburned areas with remote sensing indices of fire severity to infer temporal changes in bird occurrence for up to 28 years following fire. Using hierarchical linear models that account for the possibility of a species presence at a site when no individuals are detected, we developed occurrence models for 24 species: 13 occurred more frequently in burned areas, 2 occurred less frequently, and 9 showed no significant difference between burned and unburned areas. Within burned areas, the top models for each species included fire severity, time since burn, or both, suggesting that fire influenced patterns of species occurrence for all 24 species. Our findings suggest that no single fire management strategy will suit all species. To capture peak occupancy for the entire bird community within xeric pine–oak forests, at least 3 fire regimes may be necessary; one applying frequent low severity fire, another using infrequent low severity fire, and a third using infrequently applied high severity fire.

Keywords: fire suppression, differenced normalized burn ratio, fire severity, pine–oak forest, time since fire

Respuesta de las aves a incendios en los bosques de pinos y robles del Parque Nacional Great Smoky Mountains tras décadas de supresión de incendios

RESUMEN

La supresión de incendios en los bosques de pino y roble del sur de los montes Apalaches durante el siglo pasado alteró dramáticamente la comunidad de aves. Los intervalos entre incendios disminuyeron, causando la extirpación local o el declive poblacional de muchas especies de aves adaptadas a las comunidades de plantas formadas después de los incendios. Los declives poblacionales más fuertes dentro del Parque Nacional Great Smoky Mountains se dieron en aves que habitan los bosques secos de pino y roble, que dependen de incendios frecuentes. La acumulación de combustible luego de décadas de supresión de incendios llevó a cambios en el plan de manejo de incendios de Great Smoky Mountains en 1996. Aunque los intervalos entre incendios aún están muy por debajo de los niveles históricos, los cambios en el manejo han ayudado al incremento de la cantidad de incendios dentro del parque en los últimos 20 años, lo que provee una oportunidad para estudiar los patrones de severidad de los incendios, el tiempo desde la quema y la presencia de aves. Combinamos datos de puntos de conteo de aves en áreas quemadas e intactas con indicios de la severidad de los incendios obtenidos de sensores remotos para inferir los cambios temporales en la presencia de aves por hasta 28 años posteriores a incendios. Desarrollamos modelos de presencia para 24 especies usando modelos lineales jerárquicos, que consideran la posibilidad de presencia de una especie en un sitio aunque allí no se hayan detectado individuos. Trece especies fueron más frecuentes en las áreas quemadas, dos especies fueron menos frecuentes y nueve especies no mostraron diferencias significativas entre áreas quemadas e intactas. Dentro de las áreas quemadas los mejores modelos para cada especie incluyeron la severidad del incendio, el tiempo desde la quema o ambas variables, lo que sugiere que los incendios afectaron los patrones de presencia de las 24 especies. Nuestros resultados sugieren que una sola estrategia de manejo de incendios no será apropiada para todas las especies. Para alcanzar la ocupación máxima de la totalidad de la comunidad de aves en los bosques secos de pinos y robles son necesarios al menos tres regímenes de incendios uno de incendios leves pero frecuentes, otro con incendios leves poco frecuentes y un tercero con incendios poco frecuentes de alta severidad.

INTRODUCTION

Many of North America's temperate forests evolved with regular or periodic fire (Oliver 1980). Following a series of particularly catastrophic fires in the early 1900s, the Weeks Act of 1911 and the Clarke-McNary Act of 1924 made federal funds available for fire management, resulting in a national strategy of active suppression. This strategy altered fire regimes and has been implicated in forest bird declines across the continent (Brawn et al. 2001). During this period of active suppression, fire-dependent bird species declined within the longleaf pine (*Pinus palustris*) savannas of the southeast United States (Hunter et al. 2001), Rocky Mountain conifer forests (Hutto 1995), and Appalachian forests (Hunter et al. 2001). Although national fire management paradigms have shifted away from fire suppression over the past 30 years, we are only beginning to understand how changes in the fire management paradigm have influenced bird populations. Within North America's temperate forests, fire severity and time between fires are consistently among the most important predictors of how fire influences forest bird populations (Smucker et al. 2005, Greenberg et al. 2013, Stephens et al. 2015).

Fire was a regular part of the southern Appalachian landscape during the 18th and 19th centuries and played an important role in removing understory vegetation, creating forest openings, and maintaining rare habitats such as bogs and balds. Within Great Smoky Mountains National Park (GSMNP), fire return intervals of 2–3 years were typical in habitats dominated by table mountain pine (*Pinus pungens*; DeWeese 2007) and similar to those in longleaf pine systems (Stambaugh et al. 2011). In mixed pine–oak forests, fire return intervals are estimated at 9–13 years (Harmon 1982, Flatley et al. 2013). In these mixed forests, regular low severity fire maintained a dominant overstory of fire-tolerant shortleaf (*Pinus echinata*), table mountain, pitch (*Pinus rigida*), or Virginia (*Pinus virginiana*) pine, along with their associated avian community. Active fire suppression within GSMNP began around 1940 and resulted in a reduction in fire frequency (LaForest 2012, Flatley et al. 2013). The subsequent era of fire suppression (~1940–1996) encouraged the establishment of shade tolerant red maple (*Acer rubrum*), black gum (*Nyssa sylvatica*), and white pine (*Pinus strobus*), altering both the plant and animal communities within these forests (Harrod et al. 2000). Prompt suppression remained the dominant fire management strategy until the late 1990s when the ecological ramifications of this practice became more broadly understood. In 1996, changes in fire management policy began to give managers greater flexibility to allow wildfires to burn, to use prescribed fire, and to incorporate fuel reduction techniques for achieving management objectives (NPS Fire Management Plan 1996). Since then, these tools have helped managers increase the use of fire within GSMNP. While implementation of the current fire policy has increased the amount of land area subject to both prescribed burns (NPS Fire Effects Data 1920-2010) and wildfires (Cohen et al. 2007), the amount of fire on the landscape is still well below historic levels. Although >25% of the park is xeric pine–oak forest, on average <1% of the park has burned each year since 1996.

Historic accounts suggest that some bird species associated with xeric pine–oak forests (e.g., Red-headed Woodpecker [*Melanerpes erythrocephalus*]: Stupka 1963; Red-cockaded Woodpecker [*Picoides borealis*]: Nicholson 1997) declined during the 20th century, a period of active fire suppression. Notably, the federally endangered Red-cockaded Woodpecker was reported in GSMNP's xeric pine–oak forests between 1935 and 1985 (Fleetwood 1936, Stupka 1963, Tanner 1965, Dimmick et al. 1980) but not after that time. Red-cockaded Woodpeckers depend on mature yellow pine (*Pinus echinata* or *Pinus palustris*) stands with open understory and mid-canopy, resulting from frequent low severity fire (Ligon et al. 1986). These habitats declined within GSMNP during the era of fire suppression.

Reduced fire frequency during this period also likely limited the number of forest openings available for bird species associated with early successional habitats. Historic accounts suggest that the Northern Bobwhite (*Colinus virginianus*) declined within GSMNP during this time period (Stupka 1963), while populations of species associated with early successional habitats, including Golden-winged Warbler (*Vermivora chrysoptera*), Yellow-breasted Chat (*Icteria virens*), and Prairie Warbler (*Setophaga discolor*), showed dramatic declines in the southern Appalachian region (Sauer et al. 2014; Blue Ridge Mountains 1966–2007 BBS data) and likely within GSMNP. Research on how fire management is affecting birds in these forests is beginning to inform management decisions (Greenberg et al. 2007, Klaus et al. 2010, Greenberg et al. 2013). The detailed fire history and active fire management program in GSMNP provide a unique opportunity to understand the relationship between fire and bird communities of the xeric pine–oak forests of the southern Appalachian Mountains. We combined remotely sensed measures of fire severity and repeated avian point counts to develop occurrence models to help managers understand long-term changes in bird communi-
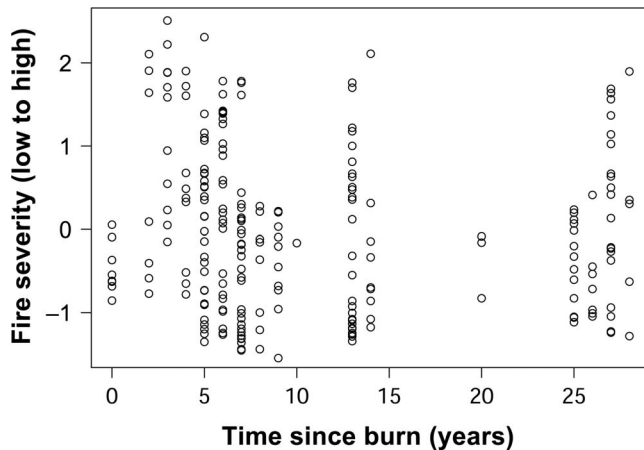
FIGURE 1. Stratification of burned sampling points across fires of different severity (standardized DNBR values) and time since burn. Each circle represents one of the 228 bird sampling points in burned areas within Great Smoky Mountains National Park.

ties in GSMNP. Specifically, we (1) contrasted species occurrence in areas that have burned within the past 28 years with species occurrence in areas that have not burned

since the establishment of GSMNP in 1934; and (2) identified patterns of species occurrence that incorporate both the amount of time since the last fire and fire severity summarized at spatial scales relevant to 24 breeding bird species.

METHODS

During the 2012, 2013, and 2014 bird breeding seasons, we surveyed 336 points within xeric pine–oak habitats of the western portion of GSMNP, including 90, 120, and 126 points in each year, respectively. We placed 108 points in locations with no record of fire since GSMNP's establishment in 1934 and 228 sampling points within the footprints of 28 fires that burned from 1986 to 2014. Prior to each season, we used ArcGIS to place sampling points. We stratified points by fire severity and time since burn (Figure 1) using Landsat-derived Differenced Normalized Burn Ratios (DNBR) as an index of fire severity and GSMNP fire history records to determine time since burn. Sampling points in burned areas were located at least 100 m from the fire perimeter, and each fire contained
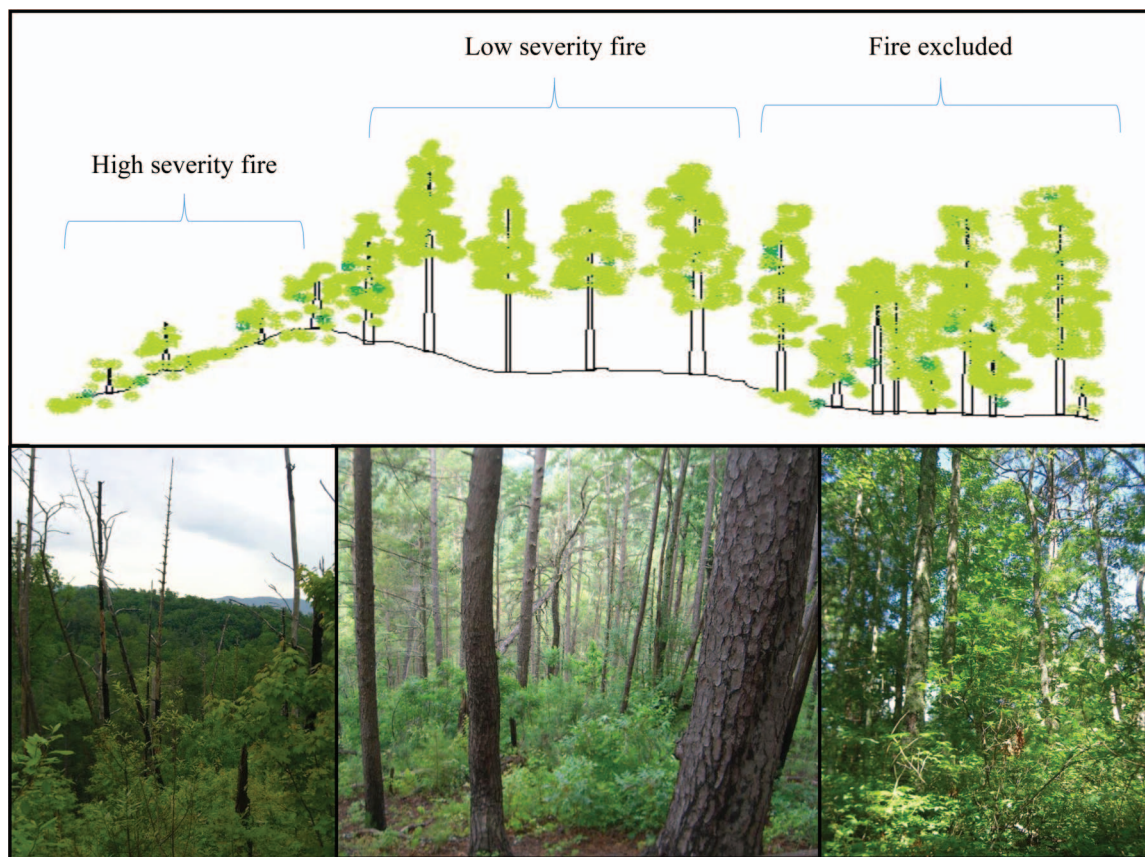

FIGURE 2. Examples of the effects of fire severity within Great Smoky Mountains National Park. High severity fires result in forest openings due to extensive overstory mortality; low severity fires remove the leaf litter and some of the understory vegetation. Red maple and black gum encroach the understory in areas where fire has been excluded.

TABLE 1. Birds detected within Great Smoky Mountains National Park during point count surveys. We used the nomenclature and species codes presented in the American Ornithologists' Union Checklist of North and Middle American Birds (56th supplement).

Common Name	Species	Species Code
Canada Goose [LD]	*Branta canadensis*	CANG
Northern Bobwhite [LD]	*Colinus virginianus*	NOBO
Ruffed Grouse [RA]	*Bonasa umbellus*	RUGR
Wild Turkey [LD]	*Meleagris gallopavo*	WITU
Great Blue Heron [LD]	*Ardea herodias*	GBHE
Turkey Vulture [LD]	*Cathartes aura*	TUVU
Osprey [RA]	*Pandion haliaetus*	OSPR
Cooper's Hawk [LD]	*Accipiter cooperii*	COHA
Red-shouldered Hawk [LD]	*Buteo lineatus*	RSHA
Broad-winged Hawk [LD]	*Buteo platypterus*	BWHA
Red-tailed Hawk [LD]	*Buteo jamaicensis*	RTHA
Mourning Dove	*Zenaida macroura*	MODO
Yellow-billed Cuckoo [LD]	*Coccyzus americanus*	YBCU
Black-billed Cuckoo [LD]	*Coccyzus erythropthalmus*	BBCU
Barred Owl [LD]	*Strix varia*	BADO
Chimney Swift [LD]	*Chaetura pelagica*	CHSW
Ruby-throated Hummingbird [LD]	*Archilochus colubris*	RTHU
Belted Kingfisher [LD]	*Megaceryle alcyon*	BEKI
Red-headed Woodpecker	*Melanerpes erythrocephalus*	RHWO
Red-bellied Woodpecker [LD]	*Melanerpes carolinus*	RBWO
Downy Woodpecker [LD]	*Picoides pubescens*	DOWO
Hairy Woodpecker [AB]	*Picoides villosus*	HAWO
Northern Flicker	*Colaptes auratus*	NOFL
Pileated Woodpecker [AB]	*Dryocopus pileatus*	PIWO
Eastern Wood-Pewee	*Contopus virens*	EAWP
Acadian Flycatcher	*Empidonax virescens*	ACFL
Eastern Phoebe [LD]	*Sayornis phoebe*	EAPH
Great Crested Flycatcher	*Myiarchus crinitus*	GCFL
White-eyed Vireo [LD]	*Vireo griseus*	WEVI
Yellow-throated Vireo [LD]	*Vireo flavifrons*	YTVI
Blue-headed Vireo	*Vireo solitarius*	BHVI
Red-eyed Vireo [AB]	*Vireo olivaceus*	REVI
Blue Jay	*Cyanocitta cristata*	BLJA
American Crow [LD]	*Corvus brachyrhynchos*	AMCR
Common Raven [LD]	*Corvus corax*	CORA
Northern Rough-winged Swallow [RA]	*Stelgidopteryx serripennis*	NRWS
Barn Swallow [LD]	*Hirundo rustica*	BARS
Carolina Chickadee [AB]	*Poecile carolinensis*	CACH
Tufted Titmouse [AB]	*Parus bicolor*	TUTI
Red-breasted Nuthatch [LD]	*Sitta canadensis*	RBNU
White-breasted Nuthatch [LD]	*Sitta carolinensis*	WBNU
Brown Creeper [LD]	*Certhia americana*	BRCR
Carolina Wren	*Thryothorus ludovicianus*	CARW
Blue-gray Gnatcatcher	*Polioptila caerulea*	BGGN
Eastern Bluebird	*Sialia sialis*	EABL
Veery [LD]	*Catharus fuscescens*	VEER
Swainson's Thrush [LD]	*Catharus ustulatus*	SWTH
Hermit Thrush [LD]	*Catharus guttatus*	HETH
Wood Thrush [LD]	*Hylocichla mustelina*	WOTH
Gray Catbird [LD]	*Dumetella carolinensis*	GRCA
Brown Thrasher [LD]	*Toxostoma rufum*	BRTH
Cedar Waxwing [LD]	*Bombycilla cedrorum*	CEDW
Ovenbird	*Seiurus aurocapilla*	OVEN
Worm-eating Warbler	*Helmitheros vermivorum*	WEWA
Louisiana Waterthrush [LD]	*Parkesia motacilla*	LOWA
Black-and-white Warbler [AB]	*Mniotilta varia*	BAWW
Swainson's Warbler [LD]	*Limnothlypis swainsonii*	SWWA
Kentucky Warbler [LD]	*Geothlypis formosa*	KEWA
Hooded Warbler	*Setophaga citrina*	HOWA

TABLE 1. Continued.

Common Name	Species	Species Code
American Redstart [LD]	*Setophaga ruticilla*	AMRE
Northern Parula	*Setophaga americana*	NOPA
Black-throated Blue Warbler [LD]	*Setophaga caerulescens*	BTBW
Pine Warbler	*Setophaga pinus*	PIWA
Yellow-rumped Warbler [LD]	*Setophaga coronata*	YRWA
Yellow-throated Warbler	*Setophaga dominica*	YTWA
Prairie Warbler	*Setophaga discolor*	PRAW
Black-throated Green Warbler [AB]	*Setophaga virens*	BTNW
Yellow-breasted Chat	*Icteria virens*	YBCH
Eastern Towhee	*Pipilo erythrophthalmus*	EATO
Chipping Sparrow [LD]	*Spizella passerina*	CHSP
Field Sparrow [RA]	*Spizella pusilla*	FISP
Scarlet Tanager [AB]	*Piranga olivacea*	SCTA
Northern Cardinal	*Cardinalis cardinalis*	NOCA
Rose-breasted Grosbeak [LD]	*Pheucticus ludovicianus*	RBGR
Indigo Bunting	*Passerina cyanea*	INBU
Eastern Meadowlark [LD]	*Sturnella magna*	EAME
Common Grackle [LD]	*Quiscalus quiscula*	COGR
Brown-headed Cowbird	*Molothrus ater*	BHCO
Red Crossbill [LD]	*Loxia curvirostra*	RECR
Pine Siskin [LD]	*Spinus pinus*	PISI
American Goldfinch	*Spinus tristis*	AMGO

[LD] The detection rate for this species was too low (≤ 0.20) to include in analyses exploring the effects of fire on patterns of bird occurrence.

[AB] This species was encountered too frequently ($\psi \geq 0.90$) to include in analyses exploring the effects of fire on patterns of bird occurrence.

[RA] This species was too rare ($\psi \leq 0.10$) to include in analyses exploring the effects of fire on patterns of bird occurrence.

between 1 and 30 sampling points. We placed unburned points at least 100 m outside a fire's perimeter along the same ridge, or a ridge adjacent to each fire. All points were placed on upper slopes and ridges in an effort to target xeric pine–oak forests of the region, thereby reducing potential variation in the effects of topography and forest type. In addition, sampling points were kept a minimum of 250 m apart to reduce the possibility of detecting individual birds at more than one sampling point. We established each point at the predetermined location prior to its first survey.

Fire Severity

Large variation in fire severity on our sites produces a variety of plant communities and forest structures (Figure 2). Low severity fire removes accumulated leaf litter, some of the duff layer, and much of the understory vegetation. In contrast, high severity fire can result in complete removal of the understory and >60% overstory mortality. To quantify fire severity across the spatial and temporal extent of this study, we used Landsat-derived DNBR. This index is useful for quantifying fire severity across the extent of a fire (Key and Benson 2006), and is available for most fires that have occurred in GSMNP since Landsat products became available in 1984.

DNBR uses the difference between the pre-fire and the post-fire Normalized Burn Ratios to quantify the change in the amount of vegetation present before and after a fire. The DNBR is calculated using band 4 (0.76–0.90 μm), representing peak vegetation reflectance, and band 7 (2.08–2.35 μm), representing peak reflectance of mineral soil. Although DNBR can provide an index of fire severity for any given location within the footprint of a fire, agreement between the index and field-derived measures of fire severity depends on factors such as atmospheric conditions during image acquisition and the time elapsed between the fire and image acquisition (Key and Benson 2006, Picotte and Robertson 2011). To reduce this variation, we selected the most timely cloud-free scenes acquired during leaf-on conditions.

Bird Sampling

We used unlimited radius point counts modified from Reynolds et al. (1980) to sample the bird community. Sampling points were visited 3 times between May 1 and June 30, in most cases by 3 different observers. During each visit, a single observer performed a 10-minute point count and mapped all birds detected. Observers identified individuals to species and estimated the distance from the sampling point to the bird's location when it was first

TABLE 2. Covariates included in the top detection model and probability (*p*) of occurrence (estimate, 95% CI lower, 95% CI upper) among sampling points for each species. Unburned points had no record of fire since 1940, and burned points had one or more fires since 1986.

Species Code	Top Detection Covariates*	Unburned ψ (95%CI lower, 95% CI upper)	Burned ψ (95%CI lower, 95% CI upper)
MODO[nr]	*p*(Observer+Time+WindSpeed+CloudCover+Temperature)	**0.39** (0.25, 0.56)	**0.71** (0.51, 0.86)
RHWO[nr]	*p*(Temperature)	**0.05** (0.01, 0.18)	**0.52** (0.30, 0.74)
NOFL[nr]	*p*(Observer+WindSpeed)	**0.57** (0.41, 0.71)	**0.78** (0.61, 0.89)
EAWP	*p*(Date)	**0.08** (0.04, 0.17)	**0.45** (0.35, 0.54)
ACFL[nr]	*p*(WindSpeed+Temperature)	**0.14** (0.08, 0.25)	**0.11** (0.06, 0.18)
GCFL[nr]	*p*(Observer+Time+WindSpeed+Temperature)	**0.27** (0.14, 0.45)	**0.27** (0.16, 0.42)
BHVI	*p*(Observer+Date+Time)	**0.74** (0.58, 0.86)	**0.61** (0.50, 0.70)
BLJA[nr]	*p*(Observer+Date+WindSpeed+CloudCover)	**0.71** (0.54, 0.84)	**0.89** (0.71, 0.97)
CARW	*p*(Observer+Date)	**0.58** (0.44, 0.71)	**0.82** (0.68, 0.90)
BGGN	*p*(Observer+Time+WindSpeed+CloudCover+Temperature)	**0.23** (0.11, 0.40)	**0.63** (0.37, 0.83)
EABL	*p*(.)	**0.04** (0.01, 0.12)	**0.24** (0.16, 0.34)
OVEN	*p*(Observer+Date+CloudCover)	**0.37** (0.30, 0.45)	**0.81** (0.67, 0.90)
WEWA	*p*(Observer+WindSpeed)	**0.54** (0.44, 0.63)	**0.78** (0.60, 0.89)
HOWA	*p*(Observer+Date+WindSpeed+Temperature)	**0.74** (0.67, 0.81)	**0.77** (0.65, 0.86)
NOPA	*p*(Date+Temperature)	**0.21** (0.11, 0.36)	**0.30** (0.19, 0.44)
PIWA	*p*(Date)	**0.48** (0.37, 0.60)	**0.59** (0.50, 0.67)
YTWA	*p*(Observer+Date+Time+WindSpeed+CloudCover)	**0.67** (0.48, 0.82)	**0.63** (0.49, 0.74)
PRAW	*p*(Date+CloudCover)	**0.01** (0.00, 0.07)	**0.29** (0.23, 0.35)
YBCH	*p*(WindSpeed)	**0.02** (0.00, 0.08)	**0.26** (0.20, 0.32)
EATO	*p*(WindSpeed+Temperature)	**0.14** (0.09, 0.23)	**0.67** (0.59, 0.74)
NOCA	*p*(WindSpeed+Temperature)	**0.22** (0.11, 0.38)	**0.32** (0.20, 0.49)
INBU	*p*(Observer+CloudCover+Temperature)	**0.61** (0.51, 0.70)	**0.89** (0.83, 0.93)
BHCO[nr]	*p*(Temperature)	**0.05** (0.01, 0.15)	**0.19** (0.11, 0.32)
AMGO[nr]	*p*(Date)	**0.54** (0.35, 0.71)	**0.84** (0.52, 0.96)

* Full models for each species include the influence of a binomial indicator of fire on species occurrence (ψ(FireY/N)).
[nr] To improve model performance and ensure that detection rates (*p*) were ≥0.20, observations for this species were not restricted to observations within 50 m of the observer. Occurrence estimates for these species will inherently be higher than those from observations restricted to 50 m and should not be compared across species.

detected. All point counts were conducted between sunrise and 1000 hr during fair weather with winds <25 km hr^{-1}.

Prior to each breeding season, observers were given 2 weeks of bird identification training, including review of recordings, as well as testing using both Thayer Birding Software simulations and field-based multiple observer point counts. During multiple observer counts, inexperienced observers were paired with experienced observers to assess consistency in species identification as well as distance estimates. Discrepancies between observers were discussed immediately following counts, and efforts were made to track down and identify birds in question. All observers carried a SanDisc MP3 player with multiple recordings of each species for immediate review when performing surveys.

Data Analysis

We used single-season occupancy models (MacKenzie et al. 2002) to account for 3 major components of the detection process: availability, detection given availability, and presence (Nichols et al. 2009). We used the "unmarked" package (Fiske and Chandler 2011) in R 15.1 (R Core Team 2014) for all analyses. We restricted observations to individuals detected within 50 m of the observer to reduce misidentification of aurally detected birds and to improve sensitivity of analyses for frequently encountered species. Wide-ranging and rare species were modeled using unlimited radius plots to ensure sufficient sample sizes for analysis. Preliminary analysis for 3 species with different vocalization and detection characteristics (Prairie Warbler, Indigo Bunting [*Passerina cyanea*], and Brown-headed Cowbird [*Molothrus ater*]) were conducted to test for evidence of "heaping" (rounding to a specified distance; Buckland et al. 1993) in limited radius counts. We developed occurrence models using both restricted and unrestricted datasets for each species following the methods outlined below and found no evidence that heaping influenced occurrence predictions for these species.

To determine which species to include in further analyses, we used observations from all 336 points to calculate detection rates under a null model. If a species'
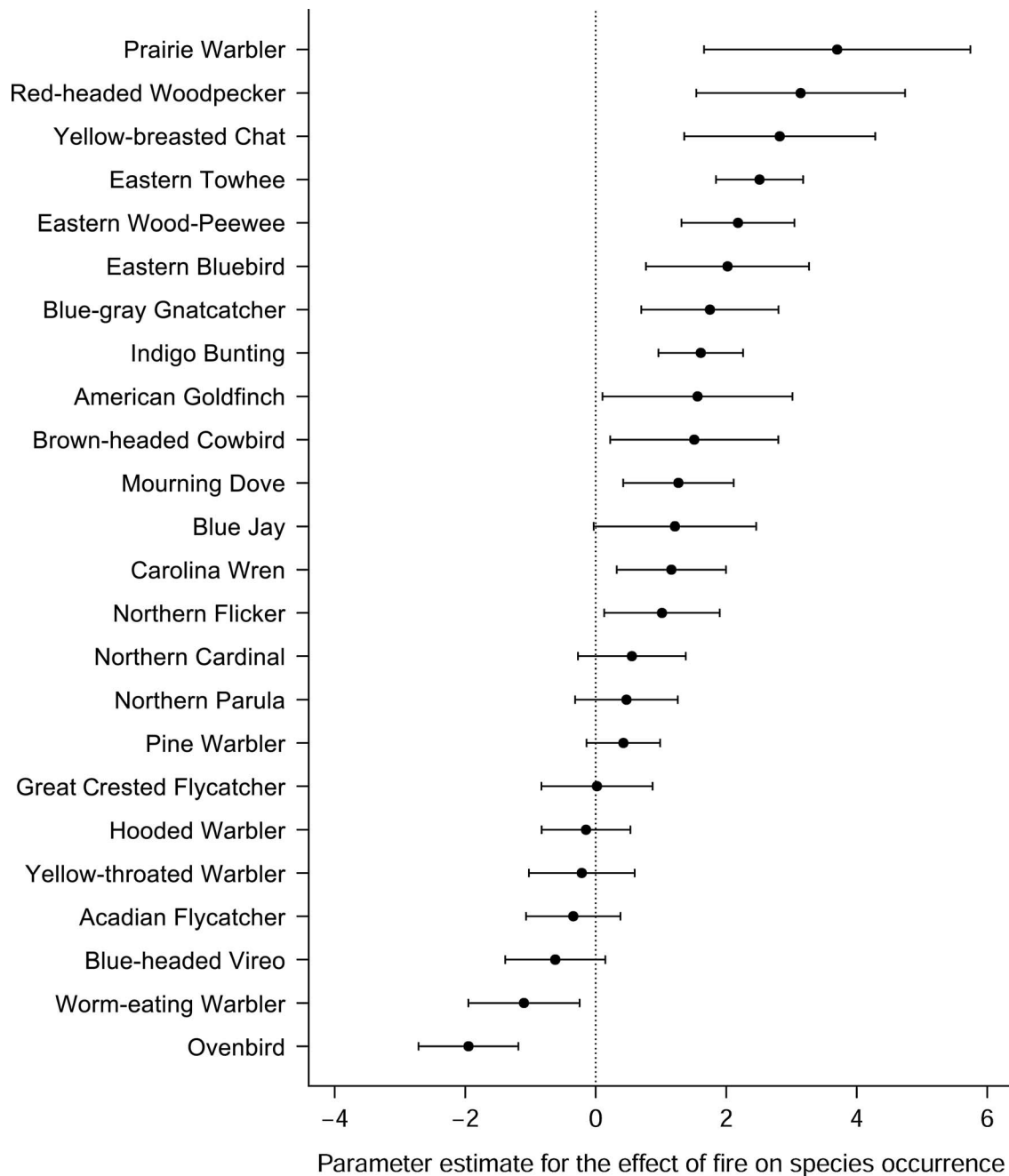
FIGURE 3. Parameter estimates ±2*SE for the effects of fire on species occurrence within Great Smoky Mountains National Park. Species with estimates entirely to the right of the dashed vertical line occurred more frequently in burned areas, and those entirely to the left of the line occurred less frequently.

detection rate (p) was <0.20, we relaxed the 50 m restriction and included all observations for that species. Whether we restricted observations to within 50 m or included them all, we only included species with detection rates >0.20 and occurrence states (ψ) between 0.10 and 0.90 in further analyses (Table 1). For these species, we evaluated models including the additive influence of all possible combinations of observer, date, time since sunrise,

wind speed, percent cloud cover, and temperature to identify detection covariates relevant for each species using an information theoretic approach. The covariates identified in the top detection model were then included in all further analyses for each species. Next, we used the covariates identified in the top detection model for each species and a binary indicator for burned (designated 1) and unburned (designated 0) sites to generate estimates of
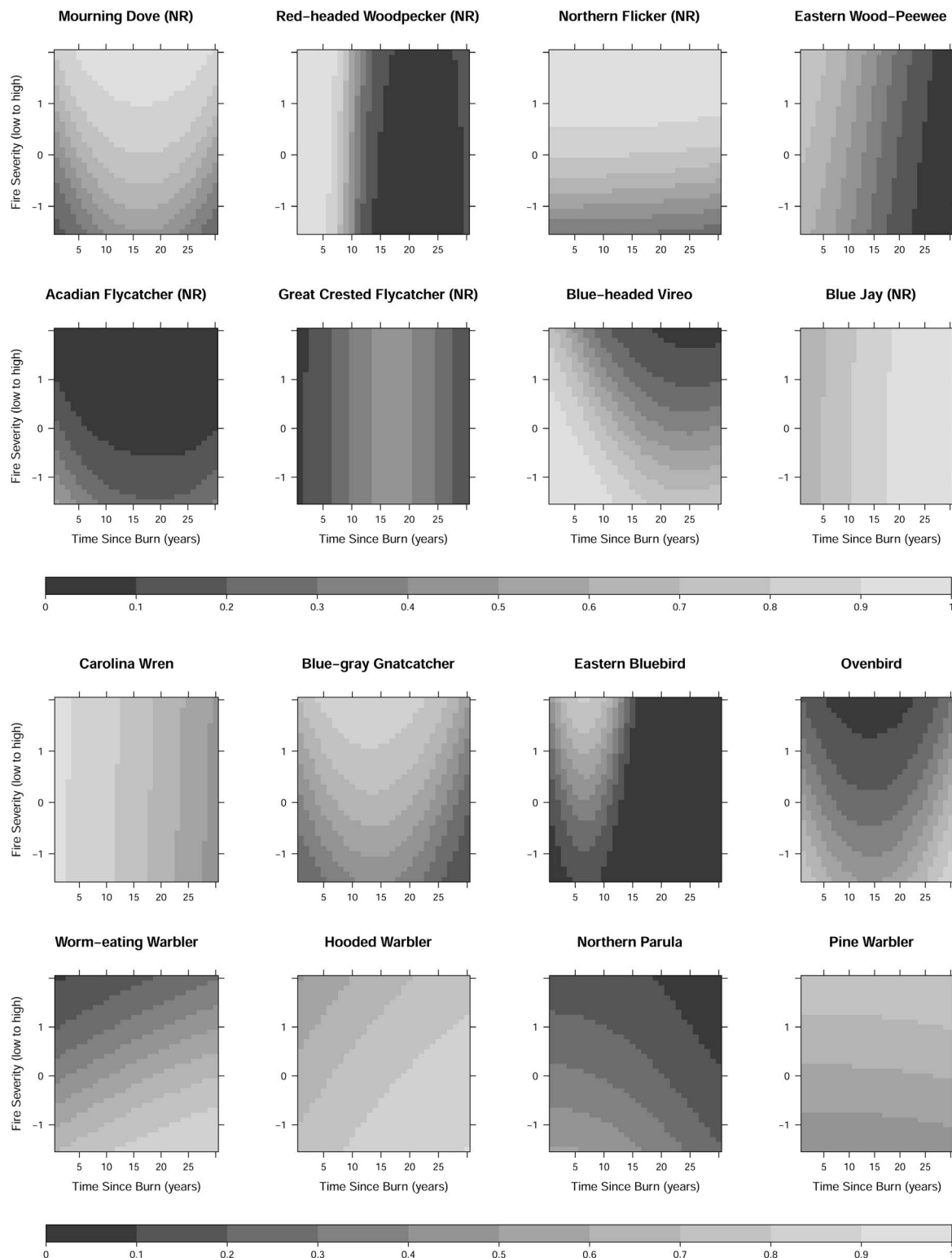
FIGURE 4. Model averaged predictions of species occurrence as influenced by both fire severity and time since burn. The probability of occurrence is greater in lighter areas. Occurrence estimates for species indicated with (NR) were not restricted to observations within 50 m of the observer and include all birds detected. Occurrence estimates for these species will inherently be higher than those using observations restricted to 50 m and should not be compared across species. *Figure 4 is continued on next page.*
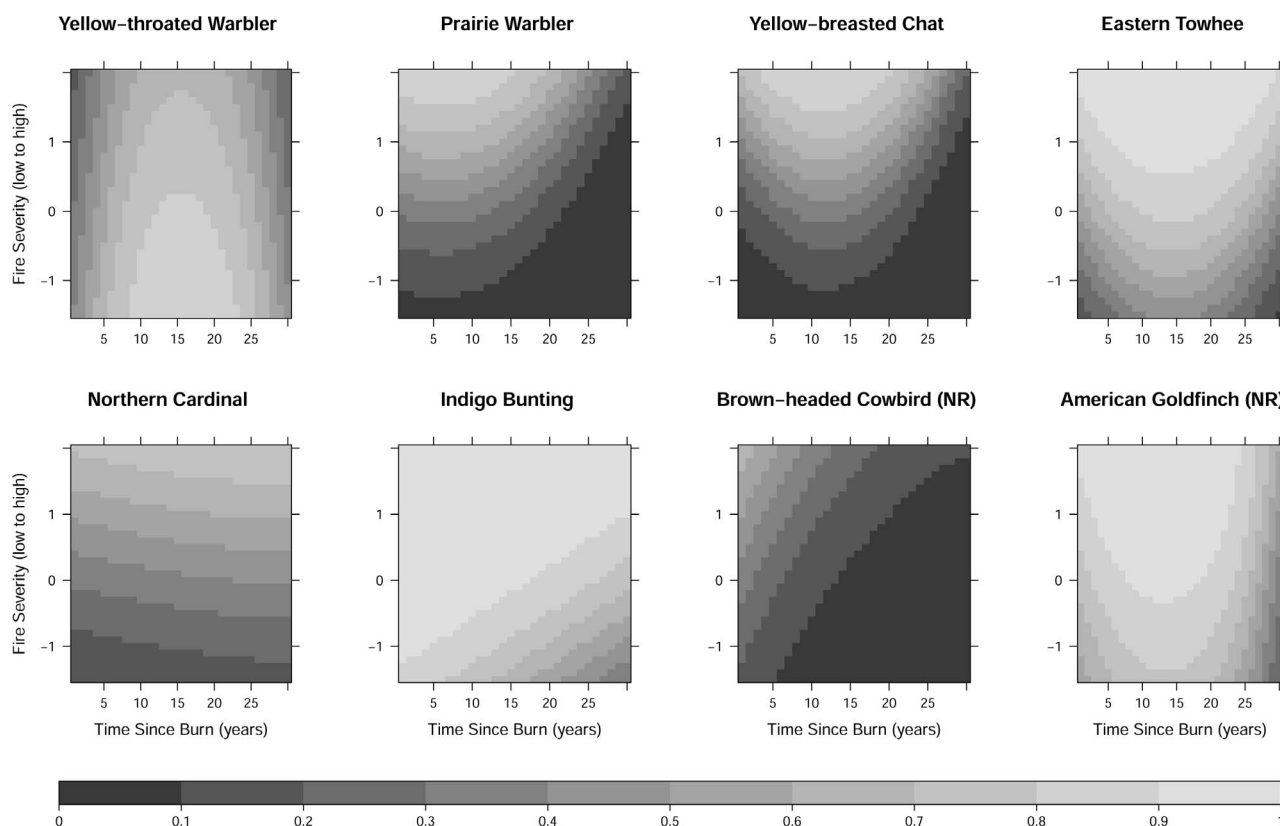
FIGURE 4. Continued.

species occurrence at both burned and unburned sampling points.

To better understand the relationship between spatial patterns of fire severity and breeding bird occurrence, we used the 228 burned sampling points to develop models incorporating fire severity (DNBR) summarized at each of 4 different spatial scales. DNBR values represent fire severity within 30 m^2 pixels (0.09 ha). Using the focal mean tool in ARCGIS we summarized DNBR at 3 additional spatial scales (90 m^2: 0.81 ha; 150 m^2: 2.25 ha; and 210 m^2: 4.41 ha). Although these 4 scales are artifacts of the Landsat imagery, they approximate the range of breeding territory sizes that we might expect for many of the species encountered in this study (i.e. Yellow-breasted Chat 1.24 ± 0.51 ha: Thompson and Nolan 1973; Ovenbird [*Seiurus aurocapilla*] 2.08 ± 0.20 ha: Mazerolle and Hobson 2004). We included the detection covariates identified previously in models exploring the effects of fire severity summarized at each of these spatial scales, and evaluated them using an information theoretic approach. The spatial scale identified in the top model was used to quantify fire severity in subsequent analyses for each species.

Finally, using the 228 sampling points from burned areas, we developed occupancy models incorporating all possible combinations of fire severity (DNBR) and the number of years since the most recent fire (time since burn). We used these models to predict temporal changes in species occurrence following fires of different severities. The final model set contained 6 models, including the conditional model (the null model with detection covariates) as well as models incorporating the effects of fire severity, the amount of time since burn, and the additive effects of fire and time (including quadratic effects of time since burn). Parameter estimates were averaged across all 6 models using Akaike's information criterion (AIC) weighting to determine the final occurrence predictions for each species. Unless otherwise noted, we consider the effects of a given parameter to be significant if twice the standard error of the estimate did not overlap zero.

RESULTS

We detected 81 bird species (Table 1) during 1008 point counts (3 visits to each of 336 sampling points). We developed species occurrence models for the 24 species with detection rates >0.20 and occupancy estimates between 10 and 90% under the null model. One or more covariates influenced the detection process for all species except Eastern Bluebird (*Sialia sialis*; Table 2). Including observer, date, wind speed, cloud cover, temperature, or

TABLE 3. Summary of AIC results for the top 3 models relating species occurrence to combinations of fire severity and time since burn (time). Models were ranked based on the difference from the top model in AIC corrected for small sample size. K is the number of parameters, and w_i is the model weight. Fire–time models were developed using the 228 sampling points in burned areas. The spatial scale that best explained the relationship between variation in fire severity and patterns of species occurrence is indicated in m^2 within ψ.

Species Code	Model	K	ΔAIC	w_i	Cumulative w_i
MODO[nr,fs,t]	p(#), ψ(fire severity150m^2 + time^q)	15	0	0.71	0.71
	p(#), ψ(fire severity150m^2)	13	−2.51	0.20	0.92
	p(#), ψ(fire severity150m^2 + time)	14	−4.51	0.07	0.99
RHWO[nr,t]	p(#), ψ(time^q)	5	0	0.58	0.58
	p(#), ψ(fire severity30m^2 + time^q)	6	−1.16	0.32	0.90
	p(#), ψ(fire severity30m^2 + time)	5	−3.96	0.08	0.98
NOFL[nr,fs]	p(#), ψ(fire severity210m^2)	10	0	0.55	0.55
	p(#), ψ(fire severity210m^2 + time)	11	−1.14	0.31	0.86
	p(#), ψ(fire severity210m^2 + time^q)	12	−2.73	0.14	1.00
EAWP[t]	p(#), ψ(fire severity90m^2 + time)	5	0	0.31	0.31
	p(#), ψ(fire severity90m^2 + time^q)	6	−0.13	0.29	0.60
	p(#), ψ(time)	4	−0.4	0.26	0.86
ACFL[nr,fs]	p(#), ψ(fire severity90m^2 + time^q)	7	0	0.49	0.49
	p(#), ψ(fire severity90m^2)	5	−0.96	0.31	0.80
	p(#), ψ(fire severity90m^2 + time)	8	−2.16	0.17	0.97
GCFL[nr,t]	p(#), ψ(time^q)	13	0	0.59	0.59
	p(#), ψ(fire severity30m^2 + time^q)	14	−2.29	0.22	0.81
	p(#), ψ(.)	11	−3.91	0.10	0.91
BHVI[fs,t]	p(#), ψ(fire severity150m^2 + time^q)	13	0	0.71	0.71
	p(#), ψ(fire severity150m^2 + time)	12	−1.79	0.29	1.00
	p(#), ψ(fire severity150m^2)	11	−12.99	0.00	1.00
BLJA[nr,t]	p(#), ψ(time)	12	0	0.46	0.46
	p(#), ψ(time^q)	13	−1.45	0.22	0.68
	p(#), ψ(fire severity30m^2 + time)	13	−1.76	0.19	0.87
CARW[t]	p(#), ψ(time)	10	0	0.51	0.51
	p(#), ψ(fire severity210m^2 + time)	11	−1.82	0.21	0.72
	p(#), ψ(time^q)	11	−1.91	0.20	0.92
BGGN[fs]	p(#), ψ(fire severity210m^2 + time^q)	15	0	0.70	0.70
	p(#), ψ(fire severity210m^2 + time)	14	−3.47	0.12	0.82
	p(#), ψ(fire severity210m^2)	13	−4.14	0.09	0.91
EABL[fs,t]	p(#), ψ(fire severity90m^2 + time^q)	5	0	0.95	0.95
	p(#), ψ(fire severity90m^2 + time)	4	−6.2	0.04	1.00
	p(#), ψ(time^q)	4	−11.91	0.00	1.00
OVEN[fs,t]	p(#), ψ(fire severity90m^2 + time^q)	13	0	0.95	0.95
	p(#), ψ(fire severity90m^2 + time)	12	−6.06	0.04	0.99
	p(#), ψ(fire severity90m^2)	11	−9.43	0.01	1.00
WEWA[fs,t]	p(#), ψ(fire severity30m^2 + time)	11	0	0.62	0.62
	p(#), ψ(fire severity30m^2 + time^q)	12	−1.74	0.26	0.88
	p(#), ψ(fire severity30m^2)	10	−3.28	0.12	1.00
HOWA[fs]	p(#), ψ(fire severity210m^2 + time)	13	0	0.48	0.48
	p(#), ψ(fire severity210m^2 + time^q)	14	−1.91	0.18	0.66
	p(#), ψ(fire severity210m^2)	12	−2.49	0.14	0.79
NOPA[fs,t]	p(#), ψ(fire severity210m^2 + *time)	6	0	0.46	0.46
	p(#), ψ(fire severity210m^2 + time^q)	7	−0.82	0.30	0.76
	p(#), ψ(fire severity210m^2)	5	−2.82	0.11	0.87
PIWA[fs]	p(#), ψ(fire severity210m^2)	4	0	0.54	0.54
	p(#), ψ(fire severity210m^2 + time)	5	−1.58	0.25	0.79
	p(#), ψ(fire severity210m^2 + time^q)	6	−3.32	0.10	0.89
YTWA[fs,t]	p(#), ψ(fire severity210m^2 + time^q)	15	0	0.53	0.53
	p(#), ψ(time^q)	14	−0.82	0.35	0.88
	p(#), ψ(fire severity210m^2)	13	−4.24	0.06	0.94
PRAW[fs,t]	p(#), ψ(fire severity150m^2 + time^q)	7	0	0.82	0.82
	p(#), ψ(fire severity150m^2 + time)	6	−3.04	0.18	1.00
	p(#), ψ(fire severity150m^2)	5	−24.07	0.00	1.00

TABLE 3. Continued.

Species Code	Model	K	ΔAIC	w_i	Cumulative w_i
YBCH[fs,t]	p(#), ψ(fire severity210m^2 + time^q)	6	0	0.98	0.98
	p(#), ψ(fire severity210m^2 + time)	5	−7.51	0.02	1.00
	p(#), ψ(fire severity210m^2)	4	−16.77	0.00	1.00
EATO[fs,t]	p(#), ψ(fire severity90m^2 + time^q)	7	0	0.94	0.94
	p(#), ψ(fire severity90m^2 + time)	6	−5.94	0.05	0.99
	p(#), ψ(fire severity90m^2)	5	−8.07	0.01	1.00
NOCA[fs]	p(#), ψ(fire severity30m^2)	5	0	0.54	0.54
	p(#), ψ(fire severity30m^2 + time)	6	−1.09	0.31	0.85
	p(#), ψ(fire severity30m^2 + time^q)	7	−2.78	0.13	0.98
INBU[fs,t]	p(#), ψ(fire severity30m^2 + time)	12	0	0.73	0.73
	p(#), ψ(fire severity30m^2 + time^q)	13	−2	0.27	1.00
	p(#), ψ(time)	11	−11.48	0.00	1.00
BHCO[nr,fs,t]	p(#), ψ(fire severity90m^2 + time)	5	0	0.57	0.57
	p(#), ψ(fire severity90m^2 + time^q)	6	−0.96	0.35	0.93
	p(#), ψ(fire severity90m^2)	4	−6.03	0.03	0.96
AMGO[nr,fs,t]	p(#), ψ(fire severity90m^2 + time^q)	6	0	0.52	0.52
	p(#), ψ(time)	4	−1.33	0.27	0.79
	p(#), ψ(time^q)	5	−3.27	0.10	0.89

[fs,t] One or more of the top 3 models incorporating fire severity ([fs]) or time since fire ([t]) had a significant effect (±2*SE of the estimate does not overlap 0) for this species.
[q] A quadratic term is included for this covariate.
[#] Detection covariates included in models for each species can be found in Table 2.
[nr] To improve model performance and ensure that detection rates (p) were $\geq$ 0.20, observations for this species were not restricted to observations within 50 m of the observer.

time of day did not improve predictions for this species. Overall, 13 species occurred more frequently in burned areas, 2 species occurred less frequently in burned areas, and 9 species showed no difference (Figure 3, Table 2).

Although only 15 species showed differences in occurrence between burned and unburned points, the influence of fire was evident for all 244 species (Figure 4). In all cases, models incorporating fire severity, time since burn, or both, outperformed the conditional model. Furthermore, 1 or more of the top 3 models contained both fire severity and time since burn for all 24, although the relative importance and the strength of the effects varied (Table 3). A quadratic effect of time since burn was included in 1 or more of the top 3 models for all 24 species, indicating a nonlinear relationship between occurrence and the amount of time following fire. Different species also responded to fire severity at different spatial scales, with occurrence patterns best described for 6, 7, 3, and 8 species when DNBR was summarized at 30, 90, 150, and 210 m^2, respectively.

Within burned areas, some species occurred more frequently immediately following fire, regardless of its severity (Carolina Wren [*Thryothorus ludovicianus*], Eastern-wood Pewee [*Contopus virens*], and Red-headed Woodpecker), whereas others occurred more frequently only after high severity (American Goldfinch [*Spinus tristis*], Blue-gray Gnatcatcher [*Polioptila caerulea*], Brown-headed Cowbird, Eastern Bluebird, Eastern Towhee [*Pipilo erythrophthalmus*], Mourning Dove [*Zenaida macroura*], Northern Cardinal [*Cardinalis cardinalis*], Northern Flicker [*Colaptes auratus*], Pine Warbler [*Setophaga pinus*], Prairie Warbler, and Yellow-breasted Chat) or low severity (Blue-headed Vireo [*Vireo solitarius*], Northern Parula [*Setophaga americana*], Ovenbird, and Worm-eating Warbler [*Helmitheros vermivorum*]) fire. Brown-headed Cowbirds, Eastern Bluebirds, Eastern Wood-Pewees, Prairie Warblers, Red-headed Woodpeckers, and Yellow-breasted Chats all occurred less frequently as the time since burn increased, whereas Worm-eating Warblers occurred more frequently.

DISCUSSION

As in similar studies (Klaus et al. 2010, Rush et al. 2012, Greenberg et al. 2013), the effects of fire severity and the amount of time without fire were common drivers shaping bird communities on our study site. Our results confirm that patterns of occurrence following fire are highly variable and suggest that the presence of fire can influence patterns of occurrence for 15 of the 24 species we considered, with only 2 species (Ovenbird and Worm-eating Warbler) occurring more frequently in unburned areas. Within GSMNP, recent changes in fire management

policy have increased the amount of fire on the landscape, benefitting the other 13 species considered. Although several species appear to benefit from recent increases in the amount of fire within GSMNP, contemporary fire frequency is still well below historic regimes, with <1% of the park burning each year.

Although fire can alter habitats dramatically, shifts in the plant and animal community often take many years (Engstrom et al. 1984, Watson et al. 2012, Greenberg et al. 2013). Patterns of bird occurrence for some species can change continually for more than 20 years following fire (Watson et al. 2012). Similarly, bird densities in Florida's old-field pines can change for 15 years after a fire (Engstrom et al. 1984). Notably, they found that the Wood Thrush (*Hylocichla mustelina*) and Northern Parula seemed to increase in density even after 15 years, whereas a number of species associated with early successional habitats completely disappeared within the first 10 years (i.e. Blue Grosbeak [*Passerina caerulea*], Bachman's Sparrow [*Peucaea aestivalis*], and Common Yellowthroat).

We found signals of bird community succession in the xeric pine–oak forests of GSMNP across sites that burned as many as 28 years prior to surveys. These patterns were most clearly evident following high severity fire. For some species, peak occupancy was found at sampling points that experienced high severity fire within the previous 0–5 years (Brown-headed Cowbird, Carolina Wren, Eastern Wood-Pewee, Indigo Bunting, and Red-headed Woodpecker), whereas other species occurred most frequently at points that burned 5–10 years prior to sampling (American Goldfinch, Blue-gray Gnatcatcher, Eastern Towhee, Mourning Dove, Prairie Warbler, and Yellow-breasted Chat). Eastern Bluebirds, Prairie Warblers, and Yellow-breasted Chats occurred at peak frequencies at points with high severity fire 5–15 years prior to sampling, whereas species such as American Goldfinch and Mourning Dove occurred at peak frequencies at points burned as many as 25 years earlier.

Patterns of occurrence within GSMNP were more subtle for low severity fires, with some species showing delayed responses. Hooded (*Setophaga citrina*) and Worm-eating Warblers occurred most frequently at points that had not burned for >15 years following low severity fires, and longer following high severity fires. Interestingly, Greenberg et al. (2007) found that both Hooded Warbler and Worm-eating Warbler densities declined temporarily following fuel reduction treatments that included fire, but then increased, suggesting that declines within the first 2 years following treatment were associated with the loss of tall shrub cover (Hooded Warbler) and decreases in leaf litter depth (Hooded Warbler and Worm-eating Warbler). In a similar southern Appalachian system, Rush et al. (2012) found that Hooded Warbler abundance increased within 1–2 years following low severity fire, with even

greater increases 3–6 years later. In both cases, changes in Hooded Warbler abundance resulted from changes in shrub cover and complexity because this species relies on a complex shrub layer for both nest and fledgling concealment (Rush and Stutchbury 2008). The Worm-eating Warbler is a ground nester that uses leaf litter to conceal its nest. Within GSMNP, model predictions suggest that occupancy for this species increases for more than 15 years. Worm-eating Warblers could be benefitting from the persistent accumulation of leaf litter over long periods of time.

Although we do not address patch size specifically, we found that the scale at which DNBR most effectively predicted species occurrence during the breeding season was directly related to species habitat requirements. Patterns of species occurrence for 4 species associated with forest openings were strongest when fire severity was summarized at larger spatial scales, suggesting that they require large patches of high severity fire. Within GSMNP, large patches of high severity fire should benefit Blue-gray Gnatcatchers, Mourning Doves, Prairie Warblers, and Yellow-breasted Chats. With the exception of the Mourning Dove, each of these species has declined in the Appalachian Region during the latter portion of the 20th century (Sauer et al. 2014; Appalachian Mountains 1966–2011).

Although large patches of high severity fire may be needed to maintain populations of Blue-gray Gnatcatcher, Mourning Dove, Prairie Warbler, and Yellow-breasted Chat, within GSMNP, frequent low severity fire may be necessary to restore or maintain the shortleaf pine-dominated habitats of the Red-cockaded Woodpecker. To bring back this species, fire frequency in these habitats should be closer to the 2–3 year return interval found in longleaf pine-dominated systems (Stambaugh et al. 2011). Interestingly, recent studies suggest that the benefits of using frequent low severity fire to increase species diversity are limited compared to the benefits of high severity fire (Artman et al. 2005, Klaus et al. 2010, Rush et al. 2012). Within GSMNP however, low severity fires often contain patches of high severity fire, which can provide habitat for many early successional species. Six species that seem to benefit from small patches of high severity fire within GSMNP include the Red-headed Woodpecker, Eastern Wood-Pewee, Eastern Bluebird, Indigo Bunting, Brown-headed Cowbird, and the American Goldfinch.

The Red-headed Woodpecker is an example of a species associated with small patches of high severity fire. Although fire severity was less important than time since fire for this species, Red-headed Woodpeckers showed the strongest patterns of occurrence when fire severity was summarized at small spatial scales, suggesting they can exploit even small forest openings. We found peak occurrence for this species at points that had burned

within the past 10 years. The presence of small patches of high severity fire within areas of low severity fire may provide a good combination of suitable nesting and foraging habitats. Peak occurrence for this species coincides with the ephemeral presence of the large-diameter snags that Red-headed Woodpeckers use for nesting (Gutzwiller and Anderson 1987). Interestingly, hotter fires in Florida slash pine forests resulted in both more intense pine beetle damage as well as more, large-diameter snags (Menges and Deyrup 2001). Although Red-headed Woodpeckers use a wide range of foraging strategies throughout the year (Conner et al. 1994), they often use fly-catching techniques in the summer (Jackson 1976). In the Blue Ridge province of North Carolina, low severity fire combined with mechanical shrub removal increased floral-visiting arthropod abundance and diversity relative to control plots (Campbell et al. 2007). Similar increases in flying arthropod abundance and diversity following fire within GSMNP could provide fly-catching birds such as the Red-headed Woodpecker increased foraging opportunities.

In general, research suggests that greater environmental heterogeneity (often induced by fire) will result in greater bird species diversity (Roth 1976, Tews et al. 2004, Fuhlendorf et al. 2006). Species-specific responses to fire, however, may be more closely tied to patterns of fire frequency than specific vegetation structural characteristics (Grundel and Pavlovic 2007). Our findings indicate that both fire severity and time since fire are important for shaping avian communities in the xeric pine–oak forests of the southern Appalachian Mountains. Variation in peak occurrence among species along gradients of both fire severity and the amount of time since fire suggests that a single fire regime will not address the habitat needs of all species. We believe at least 3 different fire regimes may be necessary to accommodate fire-adapted species in xeric pine–oak forests. These fire regimes should include areas exposed to frequent low severity fire (<5 year return interval), areas exposed to infrequent low severity fire (>10 year fire return interval), and areas exposed to infrequent high severity fire (>10 years fire return interval).

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