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ARTICLE

Agroecosystems

Bird and arthropod response to herbicide and grazing: Trade-offs and time lags in invasive plant management

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Abstract

Managing ecologically harmful plant species requires an understanding of the impacts of complex spatial and temporal disturbances on ecological communities. Actions aimed at controlling non-native plants can have dynamic effects on patterns of succession, with lag effects and trade-offs possible. In grasslands, invasive plants can be reduced using intensive grazing during the peak growth of target species or applying herbicide when non-target plants are dormant. It is unclear how combining herbicide with grazing impacts fauna and whether there are lag effects as ecosystem recovery occurs. Using landscape-scale experiments, we studied how these techniques affect multiple trophic levels several years after management disturbance, focusing on grassland birds (2015–2018) and their arthropod prey (2015–2017). Our large study patches ($n = 54$, mean size = 10 ha) were invaded by tall fescue (*Schedonorus arundinaceus*), an ecologically harmful non-native grass. We first conducted a large-scale controlled experiment on a subset of 21 patches, which were grouped spatially into threes and treated with (1) herbicide (glyphosate), (2) herbicide and native seeding, or (3) no treatment (control). When examining the entire sample of 54 patches, we were able to explore the interactive effects of herbicide and (1) intensive-early stocking (double-stocking cattle April–June), (2) season-long stocking (moderate stocking April–September), or (3) no grazing. Birds and arthropods were monitored for 3–4 years post-treatment, allowing us to examine temporal shifts after these management

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disturbances. In our experiment, we found that herbicide-treated patches, in comparison with controls, had an increased abundance of several native bird species and arthropod orders in Year 2 or 3 after treatment, with some negative responses in Year 1. These lag times indicate that applying herbicide over broad areas without providing refugia may have short-term negative consequences, especially for arthropods. When examining the interactive effects of treatments, we found that herbicide in conjunction with grazing resulted in declines for several disturbance-sensitive bird species. Improved understanding of lag effects, trade-offs, and taxon-specific responses to treatment combinations can inform restoration that limits deleterious effects of treatments on native wildlife.

KEYWORDS
grassland arthropods, grassland birds, grassland ecology, herbicide, intensive-early stocking, invasive plant management

INTRODUCTION

Anthropogenic changes to historic disturbance patterns have contributed to the increased spread of invasive plants worldwide (Oswalt et al., 2021; Sharma et al., 2023). Yet, effectively managing invasive plants often requires disturbance and results in further changes to successional trajectories (Huston, 2004). There are increasing concerns about the unintended consequences of the disturbance caused by invasive plant management (Prior et al., 2018; Skurski et al., 2013; Zarnetske et al., 2010). Strategies including herbicide, physical removal, fire, grazing, or disking can have complex and drastic impacts on plant and animal communities. Lag effects are possible, where ecological impacts emerge over longer timescales as communities respond to disturbance (Anderson, 2018; Lira et al., 2019; Watts et al., 2020). Because many invasive plants thrive in early successional environments, non-native plant management can even facilitate further invasion (Catford et al., 2012). Temporally complex trade-offs for native species are also possible, with benefits for some taxa emerging over time and deleterious consequences emerging for others (Prior et al., 2018; Skurski et al., 2013; Zarnetske et al., 2010). Effectively managing invasive plants thus requires an understanding of the temporal dynamics of how communities assemble after removal disturbances (Coon et al., 2021; Sheley & Krueger-Mangold, 2003).

Understanding recovery after restoration has become a global priority in disturbance-reliant ecosystems with rapid and complex assembly patterns (Buisson et al., 2021). Early successional ecosystems require regular disturbances and have rapid and dynamic cycles of community recovery, such as the historic maintenance of early stages of succession in grasslands by a shifting mosaic of fire and grazing by native herbivores (Fuhlendorf & Engle, 2004). However, these historic disturbance regimes have been extensively altered, with much more intensive grazing compared to historic baselines and the exclusion of fire (Perkins et al., 2019). Additionally, non-native plants have been introduced in grasslands around the world to control erosion and provide forage for domestic grazers, and many species have since become invasive (Godfree et al., 2017; Svejcar et al., 2017). Invasive plants in grasslands can cause serious agroeconomic and ecological harm, including poor forage and homogenized plant communities (Barnes et al., 2013; Bradley et al., 2018; Ellis-Felege et al., 2013; Godfree et al., 2017; Stotz et al., 2019). The increasing prevalence of invasive grasses has been shown to degrade habitat quality for grassland birds (Nelson et al., 2017; Schirmel et al., 2016) and their arthropod prey (Litt et al., 2014). This is especially problematic given the extensive loss of grassland habitats globally and concomitant declines in both birds and arthropods (Brennan & Kuvlesky, 2005; Douglas et al., 2023; Rosenberg et al., 2019; Seibold et al., 2019).

Restoring the ecological integrity of invaded grasslands often involves managed disturbances such as herbicide application or targeted grazing (Madison et al., 2001; Maresh Nelson et al., 2019). In particular, although the use of herbicide is common (Kettenring & Adams, 2011) and generally effective at reducing the prevalence of targeted plants (Adkins & Barnes, 2013; Elseroad & Rudd, 2011; Slopek & Lamb, 2017), not much is known about the impacts of herbicide on higher trophic levels, like grassland fauna. This is despite the possibility for trade-offs and negative impacts, including declines in avian abundance or reproductive success after application (Lampert et al., 2014; Skurski et al., 2013). For instance, although invasive grasses have been linked to increases in predation and cowbird parasitism rates for grassland bird nests (Lyons et al., 2015; Maresh Nelson

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et al., 2018), herbicide may reduce vegetation cover used to conceal nests from predators or nest parasites, at least temporarily (Rivers et al., 2019). Another potential trade-off is the availability of arthropod prey items. Invasive plants can reduce the abundance of arthropods (Flanders et al., 2006; George et al., 2013; Hickman et al., 2006), but herbicide can also decrease arthropod abundance through reduced vegetation biomass (Sullivan & Sullivan, 2003), potentially leading to reduced food resources. Such trade-offs necessitate careful consideration of whether the benefits of herbicide are likely to offset risks.

Understanding invasive plant management using herbicide has been limited by the short duration of most studies (~1 year; Farrell & Gornish, 2019; Kettenring & Adams, 2011). Short-term studies are likely to obscure costs or benefits regarding habitat quality (e.g., increased cover or food availability) that may emerge after several years (Cosentino et al., 2014; Endress et al., 2012). For instance, 1–2 years after applying herbicide, the plant community is often dominated by exotic annual forbs, with seeded native plants only becoming established after 3–5 years (Endress et al., 2012; Hulet et al., 2010; Mingione et al., 2025; Rothrock & Squiers, 2003). These shifting dynamics in vegetation structure and composition could temporarily reduce nest-site availability, nest concealment, or arthropod availability (Rivers et al., 2019; Taylor et al., 2006). Grassland birds that prefer low forb cover and high native grass cover, like bobolinks (*Dolichonyx oryzivorus*), grasshopper sparrows (*Ammodramus savannarum*), Henslow's sparrows (*Centronyx henslowii*), and eastern meadowlarks (*Sturnella magna*), may be negatively impacted by such changes (Osborne & Sparling, 2013; Vickery et al., 1999). Nearly all of these obligate grassland birds are facing steep declines across North America (Rosenberg et al., 2016, 2019).

In contrast to herbicide, targeted livestock grazing has received little attention as a method to restore ecological integrity by manipulating disturbance regimes. Targeted grazing involves managing livestock grazing intensity and timing to alter vegetative communities, often by increasing grazing pressure when invasive plants are most actively growing (Bailey et al., 2019). One example of targeted grazing is intensive-early stocking in the Great Plains, which involves heavy grazing in early summer before removing cattle in late summer (Maresh Nelson et al., 2019; Raynor et al., 2018; Smith & Owensby, 1978). In these ecosystems, this strategy targets non-native cool-season grasses that grow most actively in spring and early summer and provides reprieve for native warm-season grasses that reach peak growth in late summer. The use of high grazing pressure to reduce invasive grasses is meant to be a temporary strategy lasting a few years, but there may still be short-term trade-offs for grassland birds by reducing vegetation cover and heterogeneity. Intensive-early stocking drastically reduces greater prairie chicken abundance (*Tympanuchus cupido*) when combined with annual prescribed burns (Robbins et al., 2002), and high stocking rates generally reduce grassland bird nest success, diversity, and abundance (Coppedge et al., 2008; Duchardt et al., 2016; Johnson et al., 2011). Arthropod response to grazing tends to vary across taxa, though some reductions in diversity have been linked to intensive grazing (Van Klink et al., 2014; Wang & Tang, 2019).

In this study, we conducted large-scale experiments over several years to evaluate the response of multiple trophic levels to managed disturbances aimed at reducing invasive plant species in grasslands. Specifically, we evaluated how combinations of herbicide, seeding of native plants, and intensive-early stocking of domestic cattle impacted animal responses over time in a degraded grassland system that has experienced disruption to historic disturbance regimes. We evaluated the potential for trade-offs and time lags using both an experiment and a broader correlative study looking at interactive effects between disturbances. We predicted that negative impacts on grassland birds and their arthropod prey may appear in the first year after treatment due to loss of vegetation biomass—in particular, grasses—but after three years, we expected the highest abundance of birds and arthropods in patches treated with both herbicide and native seeding and lowest in control patches without herbicide. We predicted that birds would respond to grazing according to species-specific preferences for vegetation height. Alternatively, we predicted that combining intensive-early stocking with herbicide could reduce grassland bird abundance due to excessive vegetation biomass reduction. We intend to use results to develop recommendations grounded in an understanding of succession and disturbance, allowing researchers, natural resource practitioners, and landowners to minimize trade-offs.

METHODS

Study region

Our study sites are distributed throughout the Grand River Grasslands of southern Iowa and northern Missouri, USA (Figure 1; Miller et al., 2012; Raynor et al., 2019). At the start of the study, our grassland study sites were dominated by invasive C_3 grasses, including tall fescue (*Schedonorus arundinaceus*), smooth brome (*Bromus inermis*), and Kentucky bluegrass (*Poa pratensis*) (Coon et al., 2021; Raynor et al., 2019). Non-native forbs are also common, including birdsfoot trefoil (*Lotus corniculatus*),

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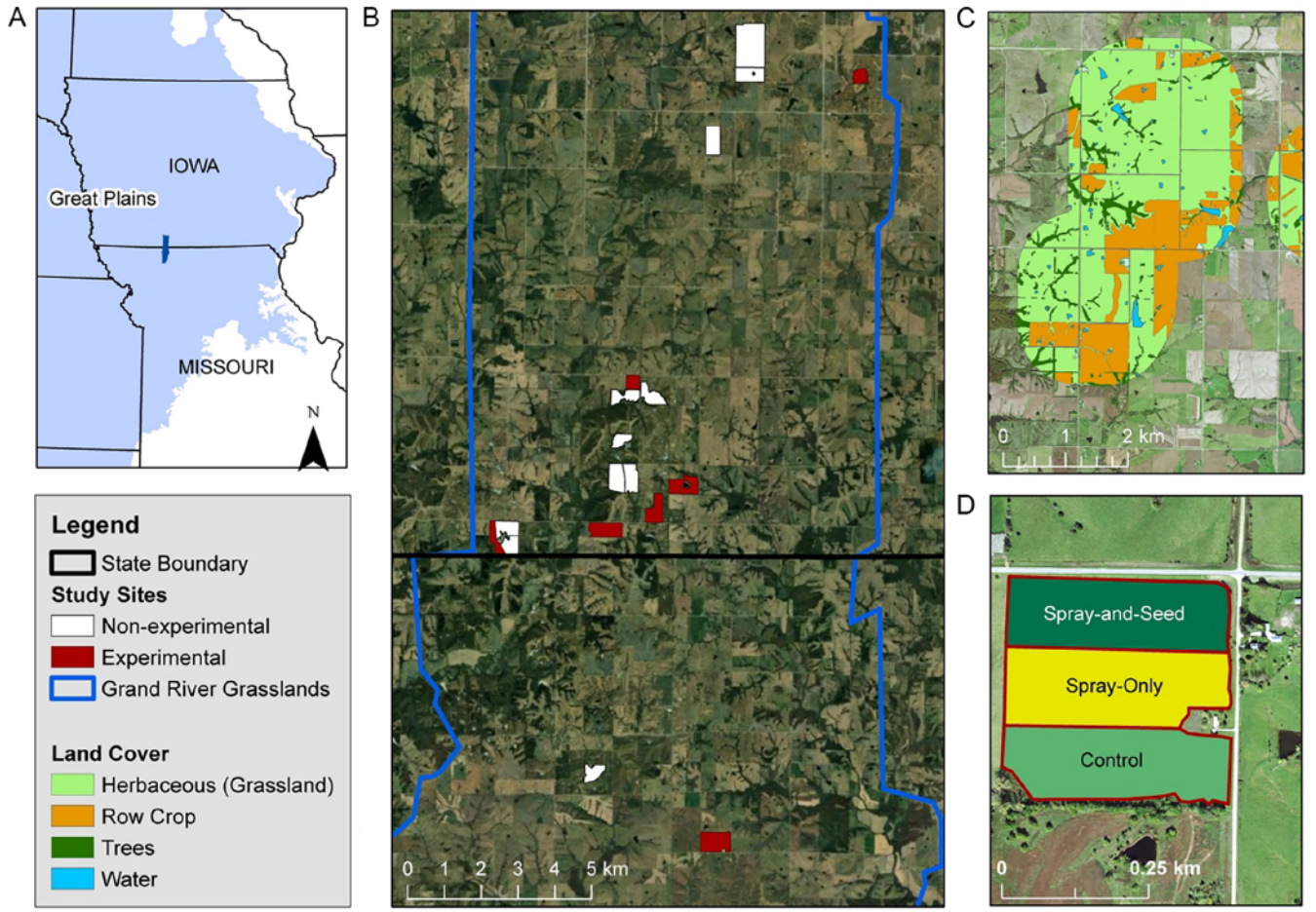

FIGURE 1 (A) The Grand River Grasslands ecoregion as situated in the Great Plains and (B) the location of study sites ($n = 18$) within the ecoregion. Also shown are (C) example 1000-m buffers around two study sites with digitized land cover within buffers and (D) an experimental study site with the three patches, each receiving different treatments. Aerial imagery was obtained from the Iowa State University Geographic Information Systems Support and Research Facility, with orthophotos taken by the National Agriculture Imagery Program in 2023.

red clover (*Trifolium pratense*), and white clover (*Trifolium repens*). Native warm-season grasses include little bluestem (*Schizachyrium scoparium*), big bluestem (*Andropogon gerardii*), and yellow feathergrass (*Sorghastrum nutans*). Native forbs include Canada goldenrod (*Solidago altissima*), prairie ironweed (*Vernonia fasciculata*), wild bergamont (*Monarda fistulosa*), and black-eyed susan (*Rudbeckia hirta*). The mean annual temperature of the Grand River Grasslands is 10°C, and annual precipitation is 940 mm. Dominant soil types within our study sites were Armstrong loam (fine, smectitic, mesic Aquertic Hapludalfs) and Gara loam (fine-loamy, mixed, superactive, mesic Mollic Hapludalfs) (Raynor et al., 2019).

Research has been ongoing in the region since 2006, with studies initially focused on the role of prescribed fire in controlling encroachment of trees and shrubs (Delaney et al., 2016; Duchardt et al., 2016; Moranz et al., 2012; Pillsbury et al., 2011). However, the focus later shifted to techniques used to control the invasive plant tall fescue, a grass that limits the success of prescribed fire by reducing burn completeness (McGranahan et al., 2012). Areas with high levels of tall fescue are avoided by grazing cattle (Maresh Nelson et al., 2019), linked to increased predation of grassland bird nests (Lyons et al., 2015; Maresh Nelson et al., 2018), and associated with reduced growth rates in some species of butterfly larvae (Jokela et al., 2015). As a part of this larger project, the percent cover of plant functional groups was monitored after experimental herbicide and native plant seeding, using a before-after control-impact study design. This study found that herbicide and seeding successfully reduced tall fescue on study sites and increased native warm-season grasses over time, though the impacts were greatest on sites without grazing (Coon et al., 2021).

Study design

We monitored 54 landscape patches (mean = 9.8 ha) over 4 years (2015–2018) undergoing invasive plant management. Patches were owned by the Iowa Department

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of Natural Resources ($n = 45$), The Nature Conservancy ($n = 3$), the Missouri Department of Conservation ($n = 3$), and private landowners ($n = 3$). Due to logistical constraints, we monitored 54 patches in 2015 and 2016, 51 in 2017, and 48 in 2018.

All 54 patches were spatially grouped in threes as a "site." For a subset of 21 patches (7 sites), we used a quasi-experimental framework (Table 1), with one of three treatments applied to a patch in the same year: (1) herbicide (spray-only), (2) herbicide and seeding of native plants (spray-and-seed), or (3) no treatment (control) (Figure 1D) such that each group contained one patch treated with each of the three treatments. We describe the approach as quasi-experimental because we did not use random assignment, but instead, we applied herbicide treatments to the patches most invaded by tall fescue. However, differences in tall fescue cover among patches were small and statistically nonsignificant (Coon et al., 2021). Six of the seven sites were treated with herbicide in 2014 and one in 2015. The herbicide treatment consisted of spraying with glyphosate in the fall (1.3 kg ha^{-1}) when native grasses and forbs were dormant. Spray-and-seed patches were treated with herbicide in the fall, followed by spring drill-seeding of a high-diversity mix of native grasses and forbs (Appendix S4). Hereafter, we refer to this subset of 21 patches as the "herbicide experiment." One of three cattle grazing treatments was applied to each of these sites: intensive-early stocking ($n = 2$), season-long stocking ($n = 2$), or no grazing ($n = 3$). With intensive-early stocking, beef cattle were stocked for the first half of the grazing season (early April to early July) at twice the herd size of the season-long stocking pastures grazed from April to September. Stocking rates were similar for intensive-early stocking (3.1 animal unit months ha^{-1}) and season-long stocking (2.5 animal unit months ha^{-1}), but instantaneous grazing pressure during the first half of the grazing season in intensive-early stocked pastures was relatively high compared to that of season-long stocked pastures. Instantaneous grazing pressure is a measure of animal demand per unit of available vegetation at a point in time. The relatively high instantaneous grazing pressure in the first half of the growing season in intensive-early stocked pastures was expected to reduce the prevalence of cool-season grasses and then favor native warm-season grasses in the second half of the growing season because of the removal of cattle (Smith & Owensby, 1978). All grazed areas had perimeter fences but no internal fencing (i.e., cattle had free access among treatment patches in a group).

Herbicide was also applied to some patches non-experimentally between 2014 and 2017. These patches differed from experimental patches because herbicide was applied by managers to entire patches as needed over the course of the study. In total, out of all 18 sites, 11 had at least one patch treated with herbicide (Table 2). Grazing treatments on these sites included intensive-early stocking ($n = 12$ patches), season-long stocking ($n = 18$ patches), or no grazing ($n = 24$ patches). This larger sample size allowed us to examine the interactive effects between herbicide and the three grazing treatments. Grazed sites were burned every three years, and ungrazed patches were burned or hayed every three to five years. Average time-since-fire or haying was equivalent across herbicide and treatment categories.

TABLE 1 Sample size for replicate patches at seven experimental management sites monitored over four years.

Herbicide treatment	Grazing treatment	Patch-year replicates
Control	IES	8
Spray-and-seed	IES	8
Spray only	IES	8
Control	None	11
Spray-and-seed	None	11
Spray only	None	11
Control	SLS	7
Spray-and-seed	SLS	7
Spray only	SLS	7

Note: Each site was assigned one of three grazing treatments, including intensive-early stocking (IES, $n = 4$), season-long stocking (SLS, $n = 6$), or no grazing (none, $n = 8$). Each site was divided into three patches, each treated either with glyphosate herbicide and no seeding (spray-only), glyphosate herbicide with native seeding (spray-and-seed), or no herbicide (control). Differences in replicates are due to logistical limitations that prevented monitoring of two sites in some years.

TABLE 2 Sample size for replicate patches on 18 grassland sites monitored over 4 years, though not every site was monitored each year due to logistical constraints.

Treated with herbicide?	Grazing treatment	Patch-year replicates
No	IES	33
No	None	53
No	SLS	44
Yes	IES	15
Yes	None	31
Yes	SLS	34

Note: Each site was assigned one of three grazing treatments, including intensive-early stocking (IES, $n = 4$), season-long stocking (SLS, $n = 6$), or no grazing (none, $n = 8$). Each site was divided into three patches, with glyphosate herbicide applied to at least 1 patch on 11 sites.

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Avian methods

During the 2015–2018 breeding seasons, we conducted grassland bird surveys from late May to early August. Surveys were completed along established transects 100–600 m in length, depending on patch size. Transects were positioned to maximize the amount of grassland area surveyed in a patch (Duchardt et al., 2016). We surveyed transects five times each breeding season, with approximately 1.5 weeks between survey rounds. Prior to each survey, observers recorded temperature, wind speed, and start time. A trained observer then walked along the transects and recorded all birds seen perching within 50 m, only surveying on days without inclement weather (Bibby et al., 2000). For each observation, we recorded sex (if known), group size, and distance from the observer. We excluded group sizes >3 from analyses to control for the effects of flocking. Data on vegetation density, which is predicted to impact the detection probability of grassland birds, were assessed using a Robel pole within 0.5-m^2 quadrats placed 25 m from the avian transects (30 per patch) (Coon et al., 2021; Robel et al., 1970).

To control for the potential effects of land cover on grassland bird abundance (Cunningham & Johnson, 2006), we digitized the extent (in hectares) of grassland, forest, and row-crop cover in 1000-m buffers around and including study patches using ArcMap 10.6 (ESRI, Redlands, CA). We chose a 1000-m buffer distance because regressions of variance in cover classes against distance from pasture edges show an asymptote at 1000 m (Pillsbury et al., 2011). We extracted each land-cover category as a proportion of the total buffer area and calculated wooded-edge density as the perimeter of tree edge (in kilometers) divided by total buffer area (in hectares).

Arthropod methods

From 2015 to 2017, we captured arthropods along two 100-m transects placed 25 m to the side of avian transects using ArcMap (ESRI). If avian transects were longer than 100 m, we placed each arthropod transect randomly along the length of one avian transect. To capture temporal variability of arthropods during the avian breeding season, sampling took place twice per summer: once mid-June to early July and again in mid-July to early August. A modified leaf-blower vacuum was used to capture ground-dwelling arthropods, and a sweep net was used to capture foliar arthropods (Buffington & Redak, 1998). We randomly assigned the sweep and vacuum capture methods to either side of the transect, simultaneously sampling with each method at a distance of 5 m. We used a subsampling technique by setting up 10-m increments along arthropod transects and then only sampling the first 2 m of every 10-m segment. This resulted in 20 m^2 netted and 20 m^2 vacuumed per 100-m transect. Arthropods were stored in 70% ethanol. In the lab, we identified arthropod specimens >2 mm in length to taxonomic order under a dissecting microscope and recorded measurements (length and/or width) for use in biometric equations estimating arthropod biomass (Sample et al., 1993).

Analysis

To mirror our study design, we ran two sets of analyses for each response variable (i.e., avian abundance and occupancy, arthropod abundance and biomass). The first set of analyses examined data from the 21 patches in the herbicide experiment, where synchronous herbicide treatments and controls allowed us to model changes in abundances over time (i.e., years-since-herbicide). Patches were coded as "spray-only," "spray-and-seed," or "control."

The second set of analyses examined interactions between grazing and herbicide across all 54 study patches. In this inclusive sample, all patches treated with herbicide were pooled into one "herbicide" treatment category, including sites treated in different years and irrespective of seeding. In these analyses, "Year" was included as a covariate. All patches where herbicide had not been applied for at least 12 years (i.e., the years our team has monitored sites) were pooled into a "no herbicide" treatment category. Each patch was also assigned a grazing category (i.e., intensive-early stocking, season-long stocking, or no grazing). All avian and arthropod analyses were carried out in R version 3.6.1 (The R Foundation for Statistical Computing).

Avian abundance and occupancy

Our assessment of the avian community in both sets of analyses focused on six grassland obligate species—bobolinks, dickcissels (*Spiza americana*), eastern meadowlarks, grasshopper sparrows, Henslow's sparrows, and sedge wrens (*Cistothorus stellaris*). We grouped western meadowlarks (*Sturnella neglecta*) with eastern meadowlarks because the two species were frequently visually indistinguishable in the field, although they can be differentiated by ear. Eastern meadowlarks are thought to be dominant in the region and were heard most frequently. In addition to six grassland obligates, we modeled the abundance of red-winged blackbirds (*Agelaius phoeniceus*), a facultative grassland bird that had sufficient detections for analysis.

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The impact of treatments on grassland bird species was estimated with either N-mixture models of abundance or occupancy in the R package "unmarked" (Fiske & Chandler, 2011). Such models use spatially and temporally replicated counts to control for imperfect detection while estimating abundance or occupancy (Dénes et al., 2015; Royle, 2004). For most of our focal species, we estimated abundance with N-mixture models using the "pcount" function (Royle, 2004). The binomial distribution was used to model detection probability and a zero-inflated Poisson (ZIP) distribution to model abundance. We employed the ZIP distribution instead of the negative binomial distribution because estimates are more ecologically realistic when "true" zeroes (i.e., birds are absent, not just undetected) are prevalent (Dénes et al., 2015; Joseph et al., 2009). We accounted for different transect lengths among patches in these models using an area offset, with every 100 m of transect equaling 1 ha surveyed, and present results as abundance per ha. Abundance models failed to converge for Henslow's sparrows and sedge wrens in the herbicide experiment due to too few detections, so we instead modeled occupancy with the "occu" function in unmarked (MacKenzie et al., 2002). In both abundance and occupancy models, we used patch-year as a replicate in analyses and did not estimate immigration or emigration due to computational complexity (Ahlering & Merkord, 2016).

Arthropod abundance and biomass

In both sets of analyses, we focused on arthropod orders commonly eaten by adult birds or fed by parents to nestlings (McIntyre & Thompson, 2003; Wiens & Rotenberry, 1979). These orders include grasshoppers, crickets, and katydids (Orthoptera); spiders (Araneae); beetles (Coleoptera); and moths, butterflies, and caterpillars (Lepidoptera adults and larvae). We also counted Hemiptera because although they are less commonly eaten by grassland birds, they are still a component of the grassland bird diet and are the most abundant order in our system (Coon et al., 2022). We estimated individual and total biomass of arthropods for all focal orders except Hemiptera using length-mass regression. We measured the length of each specimen to the nearest 0.5 mm, as well as width for Coleoptera and Lepidoptera. We input these measurements in biometric equations to estimate biomass (in milligrams) of Lepidoptera larvae, Lepidoptera adults, and Coleoptera (Sample et al., 1993) and of Orthoptera and Araneae (Sabo et al., 2002).

Prior to analyses, we examined the data for outliers. When extreme outliers were present, we used winsorization to cap values that fell beyond the 99th percentile, replacing them with the most extreme value within the 99th percentile. Unlike removing outliers from the dataset, this method preserves information while also improving estimates (Salkind, 2010). We evaluated the impact of treatment on arthropod abundance and total patch biomass using mixed models in the R package "glmmTMB" (Brooks et al., 2017). Arthropod counts were modeled using a negative binomial response distribution to account for overdispersion and biomass using a Gaussian distribution. "Site" was included as a random effect in all arthropod models to account for spatial autocorrelation.

Model selection

Our model-selection process comprised three stages for grassland bird species and two stages for arthropod orders (Table 3). In each stage, we used Akaike information criterion corrected for small sample sizes (AIC_c) and Akaike weights (w_i) to rank and assess models (Burnham & Anderson, 2002) using the "AICmodavg" package (Mazerolle & Mazerolle, 2019). In these stages, we carried variables from the top model to the next stage unless 85% CIs around effect sizes overlapped zero (to avoid bringing forward uninformative parameters; Arnold, 2010). In the first modeling stage, we examined variables affecting detection (e.g., temporal and weather variables, habitat structure, observer, sampling method). In the second stage of the avian analyses, we examined effects of landscape context. In the final stage, for both birds and arthropods, we examined the impacts of treatments. We produced predicted values and 85% CIs from the top-selected model to evaluate ecological significance of results (Arnold, 2010). In cases of model-selection uncertainty (top model $w_i < 0.6$), we examined predicted values from multiple models. We used this hierarchical modeling approach to control for nuisance variables or other covariates before examining multiple competing hypotheses regarding the additive and interactive effects of treatment.

To explore the impact of herbicide and seeding on grassland birds in the herbicide experiment, after the two initial stages (detection and landscape context), we ranked eight models related to herbicide treatment (spray-only, spray-and-seed, and control) in additive and interactive models with "years-since-treatment." This was in addition to a model with only "years-since-treatment" to determine whether year-to-year variation was the primary driver of abundance. We also included grazing (IES, SLS, and no grazing) as a covariate in models, although limited sample sizes of the SLS treatment means that these analyses cannot provide robust estimates of the impact of grazing treatments in each

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TABLE 3 Variables and model stages used to assess the impact of herbicide and grazing on grassland bird species and arthropod orders.

Modeling stage	Variables	Description
Detection: Avian analyses	Observers	Eight observers over five years
	Robel (visibility)	An index of vegetation height and density
	Wind (weather)	Ordered from 1 (0 mph) to 7 (>12 mph)
	Clouds (weather)	Categories: clear, <25% cover, 25%–50% cover, >50% cover, overcast
	DOY (temporal)	Date-of-year; ordinal date of sampling day
	Time (temporal)	24 h start time of line transects
Detection: Arthropod analyses	Method	Sweep or vacuum
	Wind (weather)	Ranked 1–7 (needs details)
	Temperature (weather)	Binned into 5° increments
	DOY (temporal)	Ordinal date of sampling day
	Time (temporal)	Start time of survey for each patch
Landscape: Avian	Herb	Proportion of 1000-m buffer around patches that is grassland
	Tree	Proportion of 1000-m buffer around patches that is tree-covered
	Crop	Proportion of 1000-m buffer around patches that is in crops
	Tree edge	km/ha within 1000-m buffer around patches
Treatments, herbicide experiment: Avian and arthropod analyses	Herbicide treatment	Spray-and-seed, spray-only, control
	YST	Years-since-treatment; years since herbicide or seeding was applied
	Grazing	Intensive-early stocking, season-long stocking, or no grazing
Treatments, herbicide-grazing study: Avian and arthropod analyses	Herbicide (yes/no)	Presence/absence of herbicide application in the last 1–5 years
	Grazing	Intensive-early stocking, season-long stocking, or no grazing
	Year	Year of sampling

Note: We conducted two sets of avian and arthropod analyses: impacts of treatments from an herbicide experiment ($n = 7$ sites) and impacts of treatments from an herbicide-grazing study ($n = 18$ sites).

experimental treatment in each year. When selected, we controlled for the impact of grazing when producing predicted estimates.

Next, we used the data from all 54 patches to explore the interactive effects of grazing treatments and herbicide on avian abundance. After the detection and land cover stage, we explored the interactions between grazing treatments (IES, SLS, and no grazing) and herbicide application (herbicide, no herbicide) in the third stage. Because herbicide treatments were asynchronous, we included "year" as a covariate in these analyses to control for temporal variability.

Similar to avian procedures, the first stage of model selection for arthropod abundance and biomass analyses consisted of selecting variables associated with weather conditions, temporal factors, and sampling methods (Table 3). The second (final) stage either explored the impacts of the interactions between herbicide and grazing using all 18 sites, or the impacts of years-since-herbicide using the seven experimental sites. Final-stage model sets were identical to those used for grassland bird analyses.

RESULTS

Grassland birds

Over 4 years of sampling, we counted 9883 birds after removing group sizes of >3 individuals. The most abundant species was the dickcissel at 16% of detections, followed by red-winged blackbirds (12%), bobolinks (11%), grasshopper sparrows (9%), and meadowlarks (8%). Henslow's sparrows and sedge wrens each composed about 4% of detections. The seven grassland obligates accounted for 52% of all counted birds. We also observed other obligates during surveys (greater prairie chickens, horned larks [*Eremophila alpestris*], lark sparrows [*Chondestes grammacus*], savannah sparrows [*Passerculus sandwichensis*], upland sandpipers [*Bartramia longicauda*], and vesper sparrows [*Pooecetes gramineus*]), although these were not common enough to allow for analysis.

Avian detection probability across all analyses was influenced by observer identity, selected in 11 of 14 species' model sets (Table 4). Robel and date of sampling were

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TABLE 4 Results from top models examining observer, temporal, or weather variables that influence avian detection (p) and landscape or treatment variables that influence avian abundance.

Treatment	Landscape	p	Null ΔAIC_c[a]	w_i[b]
A. Herbicide experiment ($n = 7$ sites)				
Bobolinks				
HerbicideT × YST[c] + grazing	Crop + tree	Obs[d] + DOY[e] + Robel[f]	12.48	0.90
Dickcissels				
HerbicideT × YST + grazing	Tree	Obs + time + DOY	50.28	1.0
Grasshopper sparrows				
...	Herb	Obs + Robel	0	0.56
Grazing	Herb	Obs + Robel	−2.35	0.17
Henslow's sparrows				
HerbicideT × YST	Herb	Clouds + Robel	13.6	0.83
Meadowlarks				
Grazing	Crop + tree	Robel	8.57	0.41
HerbicideT × YST + grazing	Crop + tree	Robel	7.88	0.29
Red-winged blackbirds				
HerbicideT × YST	Herb	Obs + DOY + Robel	12.60	0.52
HerbicideT × YST + grazing	Herb	Obs + DOY + Robel	12.38	0.46
Sedge wrens				
Grazing	Tree	Obs + time + DOY + Robel	13.82	0.46
HerbicideT + grazing	Tree	Obs + time + DOY + Robel	13.82	0.46
B. Entire study ($n = 18$ sites)				
Bobolinks				
Herbicide Y/N × grazing + year	Herb + tree	Obs + DOY + wind	112.81	1.0
Dickcissels				
Herbicide Y/N × grazing + year	Crop + tree	Obs + wind	128.22	1.0
Grasshopper sparrows				
Herbicide Y/N + grazing + year	Herb	Obs + wind + Robel	3.60	0.36
Herbicide Y/N + year	Herb	Obs + wind + Robel	3.23	0.30
Henslow's sparrows				
Herbicide Y/N × grazing + year	Herb	Obs + time	11.75	0.89
Meadowlarks				
Herbicide Y/N × grazing + year	Herb	Obs + Robel	25.26	0.70
Red-winged blackbirds				
Herbicide Y/N + grazing + year	Herb + tree	Obs + time + DOY + Robel	189.60	0.74
Sedge wrens				
Herbicide Y/N × grazing + year	Crop + tree	Obs + time + DOY	63.85	0.95

Note: Section A includes results from a subset of sites ($n = 7$) treated with herbicide experimentally (HerbicideT), with each site divided into three patches and either sprayed with herbicide, sprayed with herbicide and seeded with native plants, or not treated (control). Section B includes results from all study sites, which allowed for examining the interactions of grazing treatment (season-long stocking, intensive-early stocking, and no grazing) with herbicide (presence/absence). More than one top model is shown if model-selection uncertainty was moderate or high.

Abbreviation: AIC_c, corrected Akaike information criterion; DOY, date-of-year; YST, years-since-treatment.

[a]Change in AIC_c between top model/s and null model.

[b]The relative likelihood of the top model/s in a set, where 1.0 = most likely.

[c]Years since treatment.

[d]Observer.

[e]Day of year.

[f]Index of vegetation height and density.

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selected as covariates in eight and five model sets, respectively. Landscape variables also influenced grassland bird abundance. For instance, sedge wrens declined in abundance with increasing proportion of the landscape in cropland, and sedge wrens and dickcissels both declined with increasing tree cover. Full AIC_c tables are in Appendix S1.

For avian response to the herbicide experiment (21 patches, Table 4A), differences between spray-and-seed, spray-only, and control patches varied with years-since-treatment (Figure 2). Models that included an interaction between herbicide treatments and years-since-treatment were ranked as the top model for four of seven species (dickcissels, bobolinks, red-winged blackbirds, and Henslow's sparrows) and were competitive for one other (meadowlarks). For dickcissels and bobolinks, estimates from the top-ranked models (with model weights >0.99) show that positive effects of herbicide and seeding treatments did not occur in Year 1 but only in Years 2–4 following the application of treatments. By Year 2, dickcissels were two to three times more abundant in the spray-only and spray-and-seed treatments than in controls, with differences between the control patches and treated patches becoming more pronounced in Year 4. By contrast, bobolinks responded negatively to herbicide application in Years 1–2 but were more abundant in spray-and-seed patches than in both spray-only and control patches by Years 3–4. Red-winged blackbirds also showed a reversal in trends over time, responding negatively to herbicide treatments in Year 1 but becoming equivalent across patches by Year 2. Henslow's sparrows may have also responded negatively to treatments in Year 1 ($w_i = 0.83$), virtually disappearing from treated patches and having only a 0.26 occupancy rate in the control patches. However, occupancy rates were highly variable in later years, and model convergence issues meant that observer identity could not be included as a detection covariate in the final model.

Trends were less clear for meadowlarks, sedge wrens, and grasshopper sparrows because of model-selection uncertainty (Table 4A, Figure 3). The top model for both meadowlarks and sedge wrens included only the grazing covariate, but in both cases, second-ranked models with a moderate amount of the AIC_c weight (0.29 and 0.43, respectively) included herbicide treatments. Meadowlarks responded variably to treatments over time, becoming less abundant in the spray-and-seed patches in Years 2 and 3, but least abundant in control patches in Year 4. Sedge wrens did not respond to years-since-treatment and were instead least abundant in spray-and-seed patches and equivalent between spray-only and controls. The top model for grasshopper sparrows did not include any treatment variables.

On the 54 patches where we evaluated grassland bird response to the interactions between herbicide application and grazing treatments, an interaction was selected as the top model for 5 of 7 species (Table 4B, Figure 3). On ungrazed patches without herbicide, dickcissels were three times more abundant than intensive-early stocking but were nearly equivalent among all herbicide patches regardless of grazing. On ungrazed patches, bobolinks were more abundant on patches with herbicide, which reversed on grazed sites to being more abundant on patches without herbicide. This pattern was also observed in sedge wrens. Similarly, Henslow's sparrows disappeared from sites with intensive-early stocking that had been sprayed with herbicide, but their abundance did not differ among other grazing-herbicide combinations.

Arthropods

Over 3 years of arthropod sampling, we identified and measured 23,556 Orthoptera, 8309 Araneae, 7189 Coleoptera, and 2573 Lepidoptera, in addition to identifying 64,164 Hemiptera. Variables affecting capture were frequently selected, including sampling method (i.e., sweep or vacuum, 7 of 10 model sets) and date of sampling (5 model sets; Appendix S2).

In the 21-patch herbicide experiment (Table 5A, Figure 4), several orders (Lepidoptera, Hemiptera, and Orthoptera) showed positive responses to spray-and-seed and spray-only treatments compared to controls by Year 2 or 3 after treatment. We observed no treatment effects for Araneae or Coleoptera in the herbicide experiment. Arthropod biomass per sample (Appendix S3) mostly responded to year-to-year variation in the herbicide experiment, where we could not control for the effects of "year" due to being confounded by years-since-treatment. For Araneae, biomass results showed larger average specimen sizes on control patches in Year 3 than on the two treated patches.

In the 54-patch dataset (Table 5B), an interaction between herbicide and grazing treatment was selected for Coleoptera, with herbicide leading to increased abundance on grazed sites but decreased abundance on ungrazed sites, although CIs and model-selection uncertainty indicate this was a weak relationship (Figure 4). An additive relationship between grazing treatment and herbicide was selected for Hemiptera, Orthoptera, and Lepidoptera, although with some model-selection uncertainty in all cases. Estimates from top models indicate that Hemiptera and Orthoptera were most abundant on grazed sites and least abundant on ungrazed sites, whereas the trend was reversed (and weak) for Lepidoptera and Coleoptera (Table 5B, Figure 4).

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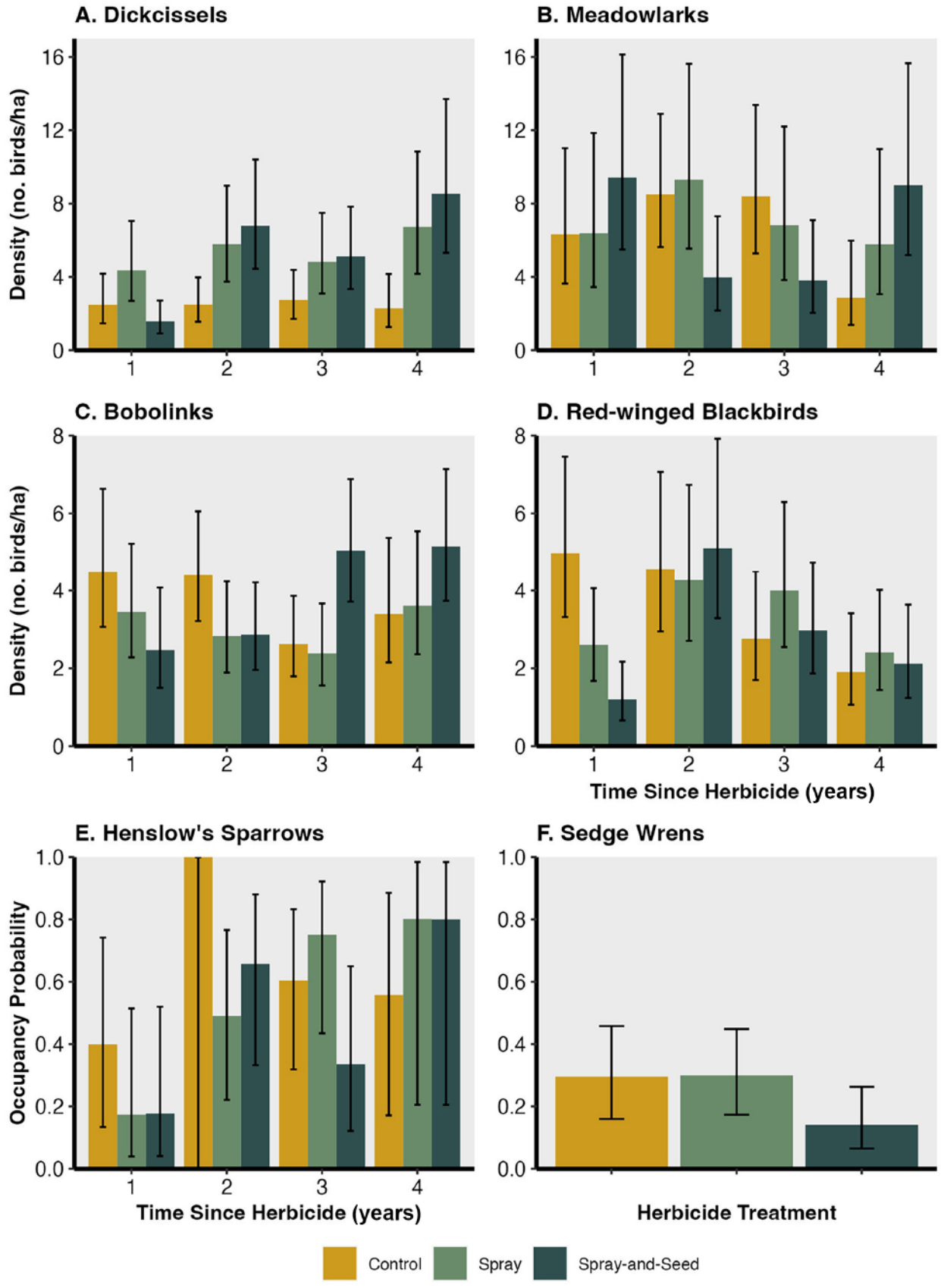

FIGURE 2 Legend on next page.

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Null models were competitive in 4 of 5 arthropod taxa when examining the effect of grazing treatments and herbicide on the average size of arthropods captured (Appendix S3). Individual biomass of Araneae was lower in sprayed areas. Orthoptera were larger in sprayed areas, except for early-intensive patches, though model-selection uncertainty was high ($w = 0.28$) and the null model was competitive.

Trade-offs and lag times

Responses at the community level for the seven-site herbicide experiment show strong evidence for time lags when comparing treated patches to controls over time (Figure 5A,B), with most grassland bird species and arthropod orders responding negatively or neutrally in Years 1 and 2. By Years 3 and 4, most responses are positive or neutral. Examinations of community-level responses to invasive plant management (Figure 6A) show trade-offs in combining herbicide and intensive-early stocking. No bird species preferred sites with intensive-early stocking over ungrazed sites or those with season-long stocking, and the combination of intensive-early stocking and herbicide had a negative impact on several birds that prefer later-successional habitats. By contrast, arthropods generally did not respond to interactions between grazing and herbicide (Figure 6B). Grassland birds mostly responded to herbicide and seeding according to species-specific preferences for disturbance levels (Figure 7).

DISCUSSION

Amid concerns about negative ecological impacts of both invasive plants (Ellis-Felege et al., 2013; Schirmel et al., 2016) and community recovery from the disturbances meant to control them (Skurski et al., 2013; Sullivan & Sullivan, 2003), there is an increasing need to investigate trade-offs of invasive plant control for native ecological communities. Nowhere is this more relevant than in grasslands—arguably the most invaded terrestrial biome and habitat for the fastest declining avian group in North America (Douglas et al., 2023; Lambdon et al., 2008; Rosenberg et al., 2019). However, few studies use sufficient spatial and temporal scales to detect habitat recovery after invasive plant control, and even fewer have experimental designs that allow for detection of lag times and trade-offs (Coon et al., 2021; Kettenring & Adams, 2011). Furthermore, we could find no other studies that have explored simultaneously intensive-early stocking and herbicide, both commonly used to manage invasive grasses globally (Dornbusch et al., 2020; Kettenring & Adams, 2011).

The multi-taxa approach, the relatively long period of our study (3 and 4 years for arthropods and birds, respectively), and our experimental design allowed us to detect responses that would have otherwise been missed. Although several bird species and arthropod orders declined in the first year after herbicide and/or seeding, nearly all stabilized or increased relative to controls in Years 2 and 3 for arthropods and Years 2–4 for birds. In our larger non-experimental sample, we observed mostly positive responses to herbicide by grassland birds and arthropod orders, though combinations of intensive-early stocking and herbicide were detrimental for several species compared to more moderate season-long stocking and ungrazed sites. These results align with vegetation community responses to herbicide in this same system—with decreases in tall fescue and increases in warm-season grasses over time, especially on ungrazed sites (Coon et al., 2021). Although insights into change over time in response to management are augmented with comparisons to pretreatment data, when available (Coon et al., 2021), the current study demonstrates the power of long-term, large-scale experiments and combinations of techniques when quantifying trade-offs.

As predicted, avian responses to grazing were linked to species-specific preferences for the level of disturbance. For instance, sedge wrens and red-winged blackbirds, which have late-successional preferences, avoided grazed sites, while meadowlarks were most abundant on grazed sites, regardless of stocking regime (Dechant, Sondreal, Johnson, Igl, Goldade, Parkin, & Euliss, 2002; Dechant, Sondreal, Johnson, Igl, Goldade, Zimmerman, & Euliss, 2002; Duchardt et al., 2016; Hull, 2002). These birds are also known to prefer a high cover of native warm-season grasses, grasses that were more abundant on ungrazed sites after restoration (Coon et al., 2021). By contrast, dickcissels and bobolinks had the lowest abundances on intensive-early stocked sites. Because intensive-early stocking can be applied temporarily for a few years, once stocking is relaxed, the reduced invasive-grass dominance

FIGURE 2 Predicted avian density and occupancy in response to experimental herbicide treatments showing variables present in top models selected by corrected Akaike information criterion. Bars represent 85% CIs. Note that *y*-axes differ between graphs. Grasshopper sparrows are not shown as no treatment variables were supported. When selected, grazing treatment was included as a covariate in models. Data were collected during 2015–2018 in Ringgold County, IA, and Harrison County, MO.

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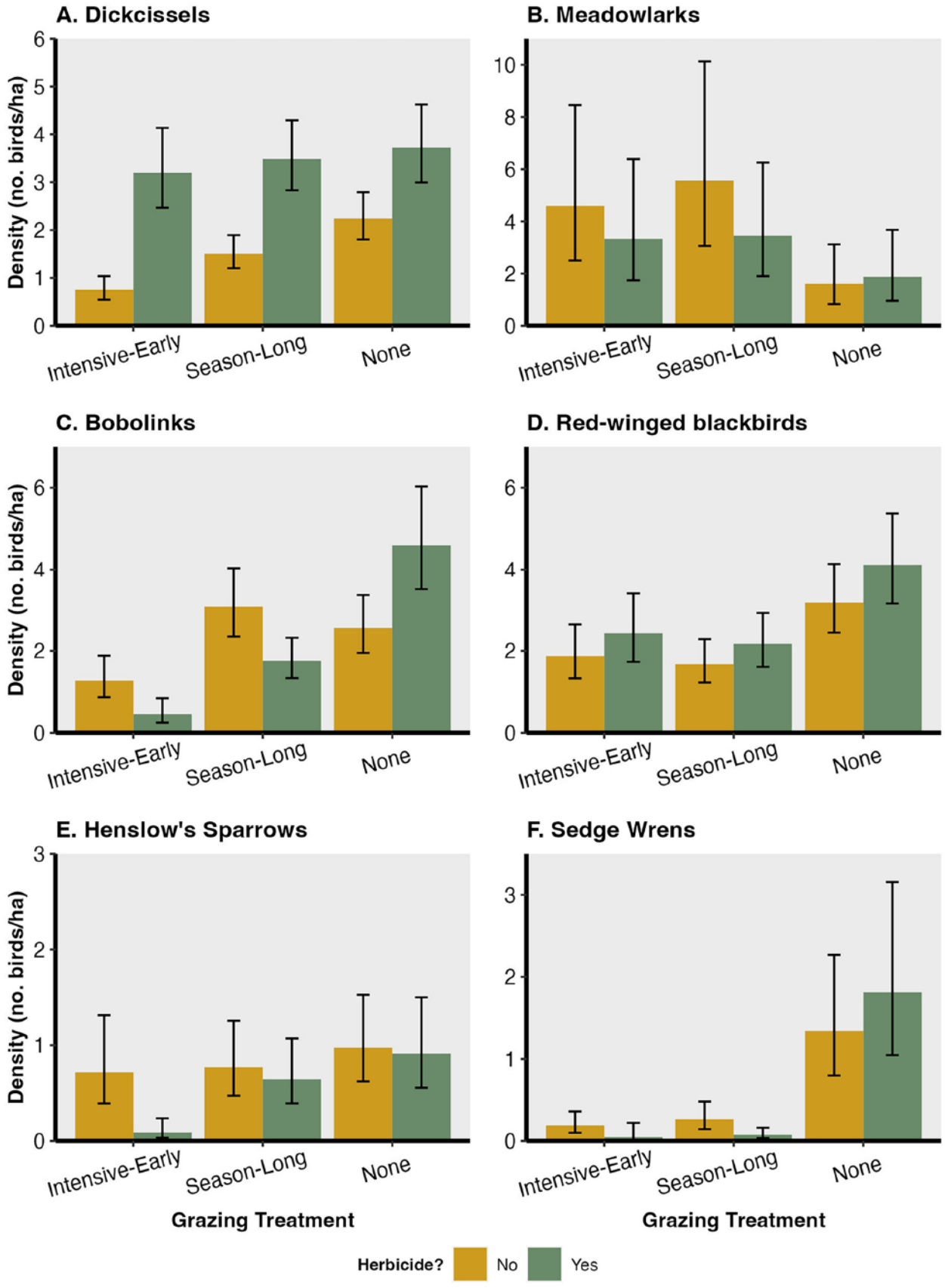

FIGURE 3 Predicted avian density in response to herbicide and grazing treatments in the first four years after treatment, showing variables present in top models selected by corrected Akaike information criterion. Bars represent 85% CIs. Note that *y*-axes differ between graphs. Data were collected during 2015–2018 in Ringgold County, IA, and Harrison County, MO.

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TABLE 5 Results from top models examining arthropod abundance, including nuisance variables related to sampling and treatment variables influencing abundance.

Treatment	Landscape	Null ΔAIC_c[a]	w_i[b]
A. Herbicide experiment ($n = 7$)			
Araneae			
YST[c]	DOY[d] + Temp	46.5	0.66
YST + grazing	DOY + Temp	45.1	0.33
Coleoptera			
...	Time + DOY + wind + method[e]	0	0.32
Lepidoptera			
Herbicide treatment × YST	Method	16.7	0.74
Hemiptera			
Herbicide treatment × YST	Time + method +DOY	10.9	0.49
Herbicide treatment	Time + method	9.7	0.26
Orthoptera			
Herbicide treatment × YST	...	104.4	0.71
B. Entire study ($n = 18$ sites)			
Araneae			
...	Year + DOY[c]	0	0.46
Coleoptera			
Herbicide Y/N × grazing	Year + time + DOY + wind + Temp + method[d]	7.4	0.63
Lepidoptera			
Herbicide Y/N + grazing	Year + DOY + method	12.6	0.47
Herbicide Y/N	Year + DOY + method	12.4	0.43
Hemiptera			
Herbicide Y/N + grazing	Year + DOY + time + method	19.5	0.39
Herbicide Y/N	Year + time + method	19.5	0.38
Orthoptera			
Herbicide Y/N + grazing	Year + Temp + method	14.7	0.42
Herbicide Y/N	Year + Temp + method	14.5	0.39

Note: Section A includes results from a controlled herbicide experiment, where herbicide treatment means that each site was divided into three patches, with each either sprayed with herbicide, sprayed with herbicide and seeded with native plants, or not treated (control). Section B includes results from all study sites, which allowed for examining the interactions of grazing treatment (season-long stocking, intensive-early stocking, and no grazing) with herbicide (presence/absence). More than one top model is shown if model-selection uncertainty was moderate or high.

Abbreviation: AIC_c, corrected Akaike information criterion.

[a]Change in AIC_c between top model/s and null model.

[b]The relative likelihood of the top model/s in a set, where 1.0 = most likely.

[c]Years since treatment.

[d]Day of year.

[e]Sweep net or vacuum.

may result in improved habitat quality once vegetation has a chance to recover in terms of biomass (Bailey et al., 2019; Raynor et al., 2018). In our study system, we have preliminarily observed an increase in native warm-season grasses and a decrease in tall fescue in response to intensive-early stocking (Coon, unpublished data). Still, our results indicate that there may be short-term trade-offs for birds that should be considered before implementing intensive stocking over broad areas (Coppedge et al., 2008; Robbins et al., 2002).

Although combining techniques tends to successfully reduce invasive plants (Farrell & Gornish, 2019; Kettenring & Adams, 2011), such combinations may lead to unpredictable responses by native species (Coon et al., 2021). In our study, intensive-early stocking and herbicide had inconsistent impacts. For instance,

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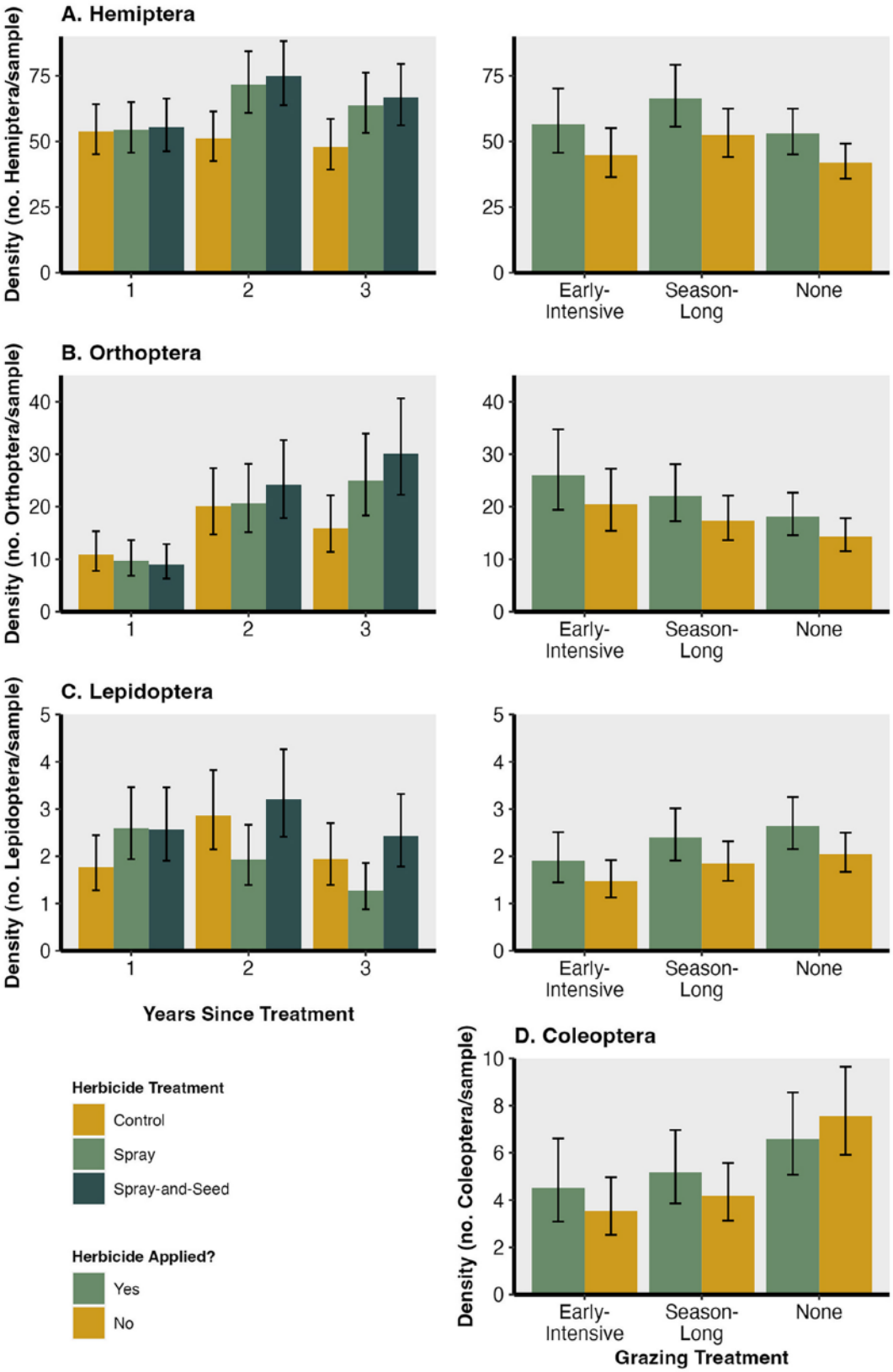

FIGURE 4 Predicted arthropod abundance per sample (collected over 20 m^2) in response to herbicide treatments (left panels of A–C) and interactions between herbicide and grazing treatments (right panels of A–C, and panel D), showing variables present in top models selected by corrected Akaike information criterion. Bars represent 85% CIs. Note that *y*-axes differ between taxa. Data were collected during 2015–2017 in Ringgold County, IA, and Harrison County, MO.

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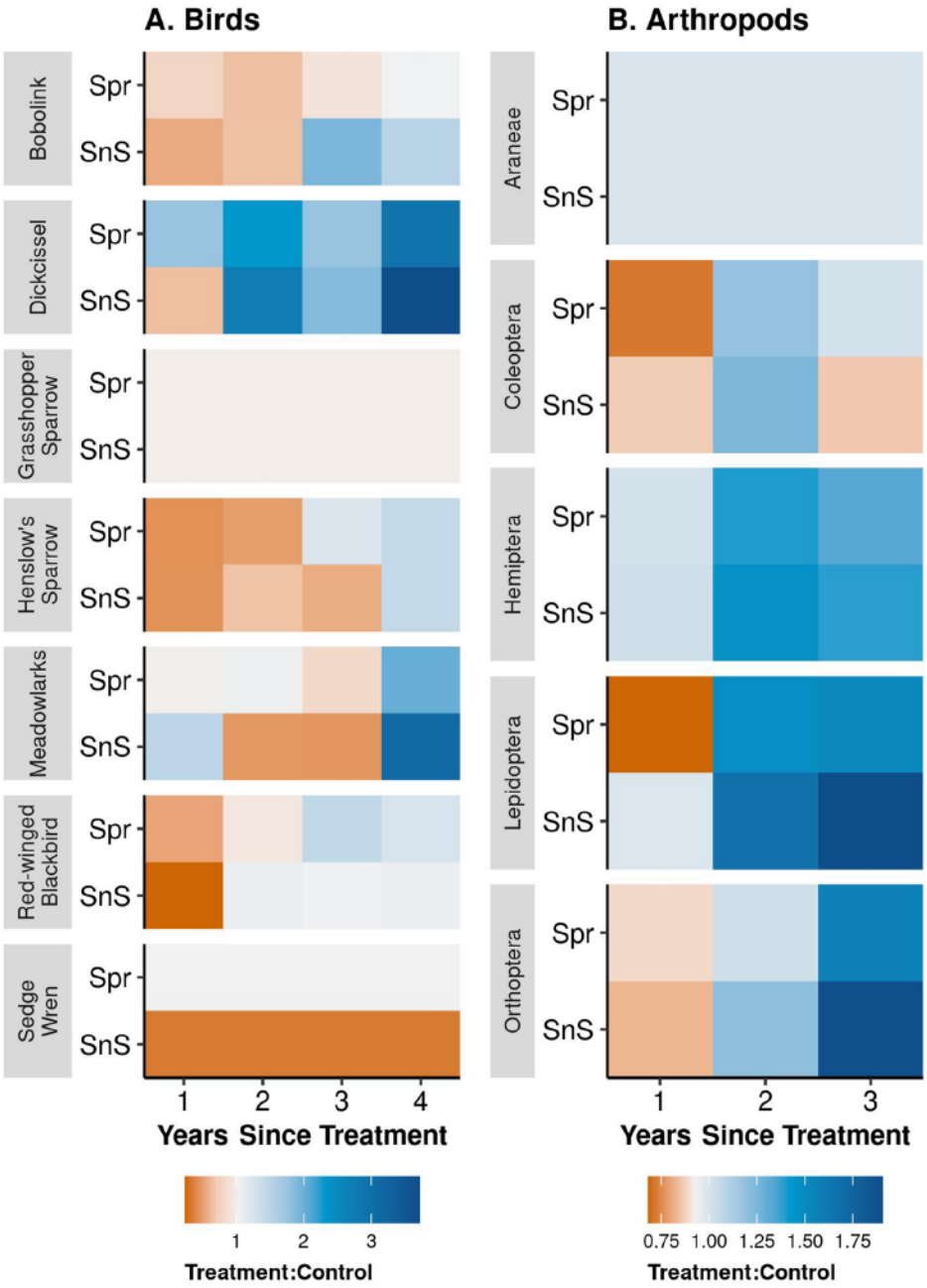

FIGURE 5 A summary of predicted avian and arthropod response to experimental herbicide over time at seven sites monitored from 2015 to 2018 (birds) and from 2015 to 2017 (arthropods) in Ringgold County, IA, and Harrison County, MO. These graphs show the ratio of abundance on treated sites (spray-only [Spr], spray-and-seed [SnS]) to control patches, with <1 indicating reductions in abundance (orange) and >1 indicating increases in abundance (blue).

herbicide seemed to make habitats associated with the former more acceptable for the dickcissel, a disturbance-tolerant species that prefers the high forb cover that herbicide creates (Dechant, Sondreal, Johnson, Igl, Goldade, Parkin, & Euliss, 2002; Duchardt et al., 2016; Hull, 2002). By contrast, disturbance-sensitive species like bobolinks and sedge wrens avoided sprayed patches on grazed sites, and Henslow's sparrows nearly disappeared from patches subjected to herbicide and intensive-early stocking (Coppedge et al., 2008; Grant et al., 2010; Powell, 2008). Reduced vegetation height from intensive grazing and increased cover of early-successional plants from herbicide could have created lower quality habitat for these species, at least in the short term. We recommend that future research explicitly considers responses of native species to interactions between alternative management techniques and does not

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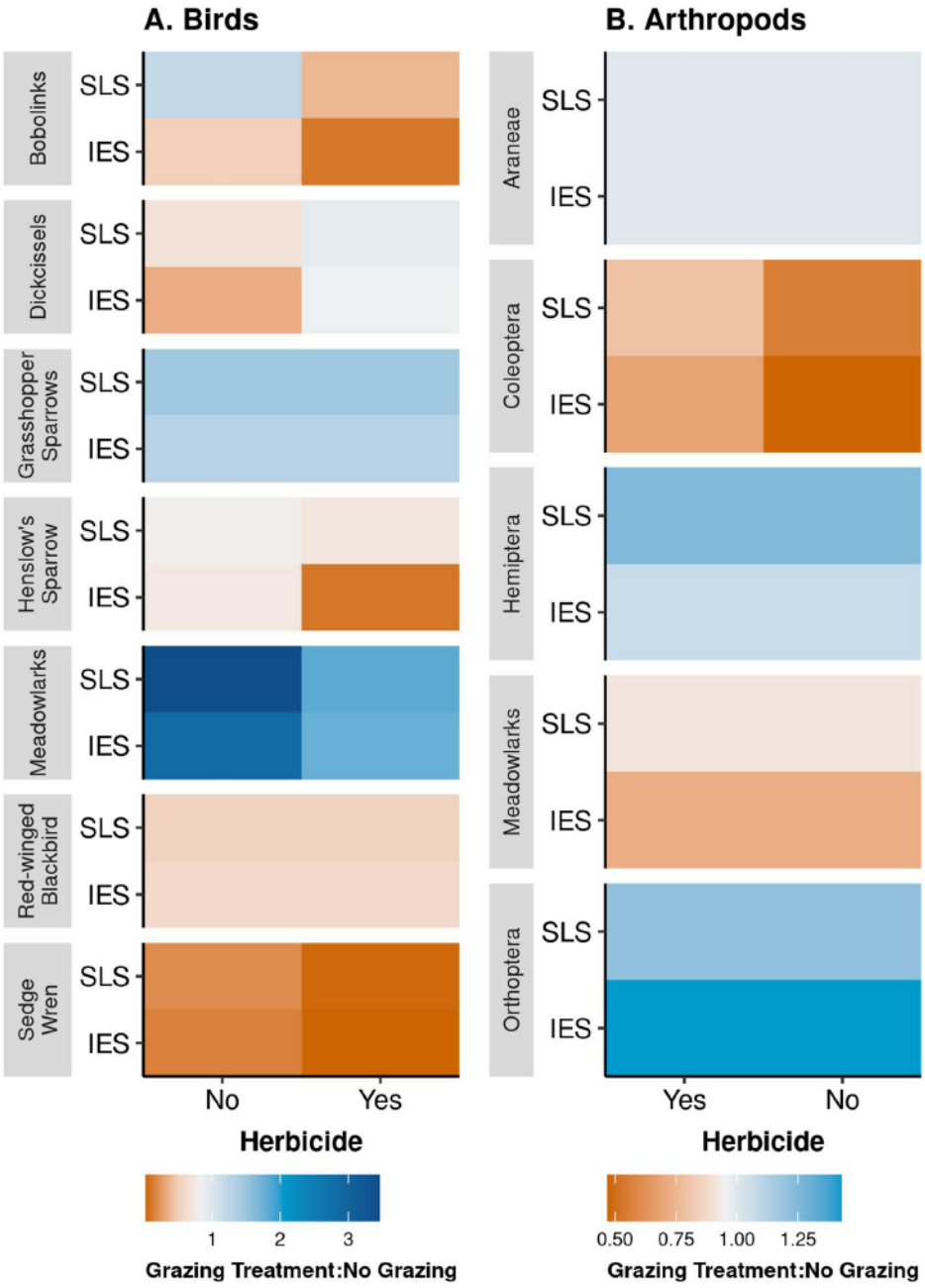

FIGURE 6 A summary of predicted avian and arthropod response to herbicide and grazing treatments at 18 sites monitored from 2015 to 2018 (birds) and from 2015 to 2017 (arthropods) in Ringgold County, IA, and Harrison County, MO. These graphs show the ratio of abundance on grazed sites (intensive-early stocking [IES], season-long stocking [SLS]) to ungrazed sites, with <1 indicating reductions in abundance (orange) and >1 indicating increases in abundance (blue).

assume simple additive effects when combining techniques for invasive plant control.

We observed striking lag times after treatment with herbicide and native seeding for several bird species and arthropod orders. Time-since-herbicide elicited strong responses from bobolinks, dickcissels, Hemiptera, Lepidoptera larvae, and Orthoptera. These bird species and arthropod orders all had initial negative or neutral responses to herbicide application that became increasingly positive over time. Negative responses relative to controls in Year 1 included bobolinks, Henslow's sparrows, and red-winged blackbirds, which all prefer tall, dense vegetation characteristic of later successional grasslands (Coppedge et al., 2008; Dechant et al., 1999; Herkert, 1994; Powell, 2008). Although we also observed lag times in three arthropod orders, it is difficult to generalize across such a broad set of taxa, and more taxa-specific research is needed. In general, lag times observed in both birds and

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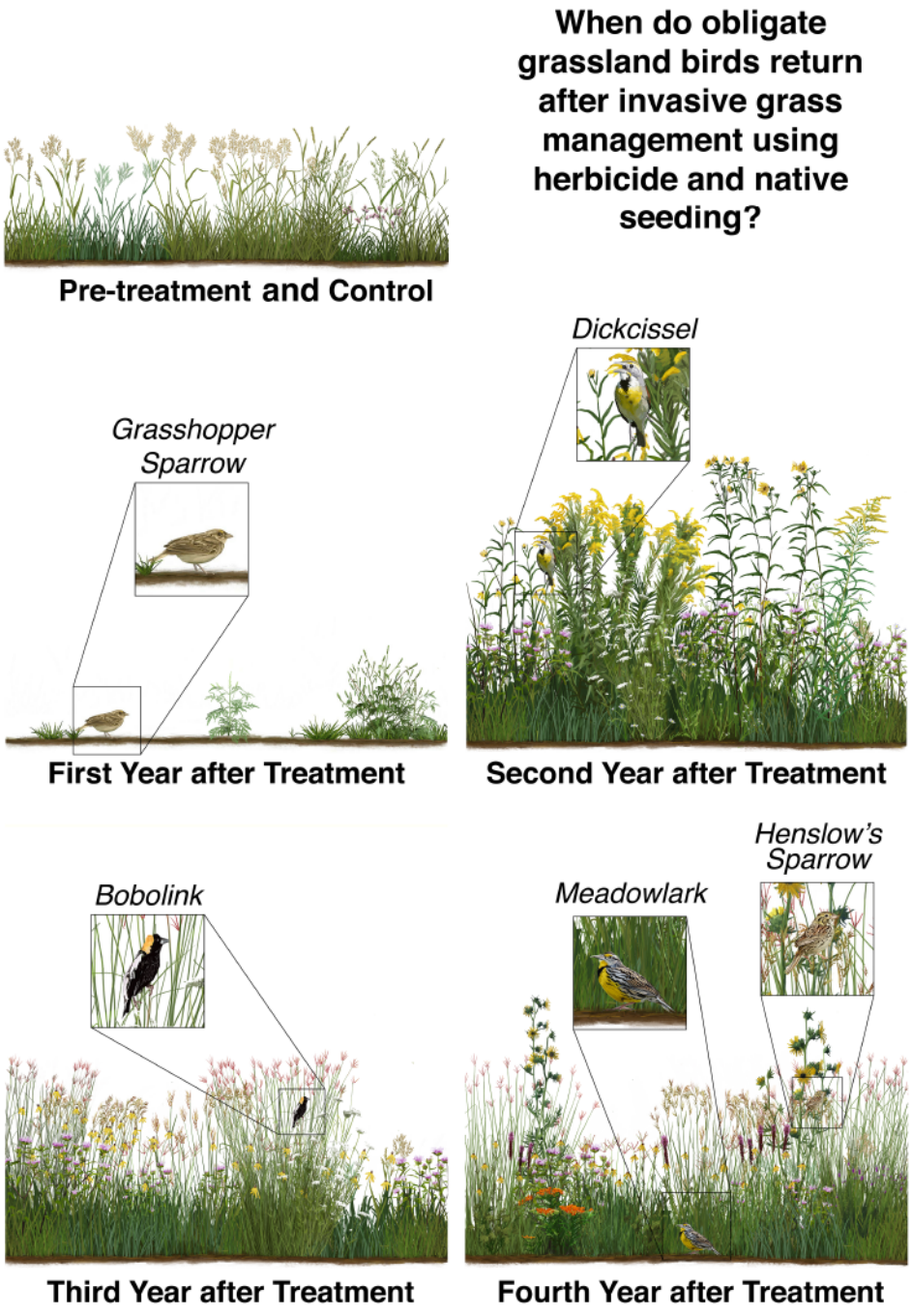

FIGURE 7 A summary figure showing when grassland birds are predicted to return to sites after invasive grass management using herbicide and native seeding and the associated changes in vegetation composition. Plant community composition derived from Coon et al. (2021) and Mingione et al. (2025). Illustration credit: Lynda Heller.

arthropods may be related to plant community recovery after herbicide application, which can take 3–5 years (Endress et al., 2012; Rothrock & Squiers, 2003). Indeed, native grasses at our study sites had a large increase in abundance in Year 3 on ungrazed sites (Coon et al., 2021). A study in the same region also found that non-native forbs dominated in the first years after seeding, followed by increases in native forbs on both grazed and ungrazed sites, though ungrazed restorations more strongly resemble high-quality reference prairies (Mingione et al., 2025).

Surprisingly, a few initial decreases in abundance relative to controls seemed to be in response to seeding, not herbicide. In Year 1, dickcissels and red-winged blackbirds were least abundant on spray-and-seed compared to spray-only patches. Sedge wrens avoided seeded patches across all years of the study. While we could find no other examples of negative responses to drill-seeding by

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birds, this technique could disrupt vegetation structure or soil properties (Giannitsopoulos et al., 2020; Pierson et al., 2007). The disruption of the litter layer by seeding just weeks before the breeding season may also have led to avoidance by some birds. These negative responses mostly disappeared by Year 2, and seeding native plants is likely to improve habitat quality over time via increased nest survival and arthropod abundance (McIntyre & Thompson, 2003; Shew et al., 2019). Notably, bobolinks were the only bird species that responded positively to native seeding. This positive response was strong, as bobolinks were nearly twice as abundant in spray-and-seed patches compared to spray-only patches and controls in the third year post-treatment.

Determining whether invasive grass management improves avian habitat quality requires examining the resources needed for reproduction and survival. However, most studies do not directly measure elements of habitat quality, such as the food resources quantified in our study (Johnson, 2007). We found that the abundance of several arthropod orders responded positively to herbicide. Although studies examining the response of arthropods to herbicide in grasslands are few, studies in agricultural fields have observed negative responses of arthropods after herbicide use in this context (Freemark & Boutin, 1995). Our results indicate that, in grasslands, reducing invasive grasses using herbicide and intensive-early stocking may increase abundance of some orders used as insect prey for birds. This outcome suggests that the short-term reductions in avian abundance that we observed are likely not linked to food abundance but may instead be due to structural changes in the vegetation that affect nest-site availability or arthropod accessibility to foraging birds (Madison et al., 2001; Rivers et al., 2019).

Despite our explorations of arthropod prey abundance and biomass as elements of avian habitat quality, assessments that only examine bird abundance can be problematic because treatment with herbicide could create an ecological trap (Lituma et al., 2012; Severns, 2011; Van Horne, 1983). Other studies have shown that dickcissels and red-winged blackbirds can have increased reproductive success on tall fescue fields managed using herbicide, fire, and disking (Osborne & Sparling, 2013; Shew et al., 2019). In a 1-year study in our study region, dickcissels enjoyed increased reproductive success and fledgling production after herbicide on experimental sites (Coon et al., 2022). Reducing tall fescue, which is relatively low in stature and homogenous in structure, may lead to the development of taller vegetation that is linked to higher nest success for many grassland bird species (Frey et al., 2008). These results underscore the importance of mechanistically exploring habitat quality when evaluating the impacts of management treatments.

Complexity in ecological recovery after planned disturbances

Navigating complexity inherent in the control of invasive plants requires acknowledging and planning for trade-offs, as well as long-term monitoring. Even if outcomes are eventually positive, herbicide application and targeted grazing are likely to have unintended consequences for birds and arthropods (Freemark & Boutin, 1995; Robbins et al., 2002; Sullivan & Sullivan, 2003). Possible benefits from controlling an invasive plant may not always outweigh potential harm from the control method—especially when invasive plants have neutral impacts on birds (Nelson et al., 2017). Our results for avian and arthropod abundance suggest that invasive grass management using herbicide—both alone and in combination with seeding of native plants—improves habitat for grassland birds over time. Managers may ameliorate short-term costs of this management by avoiding combining herbicide and intensive-early stocking over large areas in the core habitats of grassland birds that are sensitive to disturbance. Ideally, invasive plants should be managed in smaller, discrete patches (e.g., 1/3 of a pasture versus an entire pasture, perhaps 5–10 ha) versus large, contiguous areas, simultaneously improving the long-term outlook for a suite of birds while also providing refuges for species that prefer later-successional grasslands (Sheley et al., 2006; Sullivan & Sullivan, 2003). Such an approach reduces short-term negative consequences while optimizing long-term possibilities for improving habitat quality for declining birds.

AUTHOR CONTRIBUTIONS

Jaime J. Coon, Scott B. Maresh Nelson, James R. Miller, Diane M. Debinski, and Walter H. Schacht contributed to the conceptualization of the project. Jaime J. Coon, Scott B. Maresh Nelson, James R. Miller, and Rachel C. Daughtridge contributed to methodology. Jaime J. Coon, Scott B. Maresh Nelson, James R. Miller, and Rachel C. Daughtridge contributed to data analysis. Jaime J. Coon, Scott B. Maresh Nelson, and Rachel C. Daughtridge contributed to data collection and curation. Jaime J. Coon wrote the original draft. All authors contributed to reviewing and editing the manuscript and providing funding. Jaime J. Coon, Scott B. Maresh Nelson, and James R. Miller contributed to project administration.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data and code (Coon et al., 2025) are available on Figshare: https://doi.org/10.6084/m9.figshare.28701560.

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SUPPORTING INFORMATION

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

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