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RESEARCH ARTICLE

Normalized burn ratios link fire severity with patterns of avian occurrence

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Abstract

Context Remotely sensed differenced normalized burn ratios (DNBR) provide an index of fire severity across the footprint of a fire. We asked whether this index was useful for explaining patterns of bird occurrence within fire adapted xeric pine-oak forests of the southern Appalachian Mountains.

Objectives We evaluated the use of DNBR indices for linking ecosystem process with patterns of bird occurrence. We compared field-based and remotely sensed fire severity indices and used each to develop occupancy models for six bird species to identify patterns of bird occurrence following fire.

Methods We identified and sampled 228 points within fires that recently burned within Great Smoky Mountains National Park. We performed avian point counts and field-assessed fire severity at each bird census point. We also used Landsat™ imagery acquired before and after each fire to quantify fire severity using DNBR. We used non-parametric methods to quantify agreement between fire severity indices, and evaluated single season occupancy models incorporating fire severity summarized at different spatial scales.

Results Agreement between field-derived and remotely sensed measures of fire severity was influenced by vegetation type. Although occurrence models using field-derived indices of fire severity outperformed those using DNBR, summarizing DNBR at multiple

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spatial scales provided additional insights into patterns of occurrence associated with different sized patches of high severity fire.

Conclusions   DNBR is useful for linking the effects of fire severity to patterns of bird occurrence, and informing how high severity fire shapes patterns of bird species occurrence on the landscape.

Introduction

Quantifying changes in patterns of species occurrence can provide important insights into how environmental perturbations affect biodiversity. Whether the goal is documenting distributional shifts associated with global warming, or identifying the effects of local habitat conversion, reliable tools that enable resource managers to quantify changes in species occurrence are needed to make informed management and policy decisions. Since 1972, Landsat imagery has been used extensively to capture both spatial and temporal patterns in the spectral characteristics of landscapes across the globe (Pettorelli et al. 2014). Although Landsat imagery is applied in a wide variety of conservation and management applications, its ability to capture patterns of avian species occurrence is often limited by a lack of information about how different ecological processes shape patterns of species distribution (Vallecillo et al. 2009). We explore whether recent advances in mapping patterns of fire severity using Landsat imagery are useful for understanding changes in bird occurrence associated with fire.

In recent years, there has been an increase in both the number of fires and the amount of land area affected by fire across North America (Calkin et al. 2005; Cohen et al. 2007; Aldrich et al. 2010). In general, recent increases in the prevalence of fire areattributed to a combination of past and current fire management practices (Romme and Despain 1989; Cohen et al. 2007), and changing climates (Liu et al. 2013). Within the southern Appalachian region, recent changes in fire management have increased the amount of land area exposed to both prescribed burns (NPS Fire Effects Data 1920–2010) and wildfires

(Cohen et al. 2007). Recent increases in the amount of fire on the landscape have broad ecological implications, ranging from changes in vegetation structure to changes in both plant and animal species composition. Within the southern Appalachian region, variation in fire severity is often cited as an important determinant of which species persist after a fire (Klaus et al. 2010; Greenberg et al. 2013).

Fire severity is defined as the "degree to which a site has been altered or disrupted by fire" (National Wildfire Coordinating Group 2014) or "the degree of environmental change caused by a fire" (Key and Benson 2006). Although these definitions are broad, efforts to quantify fire severity generally include measurements of the effects of fire on the soil substrate, herbaceous layer, shrub layer, and small and large trees. Quantifying the effects of fire across broad spatial scales is a complex task, and tools for doing so are continually improving.

Recent advances include the use of Landsat imagery acquired using the Thematic Mapper sensor (Landsat[TM]) to assess fire severity in temperate regions of North America (Miller and Thode 2007). One promising tool for assessing severity across the footprint of a fire is the development of the Differenced Normalized Burn Ratio (DNBR), which uses the spectral characteristics of vegetation and mineral soil to quantify changes in vegetation following fire (Key and Benson 2006). This proxy for fire severity can identify patterns of ecological change across large spatial scales. Although agreement between DNBR and ground-based fire severity indices is subject to variation, one recent study showed that agreement between DNBR and ground-based Composite Burned Index can be as high as 92 % in some forest types (Picotte and Robertson 2011).

The ecological effects of fire are thought to depend largely on interactions among fire severity (Key and Benson 2006; Elliott et al. 2009), fire size (Baker 1993; Key and Benson 2006), the amount of time since burn (Harrod et al. 2000; Hurteau et al. 2008; Elliott et al. 2009), and the taxa of interest (Baker 1993; Elliott et al. 2009). Although most recent studies describe these relationships for plant communities, there is a growing body of literature linking these patterns to other taxa, including birds (Aquilani et al. 2003; Artman et al. 2005; Saab et al. 2005; Haney et al. 2008; Fontaine et al. 2009; Klaus et al. 2010).

In this analysis, we explore the utility of DNBR fire severity indices for linking the effects of fire with patterns of avian species occurrence. We use both field-derived and remotely sensed fire severity indices and avian point counts to: (1) Explore relationships between field-based and remotely sensed DNBR fire severity indices, and to (2) identify the most relevant spatial scale for summarizing DNBR fire severity indices for target species. We develop occupancy models for six bird species; two associated with early succession habitats [Prairie Warbler (*Setophaga discolor*), Yellow-breasted Chat (*Icteria virens*)], two associated with forest edges [Eastern Wood-pewee (*Contopus virens*), Indigo Bunting (*Passerina cyanea*)], and two species known to be sensitive to forest fragmentation [Ovenbird (*Seiurus aurocapilla*), Worm-eating Warbler (*Helmitheros vermivorus*)].

Methods

Sampling design

Great Smoky Mountains National Park, in the southern Appalachian region of the United States of America (Fig. 1), has extensive fire history records that include the ignition date and fire perimeter for most fires that burned within the park since it was established in 1934. This information, along with Landsat[TM] imagery, provided us an opportunity to link the effects of fire at different spatial scales with patterns of bird occurrence in the fire adapted xeric pine-oak forests of Great Smoky Mountains National Park. These xeric forests are primarily found below 900 m in elevation within the western portion of the park, and are characterized by shortleaf (*Pinus echinata*), pitch (*Pinus rigida*), table mountain (*Pinus pungens*), and virginia (*Pinus virginiana*) pines along with chestnut oak (*Quercus prinus*) and hickory (Carya spp.).

During the 2012, 2013 and 2014 breeding seasons, we surveyed 228 sampling points(45, 90, and 93 points each year respectively)within xeric pine-oak forests that burned between 1986 and 2014, the period for which Landsat[TM] products were available. Prior to each field season, we used Landsat[TM] derived Differenced Normalized Burn Ratios (DNBR) and historical fire records to stratify sampling points across four fire severity categories (unburned-low, low-moderate,

moderate-high, and high severity) defined using DNBR thresholds developed within the Park (NPS thresholds),and three time since burn categories (0–5, 6–10, 11–28 years) (Table 1). Since fire management efforts are currently aimed at mimicking historic fire regimes in xeric pine-oak forests, sampling points were located on upper slopes and ridges, which are dominated by these habitats. Each point was located at least 100 m inside the perimeter of 28 recent fires (Appendix 1 in Supplementary material) and placed within the xeric pine-oak habitats that are frequented by the six bird species of interest. We spaced all points a minimum of 250 m apart, to maximize the number of points that could be sampled each day while minimizing the influence of spatial autocorrelation among points. During point establishment, we visually assessed the relative contribution of both pines and oaks to percent canopy cover within 50 m of the sampling point (pine: >75 % coniferous, pine-oak: 50–75 % coniferous, oak-pine: 50–75 % deciduous, oak: >75 % deciduous).

Fire severity indices

Fire terminology corresponds with the National Wildfire Coordinating Group's Glossary of Wildland Fire Terminology (2012).

Differenced normalized burn ratios

Landsat-based DNBR provide resource managers with a remotely sensed measure of the change in vegetation resulting from fire (Epting et al. 2005). The Normalized Burn Ratio uses the peak reflectance of both vegetation and mineral soil to provide an index of the amount of vegetation present on the landscape. DNBR are calculated as the difference between the Normalized Burn Ratios before and after a fire.

We acquired Landsat[TM] images from National Park Service personnel and from the USGS Earth Resources Observation and Science Center. We worked with NPS personnel familiar with the fire history of the Park to select and process Landsat[TM] scenes. We chose only images without clouds or other atmospheric anomalies overlapping the area of interest (Appendix 1 in Supplementary material). Once representative scenes were chosen, we calculated DNBR fire severity values for all 30 m^2 grid cells within each scene using ArcMap 10.1. The resulting DNBR
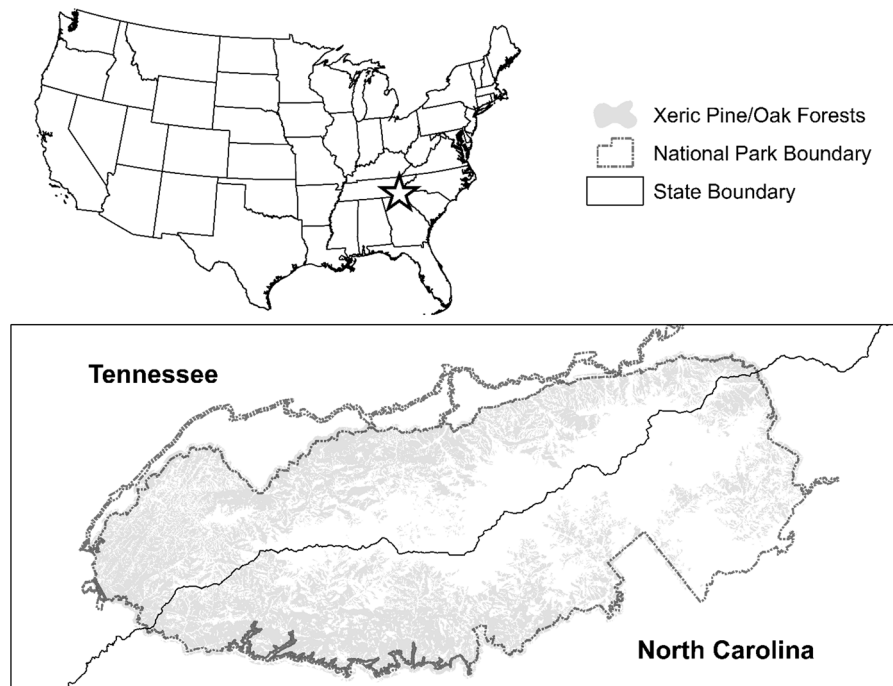
Fig. 1 Great Smoky Mountains National Park, in the Southern Appalachian Region of the United States of America, has extensive fire history records which provide the ignition date and fire perimeter for all fires that occurred within the xeric pine-oak forests of the park since Landsat[TM] imagery became readily available in 1984

Table 1 Sampling points in burned areas (228) were stratified by fire severity (using DNBR values and categories defined with the NPS Thresholds) and the number of years following the most recent fire, in xeric pine-oak forests of the western portion of Great Smoky Mountains National Park

	0–5 years	6–10 years	11–28 years	Total
Unburned—low severity	5	22	25	52
Low—moderate severity	23	21	24	68
Moderate—high severity	24	22	27	73
High severity	15	12	8	35
Total	67	77	84	228

provided a continuous index of the change in vegetation following fire which ranged from −2000 to 2000, with negative values indicating enhanced plant growth and positive values indicating retarded plant growth.

Differenced Normalized Burn Ratio indices derived from Landsat[TM] images provide fire severity at a scale of 30 m^2, however species respond to the effects of fire at different spatial scales. We used the continuous coverage of DNBR indices and the focal mean tool in ArcMap 10.1 to explore the relationship between fire severity and species occurrence at four spatial scales; 0.09 ha (30 m^2), 0.81 ha (90 m^2), 2.25 ha (150 m^2), and 4.41 ha (210 m^2). We were interested in identifying whether the relevant scale for explaining fire effects varied among our study species. The four scales that we chose encompass the range of breeding territory sizes for our target species (Prairie Warbler 1.62 ± 0.72 (Nolan et al. 2014), Yellow-breasted Chat 1.24 ± 0.51 ha (Thompson and Nolan 1973), Eastern Wood-pewee 2.2−7.7 ha (McCarty 1996), Indigo Bunting 0.4−1.4 ha (Payne 2006),

Ovenbird 2.08 ± 0.20 ha (Mazerolle and Hobson 2004), Worm-eating Warbler 1.72 ± 0.78 (Vitz et al. 2013). The minimum resolution of DNBR (30 m^2) represents the smallest scale at which we could assess patterns of species occurrence. The logistical constraints of conducting point count surveys in steep wilderness terrain and spacing points at least 250 m apart to avoid spatial autocorrelation limited the number of points sampled to approximately three points per person per day.

Although Key and Benson (2006) recommend thresholds for defining fire severity classes, *Landscape Assessment: Sampling and Analysis Methods* (hereafter LA thresholds), these thresholds were not developed within the xeric pine-oak forests of our study area. Within the Park, NPS fire ecologists have developed thresholds that more accurately reflect the effects of fire within the southern Appalachian region. We used the NPS thresholds to stratify sampling points across discrete fire severity categories and subsequently assigned LA fire severity classes to each point for comparison.

Field-derived fire severity

We used a field-derived fire severity index for validation and comparison with remotely sensed threshold indices. With the help of National Park Service fire effects personnel, we developed a rapid assessment tool for estimating fire severity during each visit to our bird sampling points (Appendix 2 in Supplementary material). This index provided a quick estimate of fire severity based on tree mortality, duff depth, and char height. This field-derived index mirrors the LA fire severity categories and has categories similar to those defined by NPS thresholds. Our field-derived fire severity index includes classes representing unburned areas in addition to low, moderate-low, moderate-high, and high severity fires (Table 2). Because duff depth increases over time and charring washes away over time, this index was likely less sensitive to these characteristics as time since burn increased. As a result, our field-derived estimates of fire severity relied more heavily on a combination of overstory and understory mortality at sampling points that burned more than 5 years earlier. We recorded field estimates of fire severity during each visit to a sampling point, averaged the scores, and rounded to the nearest whole number to arrive at a final field-based fire severity estimate. Each sampling point was visited a minimum of three times.

Avian surveys

We used unlimited radius avian point counts modified from Reynolds et al. (1980) to document the presence of target species. Each point was visited three times during the peak of the breeding season, from 1st May to the 30th of June, in most cases by three different observers. Repeated visits to each sampling point were generally two to three weeks apart, with each subsequent round of surveys starting within a few days of finishing the previous one. During each visit, observers recorded the species of each bird encountered, and its distance from the center of the sampling point when first detected. Distance to individual birds was estimated in 5 m distance bands out to 200 m, and all birds detected beyond that distance were combined in a single distance band. All point counts were conducted between sunrise and 10:00 am during fair weather with winds <15 mph. Prior to initiating each point count, observers recorded date, time, wind speed, temperature and percent cloud cover to account for the influence of these factors on detection. Wind speed was assigned to a Beaufort Wind Scale category, temperature was recorded to the nearest degree Celsius, and percent cloud cover was estimated visually. All observers were given a SanDisc MP3 player containing multiple recordings of each species song for reference during surveys and received a minimum of 2 weeks of bird identification and distance estimation training. Observers were tested for their ability to identify bird songs using both Thayer Birding Software^{TM} and field-based multiple observer point counts. Discrepancies between observers were discussed immediately following counts and birds in question were tracked down when possible.

Data analysis

We used the non-parametric Kendall's Tau-b to assess agreement between field based and remotely sensed indices of fire severity. We assumed that our ability to accurately estimate fire severity in the field would decline with the amount of time since a fire burned so we quantified the agreement between field based and remotely sensed indices of fire severity for 0–5, 6–10, and 11–28 years. In addition, we classified forest

Table 2 Fire severity classes defined using both field-derived and remotely sensed indices. Severity classes were defined for remotely sensed DNBR fire severity indices using thresholds developed within Great Smoky Mountains National Park (NPS) and those presented by Key and Benson (2006) for Landscape Assessment of fire effects (LA)

Severity class	Field class	NPS thresholds[a]	LA thresholds
Unburned	0	NA	<100
Low severity	1	<79	100–269
Low—moderate severity	2	80–269	270–439
Moderate—high severity	3	270–549	440–659
High severity	4	>550	>660

[a] NPS thresholds include both unburned and low severity in the same class

cover as either pine dominated or oak dominated to look for differences resulting from forest composition.

Although variable radius point counts are often used to estimate abundance, we used species occurrence models because they allowed us to restrict bird observations to those within 30 m of the observer, thereby more closely approximating both the territory size of our focal bird species and the smallest spatial scale that fire severity was measured. Furthermore, density estimates based on auditory detections are shown to range from 17 to 132 % of the actual total in deciduous forest bird communities (Simons et al. 2007). This variation is driven by distance estimation errors which can increase dramatically beyond approximately 75 m (Alldredge et al. 2007). We believe that the assumptions of occupancy models are more realistic in forested habitats than the assumptions of distance sampling, while still accounting for biases associated with variations in detection probability (Kissling and Garton 2006; Mackenzie et al. 2006; Simons et al. 2007). Single season occupancy models (MacKenzie et al. 2002) allowed us to simultaneously estimate detection probabilities and occupancy state for each species. We used package "unmarked" (Fiske and Chandler 2011) in the statistical software R, version 15.1 (R Core Team 2014) to perform all occupancy analyses. These models incorporate the probability that a species is present, available, and detected into species occurrence estimates, allowing us to account for variations in detection rates associated with individual bird species, their environment, and observers (MacKenzie et al. 2006).

We used a two-step approach to incorporate possible covariates influencing the detection process into estimates of species occurrence. First, we evaluated models incorporating all possible combinations of date (day of the year), time of day (minutes from sunrise), wind speed, cloud cover, and observer as detection covariates using an Information Theoretic approach (Burnham et al. 2011). The covariates included in the model that received the most AIC weight were included in subsequent analyses for each species. Next, we developed models that incorporated the relevant detection covariates, as well as the linear and quadratic effects of time since burn, and DNBR. For each species, we evaluated five models including one with DNBR quantified at each of four spatial scales (30, 90, 120, 210 m^2) in addition to the conditional model (null model with detection covariates).

Results

Fire severity indices and thresholds

Overall agreement between field-derived and remotely sensed measures of fire severity among all burned sampling points was 58 and 59 % when fire severity was classified using either NPS thresholds (Tau = 0.577, DF = 227, Z = 10.386) or LA thresholds (Tau = 0.587, DF = 227, Z = 10.708). The amount of time between a burn and field sampling had little effect on agreement between field-derived and remotely sensed fire severity estimates (Table 3). Agreement between the two metrics however, was 17 % (NPS) and 16 % (LA) stronger for deciduous dominated stands (NPS: Tau = 0.624, DF = 129, Z = 8.521. LA: Tau = 0.632, DF = 129, Z = 8.708) than it was for pine dominated stands (NPS:

Table 3 Kendal's Tau B results showing the agreement between field-derived and remotely sensed fire severity classes

Time since burn	NPS Thresholds	LA Thresholds
Within five years	Tau = 0.625, DF = 67, Z = 5.974	Tau = 0.588, DF = 67, Z = 5.785
6–10 years	Tau = 0.579, DF = 77, Z = 6.016	Tau = 0.597, DF = 77, Z = 6.251
More than 10 years	Tau = 0.592, DF = 84, Z = 6.425	Tau = 0.614, DF = 84, Z = 6.733

Tau = 0.447, DF = 97, Z = 5.104. LA: Tau = 0.471, DF = 97, Z = 5.479). Fire severity classes defined by NPS thresholds showed strong agreement with those defined using LA thresholds (Tau = 0.945, DF = 227, Z = 17.140), but were 4 % lower in coniferous stands (Tau = 0.918, DF = 97, Z = 10.823) than deciduous (Tau = 0.963, DF = 130, Z = 13.101).

Species occurrence and fire severity at different spatial scales

During the 2012, 2013, and 2014 breeding seasons, we recorded 246 Prairie Warblers, 195 Yellow-breasted Chats, 211 Eastern Wood-pewees, 872 Indigo Buntings, 329 Ovenbirds, and 232 Worm-eating Warblers. We recorded no more than 4, 4, 3, 5, 6, 4 detections respectively for these species during a single visit to any sampling point, thereby limiting the potential for bias when detection depends on abundance (Welsh et al. 2013). When we restricted the plot radius to include only individuals detected within a 30 m radius, we only encountered 95, 57, 49, 379, 45, 69 individuals of each species respectively across all 228 sampling points. Within the 30 m radius, we recorded Prairie Warblers at 18 %, Yellow-breasted Chats at 14 %, Eastern Wood-pewee at 18 %, Indigo Buntings at 67 %, Ovenbirds at 16 %, and Worm-eating Warblers at 21 % of all sampling points. Model predictions for overall occupancy state within the 30 m radius suggest that naive occurrence estimates are biased low. Occurrence predictions incorporating the relevant covariates identified in the top detection model for these same species were 0.19 ± 0.03, 0.17 ± 0.03, 0.38 ± 0.11, 0.76 ± 0.04, 0.38 ± 0.12, and 0.38 ± 0.08 respectively (Table 4). These predictions illustrate the importance of accounting for the detection process for our focal species.

Model results indicate that different species respond to the effects of fire at different spatial scales (Table 4; Fig. 2). Model predictions for the two species associated with early succession habitats (Prairie Warbler: 210 m^2, and Yellow-breasted Chat: 150 m^2), while predictions for the two species associated with forest edge habitats (Eastern Wood-pewee: 30 m^2, and Indigo Bunting: 30 m^2) and the two species associated with contiguous forest habitats (Ovenbird: 30 m^2, Worm-eating Warbler: 30 m^2) were improved by summarizing DNBR fire severity indices at smaller spatial scales. In addition, occurrence predictions for all species were improved by incorporating DNBR indices of fire severity (Table 4).

Discussion

Overall, we found 58 % (NPS) and 59 % (LA) agreement between field-derived and remotely sensed fire severity classes, which is lower than other studies in similar forest types. Picotte and Robertson (2011) found an average of 75 % agreement between DNBR and ground-based Composite Burn Index (CBI) fire severity values across a range of southeastern vegetation types. A similar study in deciduous dominated habitats of the southern Appalachians (Wimberly and Reilly 2007) found 71 % agreement between DNBR and ground-based CBI values. Lower agreement between these two indices in our study could be attributable to both a mismatch in spatial scale, and a field-derived index that traded sensitivity for flexibility. Agreement might have been stronger if we quantified both field-derived and remotely sensed estimates of fire severity at the same spatial scale. Unfortunately, we collected field-derived estimates of fire severity within 50 m radius circular plots, while DNBR indices quantified fire severity within 30 m^2 pixels. Furthermore, previous studies used CBI rather than DNBR to quantify fire severity. CBI provides a

Table 4 Model selection results evaluating the relationship between fire severity and occurrence for six species: two that are sensitive to forest fragmentation (Ovenbird, Worm-eating Warbler), two that exploit forest openings (Eastern Wood-pewee, Indigo Bunting), and two found in early succession habitats (Prairie Warbler, Yellow-breasted Chat)

Species	Model	nPars	AIC	AICwt	State Estimate ± SE
Prairie Warbler	p(^{p1}), psi(time + time^q + DNBR_210 m^2)	13	326.90	0.55	intercept: −1.68 ± 0.62
	p(^{p1}), psi(time + time^q + DNBR_150 m^2)	13	327.36	0.43	fire severity: 1.19 ± 0.24
	p(^{p1}), psi(time + time^q + DNBR_90 m^2)	13	333.44	0.02	time: 0.13 ± 0.12
	p(^{p1}), psi(time + time^q + DNBR_30 m^2)	13	343.07	0.00	time^q: −0.01 ± 0.00
	p(^{p1}), psi(.)	10	378.39	0.00	
Yellow-breasted Chat	p(^{p2}), psi(time + time^q + DNBR_150 m^2)	6	280.93	0.45	intercept: −2.15 ± 0.73
	p(^{p2}), psi(time + time^q + DNBR_90 m^2)	6	281.22	0.39	fire severity: 0.88 ± 0.24
	p(^{p2}), psi(time + time^q + DNBR_210 m^2)	6	283.27	0.14	time: 0.18 ± 0.14
	p(^{p2}), psi(time + time^q + DNBR_30 m^2)	6	286.99	0.02	time^q: −0.01 ± 0.01
	p(^{p2}), psi(.)	3	303.50	0.00	
Eastern Wood-pewee	p(^{p3}), psi(time + time^q + DNBR_30 m^2)	6	327.75	0.41	intercept: −0.63 ± 0.89
	p(^{p3}), psi(time + time^q + DNBR_90 m^2)	6	328.41	0.29	fire severity: 0.58 ± 0.41
	p(^{p3}), psi(time + time^q + DNBR_150 m^2)	6	329.30	0.19	time: 0.17 ± 0.17
	p(^{p3}), psi(time + time^q + DNBR_210 m^2)	6	330.42	0.11	time^q: −0.01 ± 0.01
	p(^{p3}), psi(.)	3	343.53	0.00	
Indigo Bunting	p(^{p4}), psi(time + time^q + DNBR_30 m^2)	12	830.76	0.77	intercept: 2.10 ± 0.81
	p(^{p4}), psi(time + time^q + DNBR_90 m^2)	12	833.49	0.20	fire severity: 0.94 ± 0.33
	p(^{p4}), psi(time + time^q + DNBR_150 m^2)	12	837.74	0.02	time: 0.01 ± 0.14
	p(^{p4}), psi(time + time^q + DNBR_210 m^2)	12	840.53	0.01	time^q: −0.00 ± 0.00
	p(^{p4}), psi(.)	9	859.31	0.00	
Ovenbird	p(^{p5}), psi(time + time^q + DNBR_30 m^2)	8	299.97	0.53	intercept: -0.49 ± 0.95
	p(^{p5}), psi(time + time^q + DNBR_90 m^2)	8	300.68	0.37	fire severity: −1.30 ± 0.42
	p(^{p5}), psi(time + time^q + DNBR_150 m^2)	8	303.75	0.08	time: −0.16 ± 0.17
	p(^{p5}), psi(time + time^q + DNBR_210 m^2)	8	306.91	0.02	time^q: 0.01 ± 0.01
	p(^{p5}), psi(.)	5	313.48	0.00	
Worm-eating Warbler	p(.), psi(time + time^q + DNBR_30 m^2)	5	387.44	0.65	intercept: −1.80 ± 0.75
	p(.), psi(time + time^q + DNBR_90 m^2)	5	389.26	0.26	fire severity: −0.91 ± 0.27
	p(.), psi(time + time^q + DNBR_150 m^2)	5	392.13	0.06	time: 0.11 ± 0.13
	p(.), psi(time + time^q + DNBR_210 m^2)	5	394.19	0.02	time^q: −0.09 ± 0.00
	p(.), psi(.)	2	410.58	0.00	

In addition to relevant detection covariates, the models evaluated for each species include Landsat-derived DNBR fire severity values summarized at four spatial scales (30, 90, 150, and 210 m^2), as well as both the linear and quadratic (^{q}) effects of the amount of time that has elapsed since the most recent fire (time)

[p1] Models for the Prairie Warbler include observer, time since sunrise and cloud cover as covariates on detection

[p2] Models for the Yellow-breasted Chat include temperature as a covariate on detection

[p3] Models for the Eastern Wood-pewee include time since sunrise as a covariate on detection

[p4] Models for the Indigo Bunting include observer and temperature as covariates on detection

[p5] Models for the Ovenbird include date, time since sunrise and temperature as covariates on detection

more rigorous assessment of fire severity and is generally acquired within a year post fire. Because our primary focus was linking DNBR fire severity indices to bird occurrence, we chose a simplified approach which allowed us to assess fire severity up to 28 years after a fire occurred.
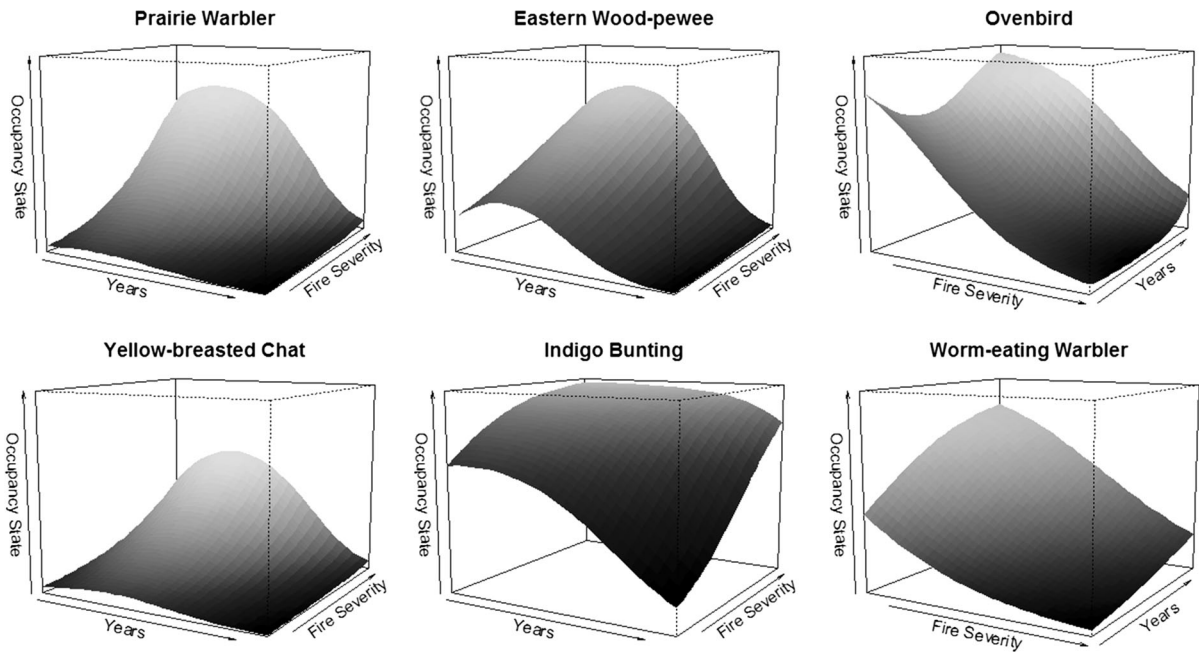
Fig. 2 Top model predictions illustrating the effects of fire severity and time since burn (years) for two early successional species (*left*), two edge associated species (*middle*), and two forest interior species that are sensitive to fragmentation (*right*). Because the Ovenbird and the Worm-eating Warbler both occurred more frequently with increasing time since burn, we switched the axesso combinations of covariates resulting in higher occupancy are further from the observer's vantage point for these two species

Although our methods of quantifying fire severity in the field were less sensitive than CBI, agreement between field-derived and remotely sensed indices varied by less than 5 % among the time since burn categories (Table 3). Because both duff depth and char height provide less information about fire severity as time since burn increases, this consistency suggests that our fire severity estimates relied more heavily on tree mortality. Interestingly, agreement between field-derived and remotely sensed fire severity increased by 17 % (NPS) and 16 % (LA) at sampling points dominated by deciduous trees compared to those dominated by conifers. Because most of our sampling points had a combination of both deciduous and coniferous trees in the canopy, we did not expect to see this difference. These findings do however corroborate those of other recent studies showing that DNBR indices vary with vegetation composition (Epting et al. 2005; Picotte and Robertson 2011).Because DNBR is susceptible to fluctuations in hydrology (Key 2005), one possible explanation is that conifers tend to inhabit areas that experience greater variation in soil moisture. Within the study area conifers are often found on

steeper slopes and more exposed ridges than deciduous trees.

DNBR values are also influenced by the atmospheric conditions during image acquisition, as well as changes in vegetation resulting from ecological processes other than fire (Key and Benson 2006). Despite these sources of variation, DNBR can be used to assess changes in vegetation at multiple spatial scales, providing insights into how fire effects scale with patterns of species occurrence. The fact that we see variation in patterns of species occurrence across different spatial scales is not surprising. Ecologists have long acknowledged that the spatial scale of observation shapes our understanding of species-habitat relationships, but we suggest that the scale providing the most information about patterns of species occurrence has a biologically meaningful explanation and provide two examples for illustration. First, we argue that the optimal scale for predicting the relationship between species occurrence and fire severity is related to the minimum patch size exploited by early successional species (Fig. 3). If the species requires a 90 m^2 patch of early succession habitat, fire
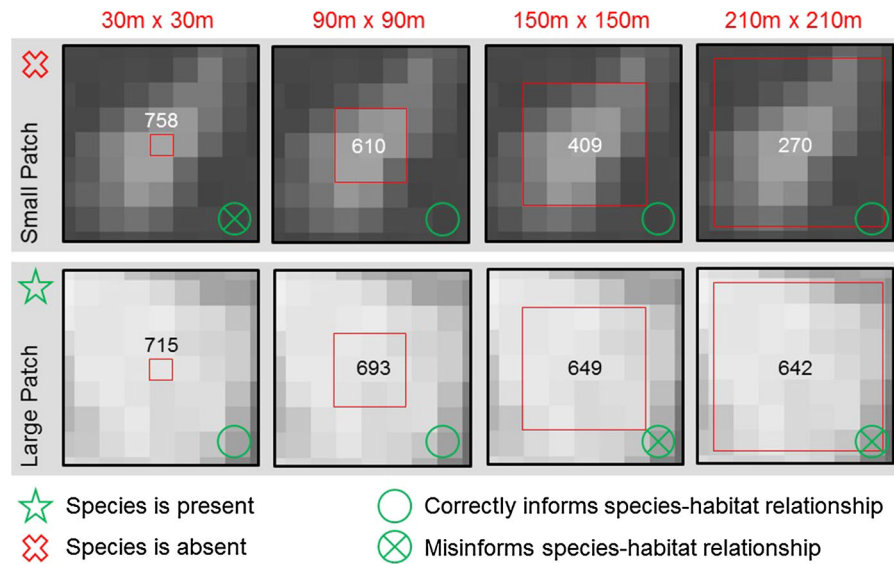
Fig. 3 Quantifying fire severity (DNBR) at multiple spatial scales can help to inform the relationship between an early successional species and its habitat requirements. To illustrate this, we assume that fire severity values >650 will result in early succession habitat and that the early successional species requires a patch that is at least a 90 m^2. *Pixel color* in the figure is indicative of fire severity, with *light colors* representing high severity fire. The *numbers* near the center of each panel indicate fire severity when values are averaged across all pixels within the *red box* (high values represent high severity fire). The early successional species is not present in the small patch of high severity fire (*top row*) because the patch is not large enough, while it is present in the large patch (*bottom row*) because it is ≥90 m^2 in size. When fire severity is quantified at

30 m^2 (first column), predicting species occurrence using the high fire severity value (758) is misleading for the small patch because the species isn't there, but the value for large patch (715) correctly informs the species-habitat relationship because the species is present. When quantified at 90 m^2, the fire severity value will correctly inform the species-habitat relationship for both the small, and large patch of early succession habitat. In the large patch, fire severity that is quantified at 150 or 210 m^2 is misleading because the species is present despite values that fail to suggest the presence of early succession habitat. With adequate replication across a range of patch sizes, this process will indicate the minimum patch size that an early successional species can exploit, in this case 90 m^2

severity quantified at scales smaller than 90 m^2 can misinform the species-habitat relationship when small patches of habitat have high fire severity values. Fire severity values quantified at a scale larger than 90 m^2 can misinform the relationship by underestimating fire severity in areas where the species is present. Similarly, the scale that best describes patterns of occurrence for species associated with contiguous forests is indicative of how sensitive those species are to forest openings (Fig. 4). If a species is sensitive to forest openings greater than 90 m^2, fire severity values quantified at smaller scales can misinform the species habitat relationship because the species may be present when fire severity values are high. Fire severity values quantified at a scale larger than 90 m^2 can also misinform the species-habitat relationship because fire severity values may be low when the species is absent due to a 90 m^2 forest opening.

Correct interpretation of the optimal scale for predicting patterns of species occurrence depends on a priori information about species-habitat relationships (i.e. whether a species is associated with early succession habitats or is sensitive to forest openings).

Correct interpretation of these species habitat relationships also requires that bird occurrence is quantified at an appropriate spatial scale. We believe this scale should reflect something important to the biology of the species, like territory size. To further explore our focal species response to fire severity at different spatial scales, we repeated our analyses using distance sampling. Distance sampling uses all birds detected, regardless of their distance from the observer to generate density estimates. In general, we saw the same trends using both distance sampling and occupancy modeling, with the same species responding to fire at larger spatial scales in both analyses.
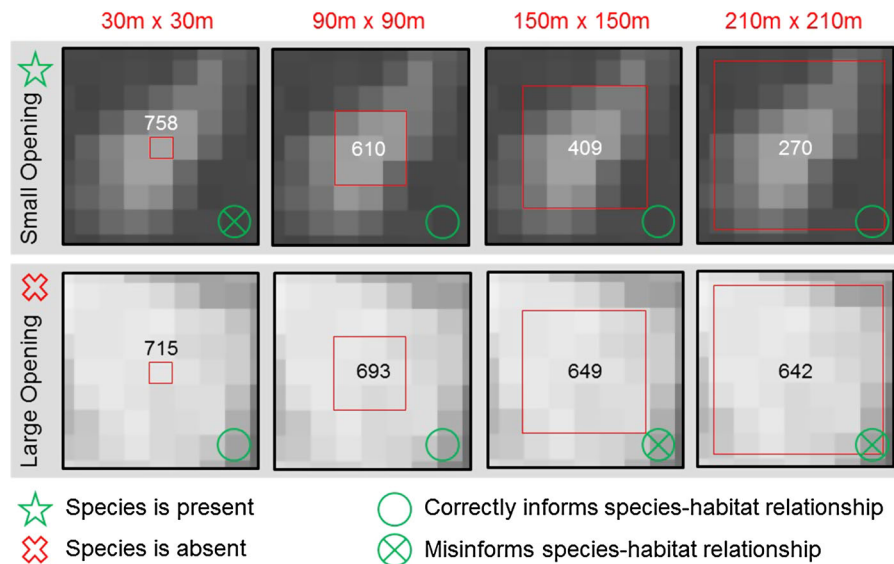
Fig. 4 Quantifying fire severity (DNBR) at multiple spatial scales can help to inform the relationship between a forest interior species and its sensitivity to forest openings. To illustrate this, we assume that fire severity values>650 will result in a forest opening, and that the forest interior species will avoid openings that are 90 m^2 or larger. *Pixel color* in the figure is indicative of fire severity, with *light colors* representing high severity fire. The *numbers* near the center of each panel indicate fire severity when values are averaged across all pixels within the *red box* (high values represent high severity fire). The forest interior species is not present in the large forest opening (*bottom row*), but is present in the small forest opening (*top row*) because the patch is ≤90 m^2. When fire severity is quantified at 30 m^2 (*first column*), predicting species occurrence using fire severity is misleading for the small forest opening because the species is present despite the high fire severity value (758). For the large forest opening, the fire severity value (715) correctly informs the relationship because the species is absent. When quantified at 90 m^2, the fire severity value correctly informs the species-habitat relationship for both the small, and large forest opening. Fire severity that is quantified at 150 or 210 m^2 is misleading for the large forest opening because the species is absent when the fire severity doesn't indicate an opening in the forest. With adequate replication across a range of forest opening sizes, this process will provide insights into how sensitive a forest interior species is to forest fragmentation, in this case the species will avoid forest openings that are 90 m^2 or larger

Interestingly, the patterns were less pronounced and more ambiguous when we used distance sampling. These results lead us to believe that the scale that fire severity best described bird density (as calculated using distance sampling) applied to an area much larger than the territory size of any of our focal species (0.4–7.7 ha), in this case the scale that bird observations were documented (>12.6 ha). We contend that using occupancy modeling and by restricting bird observations to a scale approximating the territory sizes of the focal species, the scale that best describes patterns of occurrence has a biologically meaningful explanation.

Eastern Wood-pewees and Indigo Buntings responded to fire at smaller spatial scales (30 m^2). Both species are known to select forest edges and small clearings for breeding (McIntyre 1995; Greenberg and Lanham 2001) and thought to be sensitive to

forest fragmentation (Robbins et al. 1989; Kendrick et al. 2013). We found a positive relationship with increasing fire severity for both species, and the relationship was strongest when fire severity was summarized at small spatial scales. A strong relationship between fire severity and species occurrence at small spatial scales indicates that these species can exploit small patches of high severity fire within our study area.

Both Prairie Warblers and Yellow-breasted Chats showed strong occurrence patterns at larger spatial scales. Although both species are often found in recently disturbed forest clearings in the region (Franzreb et al. 2011), prior research suggests that they are both associated with large patches of second growth and early succession habitat (McIntyre 1995; Rodewald and Vitz 2005). Because high DNBR values at larger scales result from larger patches of high

severity fire, our findings again support those of past studies. The Yellow-breasted Chat showed the strongest relationship when fire severity was summarized at a scale of 150 m^2, suggesting that they are associated with intermediate size forest clearings. The Prairie Warbler showed the strongest relationship with fire at 210 m^2 suggesting that this species is associated with even larger patches of early successional forest than the Yellow-breasted Chat.

In contrast, both the Worm-eating Warbler and the Ovenbird show a negative relationship with increasing fire severity. Prior research suggests that Worm-eating Warblers are sensitive to forest fragmentation. Robbins et al. (1989) found that occurrence was reduced by 50 % when forest patches were smaller than 150 ha. The negative relationship between Worm-eating Warbler occurrence and fire severity at small spatial scales suggests that this species is sensitive to small patches of high severity fire. While high DNBR values at larger scales indicate larger patches of high severity fire, even small areas exposed to high severity fire may negatively influence this species. Patterns of Ovenbird occurrence are similar to those of the Worm-eating Warbler. Ovenbirds are also found in large tracts of continuous forest (Robbins et al. 1989; Greenberg and Lanham 2001) and our results, as well as those of Klaus et al. (2010), show a negative relationship between species occurrence and increasing fire severity. Stronger patterns of occurrence at small spatial scales suggest that Ovenbirds and Worm-eating Warblers are both sensitive to small patches of high severity fire.

Although both forest type and the threshold values influenced the agreement between field derived and remotely sensed indices, DNBR fire severity indices improved model predictions for all six of our focal species. While it is important to consider the implications of using DNBR when ecological processes other than fire are confounding, we show that DNBR can be used to inform long term patterns of species occurrence at broad spatial scales. Because we were able to generate DNBR values for the entire footprint of many of the fires that burned within the study area since 1984, this study provides a good illustration of how pixel based indices can be used to explore relationships between species occurrence and the spatial extent of the habitat characteristics that they are associated with. A similar approach should be useful for informing patterns that arise from a wide

variety of ecological processes, including species responses to insect outbreaks, blow downs, ice storm damage, or urban development, as long as they are quantified using pixel based indices. In addition to Landsat imagery, the expanding use of unmanned aircraft and the proliferation of Light Detection and Ranging products will undoubtedly provide many opportunities to explore species habitat relationships at unprecedented spatial and temporal scales.

Compliance with ethical standards

Conflict of Interest The authors declare that they have no conflict of interest.

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