

The importance of core habitat for a threatened species in changing landscapes

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Abstract

1. Habitat loss, fragmentation, and alteration of the landscape matrix are interdependent processes, collectively responsible for most recent species extinctions. Thus, determining the extent to which these landscape processes affect animals is critical for conservation. However, researchers have often assumed that interdependent effects are independently related to animals' responses, underestimating the importance of one or several landscape processes in driving species declines.
2. We demonstrate how to disentangle the interdependent effects of habitat amount, fragmentation, and edge context on population size by assessing abundance of a rapidly declining grassland songbird species (grasshopper sparrow *Ammodramus saviannarum*) in eastern Kansas (USA). We conducted >7,000 point count surveys at >2,000 sites over two breeding seasons, then modelled the direct, interactive, and indirect effects of landscape factors on abundance within spatial scales (200-, 400-, 800-, and 1,600-m radii) relevant to our focal species' dispersal behaviour.
3. Sparrow abundance correlated most strongly with landscape structure within 400-m radii, increasing nonlinearly with grassland area and decreasing with the proportion of grassland near cropland or woody edges. Sparrows' negative response to cropland edges was mostly an added, indirect consequence of reduced grassland area, whereas sparrows' stronger negative response to woody edges was not attributable to variation in grassland area. Fragmentation and edge context mattered most in landscapes comprising c. 50%–80% grassland.
4. *Synthesis and applications.* In our research, abundance of a threatened grassland songbird was influenced more by core grassland area (a function of total grassland area, fragmentation, and edge context) than total grassland area per se. Moreover, a local extinction threshold of c. 50% grassland indicated that small amounts of habitat were unsuitable for our focal species regardless of habitat configuration or matrix type. Local extinction thresholds in response to habitat area provide clear baseline targets for land managers; above those thresholds, configuration and the matrix can be modified to increase abundance of edge-sensitive animals. Conflicting evidence in the literature regarding the importance of fragmentation and matrix features could be partially explained by species-level traits, or methodological issues such as defining landscapes at ecologically arbitrary spatial

scales, assessing landscape quality using species richness, and ignoring interactive and indirect effects.

KEYWORDS

edge contrast, edge effects, grassland birds, habitat fragmentation, habitat loss, matrix effects, rangeland management, woody encroachment

1 | INTRODUCTION

Species extinctions and range contractions over the past two centuries have mainly been caused by habitat destruction (Newbold et al., 2016; Pimm et al., 2014). Conversion of native vegetation to other land uses alters several aspects of landscape structure simultaneously, and it is usually unclear which aspect most strongly influences population size and demography. Landscape change not only reduces the total area covered by native vegetation or “habitat” but can also fragment contiguous habitat into smaller remnant patches of varying shape and isolation (Haddad et al., 2015; Saunders, Hobbs, & Margules, 1991). Many studies have therefore attempted to assess the relative effects of habitat loss vs. fragmentation (spatial arrangement or configuration) on animal populations (reviewed in Ewers & Didham, 2006; Fahrig, 2003, 2017) and debated about their relative importance for species conservation and management (Fahrig, 2013; Hanski, 2015; Villard & Metzger, 2014). However, most studies have assumed that habitat loss and fragmentation are independent processes, ignored their interactive and indirect effects, and consequently, underestimated the importance of one or both processes in driving species declines (Didham, Kapos, & Ewers, 2012; Wilson et al., 2016; With, 2016).

Habitat area independent of fragmentation does not always explain animals’ responses to landscape structure adequately (Ewers & Didham, 2006; Rybicki & Hanski, 2013). For example, fragmentation can increase the edge-to-area ratio of habitat patches beyond that resulting from habitat loss alone, further reducing the amount of interior or core habitat to buffer sensitive species from negative edge effects such as increased predation risk, interspecific competition, and/or parasitism (Pérez-Rodríguez et al., 2018; Ries, Fletcher, Battin, & Sisk, 2004; Tschardt et al., 2012). Moreover, core habitat availability may depend on characteristics of the landscape matrix, which can influence the abundance of predators, competitors, and/or parasites (Driscoll, Banks, Barton, Lindenmayer, & Smith, 2013; Ries et al., 2004). Theory suggests that the population size and viability of edge-sensitive species are driven by availability of core habitat (Cumming, 2002; Ewers & Didham, 2007; Temple & Cary, 1988), which can be mediated by edge context (Ries & Sisk, 2004). However, researchers frequently define habitat availability with simple area metrics that ignore the amount and type of habitat edge(s), thereby obscuring variation in core habitat area among patches and landscapes (Ries et al., 2004).

Avian studies are central to our current understanding of the ecological consequences of landscape change. Most evidence for the importance of core habitat and edge context for birds come from studies of forest-dwelling species (e.g., Donovan, Lamberson, Kimber, Thompson, & Faaborg, 1995; Hawrot & Niemi, 1996; Major, Christie, & Gowing, 2001; Watson, Whittaker, & Dawson, 2004). However, fewer studies have focused on the importance of core habitat or edge context for grassland birds (e.g., Davis, 2004; Fletcher & Koford, 2003; Helzer & Jelinski, 1999; Renfrew & Ribic, 2008). Land use has altered temperate grasslands more than any other biome on the planet (Newbold et al., 2016), and grassland bird populations are declining globally (Brennan & Kuvlesky, 2005; Donald, Green, & Heath, 2001). In North America, >80% of native prairie has been converted to row crop agriculture (Samson, Knopf, & Ostlie, 2004), causing >20 common grassland bird species to decline by >50% during the past half-century (Butcher & Niven, 2007). Understanding the extent to which core habitat area and edge context influence population size is critical to reversing current declines of grassland birds.

We conducted a case study of a relatively common but rapidly declining grassland songbird, the grasshopper sparrow *Ammodramus savaanarrum*. The species is a bird of conservation concern in 35 U.S. states and Puerto Rico (Ruth, 2015) and recognized as a Common Bird in Steep Decline by Partners in Flight because populations have declined by c. 68% since 1970 (Rosenberg et al., 2016). Grasshopper sparrow habitat requirements overlap broadly with a large suite of grassland-dependent birds including migrants (e.g., Savanna sparrow *Passerculus sandwichensis*; dickcissel *Spiza americana*; Henslow’s sparrow *A. henslowii*; bobolink *Dolichonyx oryzivorus*) and residents (e.g., Eastern Meadowlark *Sturnella magna*; greater prairie chicken *Tympanuchus cupido*; Rosenberg et al., 2016; Vickery, 1996). Thus, grasshopper sparrow responses to landscape change are likely representative of other declining grassland birds in North America (Brennan & Kuvlesky, 2005; With, King, & Jensen, 2008). Like many grassland-dependent birds worldwide (Azpiroz et al., 2012; Donald et al., 2001), this species occupies working rangelands, and therefore, provides insight into the importance of fragmentation and matrix features for grassland birds on other continents.

We tested whether abundance of grasshopper sparrows was driven by (a) total habitat area per se, (b) core habitat area per se (configuration matters but edge context does not), or (c) core habitat area and edge context in combination. If (a) sparrows only require sufficient habitat area to establish their c. 0.5-ha territories,

we predicted that sparrow abundance would be best determined by grassland area irrespective of configuration or edge context. Alternatively, sparrows may favour core habitat, which is determined by habitat area, configuration, and possibly, edge context. The species historically inhabited large expanses of prairie in western portions of their breeding range in the Great Plains of North America where natural selection could have favoured innate preferences for grasslands far from edges (Renfrew, Ribic, & Nack, 2005). Indeed, grasshopper sparrow abundance and nest densities decrease within c. 50 m of croplands and woody vegetation (Delisle & Savidge, 1996; Johnson & Temple, 1990; Patten, Shochat, Reinking, Wolfe, & Sherrod, 2006; Renfrew et al., 2005). Avoidance of habitat bordered by trees and shrubs is common in grassland birds and has been linked to increased risk of predation (Ellison, Ribic, Sample, Fawcett, & Dadisman, 2013; Klug, Jackrel, & With, 2010; Renfrew & Ribic, 2003). However, it is unclear whether edge avoidance by grasshopper sparrows varies with edge context. If (b) sparrows favour core habitat and perceive all edge types as equally risky, we predicted that abundance would be best determined by grassland area and configuration but not edge context. Conversely, if (c) sparrows favour core habitat and perceive woody edges as riskier than cropland edges, we predicted that abundance would be best determined by grassland area and configuration, with birds responding more negatively to the presence of woody edges than cropland edges. We tested these hypotheses by modelling the direct, interactive, and indirect effects of landscape factors on sparrow abundance at thousands of sites in eastern Kansas, home to North America's largest remaining tallgrass prairies.

2 | MATERIALS AND METHODS

2.1 | Study area and survey transects

Our study area consisted of the eastern one-third of Kansas, encompassing almost all of the Flint Hills ecoregion and parts of the Central Irregular Plains and Western Corn Belt Plains ecoregions (Figure 1; Omernik, 1987). More than 80% (c. 2 million ha) of North America's remaining tallgrass prairie lies in the Flint Hills where shallow rocky soils make the land unsuitable for tilling, and native perennial warm-season grasses support a major cattle industry (With et al., 2008). The main land use in the Central Irregular Plains and Western Corn Belt Plains is row crop agriculture, but both regions also contain hayfields and pastures. The region provides an excellent opportunity to assess the influences of habitat amount, fragmentation, and edge context on sparrow abundance because local landscapes contain 0%–100% grassland cover which is configured in a multitude of spatial arrangements and interspersed by variable amounts of croplands, trees, and water.

We conducted bird surveys along existing North American Breeding Bird Survey (BBS) transects and new transects that we established (Figure 1; Herse, Estey, Moore, Sandercock, & Boyle, 2017). Each of the 21 BBS transects located within our study area

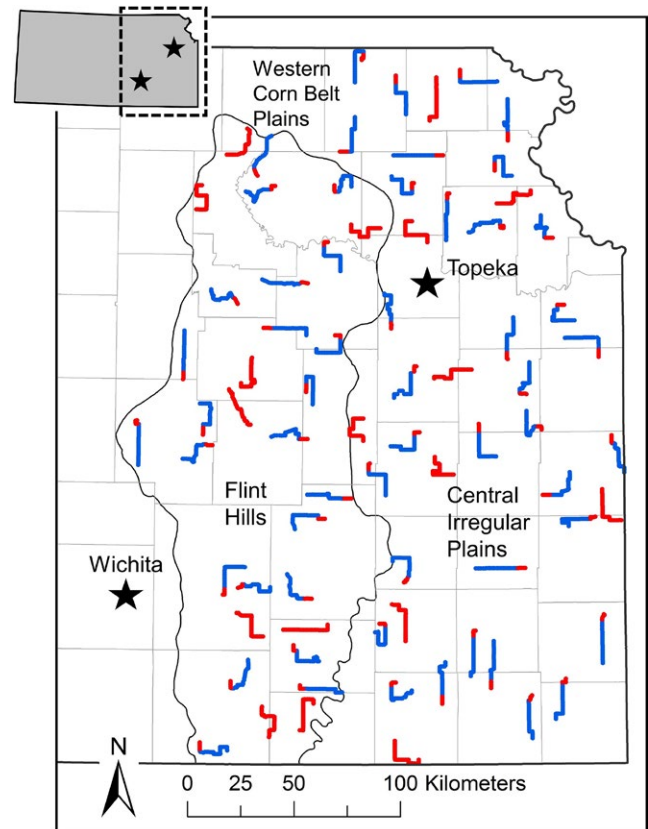


FIGURE 1 Map of our study region and 75, 30-point (23.2 km) survey transects in eastern Kansas, USA. Blue lines represent segments of transects where we conducted bird surveys in 2015 and 2016, whereas red lines represent segments we visited only in 2016. Thin black and grey lines mark boundaries of the Flint Hill ecoregion and state counties respectively

consists of 50 points spaced 800 m apart along secondary roads. We surveyed a continuous segment of 25 points along each BBS transect to accommodate a longer survey duration while restricting counts to morning hours. We surveyed the first 25 points located (a) within our study area and (b) outside of urban areas (commercial, industrial, or residential) identified using ArcMap 10.3 (Environmental Systems Research Institute, Redlands, CA). Additionally, we created 36, 25-point transects following BBS protocols using a stratified random selection of starting points (see Supporting Information), resulting in a total of 1,425 points located along 57, c. 19-km transects in 2015. In 2016, we added five new survey points to all transects and added 18 new 30-point transects, totalling 2,250 survey points located along 75, c. 23-km transects (Figure 1).

2.2 | Field methods

We surveyed for grasshopper sparrows from c. 1 month following their earliest arrival in mid-April until the end of the breeding season in late July. Each year, we conducted surveys in two "rounds." Start and end dates of survey rounds overlapped for 5 days in 2015 due to heavy rains and poor road conditions which constrained survey

schedules. We separated consecutive visits to the same transect by at least 2 weeks. Start dates of each round were similar between years: “round 1” began 13 May in 2015 and 20 May in 2016, and “round 2” began 15 June in 2015 and 27 June in 2016. All surveys in round 2 ended by 23 July in 2015 and 29 July in 2016. We visited points in a consistent order beginning 30 min before local sunrise and ending less than 6 hr after sunrise. We counted birds during dry conditions when sustained wind speeds were ≤ 25 km/h. We recorded the time, temperature ($^{\circ}\text{C}$), and wind strength (Beaufort Index) at the beginning of each survey. Trained observers (see Supporting Information) typically completed one transect per morning each, but if weather conditions deteriorated, we either discarded data and revisited the transect another day or considered the transect to be complete if the observer had completed ≥ 20 points. Surveys were conducted by five observers in 2015 and four in 2016, with one observer shared between years. We rotated observers among transects to minimize unmodelled heterogeneity in our data (Mackenzie et al., 2003).

At each point, the observer stood c. 10 m from the vehicle and conducted a 6-min count. Observers remained quiet and still during a 30-s presurvey period, so birds could adjust to their presence, then recorded detections of individual grasshopper sparrows seen or heard, recording the distance (m) to each individual at first detection. Observers measured distances to birds using laser rangefinders (Nikon Prostaff 5; Melville, NY, USA) and estimated distances if they could not see birds perched.

2.3 | Landscape factors and spatial scales

We obtained land-cover data developed by the Kansas Applied Remote Sensing Laboratory using classified satellite imagery collected prior to 2005 (Peterson, Whistler, Egbert, & Martinko, 2010). The overall accuracy of classifications used in our study was 86.2% (Peterson et al., 2010). We summarized land-cover data at four spatial scales relevant to the dispersal behaviour of grasshopper sparrows using ArcMap 10.3 and Fragstats 4.2 (McGarigal, Cushman, & Ene, 2012) (see Supporting Information). We defined the most local scale as the area within a 200-m radius (13 ha) of each survey point, corresponding with the median within-season dispersal distance estimated within our study region (Williams & Boyle, 2018). Then, holding the resolution of land-cover data unchanged (30×30 -m raster pixel), we doubled the radius and summarized spatial data within 400-m (51 ha), 800-m (201 ha), and 1,600-m (804 ha) radii of each survey point. The resulting range of scales represents potential search areas over which sparrows may prospect during territory establishment.

We considered five landscape factors as potential sources of variation in sparrow abundance, measuring each within the four spatial scales described above. We calculated the (a) percent area comprising grassland, combining warm and cool season grasslands because grasshopper sparrows breed in both types (Vickery, 1996). To account for differences in habitat configuration among landscapes, we calculated (b) grassland edge density as the total length of grassland edge (m) divided by total grassland area (ha). To assess

whether responses to configuration varied with edge context, we decomposed grassland edge density, calculating densities of grassland edges adjacent to (c) row crop fields, (d) trees or shrubs, and (e) waterbodies (Peterson et al., 2010) using data from raster pixel adjacency matrices (see Contagion metric, Fragstats 4.2; McGarigal et al., 2012). Collectively, grasslands, croplands, trees, and waterbodies comprised $>99\%$ of the land area and edges we summarized. Summary statistics for landscape factors are in the Supporting Information Table S1 and Figure S1).

2.4 | Direct and interactive effects of landscape factors on sparrow abundance

We modelled counts of sparrows using generalized linear mixed models (GLMMs; Bolker et al., 2009), including random effects of transect and survey point to account for spatial dependence in our sampling design, and observer and year to account for potential observer bias and interannual effects on sparrow abundance, respectively. We defined 6-min surveys as sampling occasions, truncating our data to include only sparrows detected within 150 m of survey points because the probability of detecting sparrows farther away was low (<0.3). We refer to 150-m radii areas surrounding survey points as “sites,” and the areas within the broader scales surrounding points as “landscapes.” We included fixed effects of temperature (quadratic) and wind strength in all models because both influenced the probability of detecting grasshopper sparrows (Herse, 2017). Accounting for the influences of observer, year, and weather on counts of sparrows, we interpreted residual variation in counts as variation in sparrow abundance. We used Poisson distributions with log links in models because zero-inflated Poisson distributions did not provide better fits. Models estimated responses using maximum likelihood and Laplace approximation (Bates, Maechler, Bolker, & Walker, 2015).

We fit alternative models based on *a priori* hypotheses, comparing model fits using information theory (ΔAIC_c and w_i ; Burnham & Anderson, 2002). We disregarded models differing from the best-fit model by one parameter and ≤ 2.0 AIC_c units if the estimated slope coefficient ($\hat{\beta}$) was uninformative with confidence limits overlapping zero (Arnold, 2010). Reliable methods for incorporating the variance of random effects into confidence limits around GLMM coefficients have not yet been developed outside of Bayesian approaches (Bates et al., 2015; Bolker et al., 2009). Thus, for each parameter of interest, we calculated confidence limits based on parametric bootstrap distributions (500 permutations) sampled from the spherical random effect and error values of the corresponding model (Bates et al., 2015). Predictor variables used together were not strongly correlated ($r \leq 0.54$; Supporting Information Figures S2–S5) (Dormann et al., 2013). We standardized means and standard deviations of all predictor variables using z-transformations to facilitate comparisons of coefficients, conducting analyses using the R packages “lme4” and “AICcmodavg” (Bates et al., 2015; Mazerolle, 2017; R Core Team, 2018).

We began model selection by comparing eight alternative global (most complex) models to identify the spatial scale over which

sparrow abundance most strongly correlated with landscape structure. Each global model included effects of percent grassland, and grassland-to-cropland, grassland-to-tree, and grassland-to-water edge densities. We considered both linear and nonlinear (quadratic) relationships between percent grassland and sparrow abundance, including two-way interactions between percent grassland and each edge density type. We fit these models at each of the four spatial scales described above, constraining subsequent analyses to include only landscape variables assayed within the spatial scale of the best-fit global model (“pseudo-optimized single scale” approach; McGarigal, Wan, Zeller, Timm, & Cushman, 2016). We then verified that overdispersion was negligible ($p > 0.05$) using a χ^2 test (Bolker et al., 2009).

Next, we evaluated the fits of a constant (null) model and a suite of models representing our three hypotheses (including the best-fit global model) (Burnham & Anderson, 2002). Models representing the first hypothesis (total habitat per se) included an effect of percent grassland but not grassland edge density. We reconsidered whether the effect of percent grassland was linear vs. nonlinear in the absence of a configuration effect. Models representing the second hypothesis (core habitat per se) included effects of percent grassland and grassland edge density. Models representing the third hypothesis (core habitat and edge context) included effects of percent grassland and different grassland edge density types individually and in combinations. We considered additive and interactive effects of percent grassland and edge densities. Our final candidate set included 16 models.

2.5 | Indirect effects of landscape factors on sparrow abundance

If variation in habitat area influenced configuration, and both are important determinants of population size, then sparrows' response to configuration is at least partially an indirect response to habitat area. Multiple regression models do not account for causal relationships among predictor variables, precluding the detection of indirect effects. Thus, we used generalized confirmatory path analysis to model the indirect effects of landscape factors on sparrow abundance (Shiple, 2009). A path model consists of a directional acyclic graph of variables connected by cause-effect relationships, each represented by a different submodel (Shiple, 2009). To determine the extent to which landscape factors influenced each other and weather variables, we built a full path model around our best-fit GLMM of sparrow abundance, assuming habitat area could influence configuration, and both could influence weather (e.g., upland grasslands are windier than lowland row crop fields, shaded woody edges are cooler than exposed cropland edges). We modelled relationships among these variables using linear mixed models (LMMs), including random effects of transect and survey point in all LMMs plus random effects of observer and year in LMMs of weather variables. Next, we reduced the full path model by excluding relationships with little to no support

($p > 0.1$). We then validated the resulting model by assessing whether observed correlations between omitted relationships could be explained by random variation using Shipley's directional separation (“d-sep”) χ^2 test (Shiple, 2009). We conducted the path analysis manually using “lme4” in R (Bates et al., 2015; R Core Team, 2018).

3 | RESULTS

Our results are based on data collected during 7,230 point count surveys (2,807 in 2015 and 4,423 in 2016). We could not access four sites in 2015 due to road closures. We counted a total of 3,406 grasshopper sparrows (1,416 in 2015 and 1,990 in 2016) during 1,887 surveys (772 in 2015 and 1,115 in 2016) (Supporting Information Figure S6). We detected sparrows at 520 of 1,421 sites (36.5%) in 2015 and 742 of 2,250 (32.9%) in 2016. During surveys with detections, we usually counted either one (49%) or two (30%) adult sparrows (Supporting Information Figure S6). Assuming an equal sex ratio, total abundance of adult sparrows is probably about double that reported here because we usually detected singing males. Holding the effects of landscape factors constant, counts of sparrows were highest when the temperature was mild (c. 16°C) and wind strength was low (Beaufort Index = 0) (Supporting Information Figure S7).

3.1 | Direct and interactive effects of landscape factors on sparrow abundance

Sparrow abundance correlated most strongly with landscape structure within 400-m radii ($w_i > 0.99$; Supporting Information Figure S8), with birds responding positively and nonlinearly to percent grassland, and negatively to grassland-to-cropland and (especially) grassland-to-tree edge density ($w_i = 0.28$; Supporting Information Tables S2–S3; Figures 2–4). The strength of the effect of percent grassland on abundance was mediated by grassland-to-tree edge density ($w_i = 0.28$; Supporting Information Tables S2–S3; Figures 2–4) but not grassland-to-cropland edge density ($w_i = 0.12$; $\hat{\beta} = 0.04$, 95% CL -0.12 , 0.17 ; Supporting Information Table S2). Grassland-to-water edge density had a small negative effect on abundance, but parameter confidence limits overlapped zero ($\hat{\beta} = -0.03$, 95% CL -0.09 , 0.02) and reduced model fit ($w_i = 0.11$; Supporting Information Table S2). The only competitive model ($\Delta\text{AIC}_c = 0.92$; $w_i = 0.18$) was a nested version (lacking the interactive effect) of the best-fit model (Supporting Information Table S2) and provided similar estimates for shared parameters, making model-averaging unnecessary (Arnold, 2010; Bolker et al., 2009). Models that accounted for habitat configuration but not edge context received little support during model selection ($\Delta\text{AIC}_c \geq 2.78$; $w_i \leq 0.07$), and models that did not account for configuration or edge context received no support ($\Delta\text{AIC}_c \geq 140.52$; $w_i \leq 0.01e - 29$; Supporting Information Table S2).

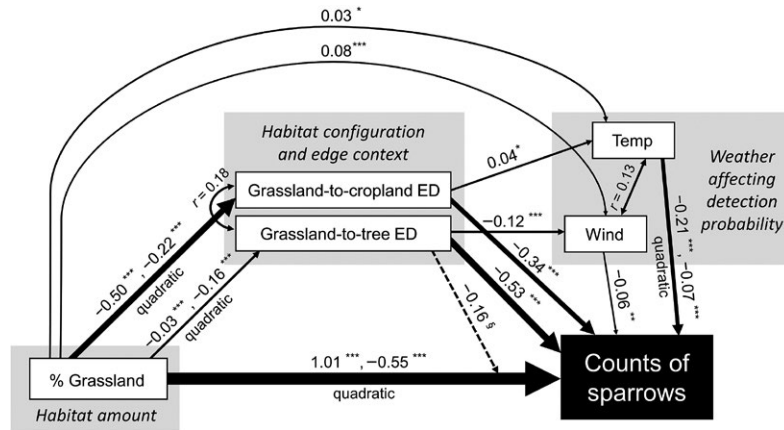


FIGURE 2 Path model showing how percent grassland, edge density (ED) and context (land-cover type abutting grasslands), and weather (temp = temperature, wind = Beaufort Index of wind strength) influenced each other and counts of grasshopper sparrows in eastern Kansas, 2015–2016. Solid arrows pointing to the black box are direct effects on sparrow counts, solid arrows pointing to white boxes represent indirect effects, and the dashed arrow pointing to another arrow is an interactive effect. Slope coefficients ($\hat{\beta}$) are above each arrow; nonlinear (quadratic) effects include a coefficient for the linear component as well as a coefficient for the squared component. Coefficients are based on standardized variables and are directly comparable (arrows weighted approximately by effect size). Asterisks indicate significance level (***<0.001, **<0.01, *<0.05, §<0.1). Bidirectional arrows beside Pearson's correlation coefficients (r) indicate relationships that lack causal direction and are not accounted for in the path model

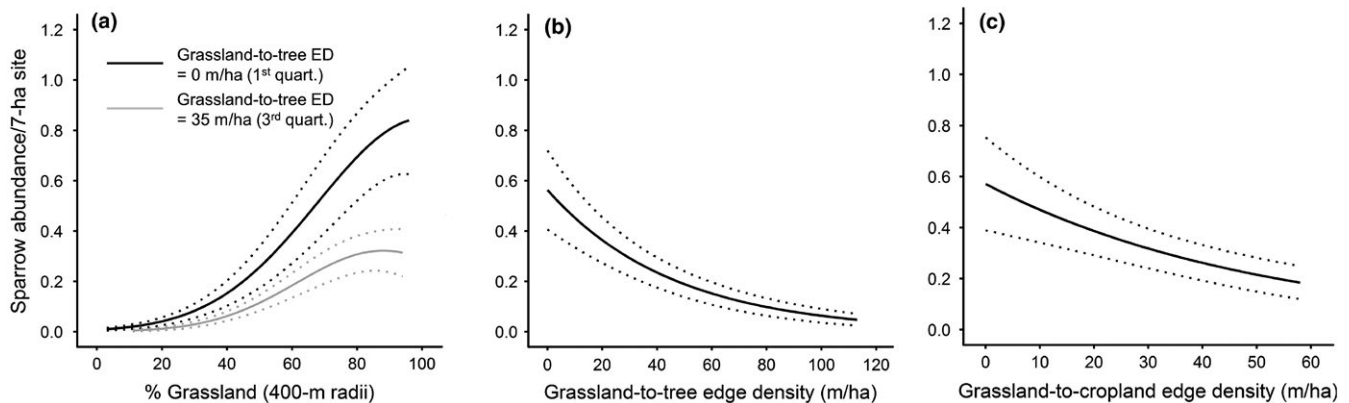


FIGURE 3 Modelled relationships between grasshopper sparrow abundance within 150-m radii (c. 7 ha) sites and (a) percent grassland (which is mediated by grassland-to-tree edge density or ED), (b) grassland-to-tree edge density, and (c) grassland-to-cropland edge density within 400-m radii (c. 50 ha) landscapes in eastern Kansas, 2015–2016. Estimates are based on median values of landscape factors not shown in a given plot and favourable conditions for detecting sparrows (temperature = 16°C, Beaufort Index of wind strength = 0; Figure S7). We plotted curves across the range of x-axis values observed in the dataset for each combination of percent grassland and edge density values. Dotted lines indicate 95% confidence limits which account for variance of fixed effects only. Estimates are from the final model

3.2 | Indirect effects of landscape factors on sparrow abundance

The path model retained the same direct and interactive effects as the best-fit GLMM for sparrow abundance plus effects of landscape factors on each other and weather. Percent grassland had a strong nonlinear effect on grassland-to-cropland edge density, indicating that sparrows' negative response to cropland edges was mostly an added, indirect response to variation in percent grassland (Figure 2). Conversely, percent

grassland had a much smaller nonlinear effect on grassland-to-tree edge density, indicating that sparrows' negative response to woody edges was mostly independent of variation in percent grassland (Figure 2). Temperature increased slightly with percent grassland and grassland-to-cropland edge density, whereas wind strength also increased with percent grassland but decreased with grassland-to-tree edge density (Figure 2). We did not detect any missing causal relationships in the reduced path model (Shipley's d-sep test, $\chi^2 = 6.03$, $df = 4$, $p = 0.20$).

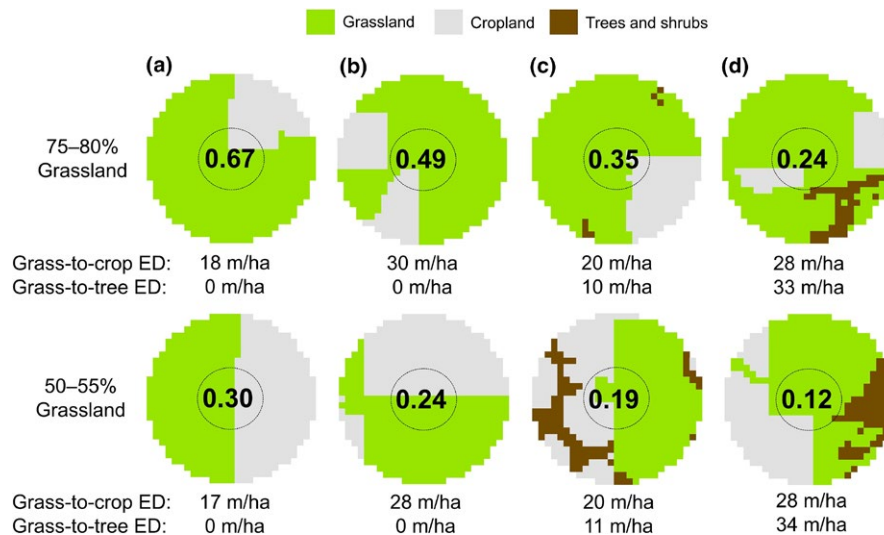


FIGURE 4 Eight landscapes from our study that illustrate how grasshopper sparrow abundance within 150-m radii (c. 7 ha) sites (delineated by dashed circles) varied with percent grassland, configuration (ED = edge density), and edge context (land-cover type abutting grasslands; e.g., grass-to-crop = grassland abutting cropland) within 400-m radii (c. 50 ha) landscapes in eastern Kansas, 2015–2016. Landscapes in the top and bottom rows contain large and intermediate amounts of grassland, respectively. Landscapes in column a contain normal amounts of grassland-to-cropland edge (c. median = 16 m/ha), whereas landscapes in b contain larger amounts (c. 3rd quartile = 30 m/ha). Landscapes in column c contain approximately the same amounts of grassland edge as those in b, but one-third of the grassland edge abuts trees rather than cropland. Landscapes in column d contain large amounts of grassland-to-cropland (c. 3rd quartile = 30 m/ha) and grassland-to-tree edge (c. 3rd quartile = 35 m/ha). Abundance estimates (bold numbers inside circles) are from the final model and based on favourable conditions for detecting sparrows (temperature = 16°C, Beaufort Index of wind strength = 0; Supporting Information Figure S7)

4 | DISCUSSION

4.1 | When does fragmentation matter?

Effective conservation requires understanding how landscape structure influences animal populations (Tschardt et al., 2012; Wilson et al., 2016). Using a large real-world dataset representing gradients of habitat amount, fragmentation, and edge context, we provide a rigorous test of theoretical predictions regarding the extent to which different landscape factors influence population size. Total habitat area per se was not a good predictor of grasshopper sparrow abundance. Instead, the relationship between habitat amount and abundance of this rapidly declining, grassland-dependent bird was clearly mediated by both fragmentation and edge context. Among landscapes comprising the same total grassland area, sparrows strongly favoured those with more core grassland and fewer woody edges, reflecting edge avoidance. Thus, as in forested ecosystems, conservation in grassland systems must account for fragmentation and edge context (Ewers & Didham, 2008; Martensen, Ribeiro, Banks-Leite, Prado, & Metzger, 2012; Watson et al., 2004; Wethered & Lawes, 2003).

Landscape theory predicts that fragmentation effects should be most pronounced in landscapes containing small to intermediate amounts (c. 10%–50%) of habitat, where spatial arrangement is likely to vary most (Swift & Hannon, 2010; Villard & Metzger, 2014). Results from empirical studies conducted in both experimental and natural

landscapes are often consistent with those predictions (e.g., Banks-Leite et al., 2014; Martensen et al., 2012; With & Pavuk, 2012). In contrast, we found that fragmentation and edge context mattered most to our focal species only when relatively large amounts of habitat remained. Moreover, only 8% of occupied sites (67 of 887) were in landscapes comprising <50% total grassland area regardless of configuration or edge context (Supporting Information Figure S6), possibly indicating a local “extinction threshold” (Fahrig, 2003; Villard & Metzger, 2014; With & King, 1999). Our results show that fragmentation and edge context may be more important than previously suspected in mediating suitability of landscapes where substantial habitat area remains (Andr n, 1994; Hanski, 2015). Likewise, edge-sensitive species may perceive all landscapes containing small amounts of habitat as unsuitable, making fragmentation and edge context unimportant in highly altered areas (Summerville & Crist, 2001; With & King, 2001).

Why was the apparent local extinction threshold so high for our focal species? We propose three potential explanations. First, the spatial scale at which researchers define landscapes influences estimates of local extinction thresholds (e.g., Homan, Windmiller, & Reed, 2004). Thus, some differences among studies could be explained by selection of spatial scales that poorly match the scale at which the focal species assesses habitat (Swift & Hannon, 2010), making comparisons across studies uninformative. Second, species-level traits such as niche breadth and dispersal capability affect animals’ responses to landscape structure (Ewers & Didham,

2006; Henle, Davies, Kleyer, Margules, & Settele, 2004; King & With, 2002). Dispersal-limited taxa may have a higher probability of encountering spatially convoluted patches or be unable to move away from such patches if the matrix inhibits dispersal (Ewers & Didham, 2006). However, our focal species is highly mobile and apparently not dispersal-limited, capable of quickly colonizing restored, seemingly isolated habitat patches (Gill et al., 2006). Thus, spatial correlates of grasshopper sparrow abundance may more accurately reflect optimal habitat selection than in less mobile species. Third, social factors could affect apparent local extinction thresholds. In species that require social groups to thrive, landscapes containing small amounts of habitat may be unsuitable regardless of configuration, leading to density-dependent relationships ("Allee effects"; Stephens & Sutherland, 1999) between abundance and habitat area. The clumped distribution of grassland songbird territories and positive responses to conspecific song implicates conspecific attraction as a key feature of their reproductive biology (Ahlering, Johnson, & Faaborg, 2006; Andrews, Brawn, & Ward, 2015), which could contribute to atypical relationships between habitat amount and the strength of fragmentation effects.

4.2 | Detecting responses to fragmentation and matrix features

Conflicting evidence in the literature regarding the importance of fragmentation and matrix features may be partially reconciled by considering three methodological issues. First, spatial scale not only influences apparent thresholds in animals' responses to landscape structure (as described above) but also the apparent strengths of species-habitat relationships (McGarigal et al., 2016). Understanding how animals perceive and respond to landscape structure requires adopting an "organism-centred" view of the world, focused at spatial scales relevant to the organism or process of interest (Wheatley & Johnson, 2009; Wiens, 1976). However, researchers frequently focus "landscape-level" studies at scales that are relevant to land managers but lack relevance for the species targeted for conservation (e.g., De Camargo, Boucher-Lalonde, & Currie, 2018; Mortelliti, Fagiani, Battisti, Capizzi, & Boitani, 2010; Radford, Bennett, & Cheers, 2005).

Second, population-level responses to landscape structure can differ from community-level responses. For instance, Fahrig (2013, 2017) has argued that fragmentation is unimportant relative to habitat amount; the "habitat amount hypothesis" posits that species richness within local landscapes is primarily determined by total habitat area irrespective of spatial arrangement. However, the goal of conservation is often to reverse declines of sensitive species rather than maximize species richness. Fragmentation and changes in the matrix frequently attract generalist or edge-adapted species that would otherwise be absent from landscapes comprising mostly core habitat (e.g., Jessen, Wang, & Wilmers, 2017; Major et al., 2001; Wethered & Lawes, 2003). Using species richness to measure ecosystem intactness means that local extinction of sensitive species is obscured by colonization by common species (Haddad et al., 2016). Thus, it

is crucial to design studies that are well-matched with conservation goals.

Third, researchers often assume that interdependent landscape factors are independently related to animals' responses and ignore potential interactive and/or indirect effects (Didham et al., 2012; Wilson et al., 2016). If two landscape factors are causally related, an animal's response to one pattern is at least partially an indirect response to the other, and ignoring their interdependence can underestimate the importance of one or both factors (Didham et al., 2012; Ruffell & Didham, 2016). In our study, grasshopper sparrows favoured landscapes comprising not only large amounts of grassland but also unfragmented grassland with small proportions of habitat near cropland or woody edges. By considering interactive effects, we found that woody edges reduced landscape suitability for sparrows when large amounts of habitat remained but did not matter when habitat was scarce. By considering indirect effects, we found that differences among landscapes in total grassland area strongly influenced the amount of grassland-to-cropland edge but not grassland-to-tree edge. Thus, sparrows' negative response to cropland edges was mostly an added, indirect consequence of reduced grassland area, whereas sparrows' stronger negative response to woody edges was not attributable to variation in grassland area. Although our results support the idea that habitat loss is the main driver of species declines, they also demonstrate the importance of fragmentation and matrix features in mediating animals' responses to habitat loss (Figures 2–4).

4.3 | Management implications

Our findings have important implications for management of threatened grassland species. Widespread habitat destruction due to agricultural conversion and urbanization, and degradation resulting from fragmentation and woody encroachment, have left temperate grasslands critically endangered (Hoekstra, Boucher, Ricketts, & Roberts, 2005; Newbold et al., 2016). Most prairies now exist in human-dominated regions where conservation must be carried out in partnership with private landowners (Green, Cornell, Scharlemann, & Balmford, 2005). Grassland restoration efforts are often confined to small fields (Besnard & Secondi, 2014; Herkert, 1994; Major et al., 2001), and unfortunately, our results suggest that small-scale restoration efforts within highly fragmented landscapes may have limited value for edge-sensitive grassland birds. Moreover, our data demonstrate that planting tree and hedge rows to minimize erosion (a common agricultural practice) decreases the quality of nearby intact habitat (Besnard & Secondi, 2014; Tack, Quamen, Kelsey, & Naugle, 2017).

Protecting large contiguous areas of habitat from further loss or degradation should be a conservation priority wherever possible (Villard & Metzger, 2014; With et al., 2008). In human-dominated landscapes, however, maximizing core habitat area rather than total habitat area per se may be a key to achieving conservation goals. For example, minimizing the edge-to-area ratio of fragments (Figure 4) and making small increases to core habitat

area could benefit sensitive species more than restoration that only increases habitat near edges, particularly for highly mobile species capable of locating and colonizing newly available habitat. In human-dominated regions, this can be done by strategically targeting private lands abutting existing prairies for protection and restoration under conservation easements (Rissman et al., 2007), and designing natural reserves that are simple in geometric shape (Ewers & Didham, 2007). Managers can also improve landscape suitability by removing trees surrounding grasslands (Besnard & Secondi, 2014; Morgado et al., 2010; Tack et al., 2017) and restoring historic fire-grazing regimes in working rangelands to prevent woody encroachment (Devine, McDonald, Quaipe, & Maclean, 2017; Fuhlendorf & Engle, 2001). Conservation efforts should also aim to minimize fragmentation caused by roads or energy development within or surrounding core natural areas (Drewitt & Langston, 2006; Hovick, Elmore, Dahlgren, Fuhlendorf, & Engle, 2014; Keyel, Bauer, Lattin, Romero, & Reed, 2012).

5 | CONCLUSIONS

We found that the relationship between abundance of a threatened grassland-dependent songbird and habitat area was mediated by fragmentation and edge context via direct, interactive, and indirect effects. Contrary to expectations, fragmentation and edge context mattered most to our focal species in landscapes containing large amounts of habitat. Our results raise concerns for conservation in grassland systems because many extant prairies are small in size and near trees. Protecting and restoring core habitat far from edges and preventing woody encroachment are essential to reversing declines of grassland-dependent species. Understanding the consequences of landscape change requires researchers to focus studies at ecologically relevant spatial scales, assess landscape suitability using response variables that do not obscure the local extinction of sensitive species, and account for interactive and indirect effects of causally related landscape factors. Determining the species-level traits that mediate responses to fragmentation and matrix features should be a priority for future research, as these may dictate the most effective approaches to species-level conservation.

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AUTHORS' CONTRIBUTIONS

M.R.H. and W.A.B. designed the study and collected the data. All authors conceived the conceptual framework and analytical approach and interpreted the results. M.R.H. led the writing of the manuscript, but all authors contributed, commented upon, and approved the manuscript.

DATA ACCESSIBILITY

Data available via the Dryad Digital Repository <https://doi.org/10.5061/dryad.9pr1476> (Herse, With, & Boyle, 2018).

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SUPPORTING INFORMATION

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

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