

Regional context for balancing sagebrush- and woodland-dependent songbird needs with targeted pinyon-juniper management in the sagebrush biome

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1 **Abstract**

2 Tree expansion among historic grassland and shrubland systems is a global phenomenon, which
3 results in dramatic influences on ecosystem processes and wildlife populations. In the western
4 US, pinyon-juniper woodlands have expanded by as much as six-fold among sagebrush steppe
5 landscapes since the late nineteenth century, with demonstrated negative impacts to the behavior,
6 demography, and population dynamics of species that rely on intact sagebrush rangelands.
7 Notably, greater sage-grouse (*Centrocercus urophasianus*) are unable to tolerate even low
8 conifer cover, which can result in population declines and local extirpation. Removing
9 expanding conifer cover has been demonstrated to increase sage grouse population growth rates
10 and sagebrush-obligate songbird abundance. However, advances in restoring sagebrush habitats
11 have been met with concern about unintended impacts to species that rely on conifer woodlands,
12 notably the pinyon jay (*Gymnorhinus cyanocephalus*) whose population declines are distinctive
13 among birds breeding in pinyon-juniper woodlands. We modeled indices to abundance in
14 relation to multi-scale habitat features for nine songbirds reliant on both sagebrush and pinyon-
15 juniper woodlands for breeding. Findings demonstrate that targeted sage grouse habitat
16 restoration under the Sage Grouse Initiative is not at odds with protection of pinyon jay
17 populations. Rather, conifer management has largely occurred in the northern sagebrush
18 ecosystem where models suggest that past cuts likely benefit Brewer's sparrow and sage thrasher
19 while avoiding pinyon jay habitat. Extending our spatial modeling further south beyond the
20 sagebrush biome could better equip conservationists with more comprehensive decision-support,
21 particularly where pinyon jays face additional pressures of drought-induced tree mortality.

22 **Keywords:** Breeding Bird Survey (BBS), conifer management, species distribution models,
23 pinyon jay, pinyon-juniper woodlands, sagebrush.

24 **Introduction**

25 Native tree species are expanding into shrublands and grasslands globally at an alarming rate,
26 increasing from 40-600% in distribution across every continent except Antarctica (Nackley et al.,
27 2017). Resulting shifts in vegetation structure and composition are affecting a broad suite of
28 ecosystem services and values, including wildlife species of conservation concern (Baruch-
29 Mordo et al., 2013; Fuhlendorf et al., 2017, 2002). In North America, pinyon-juniper
30 woodlands, composed of both juniper (*Juniperus spp.*) and pinyon pine (*Pinus spp.*; hereafter
31 collectively referred to as conifer), are among the most dominant vegetation types across the
32 intermountain western United States, supporting critical biodiversity, ecosystem services, and
33 economic potential (Romme et al., 2009). Since European settlement, the distribution of these
34 conifer species has expanded between two- and six-fold, likely due to the compounding effects
35 of historic high-intensity grazing, subsequent increases in natural fire return intervals that limited
36 woodland establishment, and favorable climatic conditions that helped tree growth proliferate
37 among sagebrush (*Artemisia spp.*) systems (Miller et al., 2019). Some 90% of pinyon-juniper
38 expansion has occurred in sagebrush ecosystems (Miller et al., 2011), leading to a loss of
39 sagebrush and herbaceous vegetation (Roundy et al., 2014) and associated specialist wildlife
40 species (Baruch-Mordo et al., 2013; Rickart et al., 2008). As a result, management to remove
41 conifers from former shrublands has been adopted as a widespread conservation practice to
42 mitigate negative ecosystem impacts over the past decade (Miller et al., 2017).

43 Central to the proliferation of recent restoration efforts is the conservation of sagebrush-
44 obligate wildlife under the umbrella of greater (*Centrocercus urophasianus*) and Gunnison sage-
45 grouse (*C. minimus*; hereafter collectively referred to as sage grouse; Doherty et al., 2018; Miller
46 et al., 2017). Sage grouse are particularly vulnerable to conifer expansion (Baruch-Mordo et al.,

47 2013). Conifer presence reduces the quality of sage grouse habitat through both behavioral
48 avoidance by nesting females (Severson et al., 2017a) and the demographic consequences of
49 reduced nest (Severson et al., 2017b), brood (Sandford et al., 2017), and female survival (Coates
50 et al., 2017). Experimental research among conifer removal projects has demonstrated that sage
51 grouse quickly return to restored habitats, with subsequent increases in nest, brood, and female
52 survival in treated areas (Sandford et al., 2017; Severson et al., 2017b, 2017c). Ultimately,
53 restoration of habitats through conifer management is translating into measurable population
54 benefits at watershed scales, accounting for a 12% increase in population growth rates compared
55 to control areas in southern Oregon (Olsen et al., 2021). Efficacy of accelerating investments in
56 large-scale restoration efforts via conifer removal was one key factor in obviating the need for an
57 Endangered listing status for sage grouse (US Fish and Wildlife Service 2015), which continues
58 to be a primary management practice for voluntary conservation of sagebrush habitats (Natural
59 Resources Conservation Service 2021).

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

69 Among songbirds in the western US, those reliant on pinyon-juniper or sagebrush for
70 breeding habitat have largely demonstrated contrasting population trends over the past 50 years
71 that is consistent with an expanding footprint of conifer among sagebrush habitats (Table 1).
72 Brewer’s sparrow, green-tailed towhee, and sage thrasher (*Oreoscoptes montanus*), all reliant on
73 unfragmented sagebrush habitats for breeding, have experienced population declines; whereas
74 woodland songbirds including ash-throated flycatcher (*Myiarchus cinerascens*), gray flycatcher
75 (*Empidonax wrightii*), gray vireo (*Vireo vicinior*), and juniper titmouse (*Baeolophus ridgwayi*)
76 exhibit stable to increasing populations (Sauer et al., 2017; Table 1). The one notable exception
77 among woodland-reliant species is the pinyon jay (*Gymnorhinus cyanocephalus*), which depends
78 on a mutualistic relationship with conifer nut production for their survival and reproduction
79 (Ligon, 1978). Pinyon jays have declined more severely since 1968 than any other land bird
80 inhabiting sagebrush-associated landscapes (Boone et al., 2018; Sauer et al., 2017), with concern
81 culminating in the US Fish and Wildlife Service being petitioned to list the pinyon jay as
82 Threatened or Endangered under the Endangered Species Act
83 ([https://defenders.org/sites/default/files/inline-](https://defenders.org/sites/default/files/inline-files/2022.4.25_FWS_Listing%20petition_Pinyon%20Jay.pdf)
84 [files/2022.4.25_FWS_Listing%20petition_Pinyon%20Jay.pdf](https://defenders.org/sites/default/files/inline-files/2022.4.25_FWS_Listing%20petition_Pinyon%20Jay.pdf); accessed 3 May, 2022).

85 Mechanisms underlying pinyon jay population declines within sagebrush ecosystems are
86 unknown. Factors hypothesized to contribute to declines include climate-mediated declines in
87 pinyon pine seed production, intentional pinyon-juniper removal, tree die-off, wildfire, and
88 drought; and transition of the preferred heterogeneous pinyon pine and sagebrush stands to
89 persistent woodlands by a process known as “infill” (Boone et al., 2018). Following the infill of
90 mixed sagebrush and conifer stands, individual trees have reduced seed productivity, thus conifer
91 infill may be analogously detrimental to pinyon jay as encroachment is to sagebrush-obligate

92 wildlife like the sage grouse (Fig. 1). Ultimately, improved spatial planning products for both
93 sagebrush-and woodland-obligate birds of conservation concern are needed to enable informed
94 decisions about potential impacts of ongoing management, and foster a holistic approach to
95 multiple species management along the shrubland-to-woodland continuum (Maestas et al. 2021).

96 We used Breeding Bird Survey (BBS) data to develop spatial models predictive of the
97 relative abundance of both sagebrush and woodland obligate songbirds inhabiting sagebrush
98 steppe. Maps were developed to: 1) depict relative species distributions spatially, 2) evaluate
99 recent conifer removal for sage grouse in relation to predicted songbird distributions, and 3) help
100 guide spatial targeting of future conservation actions. Applying spatial models to BBS data
101 provides an effective tool to learn about large-scale distribution of breeding birds (Niemuth et al.,
102 2017). We chose to model species-habitat relationships among songbirds that are likely to be
103 either passively targeted for conservation as sagebrush obligates, or influenced by conifer
104 management, and typically appear in conservation planning documents (e.g., Gillihan, 2006).
105 We overlaid past conifer cuts conducted through the Sage Grouse Initiative with predictive
106 distributions of declining songbirds to determine if conifer management for sage grouse has
107 passively targeted or avoided certain species.

108 **Methods**

109 *Study Area*

110 Our aim was to model species distributions inhabiting the sagebrush (*Artemisia* spp.) ecosystem
111 within the western US. This geography encompasses a diversity of public and private land
112 tenures and jurisdictional boundaries, and is largely defined by cover of both sagebrush- and
113 grassland-dominant understories. Domestic livestock grazing is the primary land use among
114 intact sagebrush steppe, while major anthropogenic factors contributing to habitat loss and

115 fragmentation vary spatially and include infrastructure associated with energy development,
116 cultivation, and urban development. Persistent ecosystem threats also include invasion of exotic
117 annual grasses (e.g. *Bromus tectorum*) and conifer expansion. To best capture a sampling frame
118 representative of sagebrush landscapes, we merged boundaries defined by sagebrush cover with
119 the addition of existing sage grouse Priority Areas for Conservation and management zones
120 (Sage Grouse Initiative, n.d.) and the historic sage grouse species range (Runge et al., 2019;
121 Supplemental Fig. 1).

122 *Avian Count Data*

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

137 *Spatial Covariates*

138 We broadly hypothesized that heterogeneity in species counts would be influenced by patterns of
139 vegetation, topography, anthropogenic disturbance, fire history, and weather and climate (Table
140 2). Specifically, we measured the proportion of summarized vegetation types around point
141 counts that were classified as sagebrush, non-sagebrush shrublands, conifer, pinyon-juniper
142 woodlands, scrub- and woodlands, and riparian areas (Table 2). We also combined cropland and
143 developed cover types to characterize anthropogenically disturbed areas. Topography is an
144 important component in structuring bird communities in sagebrush steppe (Knick et al., 2008), so
145 we included measures of elevation, terrain ruggedness (TRI), and a multiscale topographic
146 position index (mTPI) that broadly characterizes landforms (e.g. valley bottoms, ridges, etc.)
147 within 270m, 810m, and 2430m, such that the metric can differentiate between both local- and
148 broad-scale geomorphological features (Theobald et al., 2015). Fire is a pervasive disturbance
149 among sagebrush steppe landscapes structuring vegetation patterns, with the potential for long-
150 lasting negative impacts to densities of breeding birds (Holmes and Robinson, 2013).
151 Therefore, we used spatial data of fire boundaries and measured the proportion of burned areas 5,
152 10, and 15 years prior to each point count to characterize the potential legacy effects of fire.

153 We used weather and climate data that likely influence annual settling patterns of
154 breeding birds. Because precipitation is the primary driver of annual herbaceous growth, we
155 measured total precipitation occurring both over winter (Dec 1 - March 14) and spring (March 15
156 - July 15) as our study area encompassed ecoregions where precipitation both largely occurs
157 during winter (Great Basin) or spring and early summer (Great Plains). We also summarized
158 patterns of temperature as mean maximum and minimum temperatures over the sampling period
159 (May 15 - July 15) to characterize thermal niches for each species. We used the Normalized
160 Difference Vegetation Index (NDVI) to broadly describe site productivity as NDVI has been

161 correlated with critical life stage requirements for breeding birds (Sweet et al., 2015). We
162 calculated mean NDVI across Landsat scenes over the sampling period, and omitted pixels that
163 were identified as cultivated or woodland in an effort to best characterize the productivity of
164 sagebrush steppe habitats. Drought is a major factor shaping sagebrush steppe systems, so we
165 used Palmer's Drought Severity Index (PDSI) to identify the spatial and temporal patterns of
166 persistent, long-term drought across the study area. We matched all temporally-referenced
167 weather and climate data to the year of observation across surveys. We also resampled all data
168 to 120m resolution rasters for prediction as spatial covariates varied in their native resolutions
169 (Table 1). Lastly, we included stop (1-50) as a covariate in all models as a proxy for time of day,
170 which is known to influence detection of birds (Niemuth et al. 2017). All continuous covariates
171 were scaled ($\frac{x-\bar{x}}{s(x)}$) to aid model convergence and coefficient interpretation.

172 *Spatial and Temporal Scales*

173 We chose three spatial scales to summarize landcover and burned area covariates for
174 consideration in modeling counts including 120 m, 1000 m, and 6400 m. The smallest scale
175 (~4.5 ha) corresponds to minimum territory sizes of songbirds among sagebrush habitats
176 (Rotenberry et al., 1999). Past work has demonstrated that the amount of shrub and grass cover
177 within 1000 m scale (~314 ha) has been an important predictor of habitat selection for songbirds
178 in sagebrush steppe (Rotenberry and Knick 1995). This buffer also matches the scale of a typical
179 conifer removal project (e.g. [www://conservationalefforts.org](http://www.conservationalefforts.org)). Lastly, we hypothesized that a
180 6400 m scale (~12,868 ha) represented watershed scale habitat influencing settling patterns by
181 migratory passerines. Past research on sagebrush obligate response to conifer treatment
182 indicated that treatments needed to be adjacent to large intact landscapes (> 14,000 ha) for
183 sagebrush obligate songbirds to recolonize conifer removal areas (Knick et al. 2014).

184 *Model Fitting, Selection, and Evaluation*

185 Not all species distributions encompassed the entirety of our sampling frame, and we wanted to
186 ensure that we were including only data in analyses that had the potential for a particular species
187 to occur (i.e. 2nd order habitat selection; Johnson, 1980). Therefore, for each species we
188 modeled only data from NACEC level 3 (CEC 1997) that contained >5 detections between 2011-
189 2016, such that predictions are constrained within the occupied range of our sampling frame for
190 each species (Supplemental Fig. 1).

191 We sought to use one spatial scale to represent each landcover variable, and one spatial
192 and temporal scale to represent a fire variable for each species model. To determine the best fit
193 scales, we fit generalized linear mixed models (glmm) using a binomial error distribution (i.e.
194 detected, undetected) for each landcover and fire variable independently, including random
195 effects for year, route, and BBS observer to account for known sources of heterogeneity in BBS
196 count data (Niemuth et al., 2017). We used detection/non-detection data for scale selection so
197 we wouldn't have to make assumptions about the proper error distribution for counts, and
198 assumed that the inherent relationship between occurrence and abundance (Royle and Nichols,
199 2003) would capture relevant variables for count-based models. Using glmm in this step allowed
200 us to calculate Akaike Information Criteria (AIC), from which we used the minimum value
201 among landcover and fire variables to determine the best spatial and temporal scale among
202 variables. Once we had determined a set of candidate variables for each species, we identified
203 highly correlated variables ($|r| > 0.6$) and removed correlated variables that had lower support
204 determined by higher AIC values.

205 Once candidate variables for each species were identified, we fit multi-variable models
206 using a random forest approach with regression trees (Breiman, 2001). We modeled count data

207 with random forests regression trees because it was efficiently implemented without making
208 assumptions about an appropriate error distribution and model structure across species, and is
209 generally found to outperform parametric species distribution models in predictive performance
210 (Elith, 2019).

211 We built regression models using 3000 trees, with a third of the total variables sampled at
212 each split (the default for RF regression; Breiman, 2000). We used fixed categorical effects for
213 years and included latitude and longitude as predictors across models. We evaluated the
214 predictive capability of each species model using k-folds cross validation with 10 folds. For
215 each fold across models we calculated a receiver operator characteristic (ROC) curve and
216 calculated the area under the curve (AUC) by converting predicted counts to measure of
217 occurrence assumed from a Poisson distribution (Royle and Nichols, 2003). We used the mean
218 value of temporally-variant weather and climate predictors and stop number over the study
219 duration, and used 2016-year intercept and fire data to generate spatial predictions for each
220 species.

221 *Applying Models to Past Conifer Management*

222 Effectively targeted conifer management for both sagebrush and woodland songbirds would take
223 place in areas with higher occurrence of imperiled sagebrush obligates, while avoiding similarly
224 high occurrence areas for declining woodland-dependent species. To test the spatial relationship
225 of past conifer management with songbird occurrences, we evaluated spatial data on conifer
226 management projects from the US Department of Agriculture's Natural Resources Conservation
227 Service, Sage Grouse Initiative (*hereafter* SGI). As one of the largest restoration efforts in the
228 sagebrush biome since 2010 (Maestas et al. 2021, NRCS 2021), we considered SGI
229 representative of modern conifer removal projects specifically targeted for sage grouse and

230 sagebrush ecosystem restoration. We extracted predicted values for declining species as
231 identified by BBS (Brewer's sparrow, Sage Thrasher, Green-tailed Towhee, and Pinyon Jay)
232 among the footprint of all SGI conifer treatments (n = 3342; mean = 549.7 ha), and among all the
233 predicted values falling outside of treatment areas. We evaluated targeting of conifer
234 management with logistic regression using treatment as the response variable (1 = treatment, 0 =
235 no treatment), and predicted values for each species as the dependent variable. We reasoned that
236 estimating a positive coefficient would be indicative of conifer management targeting for a
237 particular species; in other words management was taking place in areas of higher predicted
238 occurrence. Conversely, a negative coefficient would imply conifer management was ostensibly
239 avoiding a particular species.

240 **Results**

241 Our sampling frame encompassed 24 ecoregions (Supplemental Fig. 1), of which focal species
242 were determined to occupy from 7 (Gray Vireo) to 22 (Brewer's Sparrow) ecoregions within the
243 sampling frame (Table 1, Supplemental Fig. 1). Omitting highly correlated variables, and using
244 model selection to choose among spatial and temporal scales resulted in models with 22
245 (Sagebrush Sparrow) to 30 (Brewer's Sparrow) candidate variables describing bird response to
246 topography, weather and climate, landcover, and fire history (Table 3). The spatial and temporal
247 windows selected for landcover and fire variables varied among species, ranging from local
248 (120m) to landscape (6400m) and near (5 yr) and longer-term (15 yr) impacts of fire (Table 3),
249 demonstrating heterogeneous responses by species to landscape features at multiple scales.
250 Across species AUC scores indicated at least good predictive ability across all models
251 (AUC>0.92; Supplemental Table 1). Applying models to spatial grids produced predictive
252 surfaces of occurrence and abundance at landscape scales (Figs. 2-3).

253 Logistic regression models fit from overlaying SGI conifer management with models for
254 declining species revealed that past cuts targeted areas with both Brewer's sparrow (3.468; 95%
255 CI 3.408, 3.529) and sage thrasher (3.12; 95% CI 3.049, 3.198), and avoided pinyon jay (-0.018;
256 95% CI -0.035, -0.002). Generally, SGI conifer management has been focused in northern
257 distribution of the sagebrush ecosystem including areas in northwest Utah, northern California,
258 and Oregon (Fig. 2).

259 **Discussion**

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

267 Sage grouse have been identified as an umbrella species for wildlife conservation among
268 sagebrush habitats, an assumption that has been tested with mixed results by measuring the co-
269 occurrence of overlapping species distributions. Generally, distribution and abundance of sage
270 grouse have been found to correspond with other sagebrush-dependent wildlife at regional and
271 biome-level scales (Hanser and Knick, 2011; Pilliod et al., 2020; Rowland et al., 2006; Smith et
272 al., 2019); though results become equivocal for more localized investigations of overlap (Carlisle
273 et al., 2018; Carlisle and Chalfoun, 2020; Smith et al., 2021). Perhaps a more meaningful
274 surrogate measure is to test benefits afforded to multiple species under conservation actions
275 intended to benefit a flagship species such as the sage grouse. We found that conifer removal

276 targeted for sage grouse through SGI also targeted important habitats for declining sagebrush
277 obligate songbirds, a guild of species with a proclivity for positive response to management
278 (Holmes et al., 2017). Community-level benefits from targeted conifer removal is encouraging
279 yet not surprising given similar findings demonstrating high overlap between Brewer’s sparrow
280 and SGI conifer removal (Donnelly et al., 2017), and research demonstrating that landscapes
281 across all US sagebrush steppe habitats targeted for sage grouse conservation (i.e. Priority Areas
282 for Conservation) have been judiciously designed in light of affording protections to sagebrush-
283 reliant wildlife communities (Runge et al., 2019).

284 Our results also reveal that conifer removal efforts targeted for sage grouse largely avoid
285 areas of high predicted occurrence for pinyon jay. These findings provide the first quantitative
286 assessment demonstrating that targeted sage grouse habitat restoration under one of the largest
287 conservation initiatives in the biome does not appear to be at odds with protecting pinyon jay
288 populations across most of the sagebrush biome despite suggestions to the contrary (Boone et al.,
289 2018; Magee et al., 2019). This disparity is explained in part by the SGI’s private lands
290 emphasis and science-based approach that prioritizes removal of early successional conifer
291 expansion among shrub and herbaceous dominated landscapes (Falkowski et al., 2017; Reinhardt
292 et al., 2017). Colloquially known as “phase 1” woodlands (Miller and Miller, 2007), these areas
293 are characterized by expansion of conifers into shrublands historically devoid of trees, which are
294 used by pinyon jays in some areas mainly for food caching (Boone et al. 2021). Even with the
295 increased attention in sage grouse focused conifer projects over the past decade, the combined
296 effects of management and wildfire are estimated to have only reduced the conifer footprint by
297 1.6% across the entire sage grouse range (Reinhardt et al. 2020). This pace and scale of removal

298 may barely be keeping up with continued patterns of expansion and infill, which is estimated at
299 0.4-1.5% annually (Sankey and Germino, 2008).

300 One area meriting further investigation is the situation in the Central Basin and Range
301 Ecoregion where the highest concentrations of pinyon jay occur, and contemporary pinyon-
302 juniper woodland change is affecting habitat conditions for pinyon jay and sage grouse. In
303 recent decades, pinyon-juniper woodlands in this region have continued to undergo extensive
304 change in stand structure and composition due to increasing conifer densities (Filippelli et al.
305 2020), resulting in the infill of shrub and tree co-dominant stands (Miller et al., 2008; Romme et
306 al., 2009). Preferred pinyon jay breeding habitat is often described as heterogenous stands of
307 pinyon-juniper and shrubs, that support high cone pine productivity and resulting pinyon nut
308 production (Balda, 2002). Pinyon pine tree vigor, a surrogate for tree productivity, was an
309 important predictor of pinyon jay nest-site selection, which declined with increasing tree size and
310 density (Johnson et al., 2017). Given changing woodland conditions, we hypothesize that pinyon
311 jay habitat use may be shifting to encroached sagebrush shrublands as historic woodland
312 ecological sites become less suitable - an outcome that imperils both pinyon jay and sage grouse
313 which historically occupied different niches and ecological sites along the shrubland-to-
314 woodland continuum (Fig. 1). This hypothesis is consistent with regional population trends
315 showing sagebrush obligate birds and pinyon jay in decline, while species reliant on dense,
316 persistent woodlands have increased (Table 1). Simply avoiding conifer removal projects in
317 occupied pinyon jay habitats is unlikely to be effective with ongoing woodland dynamics, so it
318 may instead be beneficial for managers to consider site-appropriate silvicultural prescriptions
319 designed to restore and maintain the heterogeneous woodland structure critical to pinyon jays.
320 Co-produced science and monitoring should be coupled with any such restoration efforts (Naugle

321 et al. 2020) to help overcome existing knowledge gaps in woodland restoration (Boone et al.
322 2018).

323 Evaluation metrics suggested that all species models provided “good” predictive
324 capability across a large geography. However, there are several important caveats when using
325 BBS data to develop spatial models. Notably, BBS sampling occurs along roadways, which
326 could bias the habitats and bird communities observed, and without repeated samples provides
327 only an index to abundance. Past studies within our sampling frame have found no significant
328 differences between counts of sagebrush obligates on road and off-road surveys (Rotenberry and
329 Knick, 1995), nor performance of spatial models applied to data when comparing BBS with
330 samples collected off-roads (Mccarthy et al., 2012). Though it remains possible that the entire
331 covariate space (i.e. niche) was not fully sampled for each species by constricting surveys to road
332 sides (e.g. high elevation roadless sites). Ultimately indices such as relative abundance from
333 BBS data can still provide management with meaningful information on patterns of avian
334 occurrence (Johnson, 2008; Niemuth et al., 2017), particularly when it represents the primary
335 data source available at the temporal and spatial scales relevant to management. Viewed in total,
336 local and design-based studies that employ random sampling and account for detection
337 probability will only improve the quality of spatial planning tools for practitioners, and should be
338 used when available. Similarly, model-based inference at the biome scale will never surpass
339 local knowledge or site evaluation prior to management when it comes to sensitive resources
340 (e.g. location of a particular nesting colony; Johnson et al., 2016).

341 Management actions to reduce conifer for purposes other than sagebrush ecosystem
342 restoration (e.g. fuels reduction) may not be similarly inconsequential for pinyon jay
343 conservation, particularly when treatments occur among established pinyon-juniper woodlands.

344 For example, thinning conifers to reduce fire risk in New Mexico, USA left previously-suitable
345 pinyon jay nesting habitat unoccupied following treatment (Johnson et al., 2018) and conifer
346 thinning in Colorado reduced pinyon jay occupancy at local scales (<4 ha), though treatments
347 also resulted increased pinyon jay occupancy at the scale of management (18-117 ha; Magee et
348 al., 2019), highlighting the importance of landscape-level considerations. Both studies
349 documenting impacts to pinyon jay from conifer removal were outside the occupied range of
350 sage grouse (Schroeder et al., 2004). Thus, extending our spatial modeling approach for the
351 pinyon jay distribution beyond the sagebrush biome could better equip conservationists in
352 southwestern ecoregions with important decision-support tools, particularly as these landscapes
353 face additional pressures of drought-induced tree mortality (Clifford et al., 2011; Fair et al.,
354 2018, Shiver et al. 2021).

355 **Implications**

356 Pinyon-juniper management is often framed as creating “winners” and “losers” among wildlife
357 species (Bombaci and Pejchar, 2016; Zeller et al., 2021), but spatial context of management
358 efforts relative to species populations is often lacking to assess this beyond local project scales.
359 In fact, nuanced analysis reveals that targeted removal of post-settlement era conifer
360 encroachment in sagebrush shrublands may not be at odds with species that rely on conifers for a
361 portion of their life history (Anthony and Sanchez, 2019; Maestas et al., 2019). Model outputs
362 developed here can help inform management for an additional suite of species of concern that
363 lack the spatial tools necessary to avoid potentially detrimental impacts and target limited
364 resources for restoration. Future efforts could combine our species models with spatial data on
365 known ecosystem threats and potential risks to populations to develop holistic, multi-species
366 management plans. For example, combining species models with high resolution vegetation data

367 (Allred et al., 2021; Rigge et al., 2020) can help practitioners make optimal decisions given a
368 bevy of seemingly competing conservation and management interests (Reinhardt et al., 2017;
369 Ricca et al., 2018).

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611 Table 1. Songbird species used to develop species distribution models and resulting spatial
 612 predictions from Breeding Bird Survey (BBS) Data. Sagebrush- and woodland-dependent
 613 species were considered for modeling, and we used BBS survey-wide estimated trends from
 614 1966-2015 to identify if populations were increasing, decreasing based on direction of 80% of
 615 the credible intervals ([CI] * denotes CI overlapping 0; Sauer et al., 2017). We only modeled
 616 species if they were detected at least 5 times within Commission for Environmental Cooperation
 617 Level 3 ecoregions from 2011-2016 (supplemental Fig. 1 for map and corresponding ecoregion
 618 names).

Species	Habitat	BBS Trend	Ecoregions
Brewer's Sparrow	Sagebrush	Declining; -1.01 (-1.89, -0.22)	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	Declining*; -0.31 (-0.83, 0.19)	1, 2, 4, 5, 6, 9, 11, 13, 16, 18, 19, 20, 21, 23, 24
Sagebrush Sparrow	Sagebrush	Increasing*; 0.43 (-3.51, 4.51)	1, 2, 5, 6, 8, 13, 16, 18, 20, 21, 23, 24
Sage Thrasher	Sagebrush	Declining; -1.20 (-1.93, -0.47)	1, 2, 5, 6, 8, 9, 11, 13, 16, 17, 18, 19, 20, 21, 23, 24
Ash-throated Flycatcher	Woodland	Increasing; 1.10 (0.68, 1.52)	1, 2, 3, 4, 5, 6, 8, 9, 12, 14, 16, 19, 21, 22, 23, 24
Gray Flycatcher	Woodland	Increasing; 2.43 (1.45, 3.51)	1, 2, 5, 6, 7, 8, 9, 13, 14, 16, 19, 21, 23, 24
Gray Vireo	Woodland	Increasing; 2.10 (-0.28, 4.24)	1, 5, 6, 14, 21, 23, 24
Juniper Titmouse	Woodland	Increasing*; 0.28 (-1.14, 1.54)	1, 5, 6, 9, 14, 16, 21, 22, 23, 24
Pinyon Jay	Woodland	Declining; -3.69 (-5.08, -2.37)	1, 2, 5, 6, 9, 13, 14, 16, 18, 19, 21, 23, 24

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

Variable (abbreviation)	Spatial Window	Temporal Window
Sagebrush (sage) ^a	120m, 1km, 6.4km	NA
Grassland/Herbaceous (herb)	120m, 1km, 6.4km	NA
Shrubland (shrb) ^a	120m, 1km, 6.4km	NA
Conifer (conf) ^a	120m, 1km, 6.4km	NA
Crop/Disturbed (dist) ^a	120m, 1km, 6.4km	NA
Pinyon/Juniper (piju) ^a	120m, 1km, 6.4km	NA
Scrubland/Woodland (scrb) ^a	120m, 1km, 6.4km	NA
Riparian (ripa) ^a	120m, 1km, 6.4km	NA
Burned Area (burn) ^b	120m, 1km, 6.4km	5, 10, 15 years
Avg Min Temp (tmin) ^c	1km	May 15 - Jul 15
Avg Max Temp (tmax) ^c	1km	May 15 - Jul 15
Total Spring Precip (sprp) ^c	1km	Mar 15 - Jul 15
Total Winter Precip (wprp) ^c	1km	Dec 1 - Mar 14
NDVI (ndvi) ^d	6.4km	May 15 - Jul 15
Elevation (elev) ^e	30m	NA
TRI (tri) ^f	1km	NA
Multiscale TPI (tpi) ^g	NA ¹	NA
PDSI (pdsi) ^h	NA	June

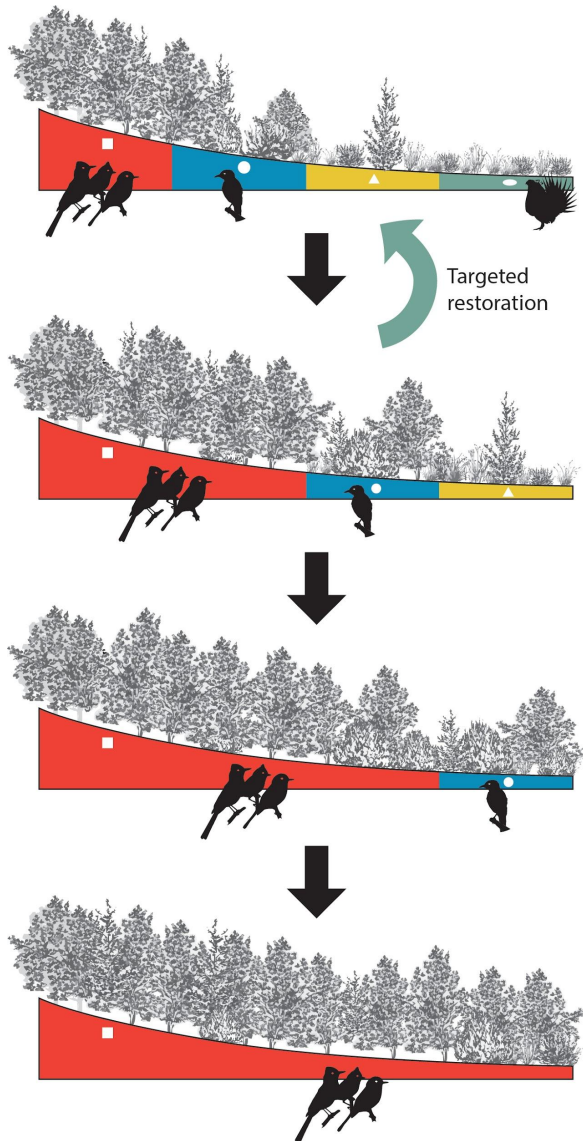
623
 624 ^a Rollins (2009); ^b Eidenshink (2007); ^c Thornton (2012); ^d Landsat-7 imagery courtesy of the
 625 U.S. Geological Survey; ^e Gesch (2002); ^f Riley (1999); ^g Theobald (2015); ^h Abatzoglou (2017).
 626 ¹ Index summarized from TPI calculated at 270m, 810m, and 2.43km (Theobald et al., 2015)

627 Table 3. Variables selected for use in models across species with shortened variable codes

628 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 15yr
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.6400 10yr
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.6400 5yr
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.1000 15yr
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 10yr
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 10yr
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 10yr
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 15yr
Sage Thrasher	elev, tpi, tri	scrb.6400, piju.1000, conf.1000, sage.1000, shrb.1000, ripa.1000, dist.1000	ndvi, pdsi, tmax, wprp	fire.1000m.5yr

629

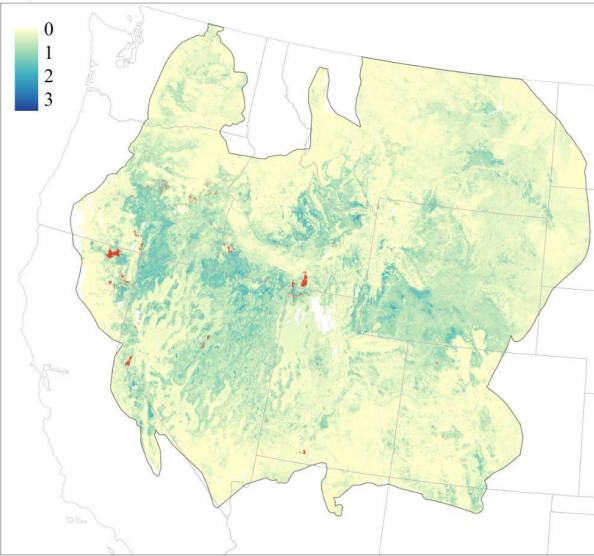


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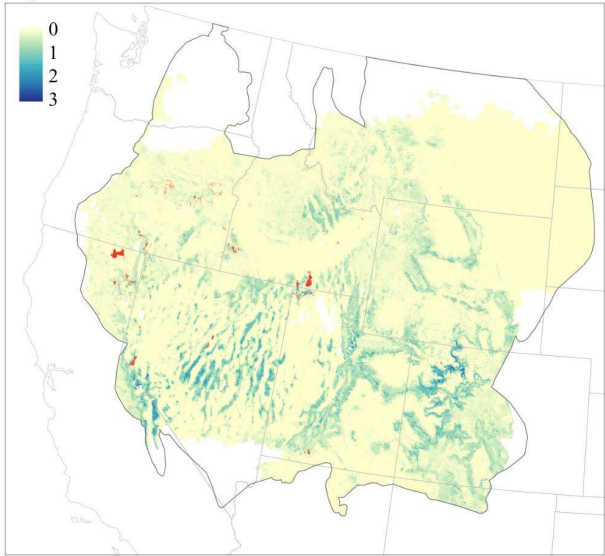
631 Figure 1. Hypothetical illustration depicting how conifer expansion and infill may impact
632 habitats for both sagebrush-obligate and woodland-reliant birds. The top panel shows a
633 landscape that supports a diversity of bird species partitioned by different ecological sites:
634 persistent woodlands supporting dense forest birds (red/square), heterogeneous woodlands
635 supporting birds reliant on more open stands, such as, pinyon jay (blue/circle), and sagebrush
636 shrublands supporting obligate birds, such as, sage grouse where encroaching conifers are
637 targeted for restoration (yellow/triangle to green/oval). Remaining panels depict shifting habitat
638 niches as conifer expansion and infill, without intervention, displace species like pinyon jay and

639 sage grouse that rely on mixed woodlands or treeless shrublands. BBS trends lend support to
640 this hypothetical scenario as both pinyon jay and sagebrush-obligates have been in decline,
641 while other songbirds reliant on persistent pinyon-juniper woodlands have been increasing
642 (Table 1).

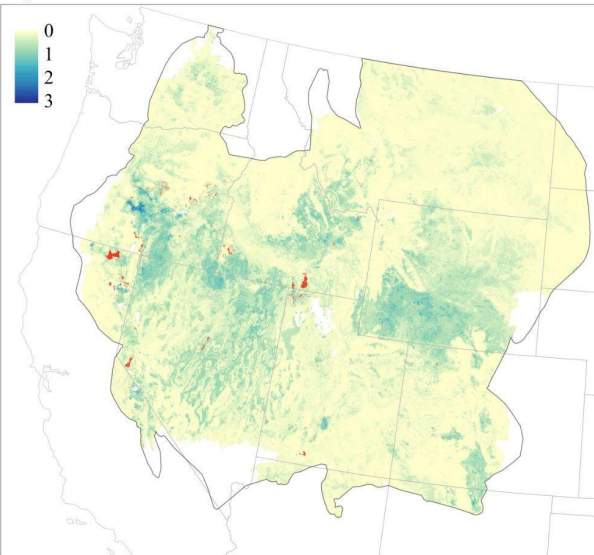
A) BRSP Predicted Count



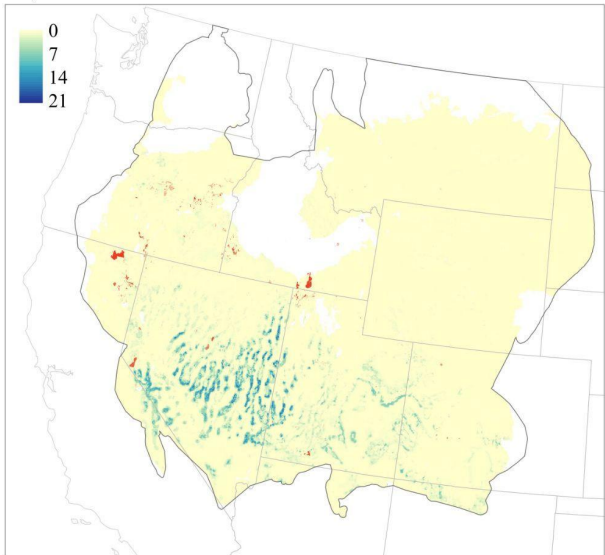
B) GTTO Predicted Count



C) SATH Predicted Count



D) PIJA Predicted Count



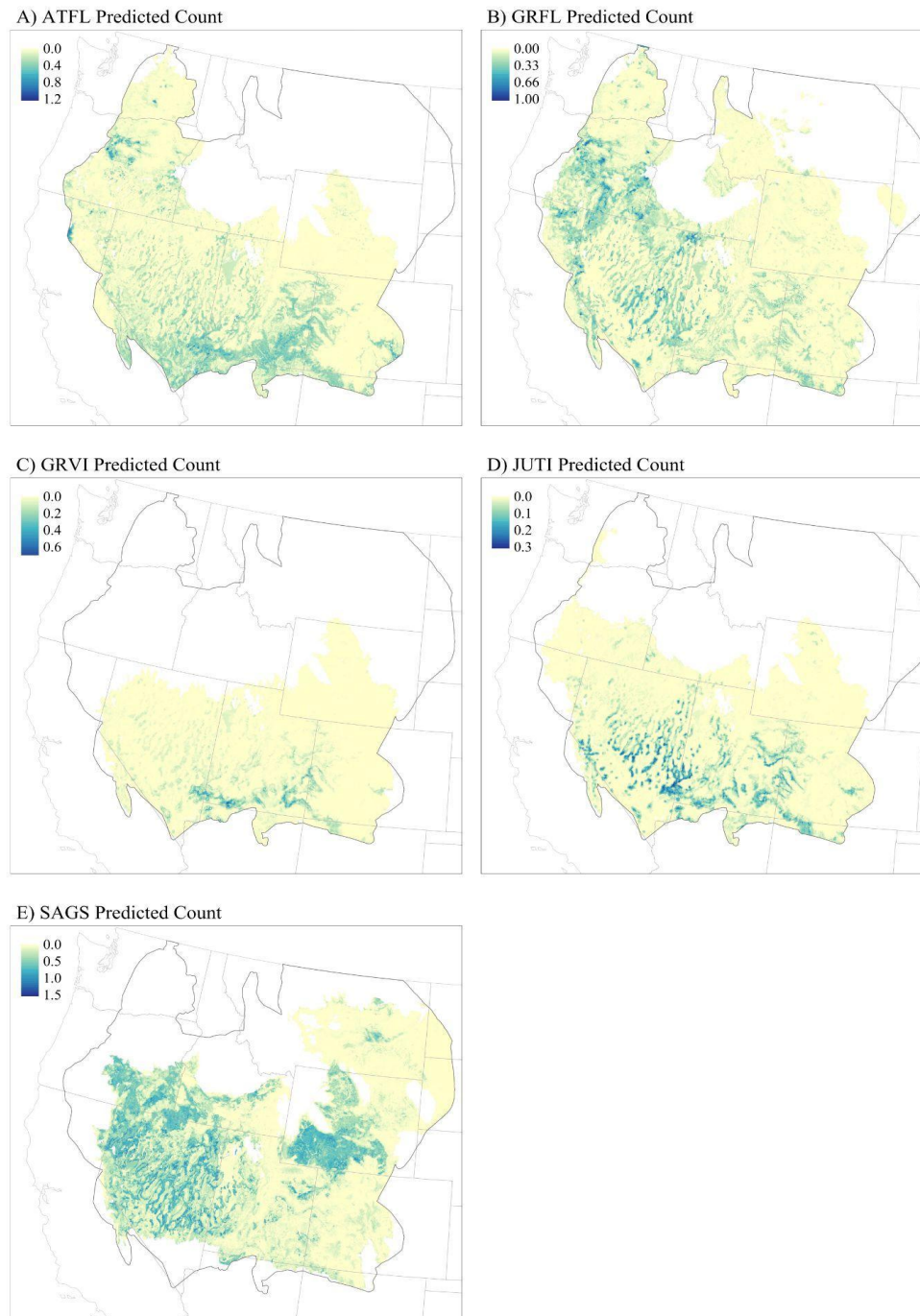
643

644 Figure 2. Predicted counts for each of the modeled species with significant declines identified

645 from BBS trends (Table 1) including , A) Brewer's sparrow (BRSP), , and B) green-tailed

646 towhee (GTTO), C) sage thrasher (SATH), and D) pinyon jay (PIJA). Conifer removal projects

647 contracted with the Sage Grouse Initiative are overlaid in red.



648

649 Figure 3. Predicted counts for each of the modeled species with stable to increasing trends
650 identified from BBS trends (Table 1) including, A) ash-throated flycatcher (ATFL), B) gray
651 flycatcher (GRFL), C) gray vireo (grvi), D) juniper titmouse (JUTI), and E) sage sparrow
652 (SAGS).

653 Supplemental Table 1. Mean area under the curve (AUC) statistic and range calculated from k-
654 folds cross-validation with 10 folds suggest good model fit across species.

Species	AUC
ash-throated flycatcher	0.950 (0.942, 0.958)
Brewer's sparrow	0.922 (0.916, 0.927)
gray flycatcher	0.961 (0.953, 0.971)
gray vireo	0.968 (0.951, 0.980)
green-tailed towhee	0.945 (0.940, 0.951)
juniper titmouse	0.932 (0.885, 0.957)
pinyon jay	0.929 (0.906, 0.967)
sage sparrow	0.964 (0.957, 0.971)
sage thrasher	0.946 (0.941, 0.949)

655



656

657 Supplemental Figure 1. Sampling frame was composed of the US portion of the sagebrush
658 ecosystem as identified by all sagebrush land cover types, with the addition of existing sage
659 grouse Priority Areas for Conservation and management zones (COT 2013), and the historic sage
660 grouse species range (USGS FRESC 2002), which encompassed 625 Breeding Bird Survey
661 routes. We restricted species models Commission for Environmental Cooperation Level 3
662 ecoregions where they were detected at least 5 times from 2011-2016, which implicated: 1-
663 Arizona/New Mexico Plateau; 2-Blue Mountains; 3-California Coastal Sage; Chaparral, and Oak

664 Woodlands; 4-Cascades; 5-Central Basin and Range; 6-Colorado Plateaus; 7-Columbia
665 Mountains/Northern Rockies; 8-Columbia Plateau; 9-Eastern Cascades Slopes and Foothills; 10-
666 High Plains; 11-Idaho Batholith; 12-Klamath Mountains; 13-Middle Rockies; 14-Mojave Basin
667 and Range; 15-North Cascades; 16-Northern Basin and Range; 17-Northwestern Glaciated
668 Plains; 18-Northwestern Great Plains; 19-Sierra Nevada; 20-Snake River Plain; 21-Southern
669 Rockies; 22-Southwestern Tablelands; 23-Wasatch and Uinta Mountains; and 24-Wyoming
670 Basin.