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Quantifying specialist avifaunal decline in grassland birds of the Northern Great Plains

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Abstract. Habitat specialists are declining worldwide, often paralleling rapid loss of habitat. Grassland habitats across North America are declining precipitously, due in part to intense conversion of grasslands to agriculture and rangelands, and specialist communities reliant upon this landscape are at particular risk of decline and collapse. We explored the relationship between grassland habitat specialism in birds and species population trends using several different grassland specialism indices (GSIs). Our data sources for these indices included (1) a regional bird dataset employing a spatially stratified sampling design (Integrated Monitoring of Bird Conservation Regions) of bird surveys in the Northern Great Plains of North America, and (2) geospatial data of species ranges (BirdLife Int'l) and grassland habitat (CEC North American Land Cover). We found a negative relationship between degree of habitat specialism and species population trends for all specialism metrics. We also found some evidence to support that specialism to grasslands on the wintering grounds partially explains population trends during the breeding season, giving added weight to the consideration of habitat conservation across the full annual cycle of a species to reverse or lessen population decline. Our work is the first to use quantitative methods to confirm the precarious state of grassland specialist songbirds in North America as well as demonstrate multiple methods for quantifying habitat specialism across different types of datasets.

Key words: conservation; grassland birds; grasslands; niche; specialism.

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Introduction

Habitat specialists can be defined as organisms that maintain narrow niche requirements for a particular environmental characteristic when compared to more generalist taxa (MacArthur 1972, Julliard et al. 2006). Specialists are experts at utilizing resources within their ecological niches, but often fail to persist outside of these narrow ecological roles. Organisms maintaining specialist life history strategies also often maintain small range extents and exhibit lowered dispersal ability (Gaston et al. 1997, Colles et al. 2009) and are therefore vulnerable to rapid changes in habitat that result in conditions outside of their particular niches (Devictor et al. 2008, Clavel et al. 2011, Correll et al. 2016). As a consequence, specialist species worldwide are being displaced from their preferred habitats as climate change and human development continues to occur across the global landscape.

Of the world's ecosystems, grasslands emerge as one of the most quickly changing landscapes (Liebold 1995, Hoekstra et al. 2005, Sylvester et al. 2013). Human impact of climate change (Brookshire and Weaver 2015), agriculture (Gage et al. 2016), oil development (Bernath-Plaisted and Koper 2016, Green et al. 2016), shrub encroachment

(Dinerstein et al. 2000, Eldridge et al. 2011), and exotic plant introduction (Saalfeld et al. 2016) are rapidly changing grassland systems, and species reliant upon these landscapes are threatened by this transformation (Coppedge et al. 2001). In North America, grassland birds as an assemblage are declining precipitously (loss of ~50% since the 1960s, Sauer et al. 2015) and are known to be vulnerable to climate change (Gorzo et al. 2016, Nixon et al. 2016). Specialist species within this guild directly experience the negative effects of grassland conversion to agriculture through habitat loss and degradation (e.g., Baird's Sparrow and Sprague's Pipit, Pool et al. 2014), and as a result, these birds have recently been afforded attention on the national conservation stage through elevation of certain species to concern lists (Rosenberg et al. 2017) across jurisdictions in both Canada and the United States as well as the development of a conservation business plan to benefit this disappearing community (National Fish and Wildlife Foundation 2016).

Disentangling the drivers of grassland bird decline is particularly complex when considering the state of the wintering grounds of these migratory birds. Many of the breeding bird species from the Northern Great Plains (NGP) winter in the grasslands of the Chihuahuan Desert and Sierra Madre Occidental and experience a different set of stressors than they do during the summer months (Gordon 2000, Saalfeld et al. 2016). Conversion of desert grasslands formerly used for ranching to center-pivot agriculture combined with limited state or federal enforcement of conserved lands (Figueroa and Sánchez-Cordero 2008) has resulted in rates of grassland loss far exceeding that in the north of the continent (Pool et al. 2014, Gage et al. 2016). Previous work suggests limitation of grassland specialist birds is likely linked to habitat on the wintering grounds (Vickery and Herkert 2001, Drum et al. 2015, North American Bird Conservation Initiative 2016).

Given the dire state of grasslands in North America and the known consequences of specialist life history strategies in rapidly changing systems, it is likely that grassland bird specialists are experiencing more extreme population losses than more generalist species. This pattern, however, has not yet been quantitatively confirmed. Until recently, the separation of specialist and generalist strategies has been largely categorical, often without strict definitions accompanying this categorization. The difference between generalist and specialist species is increasingly considered on a continuous scale (Mouysset et al. 2014, Gaüzère et al. 2015) with intermediate degrees of specialism existing between two extremes, allowing explicit definition of these strategies and quantification of degree of specialization across the environmental gradient in question. Recent work outlining simple but robust quantification concepts to explore this gradient concept across all habitats (Devictor et al. 2010) or within a single habitat type (Correll et al. 2016, 2017) shows promise in helping to quantify the precarious state of grassland specialist birds in North America in relation to changing habitats on the breeding and wintering grounds.

We adapted existing methods for quantifying degree of habitat specialization along a continuous scale to calculate four different grassland specialism indices (GSIs) for grassland bird species breeding in the Northern Great Plains (NGP) of the United States. Our data sources include a regional, spatially stratified survey of bird communities (Integrated Monitoring of Bird Conservation Regions, or IMBCR, Pavlacky et al. 2017) as well as geospatial data quantifying species ranges (BirdLife International and NatureServe 2012) and grassland habitat (CEC 2010). We then used these indices to explain the relationship between degree of specialism to grassland landscapes and the ability of a species to persist over time, measured by species' population trends. We also explored the explanatory power of winter specialism to grasslands using our geospatial GSI methods. We predicted a negative relationship between the degree of habitat specialism and species population trends on both the breeding and the wintering grounds.

Materials and Methods

Bird and habitat data: field data collection

We used data from the IMBCR program (Pavlacky et al. 2017) run by Bird Conservancy of the Rockies in the plains and intermountain west of the United States to quantify bird use of the landscape on grassland bird breeding grounds of the NGP. The IMBCR design spatially stratifies bird survey locations structured around Bird

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Conservation Regions (BCR, NABCI 2016) and defines sampling units as 1-km^2 cells, each containing 16 evenly spaced sample points 250 m apart. The IMBCR program employed a nested, stratified, probabilistic sampling design (Pavlacky et al. 2017). IMBCR strata were nested within the intersection of BCRs and states and were delineated using fixed attributes, such as land ownership boundaries, elevation zones, major river systems, and wilderness/roadless designations. The IMBCR sampling frame consisted of a 1-km^2 grid overlaid on each stratum. Grid cells were selected for sampling using Generalized Random-Tessellation Stratification (GRTS, Stevens and Olsen 2004), and all grid cells within strata had an equal probability of selection. Within each stratum, the IMBCR used the GRTS sampling algorithm to select sample units. A minimum of two sampling units was required within each stratum to estimate the variances of population parameters. The remaining allocation of sampling effort among strata was based on the priorities of the funding partners.

We used data from 16,728 point-count surveys within 721 grids throughout the US portions of BCRs 11 and 17 in the NGP (Fig. 1). These data all occur within the spatial delineation of the NGP as defined by the National Fish and Wildlife Foundation (National Fish and Wildlife Foundation 2016). Experienced surveyors trained through an intensive standardized program covering aural and visual bird identification skills conducted all point-count surveys. Technicians followed standard point-count methodology (Buckland et al. 2001) for each survey, beginning surveys ½ h before sunrise and concluding no later than five hours after sunrise. Surveys were conducted between May 15 and July 15 of each calendar year from 2010 to 2015. Technicians conducted six-minute counts, recording detections for all species observed and measuring distances to each bird using laser rangefinders when possible. Technicians also recorded the dominant habitat type of the 50 m radius area of each survey location. We split survey points after the field season by primary habitat type into two categories: grassland-dominant points (n = 5,465) and non-grassland points (n = 7,209). Detailed information about survey methods is included on the Avian Data Center website at http://rmbo.org/v3/avian/Home.aspx.

Bird and habitat data: geospatial data sources

We used global range data (BirdLife International and NatureServe 2012) to broadly define habitat use on the wintering grounds for each species on the gradient of generalism to specialism to grasslands of the NGP. BirdLife range maps are broken into seasonal ranges (e.g., breeding, wintering, resident); we used the breeding, wintering, and resident ranges from North America for each species in our analyses (see *Estimating relative abundance: raw GSI*). To define grassland habitat availability, we used the Commission for Environmental Cooperation North America Land Cover (CEC 2010) to define grassland extent across North America. We defined "grassland" as temperate or subpolar grassland included in the CEC layer.

Quantifying habitat specialization

Estimating relative abundance: raw GSI.—We modified methods developed by Correll et al. (2016) to quantify avian habitat specialization to grasslands using the IMBCR database from 2010 to 2015. We summed counts across all species with >10 detections across that time period (n = 149) and corrected for effort by dividing the summed count of each species by the number of points visited to get an estimate of average relative abundance for each species at grassland-dominant and non-grassland points.

To produce a GSI using relative abundance (hereafter raw GSI) for each species, we divided grassland-dominant relative abundance by the sum of grassland and non-grassland relative abundance. This produces a raw GSI value for each species quantifying degree of grassland habitat specialization, with values ranging from 0 (avoids grasslands completely) to 1 (occurs in grassland exclusively). Intermediate values indicated moderate use of grasslands in comparison with other habitats, indicating habitat generalism relative to the habitat types surveyed. We excluded exotic species (n = 3) because their preference for grassland habitat likely does not follow the same patterns as native species. We also excluded colony-nesting species (n = 9) because the presence or absence of these species in grasslands was likely tied to the proximity of available nesting habitat occurring near grasslands and not quality of grassland habitat. These cutoffs apply to all GSI metrics calculated.

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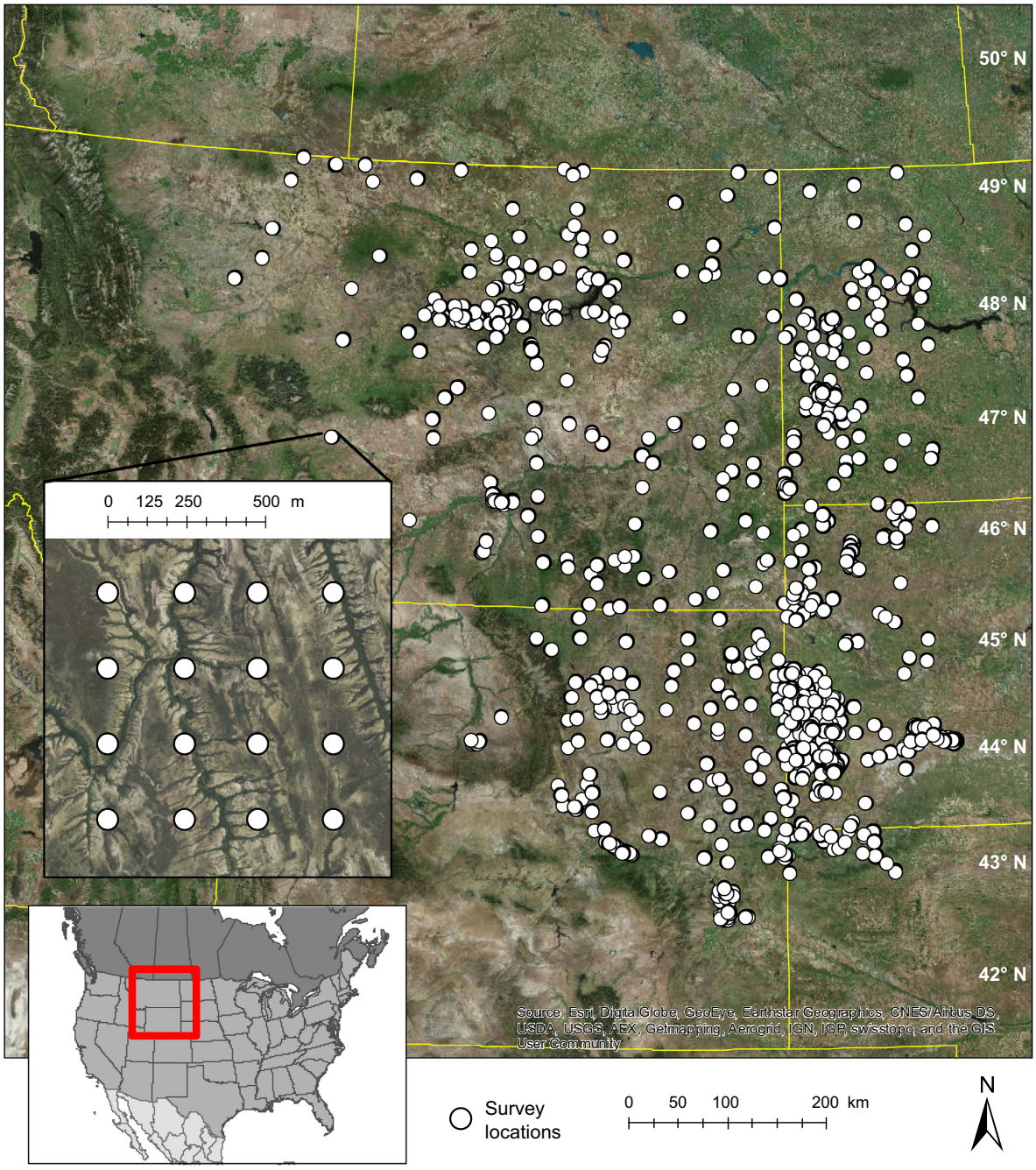


Fig. 1. Map of the Northern Great Plains, US study area. Survey locations are shown with white circles. Points were arranged in grids of 16 point-count locations each across the landscape (top inset).

Estimating abundance: adjusted GSI.—We used a hierarchical, N-mixture model within a Bayesian framework to estimate density and abundance for each species within our study area (i.e., BCR 17 and the U.S. portion of BCR 11; Royle 2004, Sillett et al. 2012), using distance sampling to account for imperfect detection of individuals (Buckland et al. 2001). We accounted for the lack of independence among points within a 1-km^2 grid cell by including grid-level random effects,

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such that the abundance, N, at point i in grid j was distributed

$$N_{ijt} \sim \text{Poisson}(\lambda_{jt}),$$

where λ is the mean abundance for the grid in year t. We obtained point-level density estimates using the equation

$$D_{ijt} = \frac{N_{ijt}}{A_{\text{circle}}},$$

where A_{circle} is the area of the circle surrounding the point count used in analyses and based on the detection distances. For each species, we removed the furthest 10% of detections from the data and used the new max (i.e., the 90th percentile of the original data) as the radius of the circle. We then calculated stratum-specific density estimates by taking the mean point-level density for all points in a stratum, and we took a weighted average, based on area, of all stratum-specific densities to obtain the overall density for our study area. Abundances for strata and the study area were calculated by multiplying density by area.

Once we obtained estimates for overall abundance, we post-stratified points as grassland and non-grassland, as with the raw GSI. Similar to the overall estimates, we took the average density of grassland points within a stratum to calculate stratum-specific grassland abundances. We also used a weighted average for grassland abundance for the entire study area but calculated areas by multiplying the proportion of grassland points within a stratum by the stratum's area. Finally, we calculated the adjusted GSIs as the abundance of a species in grasslands divided by the same metric for the entire study area.

Measuring range and habitat overlap: geoprocessed GSI.—We produced GSI values for each species using geospatial data (hereafter geoprocessed GSI) by calculating the area of grasslands from the CEC grassland layer intersecting the BirdLife resident and breeding season combined ranges of each species to the total area of each species' resident and breeding ranges (Fig. 2). This produced a geoprocessed GSI for each species for the breeding grounds comparable to the raw and adjusted GSI values.

We also calculated breeding season and wintering season geoprocessed GSI values using identical methods to those described above but using only breeding season and wintering season ranges to directly compare the explanatory value of breeding and wintering grassland specialism in birds. We did not calculate these metrics for 10 of the species because they did not have winter ranges defined by BirdLife. All geoprocessing was completed using the raster package (Hijmans 2016) in Program R (R Core Team 2016).

Population trends.—We used adjusted population trends spanning 1966–2014 produced through the North American Breeding Bird Survey (BBS; Sauer et al. 2015) to represent the ability of a species to persist through time. The BBS is a monitoring program first initiated in 1966 that spans southern Canada and the United States and is comprised of a large network of 3-min point counts within a 400 m detection radius conducted along a series of roadside survey routes. This program uses a hierarchical modeling structure (Link and Sauer 2016) to produce trend estimates for all birds detected in the North American BBS survey area during the breeding season, along with estimates of uncertainty around these population trends.

Analysis

We used linear mixed-effects models in a likelihood framework using the lmer function from the lme4 package (Bates et al. 2015) in Program R (R Core Team 2016) in two sets of model comparisons to explore relationships between GSI metrics and population trends. For the first comparison, we used the three GSI metrics calculated for the breeding grounds (raw GSI, adjusted GSI, geoprocessed GSI) as explanatory variables with species population trend as the response variable. We only included metrics for species with a geoprocessed GSI of >0.5 (n = 56) because these species represent a gradient of habitat generalism (~0.5) to grassland habitat specialism (~1.00), excluding species that may show preference or are specialized to other habitats (GSI < 0.5). We used the geoprocessed GSI as the cutoff metric because this metric was the only common metric across our two sets of model comparisons. We also included taxonomic order as a random effect in all models to account for taxonomic similarities across species (Table 1; Appendix S1). We included a model with only the random effect of taxonomic order as a null model in the candidate model set.

For the second model comparison, we used the two GSI metrics calculated using seasonal data

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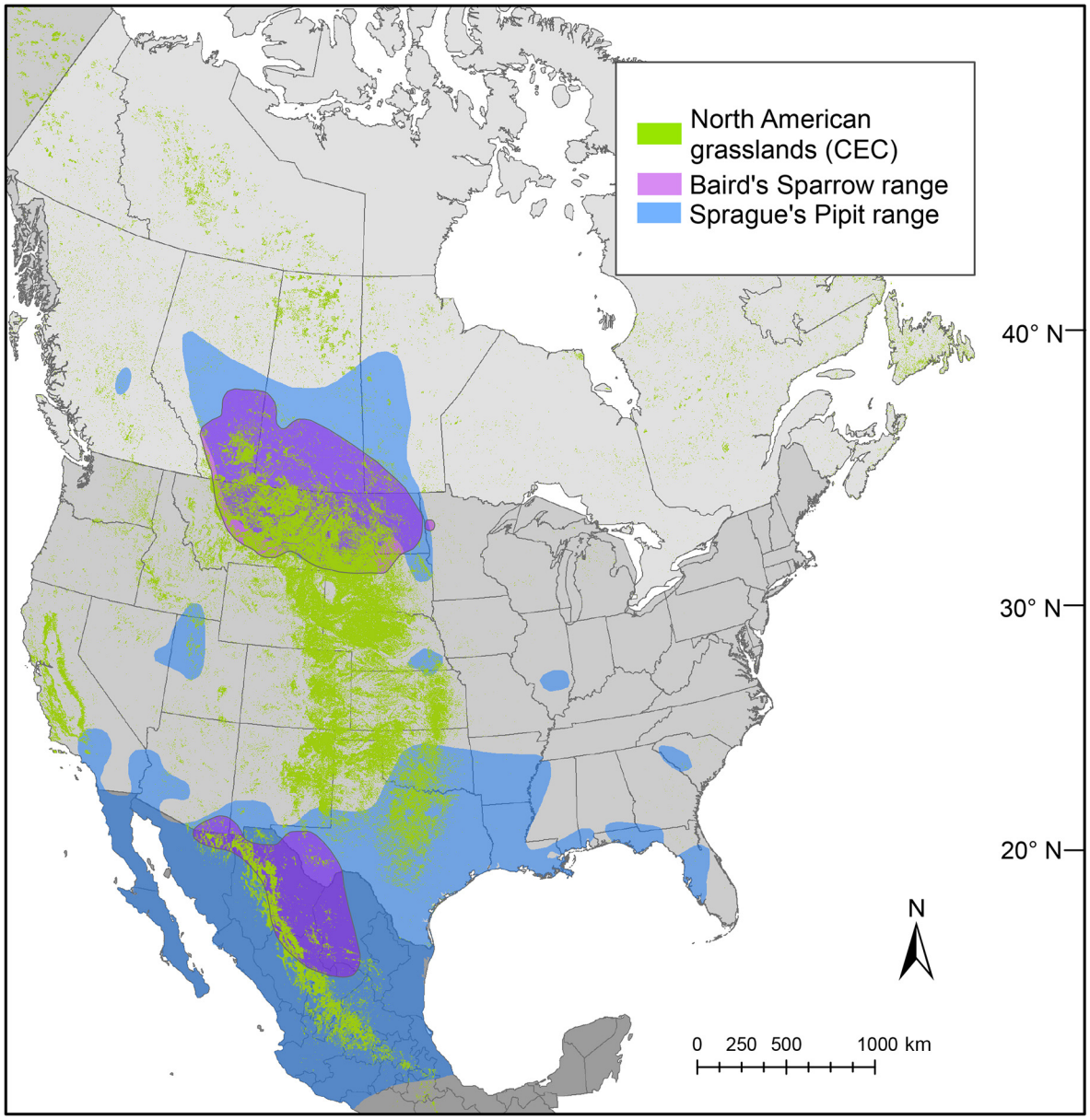


Fig. 2. Example geoprocessing setup for calculation of a grassland specialism index (GSI) measuring species' habitat specialism to grasslands. North American grasslands are depicted using the Commission for Environmental Cooperation North America Land Cover (CEC 2010), and example range maps from BirdLife International (2012) show example species of the Baird's Sparrow (purple) and Sprague's Pipit (blue).

(geoprocessed GSI from the breeding grounds and geoprocessed GSI from the wintering grounds) as explanatory variables with species population trend as the response variable (n = 63). Again, we included taxonomic order as a random effect in all models to account for taxonomic similarities and differences (Table 2) and included a model with only the random effect of taxonomic order as a null model in the candidate model set. These metrics had a correlation of 0.24, so we also included a model with both breeding and GSI metrics in the model comparison to evaluate the explanatory strengths of these metrics.

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We used Akaike's information criterion for small sample sizes (AIC_c, Burnham and Anderson 2004) to compare model performance across our candidate sets. We considered an explanatory variable to be moderate if the 90% confidence intervals (calculated using the Wald approximation method) for the beta estimate did not overlap zero and strong if the 95% confidence intervals did not overlap zero. We report 95% CIs unless otherwise noted.

Results

Grassland specialism

Values for raw GSI (n = 136 species) ranged from 0.00 (Cassin's finch, *Haemorhous cassinii*, Appendix S2) to 0.99 (Mountain Plover, *Charadrius montanus*). Values for adjusted GSI and geoprocessed GSIs showed comparable ranges, although values for the same species varied across GSI metrics (Appendix S2; see Table 2 for examples). Of these species, 105 had defined wintering ranges from BirdLife range maps and were eligible for winter GSI calculation. Global values of winter GSI ranged from 0 (many species, Appendix S3) to 0.85 (Common Grackle, *Quiscalus quiscula*).

Table 1. Comparison of linear mixed-effects models table using Akaike's information criterion for small sample sizes (AIC_c) comparing the influence of several grassland specialism indices (GSIs) measuring habitat specialism to grasslands in birds on species population trend, measured using the Breeding Bird Survey (BBS).

Model structure	AIC_c	Delta AIC	Model weight
BBS trend ~ geoprocessed GSI + *order*†	193.63	0.00	0.97
BBS trend ~ raw GSI + *order*	201.29	7.66	0.02
BBS trend ~ adjusted GSI (abundance) + *order*	204.03	10.40	0.01
BBS trend ~ *order* (null model)	206.68	13.05	0.00

† Random effects denoted in italics.

Analysis

On the breeding grounds, we found a negative relationship between population trend and all GSI metrics (Fig. 3). We estimated scaled β values of −0.65 (−1.03, −0.27) for raw GSI, −0.51 (−0.88, −0.14) for adjusted GSI, and −0.74 (−0.99, −0.39) for geoprocessed GSI. None of these 95% CIs overlapped zero, indicating a strong influence of these metrics on population trend. In our model comparison, all models including GSI metrics performed better than the null (ΔAIC > 2, Table 1).

We found a similar, albeit much weaker, pattern when directly comparing the geoprocessed GSIs for the breeding and wintering grounds (Fig. 4). In our univariate models, we estimated scaled β values of −0.69 (−0.99, −0.39) for the breeding grounds and −0.54 (−0.87, −0.22) for the wintering grounds. Neither of the beta 95% CIs overlapped zero, and both breeding and wintering ground geoprocessed GSIs performed better than the null model in our model comparison (Table 3). In the combined model, we estimated scaled β values of −0.56 (−0.89, −0.24) for the breeding grounds and −0.3 (−0.63, 0.02) for the wintering grounds. The 90% confidence intervals (−0.58, −0.03) for the winter β did not overlap zero.

Discussion

Decline of the grassland bird assemblage in the NGP

Habitat specialists are likely bearing a disproportionate amount of the ecological consequences of

Table 2. Comparison of four habitat specialism metrics in birds of the Northern Great Plains.

Common name	Scientific name	Raw GSI (relative abundance)	Adjusted GSI (abundance)	Geoprocessed GSI
Baird's Sparrow	*Ammodramus bairdii*	0.89	0.72	0.87
Chestnut-collared Longspur	*Calcarius ornatus*	0.90	0.80	0.91
Lark Bunting	*Calamospiza melanocorys*	0.70	0.53	0.96
McCown's Longspur	*Rhynchophanes mccownii*	0.41	0.15	0.92
Mountain Plover	*Charadrius montanus*	0.99	0.95	0.88

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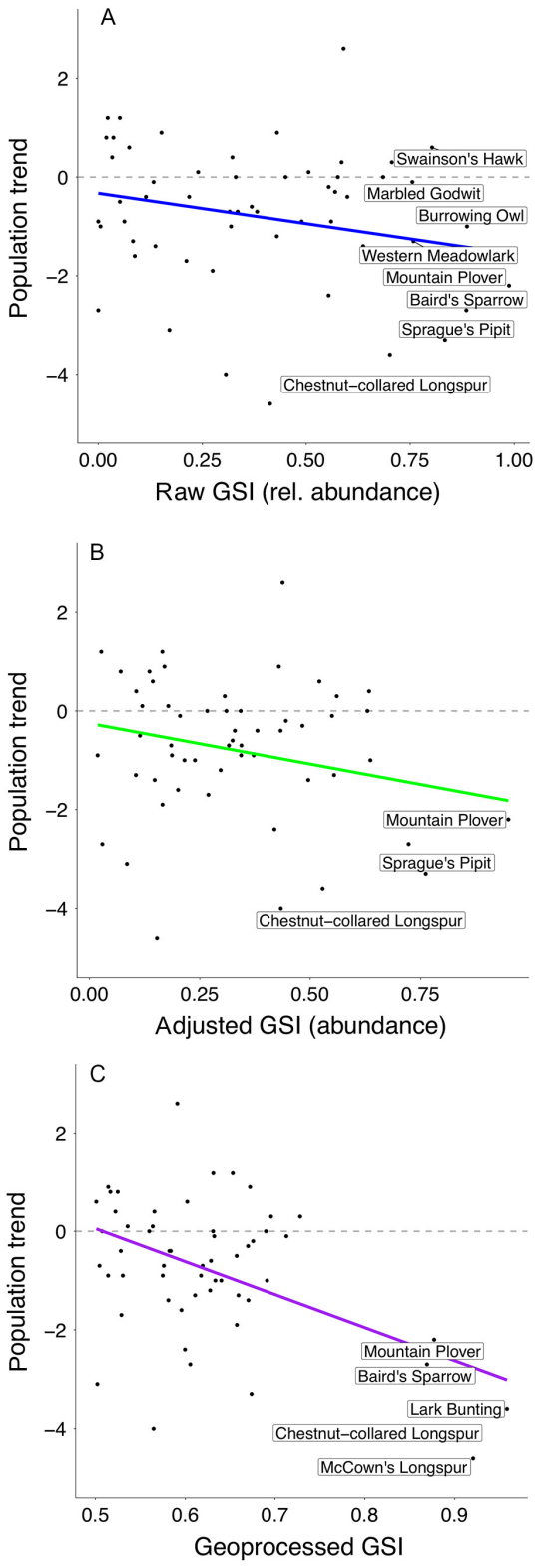


Fig. 3. Results of linear mixed-effects model results comparing four grassland specialism indices (GSIs) and North American Breeding Bird Survey (BBS) population trends (1966–2014) for 56 bird species observed in grasslands. Plot (A) shows GSI values estimating relative abundance, (B) shows GSI values using estimated species abundance, and (C) shows geoprocessed GSI values. Gray dashed line indicates zero slope or level of a stable population trend. Species with a specialism index >0.75 are labeled with the U.S. common name for the species.

rapid global change. In North America, grasslands are experiencing some of the most drastic change of any ecosystem, and this loss of habitat could be driving the loss of specialist species. We found that degree of habitat specialism has a strong, negative relationship with long-term population trends in bird species across our quantitative metrics of specialism. This finding quantitatively supports what previous work (North American Bird Conservation Initiative 2016) has qualitatively described—the more specialized a species is to grasslands, the worse it is likely to fare over time. This finding adds to a growing knowledge base linking the decline of specialist species to quickly changing habitat resources across the globe. As climate change, local-scale management, and land cover changes continue to modify the grassland landscape, particular conservation concern should be directed toward specialist species.

Further, specialist species often use similar habitat types across their annual cycle (Zurell et al. 2018). We found some support for the explanation of breeding season population trends by winter specialism to grasslands, potentially linking grasslands on the wintering grounds with population trends of breeding bird populations in North America. This finding, when combined with substantial previous qualitative support (Dinerstein et al. 2000, Pool et al. 2012, 2014), helps highlight the need for conservation of both northern and southwestern grasslands in order to support grassland species breeding in the Northern Great Plains. Most efforts to conserve grassland acreage to benefit bird populations are limited to the breeding grounds; however, many hypothesize that the limiting factor for North American grassland birds is availability and quality of wintering

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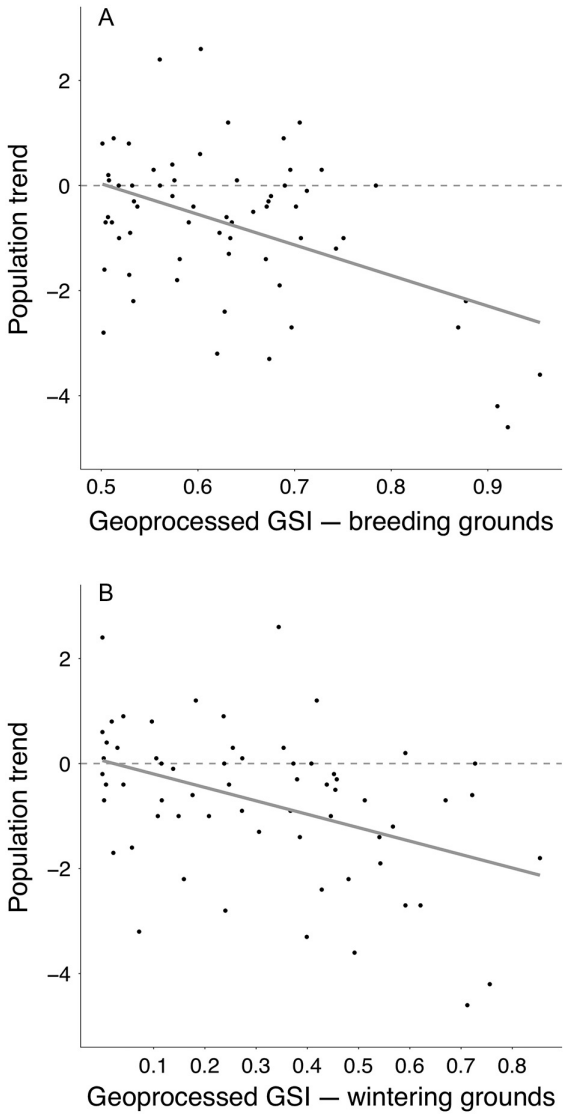


Fig. 4. Results of linear mixed-effects model results comparing four grassland specialism indices (GSIs) and North American Breeding Bird Survey (BBS) population trends (1966–2014) for 63 bird species observed in grasslands. Plot (A) shows geoprocessed GSI values for breeding grounds, and (B) shows geoprocessed GSI values for the wintering grounds. Gray dashed line indicates zero slope or level of a stable population trend.

habitat (Drum et al. 2015) which can have negative consequences for grassland bird winter survival (Macías-Duarte and Panjabi 2013, Macías-Duarte et al. 2017). We suggest further quantitative work including the development of Integrated Population Models (Fitsum et al. 2010, Hostetler et al. 2015) for this suite of birds to further support or refute these claims.

Table 3. Comparison of linear mixed-effects models using Akaike's information criterion for small sample sizes (AIC_c) comparing the influence of breeding and wintering ground grassland specialism indices (GSIs) measuring habitat specialism to grasslands in birds on species population trend, measured using the Breeding Bird Survey (BBS).

Model structure	AIC_c	Delta AIC	Model weight
BBS trend ~ geoprocessed GSI(breeding) + *order*†	213.55	0.00	0.60
BBS trend ~ geoprocessed GSI(breeding) + geoprocessed GSI(winter) + *order*	214.41	0.86	0.39
BBS trend ~ geoprocessed GSI(winter) + *order*	220.81	7.26	0.02
BBS trend ~ *order*	226.85	13.30	0.00

† Random effects denoted in italics.

A repeatable conceptual method to quantify habitat specialism

The quantitative methods used in our study were chosen in part to explore their usefulness outside of the ecosystem and datasets within which they were developed (tidal marshes). When we applied these conceptual methods to our work, we found a negative relationship between population trend and all calculated GSIs. These patterns mirror those produced in the original study (Correll et al. 2016) and strengthen support for use of this analysis strategy across different taxa and large-scale survey datasets.

Each metric calculated has strengths and weaknesses that should be considered when calculating specialism indices across different data sources and ecological scenarios. The raw GSI used raw count data and set of relatively simple summary calculations, making the production of this metric possible for scientists and managers with limited analytical resources, time constraints, or a combination of the two. The adjusted GSI, however, used estimates of abundance that (1) accounted for detectability and (2) accounted for details within the design of the IMBCR program that may drive oversampling of high-density areas for some species and thus potentially inflate GSI values in metrics that do not account for this (e.g., raw GSI, see Fig. 3,

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Table 2). The IMBCR sampling effort is allocated by stratum, with varied sampling effort in each stratum. The adjusted GSI accounted for this by taking the average abundance per sampled point for each stratum and then taking a weighted average of all strata using their proportional areas as weights. The resulting adjusted GSI metric had overall lower values (Fig. 3, Table 2, Appendix S2), which we would expect to see whether (1) detection probability varied across sampling events, and (2) some strata unequally sampled higher-density areas of birds. Therefore, adjusted specialism indices may be a more accurate metric of habitat specialism.

The model including geoprocessed GSI was the best-performing model in our comparison and held 97% of the model weight, suggesting this metric was much more effective at explaining variation in population trends than the other GSI metrics. This could be due to the methods with which habitat was assigned in the IMBCR dataset; dominant habitat was assessed as the habitat classification that had majority cover at a certain point. Birds detected at that point could have been using another habitat type representing a smaller amount of cover at the survey point, creating a potential inconsistency in the habitat assigned with the habitat that the detected bird was using. However, there are also known shortcomings to consider when using geospatial datasets to quantify habitat use for a species. First, the availability of a North American land cover classification that spanned all three countries involved in analysis was limited. While the CEC classification of grasslands met our criteria, this layer is known to underestimate the amount of grasslands, particularly in the wintering grounds, which likely affected the accuracy of our individual specialism metrics and could explain some of the lukewarm results from our winter GSI analyses as well as the aberrant winter GSI values for some individual species (e.g., Common Grackle winter GSI = 0.85). Further, a scale mismatch existed between our habitat and range map data; BirdLife maps delineate range extent only and do not include information on finer-scale habitat use within these coarse range outlines. Maps of species' ranges and grassland cover likely define the extent of ranges instead of a detailed delineation of range. Results should therefore be interpreted with the understanding of limited precision overall for geoprocessed GSI values in mind. However, the use of geospatial data instead of count data to calculate these metrics opens the door to quantitative estimation of specialism to a much larger variety of species and habitats because thorough, regional-scale count surveys (e.g., IMBCR, BBS) are limited to certain taxa (e.g., birds) and regions of the globe (e.g., Europe and North America).

Finally, we used BBS trends as a response variable in our analysis, which were derived from a continent-scale survey dating back to 1966. While the longevity of this dataset is impressive, it is based on roadside surveys and therefore likely underestimates the abundance of some species not easily observed near roads. Further, it is based on volunteer effort with short survey periods, which add additional sources of error to the trend estimates we use in our analysis.

Despite the potential shortcomings in the metrics in our analysis, the negative relationship between habitat specialism was consistent across all GSI metrics and seasons, inviting further investigation into this topic. To further vet the use of these metrics both in exploration of ecological theory or as tools in conservation, we suggest several outlets for additional study. The application of these methods within taxa other than birds will further broaden use of specialism indices to assess conservation need and quantify specialism to habitats. Further, we recommend confirmation or refutation of the negative relationship between specialism and population trends across a gradient of environments ranging from rapidly shrinking to rapidly growing landscapes. Analysis across different disturbance regimes will help quantify large-scale impacts of global change within the context of niche theory and hopefully illuminate the consequences of rapidly changing physical factors in the environment.

The analysis techniques presented here should always be used as a relative measure of habitat specialism in tandem with a thorough knowledge of the study system in question to avoid known limitations to this quantification method. Birds with low detectability can have a high amount of uncertainty associated with any specialism values, and calculation of specialism indices for these species should be avoided. In the case of geoprocessed GSI values, the datasets used are continental in extent; in global datasets

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such as these, accuracy and precision are both lost in exchange for a large spatial data extent.

Conclusions

In an era of abrupt environmental change across the globe, specialist communities reliant upon these changing landscapes are in decline. In the case of grassland birds in the NGP, we find that the more specialized a species is to grasslands, the worse it is likely to fare over time. We also found that breeding season population trend can be partially explained by specialism to grasslands on both the breeding and wintering grounds, potentially linking grassland landscapes in the southwestern United States and Mexico to the persistence of species that breed in the NGP. We suggest further work (including IPM development) across the full annual cycle of grassland birds of the NGP to (1) identify specific geographies where population limitation occurs within the full annual cycle for grassland birds and (2) promote active conservation actions across this landscape to prevent the collapse of the grassland songbird community in the NGP. Finally, we confirm the utility of specialism indices as a method of quantification for differing life history strategies within an ecosystem and suggest further work across a gradient of changing landscapes to explore the relationship between habitat specialism and our rapidly changing global ecosystems.

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