Received: 16 October 2025 | Revised: 10 April 2026 | Accepted: 8 June 2026

DOI: 10.1002/eap.70298

ARTICLE

ECOLOGICAL APPLICATIONS
ECOLOGICAL SOCIETY OF AMERICA

Limited capacity of habitat features to buffer grassland bird declines

Neil A. Gilbert[1] | **Peter J. Williams**[2] | **Daren J. Carlson**[3] | **Robert M. Dunlap**[3] | **Mike Worland**[3] | **Christopher S. Jennelle**[3] | **Elise F. Zipkin**[2]

[1]Department of Biology, Oklahoma State University, Stillwater, Oklahoma, USA

[2]Department of Integrative Biology, Ecology, Evolution, and Behavior Program, Michigan State University, East Lansing, Michigan, USA

[3]Minnesota Department of Natural Resources, Ecological and Water Resources Division, St. Paul, Minnesota, USA

Correspondence
Neil A. Gilbert
Email: neil.gilbert@okstate.edu

Funding information
Division of Environmental Biology, Grant/Award Number: 2213565; Directorate for Biological Sciences, Grant/Award Number: 2208894

Handling Editor: Daniel S. Karp

Abstract

Grassland birds are among the most rapidly declining groups of species, largely due to historical habitat losses that have led to extinction debts. Beyond direct habitat manipulations (e.g., prescribed fire), conservation strategies for grassland birds often adopt a landscape-scale perspective, particularly when guiding decisions on reserve acquisition, prioritizing management across existing reserves, and restoring habitat. Additionally, climate is increasingly recognized as a critical consideration for grassland bird conservation, since temperature influences survival and nest success, while precipitation has an outsized effect on primary productivity and habitat structure in grassland ecosystems. Here, we used a 16-year breeding season avian point count dataset from some of the highest quality patches of remaining grassland habitat in Minnesota, USA, to (1) estimate occurrence trends for 33 species that use grasslands and (2) assess the influence of two traditional habitat variables (amount of grassland habitat, grassland edge density) and two climate factors (temperature and precipitation anomaly) on baseline occurrence and trends. Our model reveals declines across bird species that use grassland reserves; four out of eight grassland-obligate species declined (with ≥95% confidence; six out of eight declined with ≥68% confidence) whereas 6 out of 25 facultative grassland species declined (with ≥95% confidence). The traditional habitat variables were associated with baseline occurrence of relatively few species (e.g., proportion of grassland habitat showed a clear relationship with baseline occurrence of four species, including two obligates) and buffered declines for only a handful of species, none of them obligates (e.g., amount of grassland habitat showed a clear buffering effect for Red-winged Blackbird). In contrast, breeding-season climate anomalies showed strong relationships with occurrence of more species (temperature: 7 species; precipitation: 11 species). However, climate effects on trends were less common (e.g., wetter breeding seasons

buffered declines of Savannah Sparrows). Considered holistically, our results suggest that grassland bird declines are apparent even in the highest quality remaining habitats of the upper midwestern United States. Conservation strategies focused exclusively on protection and management of high-quality prairie may have limited benefits for grassland bird populations, especially as temperature and precipitation anomalies exert increasingly strong impacts on population trajectories and climate conditions continue to change.

KEYWORDS
area-based conservation, Bayesian, grassland birds, landscape configuration, occupancy model, prairie, precipitation anomaly

INTRODUCTION

Anthropogenic global change is driving declines and extinctions across taxa (Butchart et al., 2010; Cardinale et al., 2012; Dirzo et al., 2014; Keck et al., 2025). Many bird species are declining: approximately 3 billion birds have been lost from North America from 1970 to 2017 (Rosenberg et al., 2019), with declines occurring most swiftly where species are abundant (Johnston et al., 2025). For North American birds, grassland species have experienced the steepest declines over the past several decades, both in terms of the number of individuals lost and the proportion of species in decline (Askins et al., 2007; Brennan & Kuvlesky, 2005; Rosenberg et al., 2019).

Grassland bird declines are largely due to widespread habitat loss, particularly the conversion of grasslands to agricultural lands (Douglas et al., 2023; Lark et al., 2019). Grassland landscapes are highly desirable for conversion to row-crop agriculture, which has led to a loss of >60% of North America's grasslands; losses have been particularly dire for tallgrass systems, with >95% of those ecosystems now gone (Comer et al., 2018). Beyond conversion of grassland to agriculture, grassland birds face a blend of interacting anthropogenic threats (Bernath-Plaisted et al., 2023) such as predation from invasive species (Loss et al., 2013), collisions with human infrastructure during migration (Van Doren et al., 2021), collapse of insect populations (Wagner et al., 2021), climate change (Maresh Nelson et al., 2024), pesticides (Li et al., 2020; Stanton et al., 2018), and woody vegetation encroachment of grassland ecosystems due to alteration of disturbance regimes (Auken, 2000; Eldridge et al., 2011; Stanton et al., 2018). These threats are often studied in the breeding ranges of species, but their impacts in the overwintering and migration ranges may be just as important (Marra et al., 2015). Conservation of grassland birds must focus on protecting and managing grassland habitats while also anticipating and mitigating the effects of other stressors (Bernath-Plaisted et al., 2023; Handler et al., 2022; Wilsey, Grand, et al., 2019).

Given the widespread loss of grasslands, reserves—protected areas with active management and high-quality habitat—are essential for conserving grassland birds and mitigating population declines. While reserves generally support biodiversity conservation (Barnes et al., 2023; Geldmann et al., 2013; Gray et al., 2016), their effectiveness varies, and reserves alone may be insufficient to halt population declines (Dornak et al., 2020; Gardner et al., 2023; Geldmann et al., 2013). The capacity of reserves to buffer declines may depend on local- and landscape-scale factors such as the amount and configuration of habitat. Many obligate grassland species—defined as species restricted to grasslands (Vickery et al., 1999)—are area sensitive, meaning they occur more frequently in larger patches of grassland habitat (Davis, 2004; Ribic et al., 2009). They also tend to occur more frequently in patches with less complex shapes and thus less edge habitat, perhaps because of higher rates of nest predation or nest parasitism near edges (Davis, 2004; Lockhart & Koper, 2018; Patten et al., 2006; Shahan et al., 2017). Therefore, reserves with large amounts of grassland habitat and few edges may support the highest occurrences of obligate grassland species, potentially providing a local buffer against broader-scale declines. Facultative grassland species—those that use multiple habitats, including grasslands (Vickery et al., 1999)—also occur in grassland reserves but may be less sensitive to the amount of grassland habitat. Indeed, some facultative grassland species that occupy other habitats may prefer reserves with less grassland habitat and abundant edges. While baseline associations between local- and landscape-scale variables and grassland bird occurrence, abundance, and demography have been well studied (Billerman et al., 2020; Davis, 2004; Ribic et al., 2009), it is still unclear whether characteristics of reserves influence population trends, and whether favorable habitat

factors, both locally and in the surrounding landscape, could mitigate local declines.

Beyond habitat factors, climate conditions also play a role in the distribution and population dynamics of grassland birds, and grasslands are experiencing more rapid changes in climate than other ecosystems in the contiguous United States (Dobrowski et al., 2013). Increasing minimum and mean temperatures may enhance processes such as adult survival and nest success, whereas increases in maximum temperatures are associated with negative effects, though these patterns vary considerably among species (Conrey et al., 2016; Felton et al., 2021; Maresh Nelson et al., 2024; Maurer et al., 2020). Precipitation generally increases primary productivity, which alters habitat structure and height (Collins et al., 2012; Lane et al., 2000), which in turn influences nest microclimate (Bernath-Plaisted et al., 2025), key food resources such as arthropods (Lenhart et al., 2015; Zhu et al., 2014), and multiple demographic parameters of grassland bird populations (Freeman, Silber, et al., 2025; Silber et al., 2023). The effects of precipitation on grassland bird populations are complex: both drought and excessive rainfall can negatively affect populations, and responses vary by taxonomic group and climate regime (Maresh Nelson et al., 2024; Zuckerberg et al., 2018). Species responses are also influenced by their habitat associations. For example, wetter-than-normal periods with vigorous vegetation growth tend to benefit species associated with wet-to-mesic grass habitat, while potentially disadvantaging species associated with dry grass habitat. Understanding these differential responses to climate variability is essential for effectively managing grassland bird communities (Maresh Nelson et al., 2024). While climate change and habitat loss threaten bird communities broadly, managers can only act locally, through reserve acquisition, restoration, or active management. However, the extent to which habitat management and local climate conditions can offset population declines remains uncertain.

Here, we analyze 16 years of bird monitoring data from 40 high-quality grassland reserves in western Minnesota, USA (Figure 1), to assess how habitat and climate factors mediate occurrence trends of grassland birds—that is, whether such factors slow or accelerate occurrence declines. By 2017, Minnesota had lost nearly 99% of the 73,000 sq km of prairie which covered the state when it was first surveyed in the 19th century, primarily to agricultural conversion (Minnesota Prairie Plan Working Group, 2018). These reserves represent some of the best remaining examples of native tallgrass prairie in the state. Against this backdrop, our objectives are to (1) estimate trends in occurrence for an assemblage of birds that use grasslands, including both obligate and facultative species, and (2) evaluate how two commonly used habitat factors in ecological and conservation analyses (amount of habitat and edge density between habitat types), as well as two climate factors (breeding-season temperature and precipitation deviations from long-term averages), influence occurrence probabilities and trends. We predict that obligate grassland species have higher occurrence and decline less rapidly in reserves with more grassland habitat and less edge. Conversely, we predict that these factors have neutral or weak positive effects on facultative grassland species, with less influence on their trends. We expected mixed responses to anomalously warm temperatures (e.g., due to range position; species near the leading edge of their range might increase with warming temperatures, whereas species near the trailing edge might decrease), though we expected obligate species to be more likely to show negative effects of warm temperatures (Maresh Nelson et al., 2024). We expect the effects of precipitation anomaly to vary by species' habitat associations—for example, facultative species associated with taller vegetation and obligate species associated with

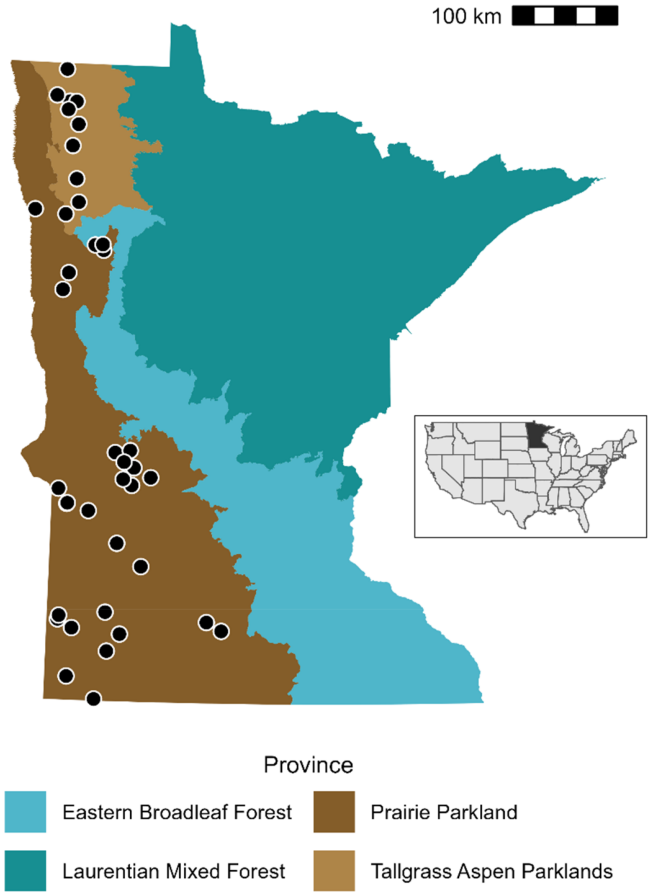

FIGURE 1 Map of Minnesota, USA, showing the distribution of surveyed grassland reserves (black points) within the state's two grassland provinces (shades of brown). Inset: the location of Minnesota within the continental United States.

mesic tallgrass habitats may respond positively, whereas obligate species associated with xeric shortgrass may respond negatively to abnormally wet years. Among-species variation in responses to such factors is inevitable, but our multispecies modeling approach allows us to evaluate both species-specific responses and assemblage-level patterns (Farr et al., 2019; Monroe et al., 2021). By clarifying how habitat and climate factors interact to shape occurrence trends, our research offers actionable insights for managing existing grassland reserves and restorations, as well as guidance for the design of future sites.

METHODS

Bird surveys

Trained observers conducted avian point counts at 40 reserves in western Minnesota from 2008 to 2023 (Figure 1). The reserves were selected following a stratified random approach: A list of grassland reserves was assembled, and reserves were randomly selected based on strata of geography, reserve size (<20 ha vs. >20 ha), and landscape context (<20% grassland vs. >50% grassland in a 1-km buffer around reserve boundary; Carlson, 2019). Except for one site that is privately owned but notable for its size and integrity of its grassland plant and animal communities, these reserves are permanently protected parcels and include public properties (e.g., state parks, wildlife management areas) and permanent private conservation easements. While the type, frequency, and intensity of management actions vary among reserves, all reserves are actively managed (e.g., prescribed fire, grazing) to sustain their status as high-quality grassland ecosystems, with particular emphases on preventing woody encroachment and limiting the dominance of non-native plant species (Ahlering et al., 2020; Carlson, 2019). Within each reserve, trained observers surveyed points that were systematically spaced at least 200 m apart. The number of points chosen for each reserve depended on reserve size and shape, ranging from 2 to 24 (median: 7), for a total of 383 unique sampling points. Due to resource limitations, we used a panel design such that four reserves were surveyed annually while the other 36 reserves were sampled on a 6-year rotation (McDonald, 2003; Wright et al., 2022). Points were surveyed three times per year within the breeding season (late May through early July).

Observers ($n = 13$ over the lifetime of the study) conducted 10-min point counts during the morning hours on days with favorable weather (no precipitation and low wind). Observers recorded the estimated distance (0–25 m, 25–50 m, 50–100 m, >100 m) to each detected bird, and we limited analysis to detections within 100 m of the point, except for three large-bodied species with large territory sizes and high detectability (Western Meadowlark, Upland Sandpiper, and Ring-necked Pheasant) for which we considered unlimited radius detections. We retained all species for analysis that were recorded on at least 3% of surveys except for waterfowl (Anatidae), which were primarily represented by flyovers. The resulting 33 species (Appendix S1: Table S1) include eight obligate grassland species (Vickery et al., 1999), as well as species with broader habitat preferences (e.g., Eastern Kingbird and Yellow Warbler), which we collectively define as facultative grassland species.

Covariates

We quantified four ecological covariates that we hypothesized would affect the occurrence of grassland birds and possibly mediate their trends through time. Rather than exhaustively searching for the variable(s) with the strongest association with occurrence, we chose a small number of variables that are often used in ecological and conservation analyses to make inference about their possible mediating influence on trends. That is, our statistical goal was inference rather than prediction (Tredennick et al., 2021), and we prioritized variables that may be useful for managers planning habitat manipulations or conservation planners designing reserve networks (Zuckerberg et al., 2026). We calculated the first two variables—proportion grassland and grassland edge density—from a contiguous grassland shapefile, which was derived from a Minnesota Department of Natural Resources layer on native plant communities (https://www.dnr.state.mn.us/npc/index.html) and the following LANDFIRE (https://landfire.gov/vegetation) land-cover classes: grasslands, pasture, hay, and idle cropland. We smoothed the layer by removing isolated shapes <2800 m^2 and filling in gaps <8200 m^2 to represent the contiguous grassland present within an area. We calculated the proportion of grassland and grassland edge density within two spatial scales of each point: within radii of 250 and 3000 m, intended to represent habitat conditions at a local scale relevant to individual bird territories and local management actions (e.g., controlled burns of pastures) and at a landscape scale relevant to broader level management decisions (e.g., acquisition of new reserves). Finally, we calculated average breeding-season (May and June) temperature deviation and cumulative breeding-season precipitation deviation from the 1985–2005 average using the R package daymetr (Hufkens et al., 2018). Positive anomalies represent warmer and wetter than average breeding seasons, while negative precipitation anomalies indicate cooler and drier than average

breeding seasons. Because the effects of weather variables may be lagged (e.g., overwinter precipitation may influence breeding-season vegetation growth and subsequent bird habitat selection or productivity; Pearce-Higgins et al., 2015; Silber et al., 2023; Williams et al., 2015), we also calculated nonbreeding season (defined as January through April, since many species included do not arrive and begin breeding until May) anomalies to be evaluated in supplemental analyses (Appendix S1).

Multispecies occupancy model

We used multispecies occupancy models to estimate species and assemblage occurrence trends, and to evaluate the influence of environmental variables on these trends (Kéry & Royle, 2015; MacKenzie et al., 2002). We chose an occupancy approach rather than abundance models because counts greater than one individual (7.4% of observations) or two individuals (2.9% of observations, potentially representing a pair) were rare, and because abundance approaches such as N-mixture models may perform poorly when assumptions are violated (Barker et al., 2018; Link et al., 2018). Occupancy models consist of two linked logistic regressions: One describes the ecological pattern of a species' occurrence, and the other describes the observational process during sampling. Variation among species in both occurrence and detection probabilities is incorporated via a random-effects structure that treats species-specific parameters as draws from assemblage-level distributions for each parameter. In this way, assemblage occurrence trends represent the aggregate pattern across all species, providing insight into how the grassland bird assemblage responds to environmental heterogeneity, while accommodating species-specific responses within the broader assemblage.

The submodel for occurrence at a point included an intercept and linear effects of year (to characterize occurrence trends), either proportion grassland or edge density (the two variables were too collinear to include together in a global model; Pearson's $|r| > 0.6$; Dormann et al., 2013), temperature anomaly, and precipitation anomaly. To understand how the habitat and climate factors influenced occurrence trends over time, we allowed each environmental variable to interact with year. While many species might be expected to show hump-shaped relationships between occurrence and climate anomalies (what we call the "Just Right" Hypothesis, or preference for average conditions), a supplemental analysis indicated that no species showed support for the "Just Right" Hypothesis for temperature anomaly, and only three species for precipitation anomaly (Appendix S1: Figure S1). Therefore, we chose to focus on linear effects for simplicity, particularly for interpreting interactions between trends and the environmental variables.

Because different species can respond differently to these factors, the model treated the influence of each covariate (and their interactions) as random effects that vary by species. Finally, to accommodate heterogeneity in occurrence among reserves and at survey points within reserves, we included random effects of reserve (specific to each species) and point within reserve (specific to each species), so the baseline probability of occurrence for each species was adjusted according to where the survey took place.

In the detection submodel, we included quadratic effects of survey date and time of day, as detectability could plausibly peak at intermediate values—for example, midway through the breeding season or during midmorning. Coefficients for these covariates, along with the intercept (representing average detectability), were treated as random effects by species to account for species-specific variation in detectability. Additionally, we included a random effect of observer to capture variation in observer skill or sensory ability. We standardized all covariates to have a mean of 0 and a SD of 1.

We fit the model with Nimble (de Valpine et al., 2017) through R v4.2.1 (R Core Team, 2025), using three Markov chain Monte Carlo chains of 30,000 iterations each, discarding the initial 10,000 iterations as burn-in and thinning by 10. We applied commonly used weakly informative priors, for example, Normal(0,1) for standardized covariate coefficients and Exponential(1) for variance components (Kéry & Royle, 2015; McElreath, 2020). We ensured that models had converged by visually inspecting parameter traceplots and checking that the Gelman–Rubin diagnostic $\widehat{R}$ was <1.1 (Brooks & Gelman, 1998). We provide additional details about the model in Appendix S1. When discussing results, we use 'with 68% confidence' and 'with 95% confidence' to refer to cases when the 68% and 95% credible intervals for a given parameter did not include zero, respectively.

RESULTS

Occurrence declines outnumber increases in the grassland bird assemblage

The assemblage of birds in grassland reserves as a whole declined in occurrence between 2008 and 2023. The assemblage average for linear effect of year (i.e., trend) was −0.12 (95% CI: −0.30, 0.08), indicating that, on average, species in the assemblage experienced weak declines in occurrence (Figure 2). This corresponds to a −22% (95% CI: −53%, 19%) change in occurrence between 2008 and 2023 for a species with an assemblage-average

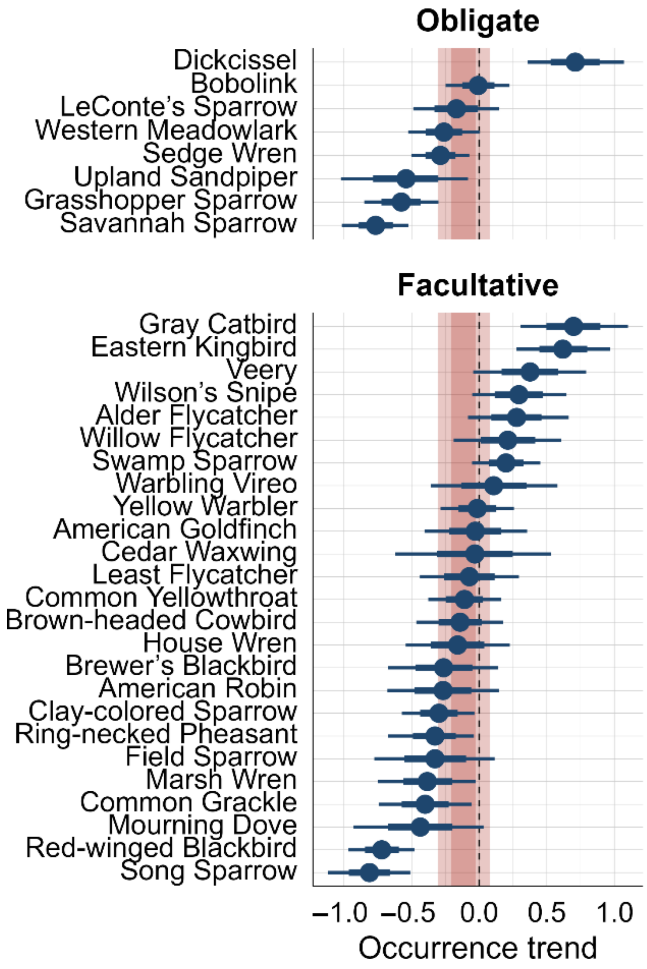

FIGURE 2 Occurrence trends (logit scale) for an assemblage of 33 bird species that use grasslands. Points and thick and thin bars are posterior means and 68% and 95% credible intervals, respectively, for species-level trend estimates. Shaded red rectangles are the 68% (darker) and 95% (lighter) credible intervals for the assemblage-level trend estimate.

response. Four out of eight of the obligate grassland species declined with ≥0.95 probability (6/8 with ≥0.68 probability); only the Dickcissel increased with ≥0.95 probability (Figure 2)—notably, this species is famously irruptive, often shifting towards and beyond range edges (which occur in our study region) during droughts within their range core (Bateman et al., 2015). Declines were less extreme for facultative grassland species; 6 out of 25 species declined with ≥0.95 probability, two species showed increasing occurrence trends with ≥0.95 probability, and the remaining 17 showed no clear trends (Figure 2).

Effect of grassland amount

At the assemblage level, there was no clear relationship between amount of grassland habitat (at either spatial scale) and occurrence probability across species (Figure 3a, Appendix S1: Figure S2). At the species level, three species (Bobolink, Savannah Sparrow, Wilson's Snipe) showed positive relationships with proportion grassland within 250 m with ≥0.95 probability (Figure 4); at the broader scale, only one species showed a relationship with proportion grassland within 3000 m (Brown-headed Cowbird, negative relationship; Appendix S1: Figure S3). We found no evidence that amount of grassland habitat (at either spatial scale) modulated occurrence trends at the assemblage level (Figure 3a). Only four species (all facultative) showed strong evidence (≥0.95 probability) of occurrence trends being affected by amount of grassland habitat: Increasing grassland accelerated declines for House Wren (250 m scale), Brewer's Blackbird (3000 m scale), and Yellow Warbler (both scales) but buffered declines for Red-winged Blackbird (3000 m scale; Figure 4, Appendix S1: Figure S3).

Effect of grassland edge density

At the assemblage level, there was no clear relationship between grassland edge density (at either spatial scale) and occurrence probability across species (Figure 3b, Appendix S1: Figure S2). At the local 250 m scale, occurrence of four species (three obligate: Bobolink, Grasshopper Sparrow, Savannah Sparrow; 1 facultative: Wilson's Snipe) decreased with increasing edge density, whereas four species (all facultative) showed increasing occurrence with increasing edge density (Figure 4). At the 3000 m scale, only two species (Western Meadowlark, obligate; Wilson's Snipe, facultative) showed strong relationships with edge density: Occurrence of both species decreased with increasing edge density (Appendix S1: Figure S3). Across species, there was no evidence that grassland edge density (at either spatial scale) influenced the probability of decline in a species with assemblage-average values (Figure 3b). Edge density buffered declines for Yellow Warbler (facultative; both scales) and House Wren (facultative; 250 m scale) but accelerated declines for Willow Flycatcher (facultative; 3000 m scale; Appendix S1: Figure S3).

Effect of temperature anomaly

Across species, there was not a strong association between occurrence and breeding-season temperature anomaly (Figure 3a). At the species level, six species (three obligate, three facultative) showed lower occurrence during abnormally warm breeding seasons, whereas one species (Dickcissel, obligate) showed higher occurrence during

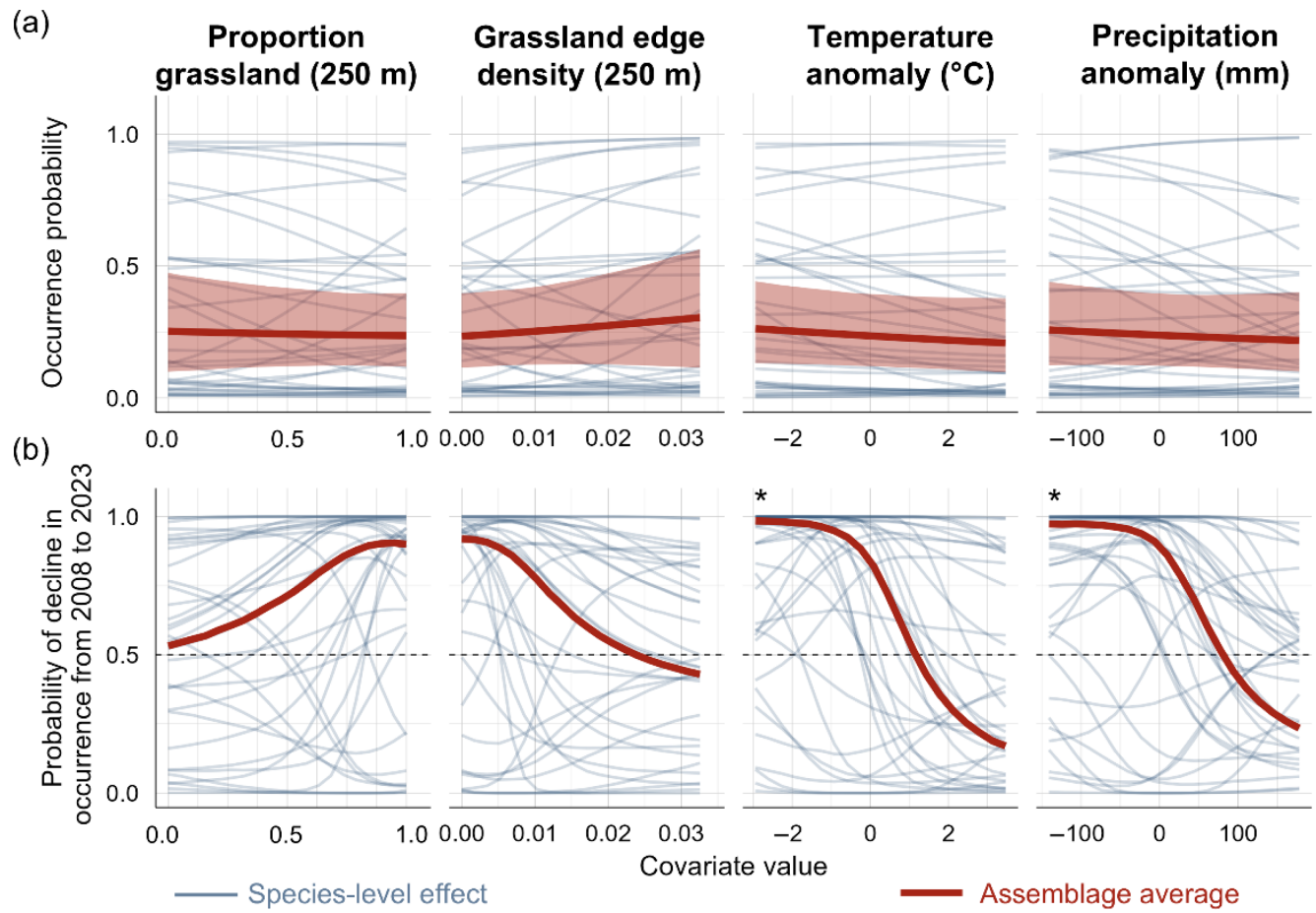

FIGURE 3 (a) Marginal effects of the environmental covariates on the occurrence of an assemblage of birds that use grasslands. The red lines and shaded regions are the posterior means and 95% credible intervals for the relationship at the assemblage level, while the blue lines are the posterior means of the species-level relationships. (b) Probability of decline in occurrence between 2008 and 2023 at differing values of the environmental covariates. The red line represents the average at the assemblage level, while the blue lines are species-level curves. An asterisk (*) or double asterisk (**) in the top left corner of a panel indicates that either the main effect of the covariate (a) or the interaction between the covariate and trend (b) had a 68% or 95% credible interval that did not include zero at the assemblage level.

abnormally warm breeding seasons (Figure 4). Across species, there was weak evidence that breeding-season temperature anomaly buffered declines at an assemblage level (Figure 3b). At the species level, abnormally warm breeding seasons buffered occurrence declines for eight species (four obligate, four facultative) and did not accelerate declines for any species. Alternative models with nonbreeding (January–April) weather anomalies identified a weak (≥68% confidence) negative main effect of temperature anomaly (i.e., lower occurrence following warmer winters) but, contrary to the breeding-season model, no evidence that nonbreeding temperature anomaly influenced trends (Appendix S1: Figure S4). At the species level, eight species (four obligate, four facultative) showed lower occurrence following abnormally warm nonbreeding seasons, whereas one species (Sedge Wren, obligate) showed higher occurrence following abnormally warm nonbreeding seasons (Appendix S1: Figure S3).

Effect of precipitation anomaly

Across species, there was no clear relationship between breeding-season precipitation anomaly and occurrence probability, likely because of similar numbers of species with strong positive and negative effects canceling out any assemblage-level pattern (Figure 3a). Six species showed strong positive relationships with breeding-season precipitation anomaly (Dickcissel, Grasshopper Sparrow, Clay-colored Sparrow, Common Yellowthroat, Swamp Sparrow, Wilson's Snipe), indicating higher occurrence probabilities in wetter breeding seasons (Figure 4a), whereas five species showed strong negative relationships with precipitation anomaly (American Goldfinch, American Robin, Brown-headed Cowbird, Common Grackle, Ring-necked Pheasant), indicating higher occurrence probabilities in drier breeding seasons (Figure 4a). Across species, there was weak evidence that breeding-season precipitation

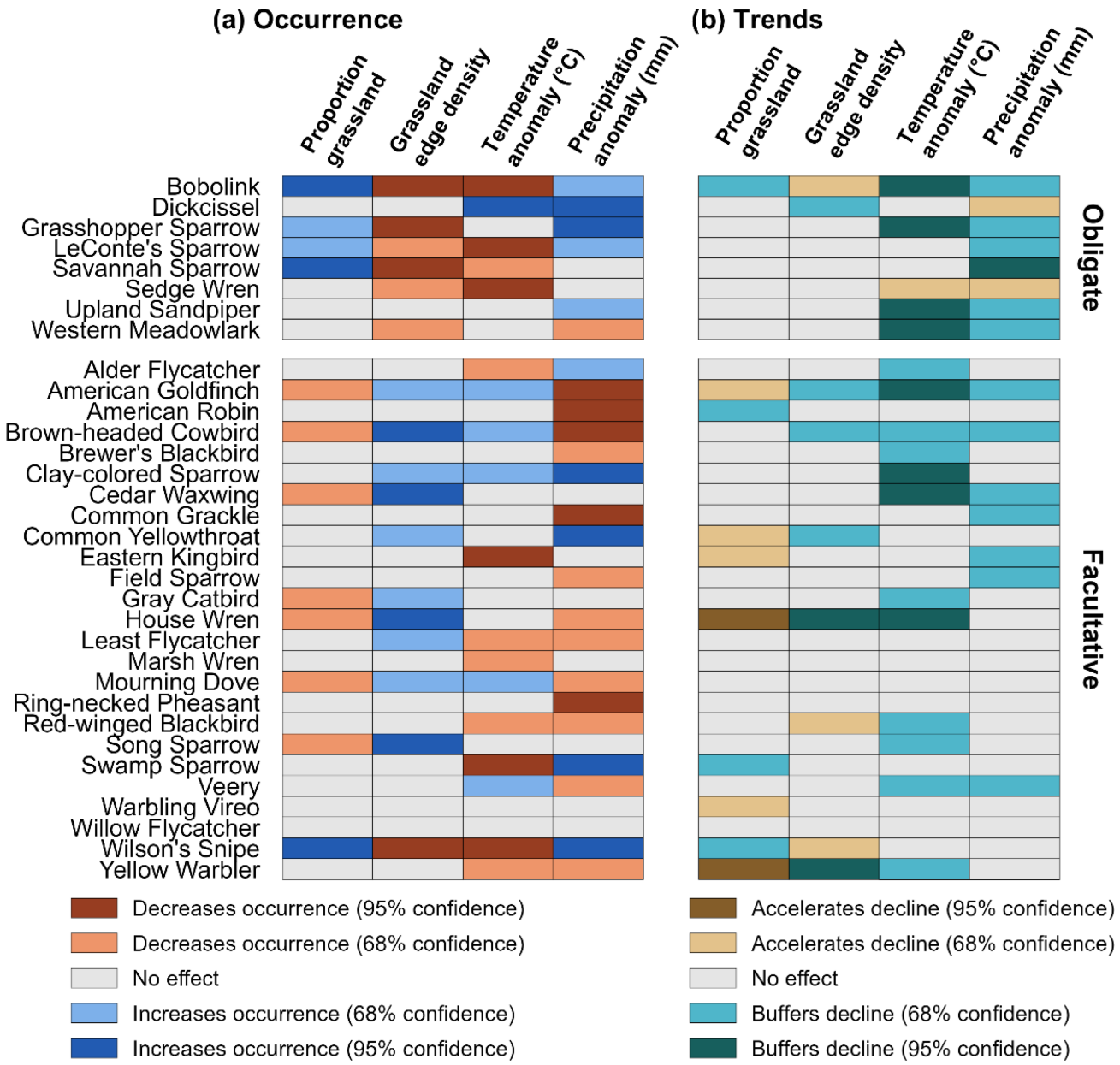

FIGURE 4 Estimated influence of ecological factors on (a) occurrence and (b) occurrence trends. In (b), "Accelerates decline" indicates that a decline occurs more rapidly (or an increase occurs more slowly) at a higher value of the covariate, whereas "buffers decline" indicates that a decline occurs less rapidly (or an increase occurs more rapidly) at a higher value of the covariate. Proportion grassland and edge density were measured within 250 m of survey points, and the weather anomalies are calculated for the breeding season (defined as May and June). See Appendix S1: Figure S3 for results for proportion grassland and edge density at the broader (within 3000 m of points) scale and for nonbreeding (January through April) climate anomalies.

anomaly buffered occurrence declines for a species with assemblage-average values (Figure 3b). At the species level, only the Savannah Sparrow showed strong evidence that wetter breeding seasons buffered declines (Figure 4). Alternative models with nonbreeding (January–April) weather anomalies identified a weak (≥68% confidence) positive main effect of precipitation anomaly (higher occurrence following wet nonbreeding seasons) and, contrary to the breeding-season model, strong (≥95% confidence) evidence that wetter nonbreeding seasons accelerated declines (Appendix S1: Figure S4). At the species level, seven species (four obligate, three facultative) showed higher occurrence following wetter nonbreeding seasons (no species showed strong evidence of lowered occurrence), but eight species (two obligate, six facultative) showed evidence of wetter nonbreeding seasons accelerating occurrence declines (Appendix S1: Figure S3).

DISCUSSION

We found limited evidence that habitat factors commonly used in ecological and conservation analyses buffer declines in occurrence of grassland birds. While several obligate grassland species showed the predicted higher baseline occurrence with increasing grassland habitat and decreasing edge (Figure 4a), neither proportion of grassland habitat nor grassland edge density (at either spatial scale) influenced occurrence trends of any of the obligate grassland species (Figure 4b, Appendix S1: Figure S3). Only two facultative species showed associations between baseline occurrence and proportion grassland, and three species showed evidence of proportion grassland accelerating declines while one species showed evidence of proportion grassland buffering declines (Figure 4, Appendix S1: Figure S3). While we did find the expected positive effect of edge density on baseline occurrence for four facultative species (and one species with a negative effect), only three species showed evidence of edge density influencing occurrence trends (Figure 4, Appendix S1: Figure S3). While our analysis focused on occurrence, it is possible that mediating influences of habitat and climate factors may be more readily apparent via abundance monitoring, since changes in abundance occur more rapidly than changes in occurrence (Brodie et al., 2025; Freeman, Eyster, et al., 2025; Johnston et al., 2015). Considered holistically, our results indicate that while traditional habitat factors may influence baseline occurrence of grassland birds, they generally do not slow declines, particularly in any consistent fashion that would support multispecies conservation.

The limited influence of habitat characteristics on trends suggests that traditional, reserve-based approaches to prairie management may be insufficient to slow the declines of grassland birds. Indeed, these declines have continued despite decades of emphasis on such approaches. These declines may reflect historical land conversion, as the widespread transformation of native grasslands to agriculture destroyed the majority of habitat, especially tallgrass prairie (Augustine et al., 2021). Such habitat loss often does not immediately precipitate local extirpations but instead creates an extinction debt, whereby species decline gradually over time following habitat conversion (Kuussaari et al., 2009). In North America, agricultural expansion has been linked to extinction debt in birds, with habitat patches in converted landscapes supporting species unlikely to persist in the long term (Haddou et al., 2022). If ongoing declines are driven by extinction debt, then management actions such as acquiring new reserves or expanding grassland habitat within existing reserves may be insufficient—at least at the rate these actions are currently implemented. Declines are likely compounded by pressures outside of breeding ranges, such as conditions during migration or on wintering grounds, which remain comparatively understudied (Bernath-Plaisted et al., 2023). Additional broad-scale threats, including climate change, may further drive declines irrespective of the amount or quality of habitat (Bernath-Plaisted et al., 2023; Grand et al., 2019; Wilsey, Taylor, et al., 2019). Reserve-based management remains critical, but expanding such efforts to a degree sufficient to slow declines may not be feasible given the dominance of private land ownership and agricultural land use in the prairie region. Complementary conservation strategies that create or enhance grassland habitat on private, working lands may offer the greatest potential to slow grassland bird declines because a majority (>80%) of remaining native grasslands are privately owned (Burger et al., 2019; Keyser et al., 2019; NABCI, 2013; Pavlacky et al., 2021). Working land conservation differs from reserve-based conservation in that management supports habitat and ecological services while also supporting production of commodities such as food, water, fiber, and fuel (Garibaldi et al., 2023; Kremen & Merenlender, 2018). After decades to centuries of habitat loss, such efforts to expand and improve grassland habitat are essential to preventing further population declines.

Compared to traditional habitat factors, the climate anomalies—especially precipitation—had more widespread effects on baseline occurrence (Figure 4a). For 24 species (73%), breeding-season precipitation anomaly was associated with occurrence with ≥68% confidence, and the relationships were often quite strong (Figure 4a). However, because roughly equal numbers of species responded positively and negatively, no net effect emerged at the assemblage level (Figure 3a). This contrasts with temperature, which showed associations with fewer species, but these associations were more consistently negative across species (Figure 4a). Among obligate grassland species, five (Bobolink, Dickcissel, Grasshopper Sparrow, LeConte's Sparrow, Upland Sandpiper) showed higher occurrence in wetter breeding seasons, while Western Meadowlark was less common under such conditions. Among the facultative species, strong negative relationships with precipitation were slightly more common than positive ones (5 vs. 4); three of the facultative species with positive relationships (Common Yellowthroat, Swamp Sparrow, Wilson's Snipe) are associated with wetland habitats (Guzy & Ritchison, 2020; Herbert & Mowbray, 2020; Mueller, 2020). The facultative species with negative effects are somewhat perplexing given that precipitation should facilitate growth of woody plants that many of these species use—perhaps short-term detriments of precipitation (e.g., nest failure) outweigh benefits, which may require longer timeframes

to come to fruition (Maresh Nelson et al., 2024). The supplemental analysis with nonbreeding precipitation supports this idea: No species showed strong negative effects of nonbreeding precipitation, and all species with strong negative effects of breeding precipitation showed either neutral or positive effects of nonbreeding precipitation (Appendix S1: Figure S3).

Interactions between climate anomalies and occurrence trends were detected for fewer species, and these are more difficult to interpret than the effects of traditional habitat factors. For example, Savannah Sparrow exhibited reduced likelihood of decline in wetter breeding seasons, but such an effect would require sustained above-average rainfall to influence long-term population trajectories, whereas precipitation varies annually. Because precipitation likely influences birds through changes in habitat structure and productivity, management interventions such as prescribed fire or grazing could potentially replicate its effects (Fuhlendorf et al., 2006). Ultimately, the strong influence of climate anomalies, especially precipitation, on occurrence underscores the importance of incorporating climate considerations into grassland bird conservation, particularly given the potential for broad-scale shifts in precipitation patterns to offset or undermine local management actions.

Our results highlight the importance of considering climate alongside traditional habitat factors when conserving grassland birds. North American grassland climates are changing rapidly: Temperate grasslands are warming swiftly (Loarie et al., 2009), and breeding birds are shifting poleward (Hovick et al., 2016; Neate-Clegg et al., 2024), though precipitation changes may ultimately exert stronger influences on range dynamics than temperature alone (Bateman et al., 2016). In Minnesota, breeding-season precipitation is predicted to increase over this century (Liess et al., 2022), potentially benefiting obligate grassland species. Yet, heavier rainfall events are also expected (Harding & Snyder, 2014), which could negate these benefits by increasing nest failure (Maresh Nelson et al., 2024). Thus, in addition to safeguarding high-quality habitat, prioritizing areas with both current and future climate suitability may provide a more effective path forward (Grand et al., 2019; Nixon et al., 2016). Ultimately, our findings highlight the precarious status of North America's grassland birds, suggest that grassland protection and habitat manipulation at current scales alone will not halt declines, and emphasize that conserving grassland birds in the face of climate change will require coordinated, international efforts across the full annual cycle to conserve grassland landscapes (Maresh Nelson et al., 2024) while incorporating human social and economic values.

AUTHOR CONTRIBUTIONS

Neil A. Gilbert, Christopher S. Jennelle, and Elise F. Zipkin conceived the study. Neil A. Gilbert conducted the analysis. Neil A. Gilbert and Peter J. Williams wrote the paper and created visualizations. All authors contributed edits to multiple drafts.

ACKNOWLEDGMENTS

We thank the field technicians who conducted surveys over the lifetime of the monitoring program. Neil A. Gilbert was supported by NSF Postdoctoral Research Fellowship in Biology 2208894. The research was supported by the NSF DEB-2213565 (Elise F. Zipkin). We thank two anonymous reviewers for constructive comments on the manuscript.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data and code (Gilbert, 2026) are available in Zenodo at https://doi.org/10.5281/zenodo.20617879.

ORCID

Neil A. Gilbert https://orcid.org/0000-0003-0949-5612
Christopher S. Jennelle https://orcid.org/0000-0003-4133-814X
Elise F. Zipkin https://orcid.org/0000-0003-4155-6139

REFERENCES

Ahlering, M., D. Carlson, S. Vacek, S. Jacobi, V. Hunt, J. C. Stanton, M. G. Knutson, and E. Lonsdorf. 2020. "Cooperatively Improving Tallgrass Prairie with Adaptive Management." *Ecosphere* 11: e03095.

Askins, R. A., F. Chavez-Ramirez, B. Dale, C. Haas, J. Herkert, F. Knopf, and P. Vickery. 2007. "Conservation of Grassland Birds in North America: Understanding Ecological Process in Different Regions." *Ornithological Monographs* 64: 1–46.

Augustine, D., A. Davidson, K. Dickinson, and B. Van Pelt. 2021. "Thinking Like a Grassland: Challenges and Opportunities for Biodiversity Conservation in the Great Plains of North America." *Rangeland Ecology & Management* 78: 281–295.

Auken, O. W. V. 2000. "Shrub Invasions of North American Semiarid Grasslands." *Annual Review of Ecology, Evolution, and Systematics* 31: 197–215.

Barker, R. J., M. R. Schofield, W. A. Link, and J. R. Sauer. 2018. "On the Reliability of N-Mixture Models for Count Data." *Biometrics* 74: 369–377.

Barnes, A. E., J. G. Davies, B. Martay, P. H. Boersch-Supan, S. J. Harris, D. G. Noble, J. W. Pearce-Higgins, and R. A. Robinson. 2023. "Rare and Declining Bird Species Benefit Most from Designating Protected Areas for Conservation in the UK." *Nature Ecology & Evolution* 7: 92–101.

Bateman, B. L., A. M. Pidgeon, V. C. Radeloff, A. J. Allstadt, H. Resit Akçakaya, W. E. Thogmartin, S. J. Vavrus, and P. J.

Heglund. 2015. "The Importance of Range Edges for an Irruptive Species During Extreme Weather Events." *Landscape Ecology* 30: 1095–1110.

Bateman, B. L., A. M. Pidgeon, V. C. Radeloff, J. VanDerWal, W. E. Thogmartin, S. J. Vavrus, and P. J. Heglund. 2016. "The Pace of Past Climate Change Vs. Potential Bird Distributions and Land Use in the United States." *Global Change Biology* 22: 1130–44.

Bernath-Plaisted, J. S., M. D. Correll, S. G. Somershoe, A. M. Dwyer, A. Bankert, A. Beh, H. Berlanga, et al. 2023. "Review of Conservation Challenges and Possible Solutions for Grassland Birds of the North American Great Plains." *Rangeland Ecology & Management* 90: 165–185.

Bernath-Plaisted, J. S., C. A. Ribic, and B. Zuckerberg. 2025. "Sweating the Small Stuff: Microclimatic Exposure and Species Habitat Associations Inform Climate Vulnerability in a Grassland Songbird Community." *Biology Letters* 21: 20240599.

Billerman, S., B. Keeney, P. Rodewald, and T. Schulenberg. 2020. *Birds of the World*. Ithaca, NY: Cornell Laboratory of Ornithology.

Brennan, L. A., and W. P. Kuvlesky. 2005. "North American Grassland Birds: An Unfolding Conservation Crisis?" *Journal of Wildlife Management* 69: 1–13.

Brodie, J. F., B. G. Freeman, P. D. Mannion, and A. L. Hargreaves. 2025. "Shifting, Expanding, or Contracting? Range Movement Consequences for Biodiversity." *Trends in Ecology & Evolution* 40: 439–448.

Brooks, S. P., and A. Gelman. 1998. "General Methods for Monitoring Convergence of Iterative Simulations." *Journal of Computational and Graphical Statistics* 7: 434–455.

Burger, L. W., Jr., K. O. Evans, M. D. McConnell, and L. M. Burger. 2019. "Private Lands Conservation: A Vision for the Future." *Wildlife Society Bulletin* 43: 398–407.

Butchart, S. H. M., M. Walpole, B. Collen, A. van Strien, J. P. W. Scharlemann, R. E. A. Almond, J. E. M. Baillie, et al. 2010. "Global Biodiversity: Indicators of Recent Declines." *Science* 328: 1164–68.

Cardinale, B. J., J. E. Duffy, A. Gonzalez, D. U. Hooper, C. Perrings, P. Venail, A. Narwani, et al. 2012. "Biodiversity Loss and its Impact on Humanity." *Nature* 486: 59–67.

Carlson, D. 2019. "Monitoring for Minnesota's Wildlife Action Plan, T-15-R-3." Page 23. Final Report, Minnesota Department of Natural Resources, St. Paul, MN.

Collins, S. L., S. E. Koerner, J. A. Plaut, J. G. Okie, D. Brese, L. B. Calabrese, A. Carvajal, R. J. Evansen, and E. Nonaka. 2012. "Stability of Tallgrass Prairie During a 19-Year Increase in Growing Season Precipitation." *Functional Ecology* 26: 1450–59.

Comer, P. J., J. C. Hak, K. Kindscher, E. Muldavin, and J. Singhurst. 2018. "Continent-Scale Landscape Conservation Design for Temperate Grasslands of the Great Plains and Chihuahuan Desert." *Natural Areas Journal* 38: 196–211.

Conrey, R. Y., S. K. Skagen, A. A. Yackel Adams, and A. O. Panjabi. 2016. "Extremes of Heat, Drought and Precipitation Depress Reproductive Performance in Shortgrass Prairie Passerines." *Ibis* 158: 614–629.

Davis, S. K. 2004. "Area Sensitivity in Grassland Passerines: Effects of Patch Size, Patch Shape, and Vegetation Structure on Bird Abundance and Occurrence in Southern Saskatchewan." *The Auk* 121: 1130–45.

Dirzo, R., H. S. Young, M. Galetti, G. Ceballos, N. J. B. Isaac, and B. Collen. 2014. "Defaunation in the Anthropocene." *Science* 345: 401–6.

Dobrowski, S. Z., J. Abatzoglou, A. K. Swanson, J. A. Greenberg, A. R. Mynsberge, Z. A. Holden, and M. K. Schwartz. 2013. "The Climate Velocity of the Contiguous United States During the 20th Century." *Global Change Biology* 19: 241–251.

Dormann, C. F., J. Elith, S. Bacher, C. Buchmann, G. Carl, G. Carré, J. R. G. Marquéz, et al. 2013. "Collinearity: A Review of Methods to Deal with it and a Simulation Study Evaluating Their Performance." *Ecography* 36: 27–46.

Dornak, L. L., J. L. Aycrigg, J. Sauer, and C. J. Conway. 2020. "Assessing the Efficacy of Protected and Multiple-Use Lands for Bird Conservation in the U.S." *PLoS One* 15: e0239184.

Douglas, D. J. T., J. Waldinger, Z. Buckmire, K. Gibb, J. P. Medina, L. Sutcliffe, C. Beckmann, et al. 2023. "A Global Review Identifies Agriculture as the Main Threat to Declining Grassland Birds." *Ibis* 165: 1107–28.

Eldridge, D. J., M. A. Bowker, F. T. Maestre, E. Roger, J. F. Reynolds, and W. G. Whitford. 2011. "Impacts of Shrub Encroachment on Ecosystem Structure and Functioning: Towards a Global Synthesis." *Ecology Letters* 14: 709–722.

Farr, M. T., D. S. Green, K. E. Holekamp, G. J. Roloff, and E. F. Zipkin. 2019. "Multispecies Hierarchical Modeling Reveals Variable Responses of African Carnivores to Management Alternatives." *Ecological Applications* 29: e01845.

Felton, A. J., R. K. Shriver, J. B. Bradford, K. N. Suding, B. W. Allred, and P. B. Adler. 2021. "Biotic Vs Abiotic Controls on Temporal Sensitivity of Primary Production to Precipitation Across North American Drylands." *New Phytologist* 231: 2150–61.

Freeman, B. G., H. N. Eyster, J. M. Heavyside, D. A. Yip, M. H. Mather, and F. L. Waterhouse. 2025. "Pacific Northwest Birds Have Shifted their Abundances Upslope in Response to 30 Years of Warming Temperatures." *Ecology* 106: e70193.

Freeman, N. E., K. M. Silber, T. J. Hefley, A. M. Louthan, and W. A. Boyle. 2025. "Climatic Variability Threatens Population Growth and Persistence of a Declining Grassland Songbird." *Ecology and Evolution* 15: e72195.

Fuhlendorf, S. D., W. C. Harrell, D. M. Engle, R. G. Hamilton, C. A. Davis, and D. M. Leslie, Jr. 2006. "Should Heterogeneity Be the Basis for Conservation? Grassland Bird Response to Fire and Grazing." *Ecological Applications* 16: 1706–16.

Gardner, A. S., D. J. Baker, J. R. Mosedale, K. J. Gaston, and I. M. D. Maclean. 2023. "The Effectiveness of UK Protected Areas in Preventing Local Extinctions." *Conservation Letters* 16: e12980.

Garibaldi, L. A., P. F. Zermoglio, E. G. Jobbágy, L. Andreoni, A. Ortiz de Urbina, I. Grass, and F. J. Oddi. 2023. "How to Design Multifunctional Landscapes?" *Journal of Applied Ecology* 60: 2521–27.

Geldmann, J., M. Barnes, L. Coad, I. D. Craigie, M. Hockings, and N. D. Burgess. 2013. "Effectiveness of Terrestrial Protected Areas in Reducing Habitat Loss and Population Declines." *Biological Conservation* 161: 230–38.

Gilbert, N. 2026. "n-a-Gilbert/prairie_birds: Accepted (Version v1.0) [Computer Software]." Zenodo. https://doi.org/10.5281/zenodo.20617879.

Grand, J., C. Wilsey, J. X. Wu, and N. L. Michel. 2019. "The Future of North American Grassland Birds: Incorporating Persistent and Emergent Threats into Full Annual Cycle Conservation Priorities." *Conservation Science and Practice* 1: e20.

Gray, C. L., S. L. L. Hill, T. Newbold, L. N. Hudson, L. Börger, S. Contu, A. J. Hoskins, S. Ferrier, A. Purvis, and J. P. W. Scharlemann. 2016. "Local Biodiversity Is Higher inside than outside Terrestrial Protected Areas Worldwide." *Nature Communications* 7: 12306.

Guzy, M., and G. Ritchison. 2020. *Common Yellowthroat (Geothlypis trichas), Version 1.0*. Ithaca NY: Cornell Lab of Ornithology.

Haddou, Y., R. Mancy, J. Matthiopoulos, S. Spatharis, and D. M. Dominoni. 2022. "Widespread Extinction Debts and Colonization Credits in United States Breeding Bird Communities." *Nature Ecology & Evolution* 6: 324–331.

Handler, S. D., O. E. Ledee, C. L. Hoving, B. Zuckerberg, and C. W. Swanston. 2022. "A Menu of Climate Change Adaptation Actions for Terrestrial Wildlife Management." *Wildlife Society Bulletin* 46: e1331.

Harding, K. J., and P. K. Snyder. 2014. "Examining Future Changes in the Character of Central U.S. Warm-Season Precipitation Using Dynamical Downscaling." *Journal of Geophysical Research. Atmospheres* 119: 13116–36.

Herbert, J., and T. Mowbray. 2020. *Swamp Sparrow (Melospiza georgiana), Version 1.0*. Ithaca NY: Cornell Lab of Ornithology.

Hovick, T. J., B. W. Allred, D. A. McGranahan, M. W. Palmer, R. Dwayne Elmore, and S. D. Fuhlendorf. 2016. "Informing Conservation by Identifying Range Shift Patterns Across Breeding Habitats and Migration Strategies." *Biodiversity and Conservation* 25: 345–356.

Hufkens, K., D. Basler, T. Milliman, E. K. Melaas, and A. D. Richardson. 2018. "An Integrated Phenology Modelling Framework in R." *Methods in Ecology and Evolution* 9: 1276–85.

Johnston, A., D. Fink, M. D. Reynolds, W. M. Hochachka, B. L. Sullivan, N. E. Bruns, E. Hallstein, M. S. Merrifield, S. Matsumoto, and S. Kelling. 2015. "Abundance Models Improve Spatial and Temporal Prioritization of Conservation Resources." *Ecological Applications* 25: 1749–56.

Johnston, A., A. D. Rodewald, M. Strimas-Mackey, T. Auer, W. M. Hochachka, A. N. Stillman, C. L. Davis, et al. 2025. "North American Bird Declines Are Greatest where Species Are Most Abundant." *Science* 388: 532–37.

Keck, F., T. Peller, R. Alther, C. Barouillet, R. Blackman, E. Capo, T. Chonova, et al. 2025. "The Global Human Impact on Biodiversity." *Nature* 641: 1–6.

Kéry, M., and J. A. Royle. 2015. *Applied Hierarchical Modeling in Ecology*, 1st ed. Amsterdam: Elsevier.

Keyser, P. D., D. A. Buehler, K. Hedges, J. Hodges, C. M. Lituma, F. Loncarich, and J. A. Martin. 2019. "Eastern Grasslands: Conservation Challenges and Opportunities on Private Lands." *Wildlife Society Bulletin* 43: 382–390.

Kremen, C., and A. M. Merenlender. 2018. "Landscapes that Work for Biodiversity and People." *Science* 362: eaau6020.

Kuussaari, M., R. Bommarco, R. K. Heikkinen, A. Helm, J. Krauss, R. Lindborg, E. Öckinger, et al. 2009. "Extinction Debt: A Challenge for Biodiversity Conservation." *Trends in Ecology & Evolution* 24: 564–571.

Lane, D. R., D. P. Coffin, and W. K. Lauenroth. 2000. "Changes in Grassland Canopy Structure Across a Precipitation Gradient." *Journal of Vegetation Science* 11: 359–368.

Lark, T. J., B. Larson, I. Schelly, S. Batish, and H. K. Gibbs. 2019. "Accelerated Conversion of Native Prairie to Cropland in Minnesota." *Environmental Conservation* 46: 155–162.

Lenhart, P. A., M. D. Eubanks, and S. T. Behmer. 2015. "Water Stress in Grasslands: Dynamic Responses of Plants and Insect Herbivores." *Oikos* 124: 381–390.

Li, Y., R. Miao, and M. Khanna. 2020. "Neonicotinoids and Decline in Bird Biodiversity in the United States." *Nature Sustainability* 3: 1027–35.

Liess, S., T. E. Twine, P. K. Snyder, W. D. Hutchison, G. Konar-Steenberg, B. L. Keeler, and K. A. Brauman. 2022. "High-Resolution Climate Projections over Minnesota for the 21st Century." *Earth and Space Science* 9: e2021EA001893.

Link, W. A., M. R. Schofield, R. J. Barker, and J. R. Sauer. 2018. "On the Robustness of N-Mixture Models." *Ecology* 99: 1547–51.

Loarie, S. R., P. B. Duffy, H. Hamilton, G. P. Asner, C. B. Field, and D. D. Ackerly. 2009. "The Velocity of Climate Change." *Nature* 462: 1052–55.

Lockhart, J., and N. Koper. 2018. "Northern Prairie Songbirds Are More Strongly Influenced by Grassland Configuration than Grassland Amount." *Landscape Ecology* 33: 1543–58.

Loss, S. R., T. Will, and P. P. Marra. 2013. "The Impact of Free-Ranging Domestic Cats on Wildlife of the United States." *Nature Communications* 4: 1396.

MacKenzie, D. I., J. D. Nichols, G. B. Lachman, S. Droege, J. A. Royle, and C. A. Langtimm. 2002. "Estimating Site Occupancy Rates When Detection Probabilities Are Less Than One." *Ecology* 83: 2248–55.

Maresh Nelson, S. B., C. A. Ribic, N. D. Niemuth, J. Bernath-Plaisted, and B. Zuckerberg. 2024. "Sensitivity of North American Grassland Birds to Weather and Climate Variability." *Conservation Biology* 38: e14143.

Marra, P. P., E. B. Cohen, S. R. Loss, J. E. Rutter, and C. M. Tonra. 2015. "A Call for Full Annual Cycle Research in Animal Ecology." *Biology Letters* 11: 20150552.

Maurer, G. E., A. J. Hallmark, R. F. Brown, O. E. Sala, and S. L. Collins. 2020. "Sensitivity of Primary Production to Precipitation Across the United States." *Ecology Letters* 23: 527–536.

McDonald, T. L. 2003. "Review of Environmental Monitoring Methods: Survey Designs." *Environmental Monitoring and Assessment* 85: 277–292.

McElreath, R. 2020. *Statistical Rethinking: A Bayesian Course with Examples in R and STAN*. Boca Raton, FL: CRC Press.

Minnesota Prairie Plan Working Group. 2018. "Minnesota Prairie Conservation Plan, 2nd edition."

Monroe, A. P., D. R. Edmunds, C. L. Aldridge, M. J. Holloran, T. J. Assal, and A. G. Holloran. 2021. "Prioritizing Landscapes for Grassland Bird Conservation with Hierarchical Community Models." *Landscape Ecology* 36: 1023–38.

Mueller, H. 2020. *Wilson's Snipe (Gallinago delicata), version 1.0*. Ithaca, NY: Cornell Lab of Ornithology.

NABCI. 2013. *The State of the Birds 2013 Report on Private Lands* 48. Washington DC: U.S. Department of Interior.

Neate-Clegg, M. H. C., B. A. Tonelli, and M. W. Tingley. 2024. "Advances in Breeding Phenology Outpace Latitudinal and

Elevational Shifts for North American Birds Tracking Temperature." *Nature Ecology & Evolution* 8: 2027–36.

Nixon, A., R. Fisher, D. Stralberg, E. Bayne, and D. Farr. 2016. "Avian Conservation and Ecology: Projected Responses of North American Grassland Songbirds to Climate Change and Habitat Availability at Their Northern Range Limits in Alberta, Canada." *Avian Conservation and Ecology* 11: 2.

Patten, M. A., E. Shochat, D. L. Reinking, D. H. Wolfe, and S. K. Sherrod. 2006. "Habitat Edge, Land Management, and Rates of Brood Parasitism in Tallgrass Prairie." *Ecological Applications* 16: 687–695.

Pavlacky, D. C., Jr., C. A. Hagen, A. M. Bartuszevige, R. Iovanna, T. L. George, and D. E. Naugle. 2021. "Scaling up Private Land Conservation to Meet Recovery Goals for Grassland Birds." *Conservation Biology* 35: 1564–74.

Pearce-Higgins, J. W., S. M. Eglington, B. Martay, and D. E. Chamberlain. 2015. "Drivers of Climate Change Impacts on Bird Communities." *Journal of Animal Ecology* 84: 943–954.

R Core Team. 2025. *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing.

Ribic, C. A., R. R. Koford, J. R. Herkert, D. H. Johnson, N. D. Niemuth, D. E. Naugle, K. K. Bakker, D. W. Sample, and R. B. Renfrew. 2009. "Area Sensitivity in North American Grassland Birds: Patterns and Processes." *The Auk* 126: 233–244.

Rosenberg, K. V., A. M. Dokter, P. J. Blancher, J. R. Sauer, A. C. Smith, P. A. Smith, J. C. Stanton, et al. 2019. "Decline of the North American Avifauna." *Science* 366: 120–24.

Shahan, J. L., B. J. Goodwin, and B. C. Rundquist. 2017. "Grassland Songbird Occurrence on Remnant Prairie Patches Is Primarily Determined by Landscape Characteristics." *Landscape Ecology* 32: 971–988.

Silber, K. M., N. M. Mohankumar, T. J. Hefley, and W. A. Boyle. 2023. "Emigration and Survival Correlate with Different Precipitation Metrics Throughout a Grassland Songbird's Annual Cycle." *The Journal of Wildlife Management* 87: e22371.

Stanton, R. A., Jr., W. W. Boone, IV, J. Soto-Shoender, R. J. Fletcher, Jr., N. Blaum, and R. A. McCleery. 2018. "Shrub Encroachment and Vertebrate Diversity: A Global Meta-Analysis." *Global Ecology and Biogeography* 27: 368–379.

Stanton, R. L., C. A. Morrissey, and R. G. Clark. 2018. "Analysis of Trends and Agricultural Drivers of Farmland Bird Declines in North America: A Review." *Agriculture, Ecosystems & Environment* 254: 244–254.

Tredennick, A. T., G. Hooker, S. P. Ellner, and P. B. Adler. 2021. "A Practical Guide to Selecting Models for Exploration, Inference, and Prediction in Ecology." *Ecology* 102: e03336.

de Valpine, P., D. Turek, C. J. Paciorek, C. Anderson-Bergman, D. T. Lang, and R. Bodik. 2017. "Programming with Models: Writing Statistical Algorithms for General Model Structures with NIMBLE." *Journal of Computational and Graphical Statistics* 26: 403–413.

Van Doren, B. M., D. E. Willard, M. Hennen, K. G. Horton, E. F. Stuber, D. Sheldon, A. H. Sivakumar, J. Wang, A. Farnsworth, and B. M. Winger. 2021. "Drivers of Fatal Bird Collisions in an Urban Center." *Proceedings of the National Academy of Sciences of the United States of America* 118: e2101666118.

Vickery, P. D., P. L. Tubaro, J. M. Cardosa da Silva, B. G. Peterjohn, J. R. Herkert, and R. B. Cavalcanti. 1999. "Conservation of Grassland Birds in the Western Hemisphere." *Studies in Avian Biology* 19: 2–26.

Wagner, D. L., E. M. Grames, M. L. Forister, M. R. Berenbaum, and D. Stopak. 2021. "Insect Decline in the Anthropocene: Death by a Thousand Cuts." *Proceedings of the National Academy of Sciences of the United States of America* 118: e2023989118.

Williams, T. D., S. Bourgeon, A. Cornell, L. Ferguson, M. Fowler, R. B. Fronstin, and O. P. Love. 2015. "Mid-Winter Temperatures, Not Spring Temperatures, Predict Breeding Phenology in the European Starling Sturnus Vulgaris." *Royal Society Open Science* 2: 140301.

Wilsey, C., J. Grand, J. Wu, N. Michel, J. Grogan-Brown, and B. Trusty. 2019. *North American Grasslands and Birds Report* 57. New York, NY: National Audubon Society.

Wilsey, C., L. Taylor, B. Bateman, C. Jensen, N. Michel, A. Panjabi, and G. Langham. 2019. "Climate Policy Action Needed to Reduce Vulnerability of Conservation-Reliant Grassland Birds in North America." *Conservation Science and Practice* 1: e21.

Wright, A. D., E. H. Campbell Grant, and E. F. Zipkin. 2022. "A Comparison of Monitoring Designs to Assess Wildlife Community Parameters Across Spatial Scales." *Ecological Applications* 32: e2621.

Zhu, H., D. Wang, L. Wang, J. Fang, W. Sun, and B. Ren. 2014. "Effects of Altered Precipitation on Insect Community Composition and Structure in a Meadow Steppe." *Ecological Entomology* 39: 453–461.

Zuckerberg, B., J. S. Bernath-Plaisted, and W. A. Boyle. 2026. "Multi-Scale Considerations for Identifying and Managing Climate-Change Refugia in Grassland Ecosystems." *Conservation Science and Practice* 8: e70168.

Zuckerberg, B., C. A. Ribic, and L. A. McCauley. 2018. "Effects of Temperature and Precipitation on Grassland Bird Nesting Success as Mediated by Patch Size." *Conservation Biology* 32: 872–882.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Gilbert, Neil A., Peter J. Williams, Daren J. Carlson, Robert M. Dunlap, Mike Worland, Christopher S. Jennelle, and Elise F. Zipkin. 2026. "Limited Capacity of Habitat Features to Buffer Grassland Bird Declines." *Ecological Applications* 36(5): e70298. https://doi.org/10.1002/eap.70298