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Original Research

Regional Context for Balancing Sagebrush- and Woodland-Dependent Songbird Needs with Targeted Pinyon-Juniper Management ☆

Jason D. Tack [1,*], Joseph T. Smith [2], Kevin E. Doherty [3], Patrick J. Donnelly [4], Jeremy D. Maestas [5], Brady W. Allred [2], Jason Reinhardt [6], Scott L. Morford [7], David E. Naugle [2]

[1] US Fish and Wildlife Service, Habitat and Population Evaluation Team, Missoula, MT, 59812, USA
[2] W. A. Franke College of Forestry and Conservation, University of Montana, Missoula, MT, 59812, USA
[3] US Fish and Wildlife Service, Science Applications, Lakewood, CO, 80235, USA
[4] US Fish and Wildlife Service, Intermountain West Joint Venture, Missoula, MT, 59812, USA
[5] US Department of Agriculture, Natural Resources Conservation Service, West National Technology Support Center, Portland, OR, 97232, USA
[6] US Department of Agriculture, Forest Service, Rocky Mountain Research Station, Moscow, ID, 83843, USA
[7] Numerical Terradynamic Simulation Group, University of Montana, Missoula, MT 59812, USA

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A B S T R A C T

In the western United States, pinyon-juniper woodlands have expanded by as much as sixfold among sagebrush landscapes since the late 19th century, with demonstrated negative impacts to the behavior, demography, and population dynamics of species that rely on intact sagebrush rangelands. Notably, greater sage-grouse *(Centrocercus urophasianus)* are unable to tolerate even low conifer cover, which can result in population declines and local extirpation, whereas removing expanding conifer cover has been demonstrated to increase sage grouse population growth rates and sagebrush obligate songbird abundance. Yet conifer management among sagebrush landscapes has been met with concerns about unintended impacts to species that rely on conifer woodlands, notably the pinyon jay *(Gymnorhinus cyanocephalus),* whose population declines are distinctive among birds breeding in pinyon-juniper woodlands. Spatial models of bird abundance can help management prioritize future actions in light of multiple species requirements, while also providing a framework to retroactively test the impact of past treatments. We used Breeding Bird Survey data to model indices to abundance in relation to multiscale habitat features including landcover, fire, topography, and climate variables for nine songbird species reliant on sagebrush and pinyon-juniper woodlands for breeding. Predictive maps allowed us to also examine the overlap of conifer management conducted by the Sage Grouse Initiative (SGI), which targets management of early successional conifers among priority sage-grouse habitats, with predicted indices to abundance of songbirds. Our findings demonstrate that targeted sage grouse habitat restoration under SGI was not at odds with protection of pinyon jay populations. Rather, conifer management has largely occurred among northern sagebrush landscapes where models suggest that past cuts likely benefit Brewer's sparrow and sage thrasher while avoiding pinyon jay habitats.

Introduction

Native tree species are expanding into shrublands and grasslands globally at an alarming rate, increasing from 40% to 600% in distribution across every continent except Antarctica (Nackley et al. 2017). Resulting shifts in vegetation structure and composition are affecting a broad suite of ecosystem services and values, including wildlife species of conservation concern (Baruch-Mordo et al. 2013; Fuhlendorf et al. 2017, 2002). In North America, pinyon-juniper woodlands, composed of both juniper (*Juniperus* spp.) and pinyon

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* Correspondence: Jason Tack, 412 ISB, 32 Campus Dr, Missoula, MT 59812, USA: 406-544-8023

E-mail address: jason_tack@fws.gov (J.D. Tack).

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pine (*Pinus* spp., hereafter collectively referred to as *conifer*), are among the most dominant vegetation types across the intermountain western United States, supporting critical biodiversity, ecosystem services, and economic potential (Romme et al. 2009). Since European settlement, the distribution of conifer species has expanded between twofold and sixfold across the Great Basin and northern Colorado Plateau, likely due to the compounding effects of historic high-intensity grazing, subsequent increases in natural fire return intervals, and favorable climatic conditions that helped tree growth proliferate among sagebrush (*Artemisia* spp.) systems (Miller et al. 2019). Trends of conifer expansion persist, with absolute tree cover increasing by 50% across western US rangelands over the past 30 yr, while more than one-quarter of rangelands are experiencing tree expansion (Morford et al. 2022). Some 90% of pinyon-juniper expansion has occurred in sagebrush landscapes (Miller et al. 2011), leading to a loss of sagebrush and herbaceous vegetation (Roundy et al. 2014) and associated specialist wildlife species (Rickart et al. 2008; Baruch-Mordo et al. 2013). As a result, management to remove conifers from former shrublands has been adopted as a widespread conservation practice to mitigate negative ecosystem impacts over the past decade (Miller et al. 2017).

Central to the proliferation of recent restoration efforts is the conservation of sagebrush obligate wildlife under the umbrella of greater *(Centrocercus urophasianus)* and Gunnison sage-grouse (*Centrocercus minimus,* hereafter collectively referred to as sage grouse; Miller et al. 2017; Doherty et al. 2018). Sage grouse are particularly vulnerable to conifer expansion (Baruch-Mordo et al. 2013). Conifer presence reduces the quality of sage grouse habitat through both behavioral avoidance by nesting females (Severson et al. 2017a) and the demographic consequences of reduced nest (Severson et al. 2017b), brood (Sandford et al. 2017), and female survival (Coates et al. 2017). Experimental research among conifer removal projects has demonstrated that sage grouse quickly return to restored areas, with subsequent increases in nest, brood, and female survival in treated areas (Sandford et al. 2017, Severson et al. 2017b, 2017c). Ultimately, sagebrush restoration through conifer management is translating into measurable population benefits at landscape scales, accounting for a 12% increase in population growth rates compared with control areas in southern Oregon (Olsen et al. 2021). Efficacy of accelerating investments in large-scale restoration efforts via conifer removal was one key factor in preventing the need for an Endangered listing status for sage grouse (CFR 2015), which continues to be a primary management practice for voluntary conservation among the sagebrush biome (Natural Resources Conservation Service 2021).

Benefits from conifer removal targeted for sage grouse likely accrue for other sagebrush obligate species, though few studies have actually measured resulting benefits of management across taxa (Bombaci and Pejchar 2016; Zeller et al. 2021). Conifer removal projects for sage grouse have had a high congruence with the predicted distributions of certain sagebrush obligate songbirds (Donnelly et al. 2017), and past management has resulted in local increases in abundances of shrubland species including Brewer's sparrow *(Spizella breweri)* and green-tailed towhee (*Pipilo chlorurus;* Holmes et al. 2017). Conversely, the potential for unintended negative impacts to species reliant on conifer woodlands remains a pervasive question, especially for nontarget songbird species of conservation concern (Boone et al. 2018; Zeller et al. 2021).

Among songbirds in the western United States, those reliant on pinyon-juniper or sagebrush for breeding habitat have largely demonstrated contrasting population trends over the past 50 yr that are consistent with an expanding footprint of conifer among sagebrush landscapes (Table 1). Brewer's sparrow, sagebrush sparrow, and sage thrasher *(Oreoscoptes montanus),* all reliant on unfragmented sagebrush landscapes for breeding, have experienced population declines, whereas woodland songbirds including ash-throated flycatcher *(Myiarchus cinerascens),* gray flycatcher *(Empidonax wrightii),* and gray vireo *(Vireo vicinior)* exhibit increasing populations (Sauer et al. 2020; see Table 1). The one notable exception among woodland-reliant species is the pinyon jay *(Gymnorhinus cyanocephalus),* which depends on a mutualistic relationship with conifer nut production for their survival and reproduction (Ligon 1978). Pinyon jays have declined more severely since 1968 than any other land bird inhabiting sagebrush-associated landscapes (Boone et al. 2018; Sauer et al. 2020), with concern culminating in the US Fish and Wildlife Service being petitioned to list the pinyon jay as Threatened or Endangered under the Endangered Species Act (https://defenders.org/sites/default/files/inline-files/2022.4.25_FWS_Listing%20petition_Pinyon%20Jay.pdf; accessed 3 May, 2022).

Mechanisms underlying pinyon jay population declines are unknown. Factors hypothesized to contribute to declines include climate-mediated declines in pinyon pine seed production, intentional pinyon-juniper removal, tree die-off, wildfire, and drought, as well as transition of the preferred heterogeneous pinyon pine and sagebrush stands to persistent woodlands by a process known as "infill" (Boone et al. 2018). Following the infill of mixed sagebrush and conifer stands, individual trees have reduced seed productivity; thus, conifer infill may be analogously detrimental to pinyon jay as encroachment is to sagebrush obligate wildlife like the sage grouse (Fig. 1). Ultimately, improved spatial planning products for both sagebrush and woodland obligate birds of conservation concern are needed to enable informed decisions about potential impacts of ongoing management and foster a holistic approach to multiple species management along the shrubland to woodland continuum (Maestas et al. 2021).

We used citizen science breeding bird data to develop spatial models predictive of the relative abundance of both sagebrush and woodland obligate songbirds. Maps were developed to depict relative species distributions spatially to help guide spatial targeting of future conservation actions in light of songbirds and to act as key data in multicriteria decision analyses. Maps also allow us to retrospectively evaluate past conifer removal projects in relation to predicted songbird distributions to determine if declining species have been passively targeted, or avoided, by conifer management intended to benefit sage grouse. Applying spatial models to BBS data provides an effective tool to learn about large-scale distribution of breeding birds (Niemuth et al. 2017). We chose to model species-habitat relationships among songbirds that are likely to be either indirectly targeted for conservation as sagebrush obligates, or influenced by conifer management, and typically appear in conservation planning documents (e.g., Gillihan 2006). We overlaid past conifer cuts conducted through the Sage Grouse Initiative with predictive distributions of declining songbirds to evaluate the potential impacts of conifer management for sage grouse on nontarget species.

Methods

Study area

Our aim was to model species distributions inhabiting the sagebrush (*Artemisia* spp.) biome within the western United States. This geography encompasses a diversity of public and private land tenures and jurisdictional boundaries and is largely defined by cover of both sagebrush- and grassland-dominant understories. Domestic livestock grazing is the primary land use among sagebrush landscapes, while major anthropogenic factors contributing to habitat loss and fragmentation vary spatially and include infrastructure associated with energy development, cultivation, and urban development. Persistent ecosystem threats also include invasion of exotic annual grasses (e.g., *Bromus tectorum, Taeniatherum*

Table 1
Songbird species used to develop species distribution models and resulting spatial predictions from Breeding Bird Survey (BBS) Data. Sagebrush and woodland dependent species were considered for modeling, and we used BBS 1966-2019 survey-wide estimated trends (with 95% CI) to identify declining species (Sauer et al. 2020). We only modeled species if they were detected at least 5 times within Commission for Environmental Cooperation Level 3 ecoregions from 2011-2016 (Fig. S1, available online at …, for map and corresponding ecoregion names).

Species	Vegetation community	BBS trend	Ecoregions
Brewer's Sparrow	Sagebrush	−0.87 (−1.51, −0.20)	1, 2, 4, 5, 6, 7, 8, 9, 10, 11, 13, 14, 15, 16, 17, 18, 19, 20, 21, 22, 23, 24
Green-tailed Towhee	Sagebrush	0.05 (−0.45, 0.51)	1, 2, 4, 5, 6, 9, 11, 13, 16, 18, 19, 20, 21, 23, 24
Sagebrush Sparrow	Sagebrush	−1.16 (−2.38, −0.04)	1, 2, 5, 6, 8, 13, 16, 18, 20, 21, 23, 24
Sage Thrasher	Sagebrush	−0.43 (−1.14, 0.28)	1, 2, 5, 6, 8, 9, 11, 13, 16, 17, 18, 19, 20, 21, 23, 24
Ash-throated Flycatcher	Woodland	0.71 (0.14, 1.18)	1, 2, 3, 4, 5, 6, 8, 9, 12, 14, 16, 19, 21, 22, 23, 24
Gray Flycatcher	Woodland	1.44 (0.03, 2.40)	1, 2, 5, 6, 7, 8, 9, 13, 14, 16, 19, 21, 23, 24
Gray Vireo	Woodland	3.91 (2.51, 5.48)	1, 5, 6, 14, 21, 23, 24
Juniper Titmouse	Woodland	0.08 (−0.78, 0.90)	1, 5, 6, 9, 14, 16, 21, 22, 23, 24
Pinyon Jay	Woodland	−1.98 (−3.44, −0.88)	1, 2, 5, 6, 9, 13, 14, 16, 18, 19, 21, 23, 24

caput-medusae, Ventenata dubia) and conifer expansion. To best capture a sampling frame representative of sagebrush landscapes, we merged boundaries defined by sagebrush cover with the addition of existing sage grouse Priority Areas for Conservation and management zones (Sage Grouse Initiative, n.d.) and the historic sage grouse species range (Runge et al. 2019; Fig. S1; available online at …).

Avian count data

Selected species were those commonly identified in sagebrush and pinyon-juniper management plans including woodland obligates ash-throated flycatcher, gray flycatcher, gray vireo, juniper titmouse *(Baeolophus ridgwayi),* and pinyon jay and sagebrush-reliant Brewer's sparrow, green-tailed towhee, sagebrush sparrow *(Artemisiospiza nevadensis),* and sage thrasher (see Table 1). We used point count data from the US Geological Survey's Breeding Bird Survey (BBS), an annual roadside survey conducted from late May to early July by citizen scientists skilled in avian identification (Pardieck et al. 2017). Along each survey route, participants conduct 50, 3-minute point counts approximately every 0.8 km (i.e., ~40-km routes) and record every bird seen or heard within 400 m. We digitized stop locations using available information on stop descriptions. When stop descriptions were unavailable, we generated equidistant points along routes between known stop locations, or between the beginning and ending points of survey routes when no stop locations for routes were available. In total, we had data available for 30 888 stops from 625 BBS routes. We constrained our sample from 2011 to 2016 such that our response data could best match contemporary spatial predictor variables.

Spatial covariates

We broadly hypothesized that heterogeneity in species counts would be influenced by patterns of vegetation, topography, anthropogenic disturbance, fire history, and weather and climate (Table 2). Specifically, we measured the percent cover of summarized vegetation types around point counts that were classified as sagebrush, nonsagebrush shrublands, conifer, pinyon-juniper woodlands, scrub and woodlands, and riparian areas (Rollins 2009; Table 2). We also combined cropland and developed lands to characterize anthropogenically disturbed areas. Topography is an important component in structuring bird communities (Knick et al. 2008), so we included measures of elevation, terrain ruggedness (TRI), and a multiscale topographic position index (mTPI) that broadly characterizes landforms (e.g., valley bottoms, ridges) within 270 m, 810 m, and 2 430 m, such that the metric can differentiate between both local and broad-scale geomorphological features (Theobald et al. 2015). Fire is a pervasive disturbance among sagebrush landscapes structuring vegetation patterns, with the potential for long-lasting negative impacts to densities of breeding birds (Holmes and Robinson 2013). Therefore, we used spatial data of fire boundaries and measured the proportion of burned areas 5, 10, and 15 yr before each point count to characterize the potential legacy effects of fire.

Table 2
Candidate variables used to describe heterogeneity in Breeding Bird Survey stop level occurrence and count data. Variables were represented as either a mean value across circular spatial windows or summarized over a temporal window when data were available.

Variable (abbreviation)	Spatial window	Temporal window
Sagebrush (sage)[1]	120 m, 1 km, 6.4 km	NA
Grassland/Herbaceous (herb)	120 m, 1 km, 6.4 km	NA
Shrubland (shrb)[1]	120 m, 1 km, 6.4 km	NA
Conifer (conf)[1]	120 m, 1 km, 6.4 km	NA
Crop/Disturbed (dist)[1]	120 m, 1 km, 6.4 km	NA
Pinyon/Juniper (piju)[1]	120 m, 1 km, 6.4 km	NA
Scrubland/Woodland (scrb)[1]	120 m, 1 km, 6.4 km	NA
Riparian (ripa)[1]	120 m, 1 km, 6.4 km	NA
Burned Area (burn)[2]	120 m, 1 km, 6.4 km	5, 10, 15 yr
Avg Min Temp (tmin)[3]	1 km	May 15-Jul 15
Avg Max Temp (tmax)[3]	1 km	May 15-Jul 15
Total Spring Precip (sprp)[3]	1 km	Mar 15-Jul 15
Total Winter Precip (wprp)[3]	1 km	Dec 1-Mar 14
NDVI (ndvi)[4]	6.4 km	May 15-Jul 15
Elevation (elev)[5]	30 m	NA
TRI (tri)[6]	1 km	NA
Multiscale TPI (tpi)[7]	NA*	NA
PDSI (pdsi)[8]	NA	June

[1] Landfire 2016 Remap; Rollins (2009).
[2] Eidenshink et al. (2007).
[3] Thornton et al. (2012).
[4] Landsat-7 imagery courtesy of the US Geological Survey.
[5] Gesch et al. (2002).
[6] Riley (1999).
[7] Theobald et al. (2015).
[8] Abatzoglou et al. (2017).
* Index summarized from TPI calculated at 270 m, 810 m, and 2.43 km (Theobald et al. 2015)

We used weather and climate data that likely influence the abundance of breeding birds. Because precipitation is the primary driver of annual herbaceous growth, we measured total precipitation occurring both over winter (Dec 1 to March 14) and spring months (March 15 to July 15) as our study area encompassed ecoregions where precipitation largely occurs during winter (Great Basin) or spring and early summer (Great Plains). We also summarized patterns of temperature as mean maximum and minimum temperatures over the BBS sampling period (May 15 to July 15) to characterize thermal niches for each species (Thornton et al. 2012). We used the Normalized Difference Vegetation Index (NDVI) to broadly describe site productivity as NDVI has been correlated with critical life stage requirements for breeding birds (Sweet et al. 2015). We calculated mean NDVI across Landsat scenes over the BBS sampling period and omitted pixels that were identified as cultivated or woodland in an effort to best characterize the produc-

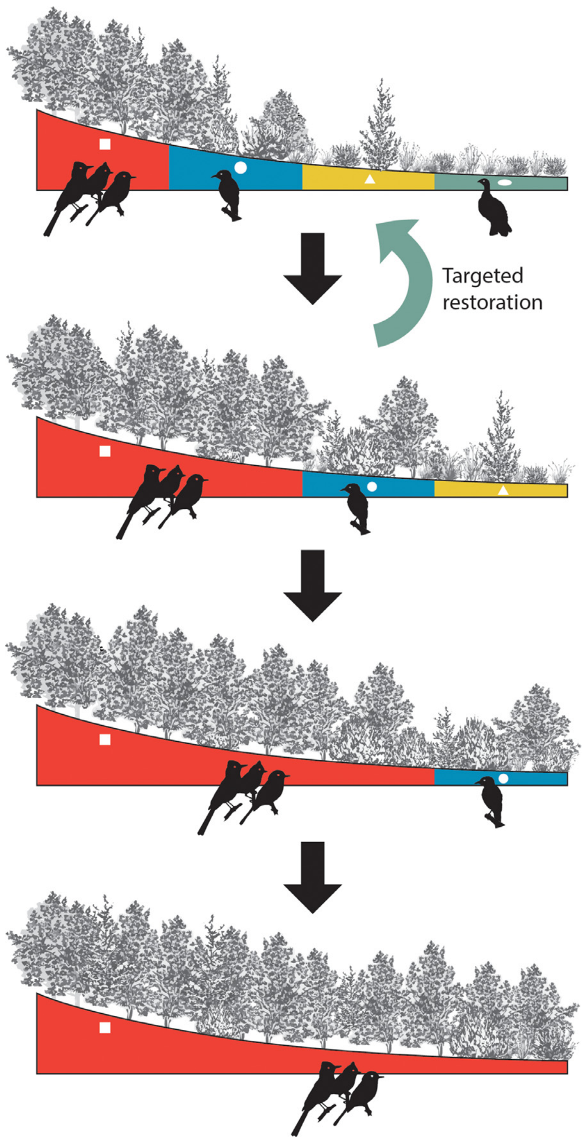

Figure 1. Hypothetical illustration depicting how conifer expansion and infill may impact habitats for both sagebrush obligate and woodland reliant birds. The top panel shows a landscape that supports a diversity of bird species partitioned by different ecological sites: persistent woodlands supporting dense forest birds (red/square), heterogeneous woodlands supporting birds reliant on more open stands, such as, pinyon jay (blue/circle), and sagebrush shrublands supporting obligate birds, such as, sage grouse where encroaching conifers are targeted for restoration (yellow/triangle to green/oval). Remaining panels depict shifting habitat niches as conifer expansion and infill, without intervention, displace species like pinyon jay and sage grouse that rely on mixed woodlands or treeless shrublands. BBS trends lend support to this hypothetical scenario as both pinyon jay and sagebrush obligates have been in decline, while some songbird populations reliant on persistent pinyon-juniper woodlands have increased (Table 1).

tivity of sagebrush communities. Drought is a major factor shaping rangelands, so we used Palmer's Drought Severity Index (PDSI) to identify the spatial and temporal patterns of persistent, long-term drought across the study area (Abatzoglou et al. 2017). We matched all temporally referenced weather and climate data to the year of observation across surveys. The resolution varied across spatial data sources (see Table 1), so we resampled all data to 120-m resolution rasters for prediction using bilinear interpolation with the R raster package (Hijmans et al. 2016). Lastly, we included stop (1 to 50) as a covariate in all models as a proxy for time of day, which is known to influence detection of birds (Niemuth et al. 2017). Survey start times vary by route location, though they generally start 30 min before sunrise. We removed samples if any BBS survey conditions were violated during the survey. All continuous covariates were standardized (subtracted the mean and divided by the standard deviation) to aid model convergence and coefficient interpretation. All data sources for spatial covariates used in analyses are listed in Table 2.

Spatial and temporal scales

We chose three spatial scales to summarize landcover and burned area covariates for consideration in modeling counts including 120 m, 1 000 m, and 6 400 m. The smallest scale (~4.5 ha) corresponds to average breeding territory sizes of songbirds among their sagebrush habitats (Rotenberry et al. 1999). Past work has demonstrated that the amount of shrub and grass cover within the 1 000-m scale (~314 ha) has been an important predictor of habitat selection for sagebrush obligate songbirds (Rotenberry and Knick 1995). This buffer also matches the scale of a typical conifer removal project (e.g., www://conservationefforts.org). Lastly, we hypothesized that a 6 400-m scale (~12 868 ha) represented landscape-scale habitat shaping the home ranges of migratory passerines. Past research on sagebrush obligate response to conifer treatment indicated that treatments needed to be adjacent to large intact landscapes (> 14 000 ha) for sagebrush obligate songbirds to recolonize conifer removal areas (Knick et al. 2014).

Model fitting, selection, and evaluation

Not all species distributions encompassed the entirety of our sampling frame, and we wanted to ensure that we were including only data in analyses that had the potential for a particular species to occur (i.e., second-order habitat selection; Johnson 1980). Therefore, for each species we modeled only data from North American Commission of Environmental Cooperation level 3 ecoregions (CEC 1997) that contained > 5 detections between 2011 and 2016, such that predictions are constrained within the occupied range of our sampling frame for each species (see Fig. S1).

We sought to use one spatial scale to represent each landcover variable and one spatial and temporal scale to represent a fire variable for each species model. To determine the best-fit scales, we fit generalized linear mixed models (glmm) using a binomial error distribution (i.e., detected, undetected) for each landcover and fire variable independently, including random effects for year, route, and BBS observer ID to account for known sources of heterogeneity in BBS count data (Niemuth et al. 2017). We used detection/nondetection data for scale selection so that we wouldn't have to make assumptions about the proper error distribution for counts and assumed that the inherent relationship between occurrence and abundance (Royle and Nichols 2003) would capture relevant variables for count-based models. Using glmm in this step allowed us to calculate Akaike Information Criteria (AIC), from which we used the minimum value among landcover and fire variables to determine the best spatial and temporal scale among variables. Once we had determined a set of candidate variables for each species, we identified highly correlated variables by calculating pairwise Pearson's correlation coefficients ($|r| > 0.6$) and removed correlated variables that had lower support determined by higher AIC values.

Once candidate variables for each species were identified, we fit multiple variable models using a random forest approach with regression trees (Breiman 2001) and included fixed effects for years to account for interannual variation. We modeled count data with random forests regression trees because it was efficiently implemented without making assumptions about an appropriate error distribution and model structure across species and is generally found to outperform parametric species distribution models in predictive performance (Elith 2019).

We built regression models using 3 000 trees, with a third of the total variables sampled at each split (the default for RF regression). We evaluated the predictive capability of each species model using k-folds cross validation with 10 folds. For each fold across models we calculated a receiver operator characteristic (ROC) curve and calculated the area under the curve (AUC) by converting predicted counts to measure of occurrence assumed from a Poisson distribution (Royle and Nichols 2003). We used the mean value of temporally variant weather and climate predictors and stop number over the study duration and used 2016-yr intercept and fire data to generate spatial predictions of relative abundance for each species.

Applying models to past conifer management

Effectively targeted conifer management for both sagebrush and woodland songbirds would take place in areas with higher occurrence of imperiled sagebrush obligates while avoiding similarly high occurrence areas for declining woodland dependent species. To test the spatial relationship of past conifer management with songbird occurrences, we evaluated spatial data on conifer management projects from the US Department of Agriculture's Natural Resources Conservation Service, Sage Grouse Initiative (*hereafter* SGI). As one of the largest restoration efforts in the sagebrush biome since 2010 (Maestas et al. 2021; NRCS 2021), we considered SGI representative of modern conifer removal projects specifically targeted for sage grouse and sagebrush restoration. We extracted predicted values of relative abundance for declining sagebrush obligate species (Brewer's sparrow, sagebrush sparrow, sage thrasher) and pinyon jay (see Table 1) within the boundaries of all SGI conifer treatments and background samples from the rest of the sampling frame. We restricted conifer treatments to only those occurring after the collection of bird data used for model training (July 15, 2016; $n = 2251$), to ensure that predicted values did reflect pretreatment conditions and would capture the targeting ability of treatments. We evaluated targeting of conifer management by estimating logistic regression generalized linear models, using treatment as the response variable (1 = treatment, 0 = no treatment) and predicted values for each species as the explanatory variable. We reasoned that an estimated positive coefficient was indicative of conifer management targeting for a particular species; or in other words, management was taking place in areas of higher predicted occurrence. Conversely, a negative coefficient implied conifer management was ostensibly avoiding a particular species. To allow for comparison in direction and magnitude among estimated coefficients, we scaled predicted relative abundances (mean = 0, sd = 1) for each species' model.

Results

Our sampling frame encompassed 24 ecoregions (see Fig. S1), of which focal species were determined to occupy from 7 (Gray Vireo) to 22 (Brewer's Sparrow) ecoregions within the sampling frame (see Table 1, Fig. S1). The spatial and temporal windows selected for landcover and fire variables varied among species, ranging from local (120 m) to landscape (6 400 m) and near (5 yr) and longer-term (15 yr) impacts of fire (Table 3), demonstrating heterogeneous responses by species to landscape features at multiple scales. Across species, area under the curve (AUC) scores indicated at least good predictive ability across all models (AUC > 0.92; see Table S1). Applying models to spatial grids produced predictive surfaces of occurrence and abundance at landscape scales (Figs. 2 and 3).

Table 3
Variables selected for use in models across species with shortened variable codes identified in Table 2. Spatial scales (m) providing the best fit follow the variable name.

Species	Topography variables	Landcover variables	Weather-climate variables	Fire variable
Ash-throated Flycatcher	elev, tpi, tri	scrb.6400, piju.1000, conf.6400, sage.6400, shrb.1000, herb.6400, ripa.120, dist.1000	ndvi, psdi, tmax, wprp, sprp	fire.120 15 yr
Brewer's sparrow	elev, tpi, tri	scrb.120, piju.120, conf.1000, sage.1000, shrb.1000, herb.6400, ripa.6400, dist.1000	ndvi, pdsi, tmax, wprp, sprp	fire.6 400 10 yr
Gray vireo	elev, tpi, tri	scrb.6400, piju.6400, conf.1000, sage.6400, shrb.6400, herb.1000, ripa.6400, dist.6400	pdsi, tmax, wprp	fire.6 400 5 yr
Gray flycatcher	elev, tpi, tri	scrb.6400, piju.1000, conf.120, sage.6400, shrb.6400, herb.1000, ripa.6400, dist.1000	ndvi, pdsi, wprp, sprp	fire.1 000 15 yr
Green-tailed towhee	elev, tpi, tri	scrb.1000, piju.6400, conf.120, sage.1000, shrb.1000, herb.6400, ripa.1000, dist.6400	ndvi, pdsi, tmin, wprp, sprp	fire.120 10 yr
Juniper titmouse	elev, tpi, tri	scrb.6400, piju.6400, conf.6400, sage.1000, shrb.6400, herb.1000, ripa.6400, dist.1000	ndvi, pdsi, tmin, wprp, sprp	fire.6400 10 yr
Pinyon jay	elev, tpi, tri	scrb.1000, piju.6400, conf.6400, sage.120, shrb.6400, herb.6400, ripa.6400, dist.1000	ndvi, pdsi, wprp, sprp	fire.120 10 yr
Sagebrush sparrow	elev, tpi, tri	scrb.6400, piju.120, conf.120, sage.120, shrb.1000, herb.120, ripa.6400, dist.120	ndvi, pdsi, tmin, wprp, sprp	fire.1000 15 yr
Sage thrasher	elev, tpi, tri	scrb.6400, piju.1000, conf.1000, sage.1000, shrb.1000, ripa.1000, dist.1000	ndvi, pdsi, tmax, wprp	fire.1000 5 yr

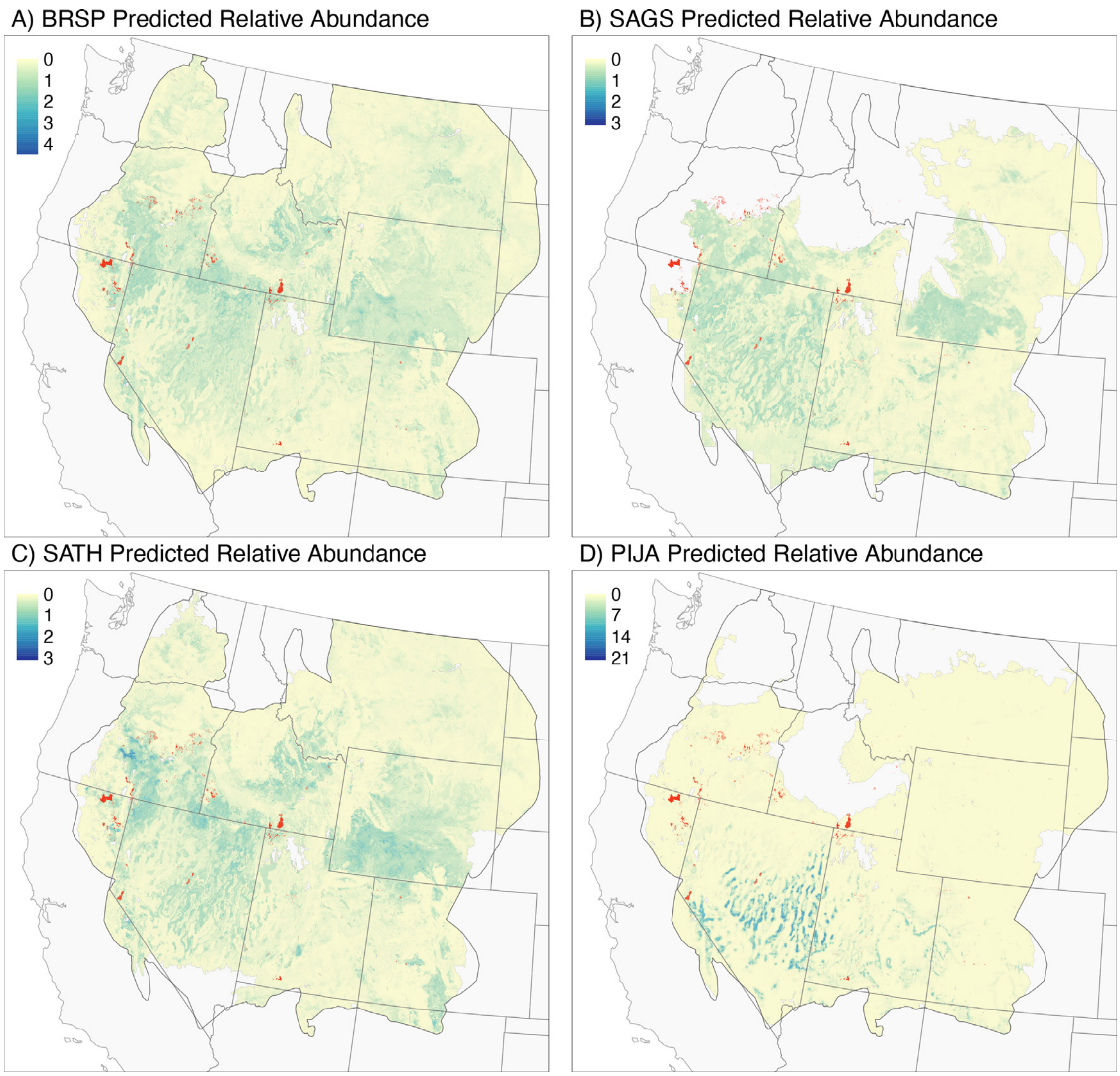

Figure 2. Predicted relative abundance for each of the declining sagebrush obligate species A) Brewer's sparrow (BRSP), B) sagebrush sparrow (SAGS), and C) sage thrasher (SATH); and D) pinyon jay (PIJA). Predictions are masked to ecoregions used to train models, with large waterbodies masked as well. Conifer removal projects contracted with the Sage Grouse Initiative following the last surveyed data used to train models (July 15, 2016) are overlaid in red.

Generally, SGI conifer management has been focused in northern sagebrush landscapes (see Fig. 2), where dominant conifer species include western juniper (*Juniperus occidentalis*) in Oregon and northern California, and Utah juniper (*J. osteosperma*) and Rocky Mountain juniper (*J. scopulorum*) in northwest Utah with some single-leaf pinyon pine (*Pinus monophylla*) (Romme et al. 2009). Logistic regression models fit from overlaying SGI conifer management with models for declining species revealed that management targeted areas with both Brewer's sparrow (0.969; 95% confidence interval [CI] 0.961, 0.977) and sage thrasher (0.411; 95% CI 0.404, 0.417) and avoided pinyon jay (−0.168; 95% CI −0.176, −0.159) and sagebrush sparrow (−0.225; 95% CI −0.231, −0.218).

Discussion

We provide the first habitat-based maps of distribution and abundance songbirds of high concern using sagebrush and woodland landscapes across the entire sagebrush biome. These new products expand the spatial targeting toolbox beyond high-profile birds like sage grouse (Doherty et al. 2010, 2016; Row et al. 2018) to empower land managers to incorporate multiple species into holistic conservation strategies. To further aid conservation planning, map representations of models are made available for visualization using an online application (https://map.sagegrouseinitiative.com/).

Sage grouse have been identified as an umbrella species for wildlife conservation among species that use sagebrush for some portion of their life history, an assumption that has been tested with mixed results by measuring the co-occurrence of overlapping species distributions. Generally, distribution and abundance of sage grouse have been found to correspond with other wildlife dependent on sagebrush at regional and biome level scales (Rowland et al. 2006; Hanser and Knick 2011; Smith et al. 2019; Pilliod et al. 2020), though results become equivocal for more localized investigations of overlap (Carlisle et al. 2018; Carlisle and Chalfoun 2020; Smith et al. 2021). Perhaps a more meaningful surrogate measure is to test benefits afforded to multiple species under conservation actions intended to benefit a flagship species such as the sage grouse. We found that conifer removal targeted for sage grouse through SGI also targeted important areas for declining sagebrush obligate songbirds, a guild of species with a proclivity for positive response to management (Holmes et al. 2017). Community-level benefits from targeted conifer removal is encouraging yet not surprising given similar findings demonstrating high overlap between

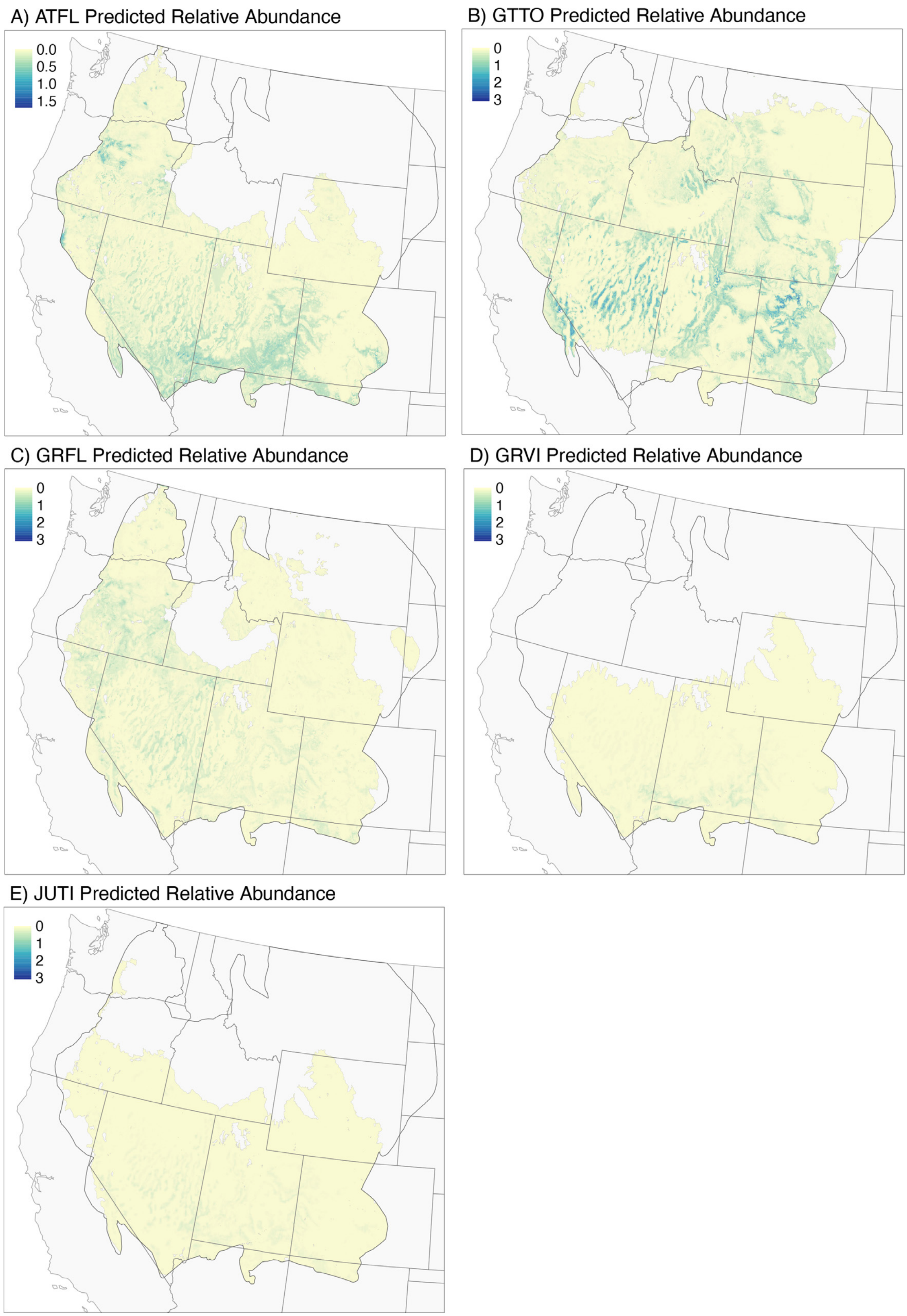

Figure 3. Predicted counts for each of the modeled species with stable to increasing trends identified from BBS trends (Table 1) including, A) ash-throated flycatcher (ATFL), B) green-tailed towhee (GTTO), C) gray flycatcher (GRFL), D) gray vireo (grvi), and E) juniper titmouse (JUTI). Predictions are masked to ecoregions used to train models, with large waterbodies masked as well.

Brewer's sparrow and SGI conifer removal (Donnelly et al. 2017). Past research has demonstrated that landscapes across the entire US sagebrush biome targeted for sage grouse conservation (i.e., Priority Areas for Conservation) have been judiciously designed in light of affording protections to the broader wildlife community (Runge et al. 2019).

Our results also reveal that conifer removal efforts targeted for sage grouse by SGI largely avoid areas of high predicted occurrence for pinyon jay. These findings provide the first quantitative assessment demonstrating that targeted sage grouse habitat restoration under one of the largest conservation initiatives in the biome does not appear to be at odds with protecting pinyon jay populations across most of the sagebrush biome despite suggestions to the contrary (Boone et al. 2018; Magee et al. 2019). This disparity is explained in part by the SGI's private lands emphasis and science-based approach that prioritizes removal of early successional conifer expansion among shrub- and herbaceous-dominated landscapes (Falkowski et al. 2017; Reinhardt et al. 2017). Colloquially known as "phase 1" woodlands (Miller and Miller 2007), these areas are characterized by expansion of conifers into shrublands historically devoid of trees, which are used by pinyon jays in some areas mainly for food caching (Boone et al. 2021). Even with the increased attention in sage grouse−focused conifer projects over the past decade, the combined effects of management and wildfire are estimated to have only reduced the conifer footprint by 1.6% across the entire sage grouse range (Reinhardt et al. 2020). This pace and scale of removal may barely be keeping up with continued patterns of expansion and infill, which is estimated at 0.4−1.5% annually (Sankey and Germino 2008).

One area meriting further investigation is the situation in the Central Basin and Range Ecoregion where the highest concentrations of pinyon jay occur, and contemporary pinyon-juniper woodland change is affecting habitat conditions for pinyon jay and sage grouse. In recent decades, pinyon-juniper woodlands in this region have continued to undergo extensive change in stand structure and composition due to increasing conifer densities (Filippelli et al. 2020), resulting in the infill of shrub and tree co-dominant stands (Miller et al. 2008; Romme et al. 2009). Preferred pinyon jay breeding habitat is often described as heterogeneous stands of pinyon-juniper and shrubs, which support high cone pine productivity and resulting pinyon nut production (Balda 2002). Pinyon pine tree vigor, a surrogate for tree productivity, was an important predictor of pinyon jay nest-site selection, which declined with increasing tree size and density (Johnson et al. 2017). Given changing woodland conditions, we hypothesize that pinyon jay habitat use may be shifting to midsuccessional woodlands encroaching sagebrush landscapes, as late successional woodlands become less suitable, an outcome that imperils both pinyon jay and sage grouse, which historically occupied different niches and ecological sites along the shrubland-to-woodland continuum (Fig. 1). This hypothesis is consistent with regional population trends showing sagebrush obligate birds and pinyon jay in decline, while species reliant on dense, late successional woodlands have generally increased (see Table 1). Simply avoiding conifer removal projects in occupied pinyon jay habitat alone is unlikely to be an effective conservation strategy for pinyon jay with ongoing woodland dynamics, so it may instead be beneficial for managers to consider site appropriate silvicultural practices designed to restore and maintain the heterogeneous woodland structure critical to pinyon jays. Co-produced science and monitoring should be coupled with any such restoration efforts (Naugle et al. 2020) to help overcome existing knowledge gaps in woodland restoration (Boone et al. 2018).

Evaluation metrics suggested that all species models provided "good" predictive capability across a large geography. However, there are several important caveats when using BBS data to develop spatial models. Notably, BBS sampling occurs along roadways, which could bias the predictor variables and bird communities observed, and without repeated samples provides only an index of abundance. Past studies within our sampling frame have found no significant differences between counts of sagebrush obligates on road and off-road surveys (Rotenberry and Knick 1995). Similarly, performance of spatial models was not significantly different when comparing BBS models with those with samples collected off roads (McCarthy et al. 2012), though it remains possible that the entire covariate space was not fully sampled for each species by constricting surveys to road sides (e.g., high-elevation roadless sites). Ultimately, indices such as relative abundance from BBS data can still provide management with meaningful information on patterns of avian occurrence (Johnson 2008; Niemuth et al. 2017), particularly when it represents the primary data source available at the temporal and spatial scales relevant to management. Viewed in total, local and design-based studies that employ random sampling and account for detection probability will only improve the quality of spatial planning tools for practitioners and should be used when available. Similarly, model-based inference at the biome scale will never surpass local knowledge or site evaluation before management when it comes to sensitive resources (e.g., location of a particular nesting colony; Johnson et al. 2016).

Many management actions are aimed at reducing conifer cover for purposes other than sagebrush restoration (e.g., fuels reduction, forage production) that likely use very different targeting schemes. Conifer management with aims beyond sagebrush and sage grouse may not be similarly inconsequential for pinyon jay conservation, particularly when treatments occur among established pinyon-juniper woodlands. For example, thinning conifers to reduce fire risk in New Mexico, United States left previously suitable pinyon jay nesting habitat unoccupied following treatment (Johnson et al. 2018) and conifer thinning in Colorado reduced pinyon jay occupancy at local scales (< 4 ha; Magee et al. 2019). We chose to evaluate only conifer removal projects contracted by SGI because this was the sole data source that ensured management was targeted for sagebrush ecological integrity under the umbrella of sage grouse. One caveat to this approach is that SGI management occurs solely on private lands. While conifer management is often coordinated across private-public boundaries in many areas (Reinhardt et al. 2020), restricting our inference to private lands presumes that our findings for targeting and avoidance may not hold elsewhere. However, using the SGI strategy of targeting early encroaching conifers among otherwise intact sagebrush rangelands while using products to identify potential areas of conflict for pinyon jay, like those developed here, provide a roadmap for future management efforts across jurisdictional boundaries. Ultimately, extending our spatial modeling approach for the pinyon jay distribution beyond the sagebrush biome could better equip conservationists in southwestern ecoregions with important decision-support tools, particularly as these landscapes face additional pressures of drought-induced tree mortality (Clifford et al. 2011; Fair et al. 2018; Shriver et al. 2021).

Implications

Pinyon-juniper management is often framed as creating "winners" and "losers" among wildlife species (Bombaci and Pejchar 2016; Zeller et al. 2021), but spatial context of management efforts relative to species populations is often lacking to assess this beyond local project scales. In fact, nuanced analysis reveals that targeted removal of postsettlement era conifer encroachment in sagebrush shrublands may not be at odds with species that rely on conifers for a portion of their life history (Anthony and Sanchez 2019; Maestas et al. 2019). Model outputs developed here can help inform management for an additional suite of species of concern that lack the spatial tools necessary to avoid potentially detrimental impacts and target limited resources for restoration. Future efforts could combine our species models with spatial data on known ecosystem threats and potential risks to populations to develop holistic, multiple species management plans. For example, combining species models with high-resolution vegetation data (Allred et al. 2021; Rigge et al. 2020) can help practitioners make optimal decisions given a bevy of seemingly competing conservation and management interests (Reinhardt et al. 2017; Ricca et al. 2018).

Declaration of Competing Interest

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

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.rama.2023.03.006.

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