

Evaluating macroecological fire impacts on bird populations

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Fire regimes are context-dependent, as are the ways that animals respond. However, most information on animal responses to fire comes from short-term local field studies, which are hard to extrapolate across large areas for fire management while also capturing spatial variation. To address this challenge, we modeled data from eBird to map the direction, magnitude, and importance of fire regime associations at 27-km resolution across the ranges of six bird species used to guide management decisions in the US: red-cockaded woodpecker (*Leuconotopicus borealis*), Bachman's sparrow (*Peucaea aestivalis*), greater sage-grouse (*Centrocercus urophasianus*), pinyon jay (*Gymnorhinus cyanocephalus*), American goshawk (*Astur atricapillus*), and olive-sided flycatcher (*Contopus cooperi*). Our findings revealed previously undocumented landscape-scale variation in fire impacts on birds. Critically, the strength of fire regime associations varied widely in magnitude even when the direction of those associations (positive, neutral, or negative) remained constant. This analytical workflow provides not only a flexible approach for assessing macroecological fire impacts but also finer-scale information sufficient for resource prioritization and decision-making.

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Fire is an important disturbance process that shapes biodiversity patterns (He *et al.* 2019). Historical fire frequency, seasonality, and severity vary substantially across space, and animal communities are in turn adapted to local fire regimes (Jones *et al.* 2023). Fire and biodiversity are intertwined, and fire management is increasingly viewed as an important tool for conservation. As a result, land managers face the task of promoting natural fire regimes while also protecting species against climate- and human-driven changes to fire conditions, which threaten species' persistence (Kelly *et al.* 2020).

Fire management to promote biodiversity requires knowledge about animal relationships to habitat and disturbance, but these relationships are context-dependent, heterogeneous, and difficult to extrapolate across scales (Nimmo *et al.* 2022). Much of what is known about animal–fire relationships comes from short-term local studies, yielding information that fails to capture the full suite of species' responses across their geographic ranges (Fontaine and Kennedy 2012). This variation presents challenges to applied conservation and fire management. For example, fire-mediated habitat associations of spotted owls (*Strix occidentalis*) vary across space, suggesting that the same conservation measures may impact the species differently in different parts of its range (Wan *et al.* 2017). Uncertainty in animal responses to contemporary fires is exacerbated by rapidly changing fire regimes

driven by climate change and anthropogenic activity (Bowman *et al.* 2020; Stillman *et al.* 2023b). To make better conservation decisions in a fiery world, we need information on animal responses to fire across large areas while also capturing variation at scales that are tractable for fire management.

Studying variation in ecological processes across space and time—called nonstationarity—can link broad-scale patterns in animal–fire relationships to localized information needs for conservation and management (Heffernan *et al.* 2014; Rollinson *et al.* 2021). For most environmental systems, however, local studies are often unable to generate adequate data for inference across spatial and temporal scales. Here, we assessed landscape-scale fire responses by a suite of bird species across the contiguous US using data from eBird (<https://ebird.org>), a global participatory science platform for avian population monitoring (Sullivan *et al.* 2014). By employing over 31 million high-quality checklists submitted by eBird participants, we used spatiotemporal ensemble modeling to account for, and measure, nonstationary effects of fire and habitat on bird populations. We then summarized information across the model ensemble to investigate spatially explicit relationships between species' abundance and three fire regime characteristics: time since fire, fire frequency, and fire severity.

We focused our study on six bird species of conservation concern that frequently influence land-management decisions such as the implementation of prescribed fire, efforts to manage landscapes for beneficial fire effects, and efforts to mitigate potentially harmful fire effects. We had three primary objectives: (1) examine the extent to which species' responses to fire regime characteristics vary across space in direction, magnitude, and importance; (2) estimate the percent of species' populations within the area of strongest fire responses; and (3)

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demonstrate a case study to visualize the observed fire regime that maximizes local abundance for the red-cockaded woodpecker (*Leuconotopicus borealis*), a federally endangered species associated with fire-maintained forests. Our study represents an innovative approach for evaluating macroecological bird responses to fire while also providing landscape-scale information to aid resource prioritization and decision-making.

Methods

We used eBird data to model six species representing exposure to a range of fire conditions in the US: red-cockaded woodpecker, Bachman's sparrow (*Peucaea aestivalis*), greater sage-grouse (*Centrocercus urophasianus*), pinyon jay (*Gymnorhinus cyanocephalus*), American goshawk (*Astur atricapillus*), and olive-sided flycatcher (*Contopus cooperi*) (Figure 1). We used eBird checklists from the contiguous US between 2011 and 2021 with data-quality filters based on best practices (Johnston *et al.* 2021). To avoid confounding spatial nonstationarity with seasonal movements of birds, we only included data from the breeding season for the two nonresident species, American goshawk (May 3–July 5) and olive-sided flycatcher (June 21–July 19). To account for biases arising from the eBird observation process, we matched checklists to a suite of 20 covariates that capture important sources of variation in detection rates, including observer effort, observer skill, weather, and year (Johnston *et al.* 2021). To capture species' landscape-scale environmental associations, we summarized 70 environmental covariates describing land cover, hydrology, anthropogenic land use, elevation, and

topography within a 1.5-km neighborhood centered on the checklist location (Appendix S1: Table S1). Finally, we included three fire regime covariates describing fire conditions within the 1.5-km neighborhood over the 10 years prior to each checklist date: *time since fire* (covariate 1) was measured as the decimal number of years (to the nearest day) since the most recent vegetation fire; *fire frequency* (covariate 2) was measured as the number of years in which vegetation fire was detected, ranging from 1–10 years; and *fire severity* (covariate 3) represented the proportion of the 1.5-km neighborhood that burned at high severity (ie vegetation consumed) in the past 10 years (Appendix S1: Panel S1 and Table S1). Together, these three covariates can be used to distinguish the broad range of fire regimes present in the US, such as high-frequency low-severity burns, fire-suppressed areas, and areas affected by recent wildfires.

Our analytical approach employed a three-step process to capture spatial variation in species–fire relationships. First, we used a species-specific Adaptive SpatioTemporal Exploratory Model (AdaSTEM; Fink *et al.* 2020) to analyze spatial variation in species' associations with local fire regimes (Appendix S1: Panel S1). AdaSTEM is an ensemble of independent regional regression models generated by partitioning the geographic study extent into a lattice of windows and then fitting independent regression models, called base models, to spatially and temporally sub-sampled training data within each window. The ensemble is based on 200 randomly located partitions, resulting in a large set of partially overlapping, uniformly distributed base models (Figure 2). Spatially explicit estimates of response–covariate associations were computed by averaging

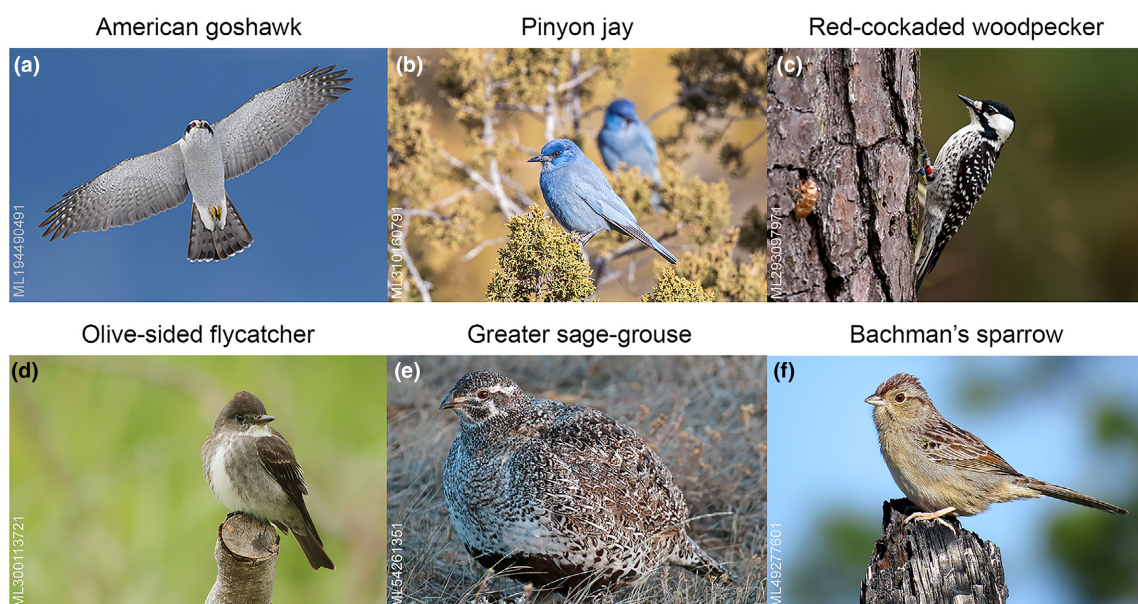


Figure 1. This study uses eBird data for six species within the contiguous US. Photographs were obtained from The Macaulay Library at the Cornell Lab of Ornithology: (a) American goshawk *Astur atricapillus* (image credit: Darren Clark), (b) pinyon jay *Gymnorhinus cyanocephalus* (image credit: Michael Henry), (c) red-cockaded woodpecker *Leuconotopicus borealis* (image credit: Shailesh Pinto), (d) olive-sided flycatcher *Contopus cooperi* (image credit: Jeremiah Trimble), (e) greater sage-grouse *Centrocercus urophasianus* (image credit: Jordan Roderick), and (f) Bachman's sparrow *Peucaea aestivalis* (image credit: Howard West).

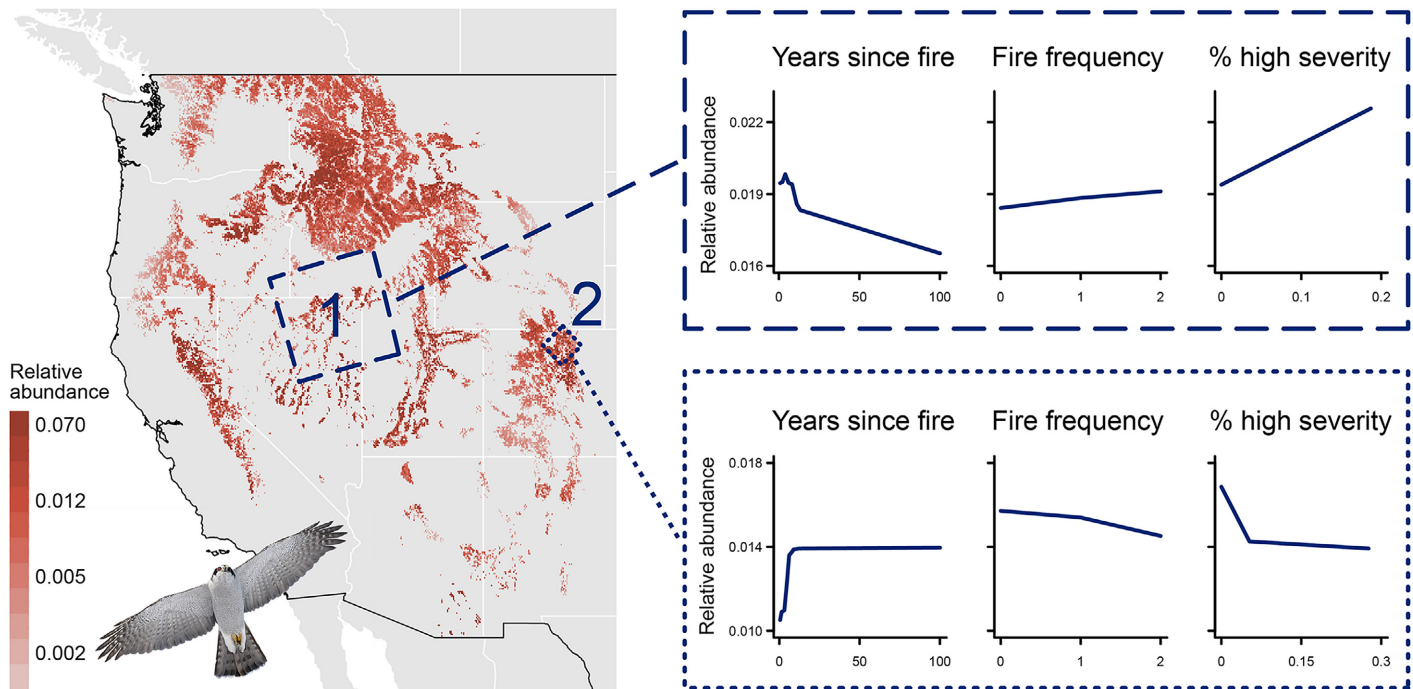


Figure 2. We used a spatiotemporal ensemble modeling approach to study spatial variation in species–fire relationships. Data were repeatedly divided into spatial windows based on data density and species’ prevalence, and separate models were fitted to the data in each window. The map shows two example windows (numbered boxes outlined in blue dashes) overlaid on eBird relative abundance data for the American goshawk (*Astur atricapillus*) during the breeding season. Each local model generated learned associations between fire covariates and relative abundance (eg line plots to the right). We then summarized these relationships through the ensemble of models to estimate local associations with fire covariates and how these associations change across space. Image credit: Darren Clark/The Macaulay Library at the Cornell Lab of Ornithology.

across all the base models that overlap the given location. We also computed spatially explicit estimates of uncertainty to facilitate comparison between landscapes. A two-step random forest hurdle model was selected as the base model to adaptively learn associations between species’ responses (occurrence and count) and the covariates described above. We used case-control sampling to account for class imbalance between detections and non-detections and spatial–temporal grid sampling to mitigate site selection bias.

Second, we summarized the learned associations between species’ responses and fire covariates using predictor importance (PI) and partial dependence (PD) statistics. PI statistics measure the strength of a covariate’s contribution to the local model, calculated as the difference in predictive performance for a model with all covariates versus the same model with permuted values of the focal covariate (Breiman 2001). Because PIs are relative to other covariates in the model, we ranked PIs in order of decreasing importance for the occurrence and count model components, separately, among 73 environmental covariates to facilitate ensemble-level inference. Next, we calculated PDs for each fire regime covariate. Here, PDs measured the functional form of the relationship between relative abundance (predicted occurrence $\times$ predicted count) and fire covariates, while marginalizing effects of all other predictors (Figure 2; Hastie *et al.* 2009). To summarize potentially complex associations as a single number, we calculated the average slope across

quantile bins of the PD estimate. Average values farther from zero indicate more consistent signals, while average values closer to zero reflect weak or highly nonlinear covariate relationships. For red-cockaded woodpeckers, we also calculated the observed fire frequency that maximized relative abundance predictions. Because this metric is conditioned on observed fire histories present in a region, it does not extrapolate potential relative abundances beyond observed values.

Finally, we generated spatial summaries of each statistic by averaging through the ensemble of overlapping local models to points on a 27-km $\times$ 27-km “landscape-scale” grid covering the species’ range (10–200 local models intersecting each point). We calculated PD uncertainty as the 80% confidence interval across the ensemble. Points where the 80% confidence interval did not overlap zero indicated that the PD signal was relatively consistent in direction among local models, and we focused our inference on these regions. Additional details on the spatiotemporal modeling workflow are provided in Appendix S1: Panel S1, and predictive performance metrics are provided in Appendix S1: Table S2.

Results

We mapped the direction, magnitude, and importance of fire regime associations at 27-km $\times$ 27-km resolution across the range of each of the six focal species (Figure 3). Our

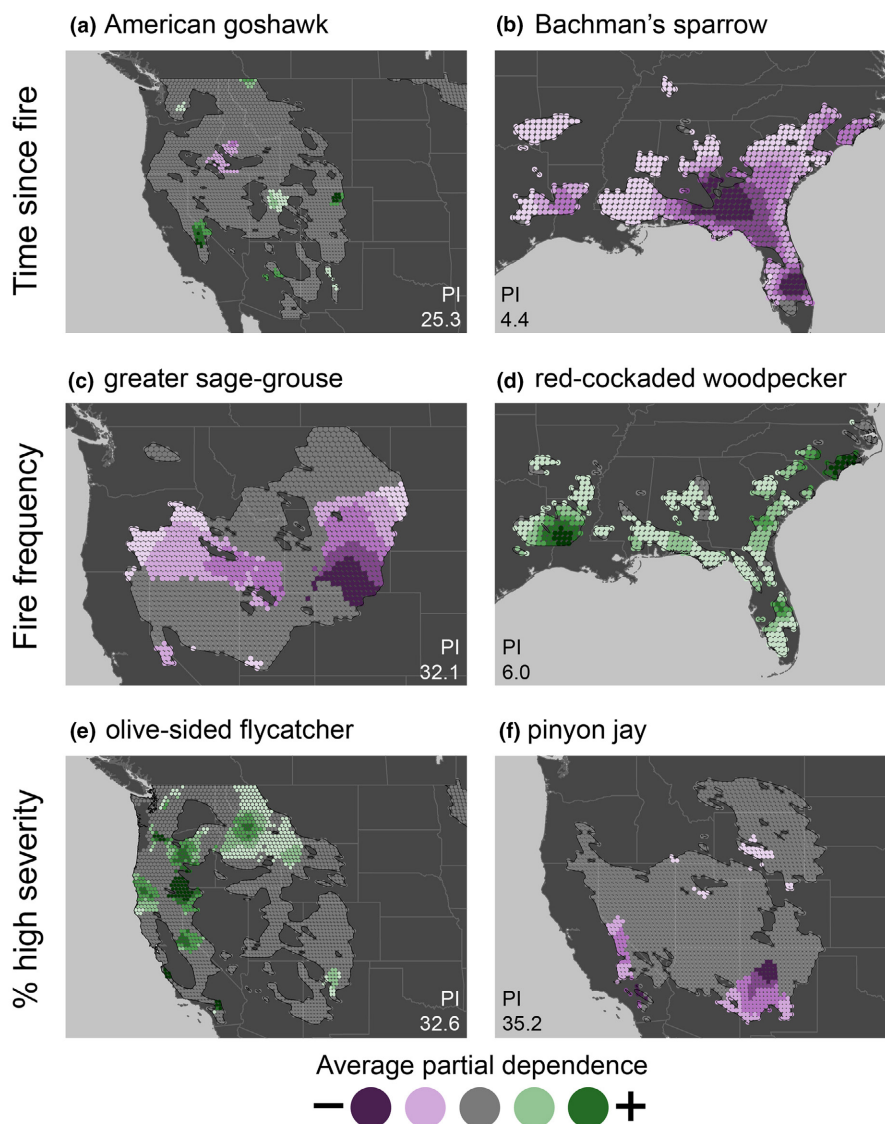


Figure 3. Macroecological assessment of fire regime associations for the six focal bird species showed landscape-scale variation in the magnitude, as well as the direction, of fire impacts. Maps depict the ensemble-averaged partial dependence summary for three fire regime covariates (time since fire [a and b], fire frequency [c and d], and fire severity [e and f]), where darker purple indicates a stronger negative relationship between the covariate and abundance, and darker green indicates a stronger positive relationship. Gray points indicate areas where 80% confidence intervals overlap zero or effect size was near zero. Thus, colored points represent areas with consistent, higher-magnitude signals across the ensemble of models as compared to areas with less consistent or lower magnitude relationships. Average predictor importance (PI) for species' occurrence is shown as a rank based on 73 environmental covariates. Possible values range from 1 (most important) to 73 (least important).

cross-scale assessment of fire impacts revealed previously undocumented spatial variation in fire regime associations. With the exception of greater sage-grouse, all focal species displayed both positive and negative effects in at least one fire covariate, even after the removal of estimates with low confidence (ie 80% confidence interval overlaps 0; Appendix S1: Table S3). For example, American goshawks showed opposite effects of time since fire in separate areas

of the species' range (Figure 3a). Critically, the strength of fire regime associations varied widely in magnitude even when the direction of fire regime associations remained constant. In Bachman's sparrows, for instance, the negative effect of time since fire on abundance was strongest in central Florida and portions of southern Georgia and Alabama, yet it was relatively weak in Mississippi, Arkansas, and eastern Oklahoma (Figure 3b). The average PI rank for fire covariates also varied substantially across space for all focal species (Appendix S1: Figure S1). Time since fire, for instance, was ranked in the top five habitat covariates across 80% of the Bachman's sparrow range, but its rank was >10 in 6% of the range.

Red-cockaded woodpeckers and Bachman's sparrows exhibited particularly strong associations with fire frequency (positive direction) and time since fire (negative direction), and our approach detected consistent signals for these relationships across 93–98% of the species' ranges (Figure 3, b and d). In contrast, pinyon jays and greater sage-grouse demonstrated overall negative responses to fire activity (Figure 3, c and f), and greater time since fire was associated with higher abundance across the majority ($\geq 55\%$) of their ranges (Appendix S1: Table S3). High-severity fire was generally less important than the other fire covariates, although this covariate still showed consistent directional effects in all six focal species. For example, in areas with a history of high-severity fire, olive-sided flycatcher abundance was higher while pinyon jay abundance tended to be lower (Figure 3, e and f).

By estimating the percent of a species' breeding population that overlaps with strong fire responses, we could evaluate range-wide fire impacts and potential threats from changing fire regimes. For instance, we found that 10.82% of the pinyon jay population, and 9.79% of the greater sage-grouse population, occurs in areas where we detected a consistent negative effect of severe fire. Bachman's sparrows, which are associated with frequent low-severity fire regimes (Tucker *et al.* 2004), showed negative responses to severe fire across 26.90% of the species' population. This contrasts with the olive-sided flycatcher, which showed a consistent positive response to severe fire across 39.7% of its population within the contiguous US.

The association between fire characteristics and bird abundance can be further linked to on-the-ground conditions by calculating the observed fire history that maximizes local relative abundance predictions. For red-cockaded woodpeckers, we found that the observed fire frequencies associated with high abundance varied considerably across the species' range (Figure 4). In portions of central and northern Florida, relative abundance was highest when five or more fires per 10 years occurred within 1.5 km of checklist locations. Fire frequency values were lower in the northern and western parts of the woodpecker's range. Because this metric is conditioned on observed fire histories present in a region, it does not extrapolate potential relative abundance beyond observed values, nor does it represent a recommended management target. However, by comparing these results against current fire intervals, managers can assess whether more frequent fire could benefit the species (ie current fire frequency is below the value that maximizes relative abundance), or whether additional research is necessary to determine whether increasing fire frequency beyond current rotations could further increase abundance.

Discussion

Efforts to conserve biodiversity must contend with increasing pressures from rapidly changing climate and fire regimes (Kelly *et al.* 2020), and effective conservation requires information for management decisions at local scales as well as information to understand patterns and priorities at broader scales. Using participatory science data for six avian species of management interest, our results describe continent-scale fire regime associations while also capturing landscape-scale variation across space. We used these results to additionally estimate the percent of species' populations with directional responses to fire and mapped the observed fire regime characteristics associated with high predicted abundance.

Using our approach, we were able to corroborate known species–fire associations for focal species and locations where fire relationships have been studied in the field. In the Florida panhandle, for example, we documented a strong positive relationship between red-cockaded woodpecker abundance and fire frequency, high importance for this covariate (eg top three covariates), and high abundance in areas with more than five fires per 10 years (Figures 3 and 4). These results mirror known associations from well-studied localities within the region, and current management guidelines for red-cockaded woodpeckers recommend prescribed burns at 1- to 2-year intervals (USFWS 2003; Martin *et al.* 2021), with similar recommendations for Bachman's sparrows (Tucker *et al.* 2004). Our findings also revealed novel variation in the magnitude—and even direction—of fire impacts within species, suggesting that the effects of fire management and shifting fire regimes understood at a particular location may not reliably inform management decision-making at other locations within the range.

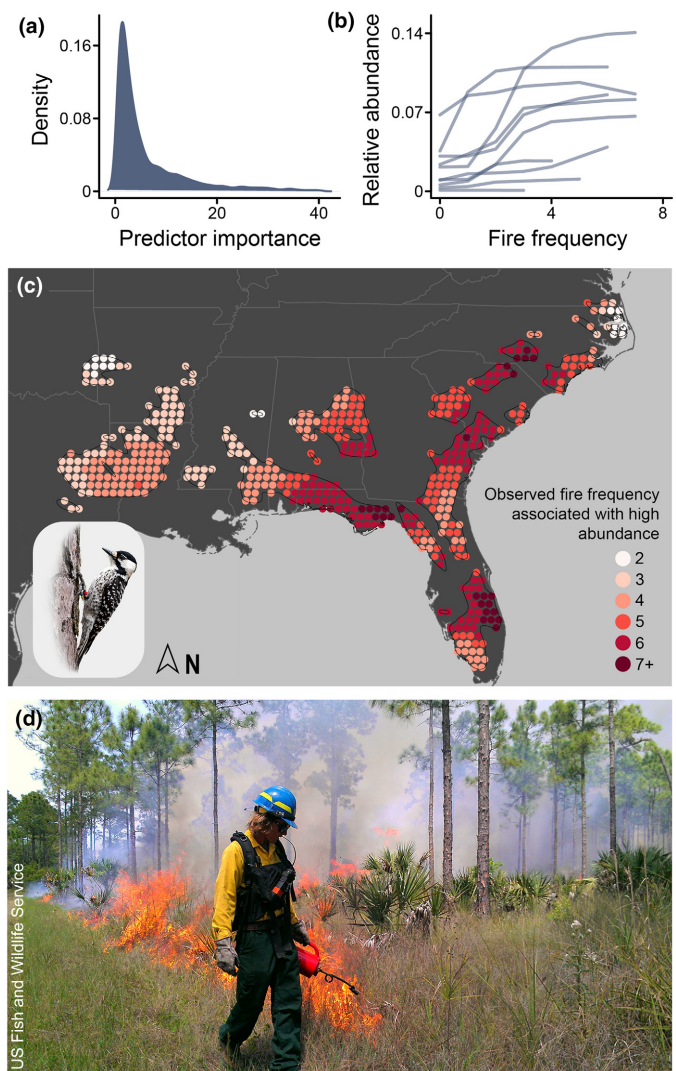


Figure 4. The observed fire frequency associated with high red-cockaded woodpecker (*Leuconotopicus borealis*) abundance varies across the species' range. (a) The distribution of average predictor importance rankings highlights the key role of fire frequency for red-cockaded woodpecker distributions. (b) Example partial dependence plots from 10 local models indicate that abundance tends to be higher with more frequent fire. (c) By collecting the fire frequency values (fires per 10 years) that maximize predicted abundance and averaging across the ensemble, we can map the observed fire frequency associated with high abundance across the species' range. (d) Prescribed fire management helps maintain habitat for red-cockaded woodpeckers, and region-specific fire management plans can be tailored to local habitat conditions. Image credits: *Leuconotopicus borealis* (Shailesh Pinto/The Macaulay Library at the Cornell Lab of Ornithology), prescribed fire (USFWS/Public Domain Mark 1.0).

These patterns likely reflect nonstationarity in the underlying processes governing bird populations, including the availability of different habitat types and the different fire regimes they support. Nonstationary patterns of fire responses have been detected for highly studied taxa where field studies can be replicated across broad spatial scales (Wan *et al.* 2017). For species that are more data-limited, our results can help prioritize key management areas and identify locations where

targeted field studies are needed to uncover potential mechanisms behind these patterns or reduce uncertainty. In some cases, large portions of mapped fire regime associations show relatively weak or uncertain relationships (eg Figure 3f), despite expectations that fire impacts should tend toward a certain direction across the range (Appendix S1: Table S3). One potential explanation is the presence of complex, nonlinear relationships between species' abundance and fire at the landscape scale, leading to variation in the direction of estimated PD slopes. We emphasize that the fire covariates used in our study describe fire history at coarser scales (1.5-km buffer around eBird checklists) as compared to field protocols such as avian point counts, and our results describe fire regime associations rather than responses to particular fire events. Thus, direct comparisons between our findings and field observations must carefully consider the influence of spatial scale on inference.

Restoring and maintaining locally appropriate fire regimes is a growing challenge for biodiversity conservation. In the western US, fires are becoming larger and more severe as a result of historical fire suppression practices coupled with climate-induced drought and climatic extremes (Bowman *et al.* 2020; Hagmann *et al.* 2021; Iglesias *et al.* 2022). Furthermore, many regions across the US show evidence of fire deficits and may require active management through prescribed fire (Ryan *et al.* 2013). It is critical to understand how species respond to these changing conditions, which parts of their range are most sensitive to change, and where targeted fire management interventions are likely to have the most benefit. By describing areas with consistent negative or positive effects of fire regime characteristics, our results provide a pathway to prioritize areas for fire restoration or fire refugia. For example, this spatial information can be leveraged to identify where pinyon jays may be most negatively impacted by an increase in severe fire, or where frequent prescribed fire may most efficiently support regional recovery of Bachman's sparrow populations. It can also support targeted investment strategies for fire management (eg prescribed fire) or mitigation (eg fuels reduction) by directing resources toward areas that need it the most, as an alternative to a "one-size-fits-all" approach (Martin *et al.* 2021). Similarly, access to landscape-scale information on fire effects can facilitate work to assess and plan for potential impacts of altered fire regimes under climate change, with key policy implications for broad-scale management planning (eg Wildfire Crisis Strategy; USFS 2022).

As applied ecological research increasingly adopts a macrosystems approach, it has become apparent that simply extrapolating phenomena observed at local scales to regional or continental scales will not sufficiently describe ecological processes (Heffernan *et al.* 2014; Soranno *et al.* 2014). Our study highlights potential avenues that, in combination, can help address this challenge. First, data streams from participatory science make it possible to monitor biodiversity across greater spatial and temporal extents, especially when resources are limited (Stuber *et al.* 2022; Stillman *et al.* 2023a). Second,

methodological advances create opportunities to improve analysis of large datasets without having to assume that species-habitat relationships remain constant (Fink *et al.* 2020). Moving forward, our approach could be extended to include large numbers of species while accommodating additional habitat covariates with relevance to land management. Effectively managing fire-prone lands to promote biodiversity hinges on our understanding of species' responses to local fire regimes. Macroecological approaches that capture landscape-scale heterogeneity, across species, hold considerable promise for addressing this challenge.

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Data Availability Statement

Ensemble-averaged data and results (Stillman 2025) for all species-fire relationships are available from Figshare at <https://doi.org/10.6084/m9.figshare.25607607.v2>. This study relies on data from eBird, available at <https://science.ebird.org/en/use-ebird-data>.

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Supporting Information

Additional material can be found online at <http://onlinelibrary.wiley.com/doi/10.1002/fee.70003/supinfo>