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ARTICLE

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Landscape-scale conservation mitigates the biodiversity loss of grassland birds

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Abstract

The decline of biodiversity from anthropogenic landscape modification is among the most pressing conservation problems worldwide. In North America, long-term population declines have elevated the recovery of the grassland avifauna to among the highest conservation priorities. Because the vast majority of grasslands of the Great Plains are privately owned, the recovery of these ecosystems and bird populations within them depend on landscape-scale conservation strategies that integrate social, economic, and biodiversity objectives. The Conservation Reserve Program (CRP) is a voluntary program for private agricultural producers administered by the United States Department of Agriculture that provides financial incentives to take cropland out of production and restore perennial grassland. We investigated spatial patterns of grassland availability and restoration to inform landscape-scale conservation for a comprehensive community of grassland birds in the Great Plains. The research objectives were to (1) determine how apparent habitat loss has affected spatial patterns of grassland bird biodiversity, (2) evaluate the effectiveness of CRP for offsetting the biodiversity declines of grassland birds, and (3) develop spatially explicit predictions to estimate the biodiversity benefit of adding CRP to landscapes impacted by habitat loss. We used the Integrated Monitoring in Bird Conservation Regions program to evaluate hypotheses for the effects of habitat loss and restoration on both the occupancy and species richness of grassland specialists within a continuum-modeling framework. We found the odds of community occupancy declined by 37% for every 1 SD decrease in grassland availability $[log_e(km^2)]$ and increased by 20% for every 1 SD increase in CRP land cover $[log_e(km^2)]$. There was 17% turnover in species composition between intact grasslands and CRP landscapes, suggesting that grasslands restored by CRP retained considerable, but incomplete, representation of biodiversity in agricultural landscapes. Spatially explicit predictions indicated that absolute conservation outcomes were greatest at high latitudes in regions with high biodiversity, whereas the relative outcomes were greater at low latitudes in highly modified landscapes. By evaluating community-wide responses to landscape modification and CRP restoration at bioregional scales, our study

fills key information gaps for developing collaborative strategies, and for balancing conservation of avian biodiversity and social well-being in the agricultural production landscapes of the Great Plains.

KEYWORDS

avian biodiversity, Conservation Reserve Program, grassland birds, grassland restoration, Great Plains, habitat loss, Integrated Monitoring in Bird Conservation Regions, landscape conservation, multispecies occupancy, private land, species distributions, species richness

INTRODUCTION

By the mid-20th century, anthropogenic modification of Earth's ecosystems had accelerated to become as important, if not more important than, natural processes (Corlett, 2015). Several key environmental parameters are now well outside historical ranges (Corlett, 2015), including human appropriation of net primary production, rates of extinction, and biotic homogenization (McGill et al., 2015). Overexploitation of natural resources and habitat loss from the conversion of native vegetation to row-crop agriculture are the main drivers of biodiversity loss in human-dominated ecosystems (Maxwell et al., 2016; Vitousek et al., 1997). Habitat loss, or the reduction in the amount of habitat available to species, often produces non-linear extinction thresholds below which populations can no longer sustain themselves (Fahrig, 2003). Because species are linked through ecological interactions, altered ecological processes, and extirpation of local populations cascade through ecosystems, often producing indelible signatures of defaunation at continental scales (Dirzo et al., 2014).

In North America, habitat loss from the conversion of native grassland to row-crop agriculture and intensification from increased mechanization between the 1960s and 1980s is thought to underlie population declines for many species of grassland birds (Stanton et al., 2018). Of the North American avifauna, grassland birds show the largest population declines, with more than 700 million individuals lost across 31 species (from 1970 to 2017; Rosenberg et al., 2019). The rapid decline of grassland bird biodiversity in response to habitat modification often proceeds by non-equilibrium processes of local extinction and colonization over time, resulting in declining extents of occurrence and increasing species turnover (Green et al., 2019). Ecological traits are thought to play a key role in species vulnerability to habitat loss (Betts et al., 2014; McGill et al., 2015). For example, specialization for grassland vegetation (Correll et al., 2019) and area sensitivity (Ribic et al., 2009) are tightly linked to population declines. Viewed cumulatively, long-term population declines have elevated the recovery of the

grassland avifauna to among the highest conservation priorities in North America (Brennan & Kuvlesky, 2005; Rosenberg et al., 2019).

Biodiversity conservation in increasingly humanmodified ecosystems must recognize that natural systems can no longer realistically be considered separate from human systems, and that restoring ecosystems to historical conditions may no longer be possible in many places (Kareiva & Marvier, 2012; Tewksbury & Rogers, 2014). Some individuals suggest that conserving biodiversity and ecosystem processes must be reframed as societal problems that are created by, and can only be solved by, humans (Hackmann et al., 2014). Others suggest that simply managing nature for human benefit will promote irreparable attrition and accelerate the current trajectory toward a biologically impoverished future (Doak et al., 2014), The wide range of values within humandominated ecosystems highlights the need to balance ecosystem services for improving human well-being and biodiversity conservation for avoiding species extinction (Hunter et al., 2014). Agricultural landscapes are a prime example of how biodiversity conservation can be complicated by competing socioeconomic, agronomic, and biological objectives (Green et al., 2005). Although conservation measures in farmed landscapes can be successful, they are costly to implement, often reduce crop yields, and displace cultivation to other regions (Green et al., 2005). Renewal ecology may offer a framework to address biodiversity and socioeconomic objectives in human-modified landscapes at the intersection of conservation biology, agro-ecology, and restoration ecology (Bowman et al., 2017). For example, objectives for wildlife-friendly farming and land-sparing can be optimized to simultaneously restore grassland function, maximize crop yields, and reduce pressure on biodiversity within farmed landscapes (Green et al., 2005).

The Conservation Reserve Program (CRP) is a voluntary program for agricultural producers administered by the United States Department of Agriculture that provides financial incentives for private landowners to remove cropland from production and restore perennial grassland cover (Hellerstein, 2017). Although CRP was originally designed to reduce cultivation on marginal or vulnerable lands, address soil erosion, and increase crop prices, over time the conservation objectives have expanded to include wildlife habitat requirements (Hellerstein, 2017). Restoring perennial grassland cover in landscapes impacted by agricultural conversion to cropland is expected to increase functional landscape connectivity (Taylor et al., 1993) and allow territory establishment of bird species with area sensitivity (Ribic et al., 2009) and dependence on grassland vegetation (Correll et al., 2019).

The effectiveness of CRP for managing habitat loss of grassland birds has been evaluated at local (Coppedge et al., 2001), regional (Best et al., 1997; Herkert, 2009), and bioregional (Murphy, 2003) scales. However, understanding the effectiveness of local management for increasing or maintaining avian biodiversity at bioregional scales requires a comprehensive evaluation over multiple spatial and temporal extents (DeWan & Zipkin, 2010; Pavlacky Jr. et al., 2017). For example, effectiveness monitoring at fine spatial and temporal scales may not accurately reflect broad-scale conservation outcomes for grassland species that regularly display nomadic movement in response to weather patterns (George et al., 1992; Macias-Duarte et al., 2018). Moreover, although conservation objectives are often developed from monitoring at bioregional scales, population responses at scales relevant to management actions are needed to evaluate success toward meeting objectives (Nichols & Williams, 2006). As such, predicting the contribution of local management to regional bird populations in a way that is useful for conservation requires concurrent effectiveness monitoring over multiple hierarchical scales, to adequately account for temporal and spatial processes (Conroy et al., 2012; Pavlacky Jr. et al., 2017). Spatially explicit predictions of species responses to restoration are useful for answering the "what to do" and "where to do it" questions in conservation planning (Wilson et al., 2007), and provides the means to go beyond simply identifying geographies with high biodiversity toward prioritizing conservation actions with the greatest biodiversity outcomes (Game et al., 2013).

We investigated landscape-scale consequences of habitat loss and effectiveness of CRP with the goal of conserving avian biodiversity, and informing sustainable landscape planning and decision-making (McAlpine et al., 2010) in agricultural production landscapes throughout much of the Great Plains. We studied patterns of apparent habitat loss and restoration by quantifying changes in species composition of grassland specialists along spatial gradients of native and restored grassland at the landscape-scale. The study objectives were to (1) determine how apparent habitat loss has

affected spatial patterns of grassland bird biodiversity, (2) evaluate the effectiveness of CRP for offsetting biodiversity declines of grassland birds and (3) develop a spatially explicit surface to estimate the conservation value of adding CRP to landscapes impacted by habitat loss. We hypothesized that habitat loss would affect landscape patterns of grassland bird biodiversity, and that extinction thresholds (Fahrig, 2003) from the cumulative local extirpation of species over time (Green et al., 2019) would show a pattern of declining species richness of grassland specialists along the spatial gradient of habitat availability. We also hypothesized that landscape-scale conservation measures (CRP) would mitigate the effects of habitat loss and increase subsequent spatial patterns of grassland bird biodiversity. Because implementing CRP in landscapes impacted by agricultural conversion to cropland is expected to increase functional landscape connectivity (Taylor et al., 1993), and the occurrence of area-sensitive (Ribic et al., 2009) and grassland-specialist (Correll et al., 2019) bird species, we predicted that species richness of grassland specialists would increase with the area of CRP in the surrounding landscape and that species composition (beta diversity) of grassland specialists would be similar in landscapes restored by CRP and landscapes with native grassland. Finally, we hypothesized that the effectiveness of CRP on the landscape would vary with the regional distribution of biodiversity and would vary according to the proportion cultivated land in the region. Because the biodiversity of grassland birds increases with latitude (Dreitz et al., 2017), we predicted that the responses of absolute species richness to CRP restoration would be greater at high latitudes where the potential for avian biodiversity is greatest. In addition, because extinction thresholds for area-sensitive species are often more pronounced in landscapes with low proportions of available habitat (Andrén, 1994; Fahrig, 2003), we predicted that the responses of relative species richness to CRP restoration would be greatest in regions with high agricultural cultivation.

METHODS

Study area

The study took place within a 1.2 million km² region of the western Great Plains including the entire Badlands and Prairies (BCR 17), Shortgrass Prairie (BCR 18) and Central Mixed Grass Prairie (BCR 19) Bird Conservation Regions (BCR; BSC and NABCI, 2014), and the Montana portion of the Prairie Potholes BCR (BCR 11; Figure 1). Grassland vegetation types were classified as Northern Mixed Grass Prairie in BCR 11 and 17, Shortgrass Prairie



FIGURE 1 Study area in the western Great Plains, USA, 2010–2018. The sampling locations are represented by round symbols and the Bird Conservation Regions (BCR) are depicted by color-coded regions. The design features point count plots nested within 1-km² Primary Sampling Units (PSU), PSUs nested within 3×3 km landscapes, landscapes nested within Bird Conservation Regions (BCR) and BCRs nested within the study area. The extent of grassland vegetation from the Commission for Environmental Cooperation (CEC) is shown in green

in BCR 18 and Mixed Grass Prairie in BCR 19 (Vickery & Herkert, 1999). In 2018, 40.4% of the study area was composed of native and agricultural grasslands such as pastures and hay fields. As of 2018, 26.9% of native vegetation in the study area (331,996 km²) has been converted to cultivated areas for production of annual crops such as corn, wheat, soybeans, vegetables, and cotton, including actively tilled land (USGS, 2019). Grassland vegetation made up the majority native vegetation converted to agricultural cultivation in the Great Plains (Samson et al., 2004). In 2018, 3.2% of the study area (39,340 km²) and 10.6% of cultivated agricultural land was restored by CRP grassland plantings (USDA, 2014). The combination of forest vegetation and developed land accounted for 16.2% of the study area, and shrubland land cover accounted for 13.3% of the region. From an evaluation of remotely sensed land-cover data in 2018 (USDA, 2014; USGS, 2016, 2019), the landscape composition of BCR 11 was 40.6% cropland, 38.2% grassland, 6.0% shrubland, and 4.1% CRP; BCR 17 was 54.8% grassland, 13.6% shrubland, 12.2% cropland, and 1.0% CRP; BCR 18 was 36.2% grassland, 30.1% cropland 15.1% shrubland, and 6.0% CRP; and BCR 19 was 34.6% cropland, 31.6% grassland, 13.0% shrubland, and 2.2% CRP.

Sampling design

The study area corresponded to the Great Plains sampling frame from the Integrated Monitoring in Bird Conservation Regions (IMBCR) program (Pavlacky Jr. et al., 2017). The sampling frame was developed by superimposing a 1 km \times 1 km grid over four BCRs in the study area (Figure 1), stratified by State and partner definedregions; 1-km² sampling units were selected within each stratum using generalized random tessellation stratified (GRTS) sampling (Stevens Jr. & Olsen, 2004). We sampled BCR 11, BCR 17, and BCR 18 in eastern Colorado every year from 2010 through 2018, but except for a small number of isolated strata, sampling in the greater BCR 18 and BCR 19 began in 2016 (Figure 1 and Table 1). We sampled the set of sampling units in successive years but, because annual sampling intensity within strata varied, some units were not sampled in successive years. We sampled 4140 1-km² sampling units within the study area from 2010 through 2018 (Figure 1 and Table 1). The IMBCR design sampled vegetation types in proportion to availability within strata (Pavlacky Jr. et al., 2017), and we included all data in the analysis.

The sampling protocols for avian monitoring involved a two-stage design with systematic subsamples of 16 point count plots located 250 m apart and ≥125 m from grid cell boundaries (Figure 1; Pavlacky Jr. et al., 2017). We monitored the occurrence of bird species at 44,849 point count plots on one visit per year from 2010 through 2018 (Table 1) using 6-min counts from 30 min before sunrise to 5 h after sunrise and at each accessible point count location (Pavlacky Jr. et al., 2017). Field technicians measured distances to each bird detection using a laser rangefinder and we truncated distances <125 m to specify 4.9-ha, non-overlapping point count plots (Pavlacky Jr. et al., 2012). We used a removal sampling protocol to estimate incomplete detection (MacKenzie et al., 2018), and binned the 6-min point count intervals into three, 2-min time occasions to maintain a constant detection rate in each occasion and ensure a monotonic decline in the detection frequency through time (Pavlacky Jr. et al., 2012).

TABLE 1 The sample sizes of 1-km² grid cells and 5-ha point count plots by year and Bird Conservation Region in the western Great Plains, USA, 2010–2018

	Bird Co	Bird Conservation Regions						
	Prairie Potholes		Badlands and Prairies		Shortgrass Prairie		Central Mixed Grass Prairie	
Year	Grid	Point	Grid	Point	Grid	Point	Grid	Point
2010	22	312	223	2232	79	858	-	-
2011	22	311	169	1697	135	1513	6	49
2012	18	232	162	1754	112	1301	8	78
2013	24	198	315	3273	150	1683	8	86
2014	31	414	249	2907	125	1401	6	81
2015	20	280	241	2653	201	2393	6	91
2016	27	344	228	2651	259	2583	62	525
2017	36	464	222	2554	280	2915	76	587
2018	32	440	201	2379	285	2934	100	676

Landscape covariates

We measured three continuous landscape composition covariates in 3 km \times 3 km (9 km²) square landscape buffers surrounding the 1-km² sampling units using remotely sensed data (Figure 1 and Table 2). We selected a 3 km \times 3 km landscape buffer based on the eight 1-km² grid cells neighboring the IMBCR sampling unit (Pavlacky Jr. et al., 2017) to construct a design-based hierarchal structure for predictions. The 9-km² landscape buffer was similar in size to a grid of point counts buffered by the mean of the best-supported landscape radii for six grassland bird species (10 km²) studied by Niemuth et al. (2017). We quantified the area of grassland and shrubland vegetation in the 9-km² landscapes using the LANDFIRE Existing Vegetation Type (EVT) spatial data layer (USGS, 2016) using a Geographic Information System (GIS; ArcGIS version 10.1, Environmental Systems Research Institute, Redlands, CA, USA), and the raster and spatialEco packages in the R statistical computing environment (R Version 3.5.2, www.r-project.org). We classified landscape composition as grassland or shrubland vegetation according to the EVT System Group Physiognomy field, except that we reclassified three grassland types, two conifer-hardwood types, and one hardwood type as shrubland, based on a review of the vegetation types (Appendix S1: Table S1). The grassland vegetation was composed of native grassland vegetation, as well as agricultural grasslands such as pastures and hay fields. In addition, we measured the area of CRP in

TABLE 2 The name, description, and mean and range of covariates for 9-km² landscapes and 1-km² sampling units within the western Great Plains, USA, 2010–2018

Covariate	Description	Mean (range)
Grass	Area (km²) of grassland vegetation within 9-km² landscapes	4.3 km ² (0.0 km ² , 9.0 km ²)
Shrub	Area (km²) of shrubland vegetation within 9-km² landscapes	1.0 km ² (0.0 km ² , 8.9 km ²)
CRP	Area (km ²) of Conservation Reserve Program (CRP) within 9-km ² landscapes	0.2 km ² (0.0 km ² , 8.7 km ²)
Lat.	Latitude (DD) for the centroid of the 1-km ² sampling units	42.2 DD (31.3 DD, 49.0 DD)
Long.	Longitude (DD) for the centroid of the 1-km ² sampling units	-103.8 DD (-112.5 DD, -97.0 DD)

the 9-km² landscapes using Common Land Unit spatial data (USDA, 2014). We included only the CRP conservation practices that involved grassland or wetland cover types, and removed practices involving tree cover and parcels containing missing practice information across all years. For missing practice information within a particular year, including all CRP raster data from 2008-2010, we updated values with data from the closest available year, with the exception of CRP parcels with an expiration date >15 years after the data year or parcels with a missing expiration date. When possible, we replaced missing parcel data at the county or State level with data from the closest available year. We intersected the annual CRP and land-cover data, and replaced the intersected land cover with CRP to arrive at seamless annual vegetation mosaics composed of grassland, shrubland, and CRP land cover. In addition to the landscape composition covariates, we used GIS to calculate latitude and longitude for the centroid of the 1-km² sampling units (Table 2).

Statistical analysis

We used a continuum-modeling approach to evaluate hypotheses for the effects of apparent habitat loss and restoration on the biodiversity of grassland birds along spatial gradients in the areas of grassland and CRP in the surrounding landscape (Betts et al., 2014; Fischer & Lindenmayer, 2006). We linked landscape pattern and process of habitat use by applying a grassland specialization index (Correll et al., 2019) to count data from the IMBCR program (Pavlacky Jr. et al., 2017) in the Great Plains, and identified the community of 44 grassland specialists with counts >10 and indices >0.5 that were expected to decline from the loss of grassland habitat and benefit from CRP restoration (Appendix S1: Table S2). For objective 1, we developed an a priori hypothesis for biodiversity loss expected under the temporal process of habitat loss from the conversion of grassland to agricultural cultivation (Fahrig, 2003; Stanton et al., 2018). We predicted that if the biodiversity of grassland specialists declined with the historical process of habitat loss over time, then we would observe a decline in species richness along a gradual pattern of grassland availability (apparent habitat loss) over space. Similarly for objective 2, we developed an a priori hypothesis for biodiversity gains expected under the temporal process of habitat restoration over time in landscapes impacted by conversion to cropland (Dunning et al., 1992; Ribic et al., 2009). We predicted that if the biodiversity of grassland specialists increased with the temporal process of habitat restoration, then we would observe an increase in species

richness along a gradient in the spatial pattern of CRP. We used a continuum model to approximate responses of individual species to gradual changes in spatial patterns of grassland area and CRP restoration in the surrounding landscape (Fischer & Lindenmayer, 2006). By comparing model results to predictions, we made inductive inference to changes in grassland bird biodiversity from temporal process of habitat loss and restoration as benchmarks for evaluating CRP restoration of landscapes impacted by habitat loss from conversion to cropland (Herkert, 2009; Stanton et al., 2018).

We estimated spatial variation using the hierarchical design of the IMBCR program with 5-ha point count plots nested within 1-km² grid cells, 9-km² grid cell buffers nested within BCRs, and BCRs nested within the study area (Pavlacky Jr. et al., 2017), and accounted for annual temporal variation using longitudinal data from 2010 through 2018. We indexed the 1-km² sampling units by latitude and longitude and included quadratic terms to account for the geographic ranges of grassland specialists in the Great Plains (Table 2).

We extended the hierarchical Bayes multiscale occupancy model of Mordecai et al. (2011) to accommodate multiple species (Dorazio & Royle, 2005; Royle & Dorazio, 2008) and two spatial scales (Latif et al., 2020). For each species, we estimated the probability of largescale occupancy (ψ) for grid cells, probability of smallscale occupancy (θ) for point count plots given presence at the grid cells, and probability of detection (p) for minute intervals given presence at the point count plots (Pavlacky Jr. et al., 2012). We used a state-space formulation (Royle & Dorazio, 2008) composed of two submodels for partially observed processes of large-scale and smallscale occupancy and an observation model for repeated detections (Mordecai et al., 2011). The latent state z_{itk} is the estimated presence (z = 1) or absence (z = 0) of species *i* in year *t* and grid cell *k*, and the latent state u_{itki} is the estimated presence (u = 1) or absence (u = 0) of species i in year t, grid cell k, and point count plot j. The observations y_{itki} are the detections of species using a removal design for three, 2-min time occasions (MacKenzie et al., 2018; Pavlacky Jr. et al., 2012). The state process model consisted of two equations, one for the occupancy state of grid cells $z_{itk} \sim \text{Bernoulli}(\psi_{itk})$, and the other for the occupancy state of point count plots conditional on the occupancy of grid cells $u_{itki} | z_{itk} \sim \text{Bernoulli}(\theta_{itk} z_{itk})$. The observation model for detections $y_{itkj} | u_{itkj} \sim \text{Binomial}(p_{itl}u_{itkj}, J_{itkj})$ is conditional on the occupancy state of the point count plots, where p_{itl} is the probability of detection for species *i*, year t and BCR l, and J_{itki} is the time occasion in which species i was first detected in year t, grid cell k, and point count plot j using a removal design (MacKenzie et al., 2018, Pavlacky Jr. et al., 2012). When a species was not detected, or when a species was detected on the last time occasion, J = 3.

We used a series of logistic equations to model the effects of CRP, grassland, shrubland and spatial location on the large-scale occupancy (ψ) of grassland specialists. We \log_e transformed the land-cover covariates $\left[\log_e(1 + \log_e)\right]$ $+ \text{km}^2$)] to allow non-linear and threshold responses to landscape features (Lindenmayer et al., 2008), and centered and standardized all covariates using the z-transformation (Schielzeth, 2010). We estimated coefficients for large-scale occupancy (d_i) to evaluate the hypotheses, and small-scale occupancy (b_i) to account for incomplete availability of the *i* species along the covariate gradients (Pavlacky Jr. et al., 2012). We estimated spatial and temporal variability in the probability of detection (p_{itl}) to account for imperfect detection of the species in year t and BCR l. We included the interaction between CRP and grassland land cover to evaluate the hypothesis that the effect of CRP was greater in highly modified landscapes than in more intact landscapes. We indexed large-scale occupancy of grid cells by latitude and longitude, and included quadratic terms to account for spatial variation in the geographic distributions of the species:

$$logit(\psi_{itk}) = d_{0i} + d_{1i}Grass_{tk} + d_{2i}Shrub_{tk} + d_{3i}CRP_{tk} + d_{4i}Grass \times CRP_{tk} + d_{5i}Lat_{tk} + d_{6i}Lat_{tk}^2 + d_{7i}Long_{tk} + d_{8i}Long_{tk}^2 + \eta_{3it};$$

 $logit(\theta_{itk}) = b_{0i} + b_{1i}Grass_{tk} + b_{2i}Shrub_{tk} + b_{3i}CRP_{tk} + b_{4i}Grass \times CRP_{tk} + \eta_{2it};$

$$logit(p_{itl}) = a_{0i} + \eta_{1it} + \varepsilon_{il};$$

where d_{0i} , b_{0i} , and a_{0i} are the random intercepts for largescale occupancy, small-scale occupancy, and detection of the *i* species, respectively. The η_{it} parameters are the random effects for species *i* and year *t*, and the parameter ε_{il} is the random effect for the detection of species *i* and BCR *l*. We estimated binomial spatial variation for the occupancy parameters using Bayesian inference, and accounted for extra-binomial variation using hierarchical models (Hobbs & Hooten, 2015). We accounted for excess zeros (overdispersion) using zero-inflated distributions for θ and ψ , and avoided underestimating precision of covariate effects for species with sparse data by shrinking parameter estimates to the mean using multivariate random intercepts and coefficients.

We assumed that the species-level coefficients and random effects were drawn from normal distributions for the 44 grassland specialists in the community (Dorazio et al., 2006; Royle & Dorazio, 2008). We specified community-level coefficients for d_{xi} and b_{xi} according to $\sim \text{Normal}(\mu_x, \sigma_x^2)$, where μ is the mean and σ^2 is the variance for the *x* coefficients among *i* species for large-scale (*d*) and small-scale (*b*) occupancy. We structured the community-level random effects for η_{it} and ε_{il} according to $\sim \text{Normal}(0, \sigma_t^2)$ and $\sim \text{Normal}(0, \sigma_l^2)$, respectively, where the mean is zero and σ^2 is the variance of year *t* or BCR *l* for the *i* species. We used the bivariate approximation to the multivariate normal distribution to specify covariance between the random intercepts of the community occupancy and detection models (Dorazio et al., 2011; Appendix S1).

We estimated model parameters using the Markov Chain Monte Carlo (MCMC) simulation implemented in program *JAGS* (Plummer, 2003; JAGS version 4.3.0, www.sourceforge.net) using packages *rjags* and *saveJAGS* in the R statistical computing environment (R Version 3.6.3; Appendix S1). We used vague uniform prior distributions for the correlation parameters, and weakly informative *t*-distribution and half-Cauchy priors for the mean and precision parameters, respectively (Dorazio et al., 2011). We generated 20,000 MCMC samples with a thinning interval of 20 iterations, an adaptation and burn-in period of 20,000 iterations, and used $\hat{R} < 1.1$ as an indication of model convergence (Gelman & Rubin, 1992).

We estimated the parameters using the mean and standard deviation of MCMC samples of the posterior distributions, calculated 95% credible intervals (CI) using percentiles of the posterior distributions, and calculated Bayesian *p*-values for regression coefficients greater than or less than zero using posterior predictive distributions (Hobbs & Hooten, 2015). The Bayesian CI represented the two-tailed probability, given the data, that the true value of the coefficient fell within the credible region. The Bayesian *p*-value represented the one-tailed probability, given the data, that the regression coefficients were greater than [$p(d_{xi} > 0)$] or less than [$p(d_{xi} < 0)$] zero. We considered coefficients with *p*-values >0.9 as considerable support for the one-tailed hypotheses.

We used the community multiscale occupancy model to estimate species richness responses to apparent habitat loss and CRP restoration for grassland specialists in the western Great Plains. The model estimated the effects of landscape covariates on the large-scale occupancy (ψ) of 1-km² grid cells while accounting for incomplete availability and detection of the species (Pavlacky Jr. et al., 2012). We estimated the mean gamma species richness (Whittaker et al., 2001) of grassland specialists for 1-km² sampling units according to $\hat{\gamma}_k = \sum_{i=1}^M \psi_{ik}$ (MacKenzie et al., 2018; Zipkin et al., 2009). We applied $\hat{\gamma}_k$ to the posterior distributions of the model to estimate the mean and precision in species richness along response gradients of the landscape covariates.

We used the Jaccard index to estimate beta diversity (Arita, 2017; Dorazio et al., 2011) for pairs of landscapes composed of CRP and grassland, and pairs of grassland landscapes. The Jaccard index measures the proportion of species that are common to paired sites, and the complement is beta diversity, interpreted as dissimilarity or turnover in species composition. We studied beta diversity in the Shortgrass Prairie BCR because the largest gradient of the CRP covariate occurred in this bioregion. We applied the Jaccard index to finite estimates of large-scale occupancy z_{tk} for pairs of landscapes in intervals defined by 1-km² cut-points along the land-cover gradients for grid cell k and vear t, with $<1 \text{ km}^2$ of shrubland landcover. We estimated beta diversity by sampling pairs of landscapes in each land-cover interval using 1000 parametric bootstrap iterations for the posterior distribution of z_{itk} . We estimated the relative change in beta diversity for pairs of landscapes composed of CRP and grassland relative to pairs of grassland landscapes within the 1-km² land-cover intervals.

We generated spatially explicit distributions of species richness and predicted responses of grassland specialists to CRP at the scale of the covariate measurements in 2016. We superimposed the 3 km \times 3 km covariate grid over the study area and attributed each of the 9-km² grid cells with landscape covariates for year 2016 within the GIS environment. We predicted large-scale occupancy $(\widehat{\psi}_{ik})$ for species *i* and grid cell *k* according to the logistic equations for each of the M species and estimated species richness for each grid cell according to $\hat{\gamma}_k = \sum_{i=1}^M \hat{\psi}_{ik}$ (MacKenzie et al., 2018, Zipkin et al., 2009). We omitted the quadratic term for longitude in the logistic equation to avoid issues involving strong non-linearity of the quadratic function near the eastern boundary of the study area. Next, we estimated the marginal species richness response from enrolling 1 km² of CRP in landscapes impacted by agricultural conversion to cultivated land. We attributed the 3 km \times 3 km covariate grid with the 2016 area of cropland from the National Land Cover Database (USGS, 2019). We added 1 km² to the CRP covariate data for all grid cells with $\leq 8 \text{ km}^2$ of native vegetation and CRP, and $\geq 1 \text{ km}^2$ of cropland, and we estimated species richness for the modified covariate grid as above. We calculated the absolute effect by subtracting baseline predictions of species richness from the CRP +1 km² predictions of species richness and calculated the relative effect by dividing the absolute effect by the baseline species richness for each grid cell. We summarized the mean, SD and CV for the absolute and relative responses to CRP by state and BCR to evaluate the



FIGURE 2 The species richness of grassland specialists by the area (km²) of Conservation Reserve Program (CRP) and pattern of apparent habitat loss in surrounding 9-km² landscapes, western Great Plains, USA, 2010–2018. The bold trend lines represent summed predictions of large-scale occupancy at mean values of latitude, longitude, and interaction between grassland and CRP, and minimum values for the other covariates in the model. The bounding regions represent 95% credible intervals for predicted species richness

predicted regional outcomes for the biodiversity of grassland birds.

RESULTS

As expected, we found strong support for the prediction that the species richness of grassland specialists declined with increasing habitat loss (Figure 2). We interpreted the mean of the species-level coefficients (μ_x) as the overall covariate effect for the community-wide occupancy of grassland specialists. Community-level occupancy for grassland specialists increased with the availability of grassland in the surrounding landscape ($\mu_{d_{\text{Grass}}} = 0.471$; SD = 0.088; CI = 0.299, 0.642; p > 0.999). The odds ratio for the mean of the community-level coefficients indicated that the odds of community occupancy declined by 37% ($\bar{x} = 0.63$; CI = 0.52, 0.75) for every 1 SD increase in the area of apparent habitat loss (km^2) on the log_e scale. The large-scale occupancy for 28 of the 44 grassland specialists increased with increasing area of grassland (Figure 3; Appendix S1: Table S3, Figure S1a; p > 0.9).

We considered the covariate effect of shrubland on the site occupancy of grassland specialists as a control variable to separate the covariate effects of shrubland and grassland land cover (Appendix S1: Table S1). The species richness of grassland specialists did not vary considerably by the area of shrubland in the surrounding landscape ($\mu_{d_{\text{shrub}}} = 0.045$; SD = 0.051; CI = -0.055, 0.146; p = 0.811). However, species composition varied along the gradient of shrubland cover. The site occupancy of 12 grassland specialists increased with increasing shrubland in the surrounding landscape, whereas eight species declined along the gradient of increasing shrubland (Appendix S1: Table S4; p > 0.9).

We found strong evidence supporting the prediction that CRP increased species richness of grassland specialists in landscapes impacted by habitat loss from conversion to cropland (Figure 2). The community-wide occupancy of grassland-specialist species increased with the area of CRP in the surrounding landscape ($\mu_{d_{CRP}} = 0.184$; SD = 0.049; CI = 0.084, 0.281; p = 0.998; Figure 2). The odds of community occupancy increased by 20% ($\bar{x} = 1.20$; CI = 1.08, 1.33) for every 1 SD increase in the area of CRP (km²) on the log_e scale. Specifically, the large-scale occupancy of 21 grassland specialists increased with increasing CRP in the surrounding landscape (Figure 3; Appendix S1: Table S5, Figure S1b; p > 0.9).

We found support for the hypothesis that CRP landscape management mitigates the effects of habitat loss on the biodiversity of grassland birds. Predicted species richness was similar in landscapes with comparable CRP and grassland land cover (Figure 2). At mean latitude and longitude in the study area, 5.2 grassland specialists (CI = 4.6, 6.2) were predicted to occur in landscapes with 8 km² of CRP, compared with 5.8 grassland specialists (CI = 5.5, 6.5) in landscapes with 8 km² of grassland land cover (1 km² of apparent habitat loss; Figure 2). Within the Shortgrass Prairie BCR, mean beta diversity was 0.65 between pairs of landscapes composed of CRP and grassland (SD = 0.01; CI = 0.62, 0.69; Figure 4a), and was 0.56between pairs of grassland landscapes (SD = 0.01; CI = 0.53, 0.59; Figure 4b). Relative change between overall measures of species turnover indicated that beta diversity was 17% (SD = 0.03; CI = 0.11, 0.24) greater between CRP and grassland landscapes than between grassland landscapes (Figure 4c). Although relative change between overall measures of species turnover was low, beta diversity for pairs of landscapes with $>9 \text{ km}^2$ (>89%) of CRP or native grassland was 61% greater than beta diversity for pairs of intact grasslands (SD = 0.27; CI = 0.21, 1.27; Figure 4c).

The spatially explicit predictions of species richness supported the hypotheses for regional variation in biodiversity of grassland specialists. As predicted, the species richness of grassland specialists increased with latitude and was somewhat lower at mid-latitudes (Figure 5a; Appendix S1: Figures S2a, S3a). The community-level coefficients indicated that the site occupancy of grassland



FIGURE 3 Coefficients for the covariate effects of (a) Conservation Reserve Program and (b) grassland availability on the large-scale occupancy of 1-km² grid cells for grassland specialists. The round symbols are the mean of the parameter's posterior distribution and the error bars are 95% credible intervals (CI). Coefficients with CIs excluding zero indicate measurable effect sizes for two-tailed hypotheses ($\alpha = 0.05$) and bird symbols indicate measurable effect sizes for one-tailed hypotheses ($\alpha = 0.1$)

specialists increased with latitude ($\mu_{d_{\text{Lat}}} = 0.692$; SD = 0.348; CI = -0.004, 1.354; p = 0.974) and the positive effect of latitude was reinforced by the quadratic



FIGURE 4 Legend on next column.

relationships ($\mu_{d_{\text{Lat}^2}} = -0.157$; SD = 0.106; CI = -0.367, 0.052; p = 0.934). Species richness of grassland specialists increased with degrees of longitude from west to east (Figure 5a; Appendix S1: Figures S2b, S3b; $\mu_{d_{\text{Long}}} = 0.252$; SD = 0.147; CI = -0.048, 0.533; p = 0.959).

Projecting the marginal effects of adding 1 km² of CRP to landscapes impacted by habitat loss from conversion to cultivation supported the predictions that absolute species richness responses would be greatest in regions with high biodiversity, whereas relative species richness responses would be greatest in regions with highly modified landscapes. We found that the absolute increase in species richness of grassland specialists from implementing 1 km² of CRP was greatest at high latitudes in the Prairie Potholes BCR of Montana ($\overline{x} = 1.54$, SD = 0.41) and Badlands and Prairies BCR of North Dakota ($\overline{x} = 1.36$, SD = 0.29; Figure 5b; Appendix S1: Table S6). Although precision was low for estimates of percentage change, the relative increase in species richness from the marginal increase in CRP was greater in highly modified landscapes at lower latitudes in the Shortgrass Prairie BCR of Kansas ($\overline{x} = 31\%$, SD = 22) and Texas ($\overline{x} = 30\%$, SD = 18), and Central Mixed Grass Prairie BCR of Texas $(\overline{x} = 29\%, SD = 11;$ Figure 5b; Appendix S1: Table S6).

DISCUSSION

Declining biodiversity from anthropogenic landscape modification is among the most pressing conservation problems in North America (Stanton et al., 2018) and worldwide (Dirzo et al., 2014). Given that the vast majority of grasslands are privately owned (Askins et al., 2007), landscape conservation solutions, such as the CRP program (Hellerstein, 2017), are essential for addressing both socioeconomic and wildlife conservation objectives. We studied the consequences of landscape modification and effectiveness of CRP in agricultural cultivation landscapes to provide system understanding for conserving the biodiversity of grassland birds. By evaluating hypotheses for the effects of habitat loss on the community of grassland specialists, we quantified the extent to which spatial patterns of grassland availability may have affected biodiversity declines of grassland birds.

FIGURE 4 Beta diversity for pairs of landscapes composed of (a) CRP and grassland and (b) grassland, and (c) the relative change in beta diversity along the gradient of land cover in the Shortgrass Prairie Bird Conservation Region, USA, 2010–2018. The beta diversity for (a) and (b) are represented by posterior distributions for the complement of the Jaccard index, and the relative change in beta diversity (c) was represented by (b - a)/b



FIGURE 5 The predicted species richness of (a) grassland specialists and (b) marginal responses of adding 1 km^2 of the Conservation Reserve Program in the western Great Plains, USA. The color ramp for (b) represents marginal species richness above the (a) estimates for 9-km² landscapes

We found that the odds of occurrence for grassland specialists declined by 37% for every 1 SD increase in habitat loss [log_e(km²)], resulting in regional patterns of biodiversity loss. By investigating species richness responses to landscape restoration, we discovered that CRP was capable of partially offsetting biodiversity declines of grassland specialists in landscapes impacted by agricultural conversion to cropland. The odds of community occurrence increased by 20% for every unit increase in CRP, accounting for a considerable, but incomplete, representation of biodiversity of grassland specialists. Overall beta diversity (turnover) between CRP and grassland landscapes was 17% greater than between grassland landscapes, indicating that CRP-restored landscapes included 83% of the grassland bird biodiversity inherent to grassland landscapes. However, species turnover between landscapes with >8 km² land cover of CRP or grassland was 61% greater than turnover between intact grasslands, suggesting that species composition in landscapes with >89% land cover of CRP represented only 39% of the grassland bird biodiversity of intact grasslands. High beta diversity between landscapes dominated by CRP and intact grasslands suggested that CRP restoration of entire

landscapes affected by intensive cultivation may not be effective for increasing the biodiversity for grassland specialists. Similar to the findings of Hagen et al. (2020), CRP may be most effective for increasing the occurrence of area-sensitive species when implemented in landscapes with remnant patches of grassland vegetation. Mapping spatially explicit predictions provided a framework to prioritize the implementation of CRP in regions with the largest outcomes for the biodiversity conservation of grassland specialists in the Great Plains.

As shown here, the large effect of CRP on the occurrence of grassland birds suggests that grassland restoration by planting perennial grasses in formerly cropped fields (Munson & Lauenroth, 2012) could be also scaled up to address conservation problems in agricultural production landscapes, including faunal homogenization and loss of biodiversity (Dirzo et al., 2014; McGill et al., 2015). Although our results do not address the exact mechanism underlying the relationship between CRP and grassland bird species richness, grassland restoration in farmed landscapes is likely to increase functional landscape connectivity (Taylor et al., 1993) by providing complementary or supplementary habitat resources, and increasing landscape permeability (Dunning et al., 1992). Accordingly, we predicted that restoring landscape connectivity would reclaim area above extinction thresholds (Fahrig, 2003) in highly modified agricultural landscapes, and increase the spatial extents of occurrence and territory establishment for species with area sensitivity (Ribic et al., 2009) and narrow tolerances for grassland vegetation (Correll et al., 2019). Our results showed that mean species turnover between CRP and grassland was 17% greater than between grassland landscapes, which suggested that enrolling CRP in agricultural landscapes can both support communities of grassland specialists, and reduce faunal homogenization and loss of avian biodiversity (McGill et al., 2015).

Specifically, implementing CRP in the surrounding landscape increased the site occupancy of grassland species of high conservation concern in the Great Plains (Partners in Flight, 2019), such as the Lesser Prairie-Chicken (Tympanuchus pallidicinctus), and included several migratory (Pool et al., 2014) and habitat specialist (Correll et al., 2019) species (Appendix S1: Table S2): Long-billed Curlew (Numenius americanus); Short-eared Owl (Asio flammeus); Chestnut-collared Longspur (Calcarius ornatus); Thick-billed Longspur (Rhynchophanes mccownii); Grasshopper Sparrow (Ammodramus savannarum); Lark Bunting (Calamospiza melanocorvs); Baird's Sparrow (Centronyx bairdii); Bobolink (Dolichonyx oryzivorus). Several of these species are known to benefit from CRP (Johnson, 2005; Ryan et al., 1998). Although Johnson and Schwartz (1993) found that Chestnut-collared Longspur abundance was greater in cropland than CRP, Veech (2006) showed positive population responses following CRP restoration, similar to our findings. Our results include previously undocumented effects of CRP at the landscape-scale for Long-billed Curlew, Short-eared Owl, Chihuahuan Raven (Corvus cryptoleucus) and Thick-billed Longspur (Haufler, 2005; Ryan et al., 1998). We did not expect species requiring heterogeneity in shortgrass conditions from disturbance, such as fire and grazing (Fuhlendorf et al., 2009), such as Sprague's Pipit (Anthus spragueii) and Mountain Plover (Charadrius montanus), to benefit from CRP restoration. Despite the requirements of one mid-contract management action and recent emphasis on burning and grazing practices (CCC and USDA, 2019), current management practices may be insufficient for species that require greater heterogeneity in grassland structure (Derner et al., 2009; Hovick et al., 2015). Nevertheless, several favoring short-grass conditions (Billerman species et al., 2020) also benefited from the landscape effects of CRP, including the Long-billed Curlew, Horned Lark (Eremophila alpestris), Chestnut-collared Longspur, and Thick-billed Longspur. While the local-scale habitat suitability of CRP grassland may be low for species requiring heterogeneity in

short-grass or bare-ground conditions (Derner et al., 2009), the positive effects for these species are likely to reflect increases in large-scale connectivity from the addition of CRP in surrounding agricultural landscapes (Davis et al., 2013). Similarly, we did not expect species requiring keystone features (Tews et al., 2004), such as Black-tailed Prairie Dog (Cynomys ludovicianus) towns or wetlands, to benefit from grassland restoration (e.g., Burrowing Owl, Athene cunicularia), but because CRP practices are often implemented as wetland buffers, we found that landscape restoration increased the site occupancy of Marbled Godwit (Limosa fedoa), California Gull (Larus californicus), Willet (Tringa semipalmata), and Wilson's Phalarope (Phalaropus tricolor). Although we found evidence for community-wide responses to landscape restoration, more frequent midcontract management or additional conservation measures are needed for species with high vulnerability to threats related to habitat degradation on the breeding-grounds (Partners in Flight, 2019; Appendix S1: Table S2), such as the Greater Prairie-chicken (T. cupido), Mountain Plover, Northern Harrier (Circus hudsonius), Ferruginous Hawk (Buteo regalis), and Sprague's Pipit.

The main limitations of our study involve using spatial patterns to make inference to temporal processes in the continuum model, simple measures of landscape composition, and uncertainty from spatial and temporal variation in weather patterns. Within a continuummodeling framework (Fischer & Lindenmayer, 2006), we used spatial patterns along gradients in grassland availability to make inferences about temporal processes of habitat loss. Although spatially explicit predictions along gradients of grassland availability provided biologically realistic patterns of regional biodiversity (Figure 5), the spatial gradients may not completely correspond to the actual temporal processes of habitat loss over time. Although 27% of the study area was converted to cultivated cropland and the majority of vegetation converted to cropland was native grassland (Samson et al., 2004), 16% of the study area was composed of forested and developed land, which indicated that the gradient in grassland availability was influenced by these land-cover types. Because several grassland species perceive forest edges as hard boundaries (Ribic et al., 2009), our inference to apparent habitat loss may be more conservative, considering the relatively softer boundaries between cropland and grassland. A second possible caveat of our results stems from the relatively simple measures of landscape composition used in this study. Although we accounted for landscape heterogeneity of grassland and shrubland vegetation, our approach may be an oversimplification of complex ecological processes involving landscape heterogeneity (Fahrig et al., 2011). Grassland bird species are known to respond to variation in

CRP seed mixes and successional ages of fields (Johnson, 2005), and heterogeneity in cropland types (Fahrig et al., 2011), as well as landscape heterogeneity in vegetation structure produced by disturbance processes, such as soil, fire and herbivory (Hovick et al., 2015). Monitoring the effectiveness of landscape restoration on grassland birds is complicated by nomadic annual movements (Green et al., 2019) and variable rangeland conditions from annual weather patterns (George et al., 1992). Although ecological processes for spatial and temporal variation are underdetermined in the current study, we controlled for annual variation using random effects and accounted for the geographic distributions of the species using non-linear relationships for latitude and longitude. Future research directions include estimating temporal dynamics of grassland bird communities relative to annual variation in precipitation and temperature, as well as evaluating the effectiveness of prescribed grazing and brush management for climate adaptation, drought management, and the conservation of grassland birds.

We suggest that the biodiversity conservation of grassland birds will be most effective within a renewal ecology framework that integrates conservation science, restoration ecology, and agro-ecology to maximize human well-being and biodiversity outcomes in highly modified agricultural production landscapes (Bowman et al., 2017; Kareiva & Marvier, 2012). Because the role of humans has become pervasive in highly modified landscapes (Kareiva & Marvier, 2012), conservation success depends on understanding human dimensions that drive decision-making processes before tangible biodiversity outcomes are possible (Knight et al., 2010). By providing financial incentives to private agricultural producers, the CRP model provides a mechanism for simultaneously achieving human wellbeing and ecosystem services, such as water, soil and wildlife conservation (Hellerstein, 2017). The initial intent of the CRP was to reduce cultivation on marginal or vulnerable land to address soil erosion and increase crop prices and yields on cultivated land, which reduce the need to cultivate native vegetation in other regions (Green et al., 2005). Recent trends in the targeted enroll-CRP ment of to achieve ecosystem services (Hellerstein, 2017) may be similar to wildlife-friendly farming practices, which can reduce crop yields and displace agricultural cultivation to other regions (Green et al., 2005). Recent declines in the legislated area limits of CRP and payment rates have resulted in a declining trend in the area of land enrolled in the program (Hellerstein, 2017). Ultimately, the area of land enrolled in CRP within agricultural production landscapes of the Great Plains has important implications for the sustainability of traditional livelihoods, efforts to feed expanding human populations (Bowman et al., 2017), and the decline of the North American grassland avifauna

(Rosenberg et al., 2019). Addressing socioeconomic and biodiversity problems on such a grand scale will require conservation strategies to balance tradeoffs for potentially conflicting objectives in a way that provides optimal outcomes for social welfare and biodiversity (Schwartz et al., 2018). The spatially explicit predictions for the responses of grassland-specialist species to CRP may prove useful within Systematic Conservation Planning (Margules & Pressey, 2000) to prioritize restoration action within financial constraints (McBride et al., 2010). We discovered that the absolute conservation outcomes were greatest at high latitudes in regions with high biodiversity, whereas relative percentage increases in species richness were greater at low latitudes in highly modified landscapes (Figure 5; Appendix S1: Table S6).

By simultaneously addressing the threats of landscape modification and landscape restoration for biodiversity conservation, and the social-economic well-being of private agricultural producers (Bowman et al., 2017), the CRP program provides an emerging solution to one of the most pressing conservation problems for the declining grassland avifauna of North America (Rosenberg et al., 2019). The current study provides a statistically rigorous evaluation of CRP at bioregional scales to provide necessary information to implement landscape-scale conservation for a comprehensive assemblage of grassland specialists in the western Great Plains. Monitoring the effectiveness of landscape restoration increases the confidence of resource professionals and promotes accountability toward meeting biodiversity conservation objectives (Briske et al., 2017). Ultimately, conservation success in the Great Plains depends on social capital to reward private agricultural producers for voluntary conservation of natural resources in the public trust (Briske et al., 2017). Considering limited financial resources (Hellerstein, 2017), sustainability of traditional livelihoods (Bowman et al., 2017), future food demands (Green et al., 2005), and impending biodiversity crisis (Rosenberg et al., 2019), we advocate for a collaborative conservation strategy (Bowman et al., 2017; McBride et al., 2010; Schwartz et al., 2018) capable of balancing tradeoffs for economic constraints, human dimensions, future competing land uses, and key elements of biodiversity to provide optimal solutions for social well-being and conservation of grassland birds.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data (Pavlacky et al., 2021) are available on Dryad at https://doi.org/10.5061/dryad.9zw3r22f3. Conservation Reserve Program data for private lands enrolled in confidential Farm Service Agency agreements (USDA, 2014) are omitted. Also omitted are coordinates for primary sampling units from the Integrated Monitoring in Bird Conservation Regions program that require a data sharing agreement from Bird Conservancy of the Rockies.

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Additional supporting information may be found in the online version of the article at the publisher's website.

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