

University of Arkansas, Fayetteville

ScholarWorks@UARK

Graduate Theses and Dissertations

5-2021

Influence of Local- and Landscape-scale Factors on Avian Assemblage in Fragmented Tallgrass Prairie Landscape

Pooja Panwar

University of Arkansas, Fayetteville

Follow this and additional works at: <https://scholarworks.uark.edu/etd>



Part of the [Animal Experimentation and Research Commons](#), [Animal Studies Commons](#), [Poultry or Avian Science Commons](#), [Terrestrial and Aquatic Ecology Commons](#), and the [Zoology Commons](#)

Citation

Panwar, P. (2021). Influence of Local- and Landscape-scale Factors on Avian Assemblage in Fragmented Tallgrass Prairie Landscape. *Graduate Theses and Dissertations* Retrieved from <https://scholarworks.uark.edu/etd/4005>

This Thesis is brought to you for free and open access by ScholarWorks@UARK. It has been accepted for inclusion in Graduate Theses and Dissertations by an authorized administrator of ScholarWorks@UARK. For more information, please contact scholar@uark.edu.

Influence of Local- and Landscape-scale Factors on Avian Assemblage
in Fragmented Tallgrass Prairie Landscape

A thesis submitted in partial fulfillment
of the requirements for the degree of
Master of Science in Biology

by

Pooja Panwar
Bundelkhand Institute of Engineering and Technology
Bachelor of Technology in Computer Science and Engineering, 2010

May 2021
University of Arkansas

This thesis is approved for recommendation to the Graduate Council.

John D. Willson, PhD
Thesis Director

Steven L. Stephenson, PhD
Committee Member

Brett A. DeGregorio, PhD
Committee Member

Abstract

Agricultural expansion and increasing urbanization are driving rapid landscape modification in the Tallgrass prairies ecosystem and are affecting biodiversity at multiple spatial scales. Thus, the conservation of fragmented grassland and steeply declining grassland avifauna is dependent on the relationship between local- and landscape-scale factors and avian assemblage. We also need to understand how these factors, operating at different spatial scales, drive the occupancy of different guilds in the assemblage. We conducted repeated point count surveys during the breeding season of 2019 at 66 grassland sites across Arkansas and Missouri, USA. We developed a multi-species occupancy model to estimate species richness, and species- and guild-specific occupancy probability while accounting for species-specific detection probabilities. We examined the effect of landscape elements: type of landcover around a site, area and shape of a fragment and local-level elements: habitat type (remnant prairie/ hayfield), proximity to trees, and vegetation composition and structure on avian assemblage and guild-specific occupancy probability. Overall, we found that factors operating at landscape-scale have a significant effect on overall richness and composition of avian assemblage and guild-specific occupancy probability. The avian assemblage richness was higher for heterogenous landscape, small patches, and patches with more edge habitat which was a result of lower proportion of habitat specialists (grassland obligate) and higher proportion of habitat generalists. For grassland obligate species, high grassland cover, low forest cover, large patch area, less edge habitat, and lower litter depth had strong positive effects on their occupancy and guild-level species richness at a site. For grassland facultative species, high development around a site, small patch, high edge habitat, and lower litter depth had strong positive effects on their occupancy and guild-level species richness at a site. For woodland species, low grassland cover and high forest cover

around a site, small patch, and high edge habitat had strong positive effects on their occupancy and guild-level species richness. Collectively, our results indicate that response to local- and landscape-scale factors varies between the guilds and habitat specialists are negatively affected by habitat fragmentation. Conservation efforts should focus on conserving landscapes, large tracts of prairies, minimize woody encroachment, reduce edge habitat and maintain heterogeneous vegetation structure to mitigate grassland bird decline.

Acknowledgments

I would like to thank my advisor Dr. J.D. Willson, for stepping up as my advisor in the difficult times and for encouraging me to broaden my horizon and develop new skills. I am grateful to my committee members Dr. Brett A. DeGregorio and Dr. Steven Stephenson for their support and guidance to get me to the finish line. None of this would have been possible without the support of my late advisor Dr. Douglas A. James, who gave me, a software engineer, an opportunity to explore my interests in the field of ecology and conservation. I was lucky to have an advisor who nurtured and encouraged my zest for learning. I would also extend special thanks to late Dr. Kim Smith for his support and confidence. I am grateful to Dr. Ragupathy Kannan for his guidance and encouragement throughout.

I am thankful to Dr. Anant Deshwal for his continued support and guidance throughout my academic journey. Thank you for helping me professionally with study design, data collection and analysis and personally with emotional support through the difficult times. I am truly blessed to have friends like Brian Becker and Heather Becker for being there as a family away from my biological family and making me feel at home on foreign land. I am grateful to my friends: Zachary Tipton, Pamela McDill, Timi Apulu, Wade Boys, Max Carnes-Mason, Larry Kamees, Dr. Chelsea Kross, Ethan Royal, Meredith Swartwout, and Dr. Jennifer Mortensen for being there when I needed you the most. Thank you to Dr. Jackie Guzy, Dr. Anant Deshwal, and Ethan Royal for helping me with the complicated modelling process. Thank you Dr. Anant Deshwal, Sonam Wangmo and Nazrana Payal for helping me out with some field work. A special thank you to Hafeez Khwaja for lending me your car when my car broke down on the peak of my field season. Thank you, department of Biological Sciences at the University

of Arkansas, especially Becky Harris, Jan Warren, and Patty Drane for helping me with all the administrative tasks.

I am highly obliged to various public land managers and private landowners to allow me to conduct my field work. Thank you to Arkansas Natural Heritage Commission, Arkansas State Parks, Pea Ridge National Park, Missouri Department of Conservation, Prairie State Park, the City of Fayetteville. I am grateful to Joe Neal and Joe Woolbright to provide me with necessary background to get familiar with natural history of wildlife in Arkansas wildlife. I am especially thankful to Joe Neal to patiently teach me birdsongs and calls, introduce me to all cool birding locations, and for great birding trips. I am also thankful to the Arkansas Audubon Society Trust and Ozark Ecological Research Inc. for providing me partial support of my research.

Last but not the least, a big thank you to my family. I am deeply grateful for your support and encouragement through a career change, moving to a foreign land, and to get through graduate school.

Table of Contents

Introduction.....	1
Literature cited.....	3
Chapter 1: Influence of Local- and Landscape-scale Factors on Avian Assemblage in Fragmented Tallgrass Prairie Landscape.....	5
Introduction.....	5
Methods.....	9
Results.....	16
Discussion.....	21
Conclusions and Conservation Implications.....	28
Literature Cited.....	29
Tables and Figures.....	36
Conclusion.....	49

Introduction

One of the greatest environmental challenges of the 21st century is to slow biodiversity loss (Pimm et al. 2014). Along with multi-fold increase in global extinctions, biotic changes such as changes to abundance of common species, invasive species, and shuffling of species assemblage have profound effects on ecosystem functioning and services (Hooper et al. 2012). One of the primary causes of these biotic changes is habitat loss and habitat fragmentation. Humans have severely altered more than three quarters of Earth (Díaz et al. 2019) and agricultural intensification and urbanization further threatens remaining habitats (Andren 1994).

Globally, grasslands are one of the most threatened biomes with nearly half (46%) having been replaced by crop agriculture and other land uses (Hoekstra et al. 2005). In North America, more than 96% of tallgrass prairie has been lost (Samson and Knopf 1994), and the remaining tallgrass prairie habitat is either managed intensively for cattle production (With et al. 2008, Rahmig et al. 2009) or managed as wildlife reserve. Due to fire suppression, climate change, and surrounding land development around unmanaged grasslands, shrubs and trees are encroaching into these grasslands (Briggs et al. 2005, Kulmatiski and Beard 2013, Ratajczak et al. 2014, Scholtz et al. 2018). Additionally, due to ever-increasing energy demands, oil and gas wells and wind turbines are now common within grasslands (Hovick et al. 2014, Shaffer and Buhl 2016). Only 2% of remaining native grasslands in the USA are publicly owned and managed for conservation (NABCI 2011), reflecting the generally low level of protection that temperate grasslands receive worldwide (Hoekstra et al. 2005). Widespread habitat loss and degradation is concomitant with steep decline in grassland bird populations (Rosenberg et al. 2019).

Habitat loss and fragmentation leads to modifications of several local- and landscape-scale factors which are known to impact occupancy, abundance, and reproductive success of grassland birds. Many grassland bird species such as Greater Prairie-Chicken (*Tympanuchus cupido*), Henslow's Sparrow (*Ammodramus henslowii*), and Grasshopper Sparrow (*Ammodramus savannarum*) have large habitat area requirements and hence do not occur in landscapes without expansive grassland (Ribic et al. 2009, Winder et al. 2014). Increased edge exposure due to habitat fragmentation leads to greater risk of adult mortality (Hovick et al. 2014), nest predation (Renfrew and Ribic 2008, Klug and Jackrel 2010), and/or brood parasitism by Brown-headed Cowbirds (*Molothrus ater*) (Winter et al. 2000). Previous empirical studies have shown that the occurrence and abundance of some grassland birds is strongly correlated with interior or 'core' grassland area away from edges than total grassland area (Helzer and Jelinski 1999, Renfrew and Ribic 2008). Though these species-specific studies or studies on few habitat specialists inform grassland bird conservation and habitat management decisions, we have little understanding of how local- and landscape-scale factors affect the avian assemblage in fragmented Tallgrass prairie landscapes.

The objective of this study was to examine effects of local- and landscape-scale factors on species-specific occupancy and detection probability and composition of avian assemblages. We collected occurrence data for birds across 66 sites in northwestern and central Arkansas and southwestern Missouri in 2019. At the local-scale, we collected data on vegetation structure, type of grassland (remnant prairie/ hayfield), and proximity to trees for each site. On a landscape-scale, we measured percent land covered by three land cover types: grassland, forest, and developed within 1 km buffer around each site, and area and perimeter-to area ratio of grassland fragment. We used Bayesian Hierarchical community occupancy modelling to estimate species

richness and occupancy probability of guilds based on habitat preference of species and the whole assemblage while accounting for species-specific detection probabilities. This research informs the habitat management strategies for grassland bird conservation.

Literature Cited

- Andren, H. 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. *Oikos*:355-366.
- Briggs, J. M., A. K. Knapp, J. M. Blair, J. L. Heisler, G. A. Hoch, M. S. Lett, and J. K. McCarron. 2005. An ecosystem in transition: causes and consequences of the conversion of mesic grassland to shrubland. *BioScience* **55**:243-254.
- Díaz, S., J. Settele, E. S. Brondízio, H. T. Ngo, M. Guèze, J. Agard, A. Arneth, P. Balvanera, K. Brauman, and S. H. Butchart. 2019. Summary for policymakers of the global assessment report on biodiversity and ecosystem services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services. Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services.
- Helzer, C. J., and D. E. Jelinski. 1999. The relative importance of patch area and perimeter–area ratio to grassland breeding birds. *Ecological Applications* **9**:1448-1458.
- Hoekstra, J. M., T. M. Boucher, T. H. Ricketts, and C. Roberts. 2005. Confronting a biome crisis: global disparities of habitat loss and protection. *Ecology Letters* **8**:23-29.
- Hooper, D. U., E. C. Adair, B. J. Cardinale, J. E. Byrnes, B. A. Hungate, K. L. Matulich, A. Gonzalez, J. E. Duffy, L. Gamfeldt, and M. I. O'Connor. 2012. A global synthesis reveals biodiversity loss as a major driver of ecosystem change. *Nature* **486**:105-108.
- Hovick, T. J., R. D. Elmore, D. K. Dahlgren, S. D. Fuhlendorf, and D. M. Engle. 2014. Evidence of negative effects of anthropogenic structures on wildlife: a review of grouse survival and behaviour. *Journal of Applied Ecology* **51**:1680-1689.
- Klug, P. E., and S. L. Jackrel. 2010. Linking snake habitat use to nest predation risk in grassland birds: the dangers of shrub cover. *Oecologia* **162**:803-813.
- Kulmatiski, A., and K. H. Beard. 2013. Woody plant encroachment facilitated by increased precipitation intensity. *Nature Climate Change* **3**:833-837.
- North American Bird Conservation Initiative (NABCI), U.S. Committee (2011) The State of the Birds 2011 Report on Public Lands and Waters. U.S. Department of Interior, Washington, DC.

- Pimm, S. L., C. N. Jenkins, R. Abell, T. M. Brooks, J. L. Gittleman, L. N. Joppa, P. H. Raven, C. M. Roberts, and J. O. Sexton. 2014. The biodiversity of species and their rates of extinction, distribution, and protection. *Science* **344**.
- Rahmig, C. J., W. E. Jensen, and K. A. With. 2009. Grassland bird responses to land management in the largest remaining tallgrass prairie. *Conservation Biology* **23**:420-432.
- Ratajczak, Z., J. B. Nippert, J. M. Briggs, and J. M. Blair. 2014. Fire dynamics distinguish grasslands, shrublands and woodlands as alternative attractors in the Central Great Plains of North America. *Journal of Ecology* **102**:1374-1385.
- Renfrew, R. B., and C. A. Ribic. 2008. Multi-scale models of grassland passerine abundance in a fragmented system in Wisconsin. *Landscape Ecology* **23**:181-193.
- Ribic, C. A., R. R. Koford, J. R. Herkert, D. H. Johnson, N. D. Niemuth, D. E. Naugle, K. K. Bakker, D. W. Sample, and R. B. Renfrew. 2009. Area sensitivity in North American grassland birds: patterns and processes. *The Auk* **126**:233-244.
- Rosenberg, K. V., A. M. Dokter, P. J. Blancher, J. R. Sauer, A. C. Smith, P. A. Smith, J. C. Stanton, A. Panjabi, L. Helft, and M. Parr. 2019. Decline of the North American avifauna. *Science* **366**:120-124.
- Samson, F., and F. Knopf. 1994. Prairie conservation in north america. *BioScience* **44**:418-421.
- Scholtz, R., J. Polo, E. Tanner, and S. Fuhlendorf. 2018. Grassland fragmentation and its influence on woody plant cover in the southern Great Plains, USA. *Landscape Ecology* **33**:1785-1797.
- Shaffer, J. A., and D. A. Buhl. 2016. Effects of wind energy facilities on breeding grassland bird distributions. *Conservation Biology* **30**:59-71.
- Winder, V., L. McNew, A. Gregory, L. Hunt, S. M. Wisely, and B. K. Sandercock. 2014. Space use by female Greater Prairie-Chickens in response to wind energy development. *Ecosphere* **5**:1-17.
- Winter, M., D. H. Johnson, and J. Faaborg. 2000. Evidence for edge effects on multiple levels in tallgrass prairie. *The Condor* **102**:256-266.
- With, K. A., A. W. King, and W. E. Jensen. 2008. Remaining large grasslands may not be sufficient to prevent grassland bird declines. *Biological Conservation* **141**:3152-3167.

Chapter 1

Influence of Local- and Landscape-scale Factors on Avian Assemblage in Fragmented Tallgrass Prairie Landscape

Introduction

The primary cause of alarming declines in global biodiversity is the destruction and degradation of natural ecosystems (Pereira et al. 2010, Rands et al. 2010). Intensification of agriculture and urbanization are major drivers of habitat destruction (Wilcove et al. 1986, Andren 1994). Habitat destruction typically leads to fragmentation, the division of a habitat into smaller and more isolated fragments embedded in a matrix of human-transformed land cover. The loss of area, increase in isolation, and greater exposure to human land uses along fragment edges initiate long-term changes to the structure and function of the remaining fragments (Lindenmayer and Fischer 2013, Haddad et al. 2015).

Globally, grasslands are among the most threatened biomes (Hoekstra et al. 2005) due to habitat loss and fragmentation (Askins et al. 2007). North America's grasslands have experienced substantial impacts from agricultural expansion and increasing urbanization. Additionally, the current economic climate continues to drive substantial grassland conversion to agriculture (Wright and Wimberly 2013, Wright et al. 2017). Such substantial and ongoing habitat loss and fragmentation has precipitated widespread declines in grassland birds (Sauer and Link 2011, Rosenberg et al. 2019). North American grassland birds are experiencing the steepest population declines compared to any other group of birds on the continent (North American Bird Conservation Initiative Canada 2012).

Widespread declines have prompted much species-specific research on grassland bird populations at the habitat patch level including effects of habitat loss and fragmentation (Herkert 1994, Helzer and Jelinski 1999, Fletcher Jr 2005) and habitat quality and both vegetation composition and structure (O'Leary and Nyberg 2000, Ribic and Sample 2001, Davis 2004, With et al. 2008) and landscape level (Bakker et al. 2002, Shahan et al. 2017). For example, in fragmented grasslands of Illinois, habitat loss and fragmentation were shown to be likely the causes of midwestern grassland bird declines, especially for area-sensitive species (Herkert 1994). In the prairies of southern Saskatchewan, the vegetation structure, patch size, and ratio of edge to interior habitat were important predictors of grassland songbird abundance and occurrence (Davis 2004). Protection of both small native-prairie fragments with minimal edge habitat and large continuous tracts are known to play a critical role in conservation of grassland birds (Davis 2004). By looking at three grassland specialists, With et al. (2008) pointed out that large habitat area is not a guarantee of population viability if the available habitat is of poor quality, such as in regions predominantly managed for agricultural and livestock production. These species-specific studies, while important, tend to do ignore the effect of fragmentation on composition of avian assemblage in remaining grassland fragments. The number of species in an area is undeniably important, but the presence or absence of certain species or overall composition of a community can often be an equally important conservation goal. In accordance with the degree of fragmentation, species composition within a community may change independent of the number of species. For example, the ratio of habitat edge to habitat interior can influence the occupancy and abundance of “invasive” or “edge specialist species” vs. “interior species” (Yahner 1988, Forman 1995). The effects of fragmentation on communities are difficult to assess as the local habitat within a site may be influenced by geographic attributes

of a fragmented landscape (area, shape, spatial arrangement of fragments (Fahrig and Merriam 1985, Robinson et al. 1992, Leach and Givnish 1996, Zschokke et al. 2000). Thus, there is a gap in our understanding of how factors at different spatial scales can influence avian species composition and assemblage structure. Addressing this knowledge gap will have major implications for conservation planning and habitat restoration in fragmented landscapes.

In fragmented landscapes, patches should be viewed in the context of the surrounding habitat matrix because the matrix can determine the degree of patch isolation (Andren 1994), the availability of supplementary resources (Dunning et al. 1992, Burke and Nol 1998) and secondary habitat (Johnson 2007). Conservation planners need to understand how the composition and structure of the surrounding landscape influence bird occupation of small and isolated patches. Insights into how birds perceive grassland habitats at the landscape scale would enhance our ability to direct grassland conservation over broad geographic regions and complement what has been learned at local scales (Flather and Sauer 1996, Naugle et al. 1999). Prior studies of grassland birds have had mixed results with some detecting landscape effects (Söderström and Pärt 2000, Ribic and Sample 2001, Bakker et al. 2002, Hamer et al. 2006, Renfrew and Ribic 2008), others finding little to no effect of the landscape (Bajema and Lima 2001, Horn et al. 2002, Koper and Schmiegelow 2006, Jacobs et al. 2012), and others finding the combination of local and landscape variables having the greatest explanatory power (Fletcher Jr and Koford 2002, Cunningham and Johnson 2006, Quamen and Naugle 2007). Some of the ambiguity can be explained through the different approaches taken for data collection and analysis of various landscape variables (Shahan et al. 2017).

Landscape-scale elements such as area and shape of a fragment are known to influence the occupancy, density, and reproductive success of grassland birds. Multiple grassland birds are

area- or edge-sensitive (Delisle and Savidge 1997, Winter et al. 2000, Jensen and Finck 2004, Ribic et al. 2009). Although, patch area influences species richness and is important for the conservation of grassland obligate species, it is equally important to note that patches of equal area may also vary significantly in the amount of their area exposed to edges. It has been well-documented that an increase in habitat edge leads to higher predation and parasitism rates on grassland breeding birds (Johnson and Temple 1986, Burger et al. 1994, O'Leary and Nyberg 2000).

The effects of local-scale elements such as vegetation structure, proximity to trees, and whether a fragment is a remnant prairie or an agricultural land (hayfield/pasture) is mostly studied in terms of specie-specific response. Many grassland birds respond to specific vegetation composition and structural features (Whitmore 1981, Herkert 1994, Davis 2004, Winter et al. 2005, Jacobs et al. 2012). Previous studies have mostly looked at the effect of local- and landscape-scale variables on either single grassland species or a small subset of species within grassland bird assemblage leaving a gap in our understanding the effects of local- and landscape-scale elements on the occupancy patterns of different habitat guilds in fragmented prairie landscape.

In this study we used Bayesian hierarchical Multi-species Occupancy Model (MSOM) to elucidate the local-and landscape-scale factors driving composition of avian assemblage and to provide unbiased estimates of the probability of occupancy for each species and guild inhabiting fragmented Tallgrass prairie landscapes. We conducted repeated point count surveys at 66 sites across a fragmented tallgrass prairie landscape which allowed us to examine effects of local and landscape-scale variables. Our objectives were to 1) evaluate the effect of landscape fragmentation on composition of grassland bird assemblage 2) determine importance of

landscape elements in explaining occupancy probability and species richness across the guilds, and 3) determine importance of local-scale covariates in explaining occupancy probability and species richness across the guilds. To address our first objective, we hypothesized that the composition of avian assemblage would change with fragmentation and higher fragmentation would result in lower occupancy of habitat specialists and higher occupancy of generalist species. To address our second objective, we quantified the landscape elements (percent grassland, forest, and developed cover around each of our sites, area, and perimeter-to-area ratio of each fragment). We hypothesized that occupancy and species richness would vary between the guilds depending upon their habitat requirements. To address our third objective, we quantified local-level covariates (vegetation structure, habitat type, and proximity to trees) that could affect guild-specific occupancy and species richness. We hypothesized that the effect of local-level factors would vary among guilds because each guild has its own suite of resources needed for foraging and reproduction. Identifying connections between local- and landscape-level factors and avian guilds would permit the development of management techniques that are suitable for more than a single target species making it easier to maximize conservation resources.

2. Methods

2.1 Study area

The study was conducted in Tallgrass prairies and pastures in northwestern and central Arkansas and southwestern Missouri, USA. We established a total of 66 point-count stations (hereafter referred as sites) with 43 sites within 23 remnant native prairie fragments and 23 sites within 20 agricultural properties which were historically prairies (mean site size 45.98 ha and range of 5 - 131 ha). All except one remnant prairie site were managed with prescribed fire on an

annual or 3-year burn cycle by different management agencies. One remnant prairie site (Prairie State Park, Missouri) was grazed by bison. The agricultural lands were both privately owned and public lands (managed by National Park Services and Arkansas State Parks) primarily used for hay cultivation, with harvest occurring annually between Jun-Aug. We did not sample agricultural lands that were used for cattle grazing. Using ArcGIS (ESRI, 2020), we overlaid a 200 x 200 m grid at each prairie and agricultural land fragment and established a site at the center of randomly selected grid within each fragment. Each site was at least 100 m from the edge, to avoid edge effects that might influence avian assemblage (Fletcher Jr 2005), and the sites were at least 200 m apart from each other to avoid double counting. We established sites commensurate to the size of fragments, smaller fragments (< 30 acres) had 1-2 sites and larger fragments (>30 acres) had 1- 4 sites.

2.2 Data collection

We conducted bird counts three times during the breeding season (May-July) of 2019 at each site ($N = 66$). A single observer conducted 10-minute variable radius point counts surveys to sample the breeding bird community (Ralph et al. 1995). Counts occurred when birds were most active and vocal from dawn to 4 hours after sunrise and on days with weather conducive to hearing and seeing birds (wind less than 20 km/hr, no precipitation; Bibby et al. 1992). During surveys, the observer recorded all birds heard or seen, how individuals were detected (by song or visual) and distance of the bird from the center point divided in three categories: 0 – 25 m, 25 – 100 m and > 100 m. During each survey, we measured environmental variables (air temperature, humidity, and windspeed) and recorded minutes from sunrise and time and date of survey. We used (Vickery et al. 1999) and Birds of the World species account (<https://birdsoftheworld.org>)

to categorize species into five habitat preference guilds: grassland obligate, grassland facultative, shrub and edge, woodland, and urban (Table 1).

For each site, we recorded habitat type (remnant prairie/hayfield), percent land cover within 1000 m buffer of each site, area and perimeter/area ratio of the fragment for each site, vegetation structure, and proximity to nearest trees (riparian buffer, wind-break tree line or forest edge) at each site. We measured land use type within 1000 m buffer surrounding each site location using land cover data for 2016 downloaded from National Land Cover Database (NLCD) (www.mrlc.gov). Because it is difficult to differentiate between agricultural lands and prairies in satellite imagery, we did not differentiate between them. We combined data for several land cover type into three categories: grassland, forest, and developed (Table 2).

In order to measure area and perimeter-to-area ratio of a fragment, we drew a polygon around each fragment on ArcGIS 10.8.1 (ESRI 2020). We also ground-truthed the boundaries of each fragment in the field. We defined a remnant prairie fragment as an area of contiguous native prairie and considered cropland, grazed pasture, hayfields, wooded riparian areas, and roads as delineating native-prairie fragment. We defined agricultural land fragments as areas of contiguous hayfield and considered cropland, grazed pasture, native prairie, wooded riparian areas, and roads as delineating the fragment.

We measured vegetation structure at each site once in breeding season (15 - 30 July). Other studies have demonstrated that vegetation structure does not change significantly between beginning (May) and end of breeding season mid-Jul (Winter and Faaborg 1999). We quantified vegetation structure at each site using visual obstruction, maximum height of vegetation, canopy coverage, ground cover, and litter depth (as recommended by (Fisher and Davis 2010). We assessed the visual obstruction of the vegetation by looking at visual obstruction from a viewing

pole 4 m away from the Robel pole at a height of 1m (Robel et al. 1970). We measured the maximum height of vegetation within 2 cm of the Robel pole. We visually estimated vegetation canopy and ground coverage within a sampling frame (1 x 1 m) around the site. We determined canopy cover percentages on a nonoverlapping basis for each of the following groups: forbs, grasses, and woody vegetation. We classified ground cover by percent ground bare or covered with litter. Litter was defined as dead plant material lying flat on the soil surface, usually in some stage of decomposition. Litter depth was measured at the center of 1 x 1 m frame. For each site, we measured vegetation variables at four plots around the site: one at the center of the site, and three plots located 30 m from the center in 0, 120, 240 degrees from the center (Best et al. 1997, Fletcher Jr and Koford 2002). We averaged these 4 plots to represent vegetation of each site (Best et al. 1997, Fletcher Jr and Koford 2002). We measured proximity to trees by measuring distance closest tree-line, riparian buffer or forest edge using ArcGIS.

2.3 Modelling and Analysis

We used Principal component analysis (PCA) in the vegan package (Oksanen et al. 2019) in R to reduce the number of variables by combining correlated variables into new principal components for vegetation and sampling variables. We performed a PCA on vegetation covariates and sampling covariates and used principal component scores from the first two axes as vegetation and sampling covariates in our occupancy analyses (Table 3). To isolate the effects of landscape-scale covariates (percent land cover type in 1000 m buffer, area, perimeter/area ratio), and local-level covariates (habitat type [prairies/hayfield] and proximity to trees), we did not include them in the PCA; Exploratory analysis showed that they were not strongly correlated with other site and sampling covariates.

We used a hierarchical Bayesian community occupancy model (Dorazio and Royle 2005) to estimate species-specific and guild-specific occupancy and detection probability as a function of site-specific covariates (habitat type, % land use cover within 1000 m buffer, patch area, perimeter/area ratio, proximity to trees, vegetation PC1, and vegetation PC2) and sampling covariates (sampling PC1 and PC2). This hierarchical approach incorporates species-specific and guild-level covariates effects into the same modelling framework, thus allowing estimation of species-specific and guild-specific occurrence and detection probabilities and site-specific species richness while accounting for imperfect detection (Dorazio and Royle 2005, Zipkin et al. 2009). By considering all occupancy and detection parameters as random effects rather than deterministic relations among parameters and processes hierarchical multi-species models improves estimation of individual parameters for each species by considering each within the context of a group of related variables (Sauer and Link 2002). Hierarchical MSOM increases the precision of estimates for rare or elusive species by also considering each within the context of the broader community (Sauer and Link 2002, Russell et al. 2009).

We generated species-specific observance matrices for three sampling occasions at each site, where detection was represented as 1 and non-detection as 0. Thus, the data provided a three-dimensional matrix $x_{i,j,k}$ for species i at site j for the k th sampling occasion. The first level of the model assumed a true presence-absence matrix z_{ij} for species $i = 1, 2, \dots, N$ at site $j = 1, 2, \dots, J$, where $z_{ij} = 1$ if species i was present at site j , otherwise $z_{ij} = 0$. We assumed that the occupancy status of each site was constant across all surveys in our study. The occupancy state is considered a Bernoulli random variable, $z_{ij} \sim \text{Bern}(\Psi_{i,j})$, where $\Psi_{i,j}$ is the probability that species i occupies site j . Similarly, we specified a second level of the model (observation model) where species detection was modeled as a Bernoulli random variable: $x_{i,j,k} \sim \text{Bern}(p_{i,j,k} * z_{i,j})$, where

$p_{i,j,k}$ is the probability that species i is detected at site j during survey k . Note that if species i was not present at site j (i.e. $z_{ij} = 0$) then no detections of species i were possible as $(p_{i,j,k} * z_{ij}) = 0$.

We assumed species-specific occupancy probability (Ψ_{ij}) followed a linear-logit function of the model covariates:

$$\begin{aligned} \text{logit}(\psi_{ij}) = & \alpha_{0i} + * I(\text{Hayfield} = 1) + \alpha_{1i} * \% \text{ Grassland} + \alpha_{2i} * \% \text{ Forest} + \alpha_{3i} \\ & * \% \text{ Developed} + \alpha_{4i} * \text{Area} + \alpha_{5i} * \frac{\text{Perimeter}}{\text{Area}} + \alpha_{6i} * \text{Proximity to Trees} \\ & + \alpha_{7i} * \text{VegPC1} + \alpha_{8i} * \text{VegPC2} \end{aligned}$$

where $I(.)$ is an indicator function taking the value of 1 if the argument is true and 0 otherwise.

Species-specific detection probabilities also followed a linear-logit function of the model covariates:

$$\text{logit}(p_{i,j,k}) = \beta_{0i} + \beta_{1i} * \text{SamplingPC1}_{j,k} + \beta_{2i} * \text{SamplingPC2}_{j,k}$$

Parameters α_2 is interpreted as contrasts of the categorical predictor for habitat type (remnant prairie or hayfield) with remnant prairie as the reference category. The percent grassland, forest, or developed was defined as the percent of pixels with respective land use category within a 1000 m buffer around sites. The area and perimeter/area ratio are defined as the area and perimeter/area ratio of the contiguous prairie/ hayfield fragment. The proximity to trees was defined as distance to nearest tree-line, riparian buffer or woodland edge. We defined VegPC1 and VegPC2 covariates as the respective z score (i.e., centered and scaled to a mean of 0 and SD of 1) of principal component scores from each of the first two site PC axes (Table 3a). Finally, when modeling detection probability, we defined the sampling PC1 and sampling PC2 covariates as the respective z score of principal component scores from each of the first two sample-specific- PC axes (Table 3b). All the continuous variables were standardized prior to the analysis by converting to z-scores (i.e., the mean was subtracted from each value and then

divided by the SD). Standardized covariates allowed direct comparison of model coefficients so that the relative importance of each covariate could be determined according to the magnitude of the coefficient.

We estimated species richness (N) for 66 sites by summing estimated occupancy for each of the 62 observed species. Species richness for site j was defined as

$$\widehat{N}_j = \sum_{i=1}^{62} \hat{z}_{i,j}$$

where $\hat{z}_{i,j}$ is the estimated occupancy of species i at site j . Similarly, we estimated guild-specific species richness for each site by summing the estimated occupancy for each species within that guild.

In community occupancy models, the parameter estimates for data-poor species are more precise as the estimation process “borrows” from data-rich species, however, the inference might depend on the implicit assumption of the relatedness among species (Pacific et al. 2014). To increase the degree of relatedness among our species, we divided our 62 species of interest into five groups based on their habitat preference: (1) grassland obligate, (2) grassland user, (3) shrub and edge, (4) woodland, and (5) urban. We drew species-specific effects from group normal distributions e.g., $\alpha_{d,i} = N(\mu_{d,h}, \sigma_{d,h}^2)$ for parameter α_d of species i in group h or $\beta_{d,i} = N(\mu_{d,h}, \sigma_{d,h}^2)$ for parameter β_d of species i in group h , where the mean and variance of the normal distribution are group level hyper-parameters. We used a $N(0,2)$ (mean, variance) prior for all group mean parameters and $U(0.1,3)$ for all group standard deviation parameters.

We fitted the model using JAGS (Plummer 2003) called from R (Team 2019) and executed using the jags function from package R2jags (Su et al. 2015). We implemented this model in a Bayesian framework using Markov Chain Monte Carlo (MCMC) sampling in JAGS

to generate samples from the posterior distribution (Lunn et al. 2000). We used three Markov chains, each of length 200,000; the first 100,000 were removed as burn-in, and the remainder were thinned by a factor of 50. Across the three chains, this provided 6,000 samples to approximate posterior summary statistics for each model parameter including mean, standard deviation, and 2.5% and 97.5% percentiles of the distribution, which represent 95% Bayesian credible intervals. We assessed model convergence via the Gelman-Rubin diagnostic and a visual inspection of chains, with both measures indicating a reasonable assumption of convergence. For all monitored parameters in our study, the Gelman-Rubin statistic value was below 1.05 (Gelman and Rubin 1992).

In post hoc analyses, we used Pearson's correlation coefficients to evaluate the relationship between the estimated species richness for each posterior sample (at both spatial scales) with the patch area, perimeter-to-area ratio, percent grassland, forest, and developed civer within 1000 m radius. The correlation coefficients for each covariate are organized by the median and 95% credible intervals across all posterior samples. We conducted these analyses to assess the cumulative effects of local and landscape-scale covariates on species richness patterns, a derived parameter, at each site. We categorized relationships as strong ($|0.7| < r < |1.0|$), moderate ($|0.5| < r < |0.7|$), weak ($|0.3| < r < |0.5|$), or negligible ($|0.1| < r < |0.3|$); (Hinkle et al. 2003).

3. Results

We detected 62 avian species (grassland obligates [n=4], grassland facultative [n=14], shrub or edge species [n=15], woodland species [n=23], and urban species [n=6]) across three surveys at 66 grassland sites (Table 1). The most frequently detected species was the Eastern

Meadowlark (*Sturnella magna*; naïve occupancy rate = 0.95), followed by the Dickcissel (*Spiza americana*, 0.91), and Northern Cardinal (*Cardinalis cardinalis*, 0.85).

3.1 PCA results

The first two vegetation-covariate principal components (PC) cumulatively explained 78.85% of total variation (Table 3a). Vegetation PC1 explained 44.89% of total variance and was an index of litter depth and ground cover (litter/bare) as indicated by strong positive factor loadings for litter depth and percent litter ground cover and a negative factor loading for percent bare ground. Vegetation PC2 explained 33.96% of total variance and was an index of vegetation height and composition as indicated by strong positive factor loadings for vegetation height and percent forbs and a strong negative factor loading for percent grass.

The first two sampling covariate principal components cumulatively explained 59.79% of total variance (Table 3b). Sampling PC1 explained 37.55% of total variance and was an index of time of day as indicated by strong factor positive loadings for minutes from sunrise and temperature and a strong negative factor loading for humidity. Sampling PC2 explained 22.23% of total variance and was most strongly influenced by Julian date.

3.2 Avian Assemblage Responses

The mean probability of occupancy across all species was 0.38 (0.01 – 0.99), whereas mean probability of detection was 0.35 (range: 0.07 – 0.95). The effects of sampling PC1 (Fig. 8) and sampling PC2 (Fig. 9) on species-specific or guild-specific detection probability were not strong. There was a slightly negative effect of sampling PC2 indicating that detection probability decreased from May to July across all guilds (Fig. 9).

The mean estimated species richness across all sites was 25.4 (range: 14.5 - 37.7). The estimated mean guild-level species richness for grassland obligates was 2.3 (0.0 – 4.0), grassland facultative was 7.3 (3.0 - 11.4), shrub and edge species was 6.8 (3.3 – 9.9), woodland species was 7.7 (2.9 – 17.8), and for urban species was 1.3 (0.1 – 4.4).

The species richness of avian assemblage increased as percent forest ($r = 0.47$, Bayesian Credible Interval [BCI]: 0.3 to 0.63; Fig. 3b) and developed ($r = 0.26$; 0.1 to 0.43 BCI; Fig. 3c) cover increased and decreased as percent grassland cover in surrounding landscape decreased ($r = -0.51$, -0.66 to -0.35 BCI; Fig. 3a). Similarly, species richness of assemblage was high for fragments with small area ($r = 0.4$, -0.54 to -0.25 BCI; Fig. 4a).

3.3 Landscape-scale Covariates

The effect of the landscape matrix on mean estimated occupancy probability and species richness varied between the guilds. There was a positive effect of percent grassland area within 1000 m radius of a site on the occupancy probability of grassland obligate (mean = 0.92, 0.89 – 2.78 BCI) but a negative effect on occupancy probability of shrub and edge species (-0.73, -2.26 – 0.80 BCI), and woodland species (-0.81, -2.41 – 0.76 BCI; Fig. 1a). There was a moderate positive correlation between percent grassland and species richness of grassland obligates ($r = 0.55$, 95%, 0.5 to 0.61 BCI; Fig. 3d), a moderate negative correlation with woodland species richness ($r = -0.65$, -0.76 to -0.51 BCI; Fig. 3m), and a weak negative correlation with urban species richness ($r = -0.41$, -0.63 to -0.17 BCI; Fig. 3p).

There was a negative effect of percent of forest cover around a site on occupancy probability of grassland obligate (-0.38, -1.88 – 1.13 BCI) and grassland facultative species (-0.27, -1.44 – 0.92 BCI) but a positive effect on woodland species (0.38, -0.85 – 1.64 BCI; Fig.

1b). There was a weak negative correlation between percent forest and species richness of grassland obligates ($r = -0.32$, -0.38 to -0.26 BCI; Fig. 3e) and a moderate positive correlation with species richness of woodland bird species ($r = 0.68$, -0.54 to -0.79 BCI; Fig. 3n).

There was a negative effect of percent developed land around a site on occupancy probability of grassland obligate species (-0.38 , -1.62 – 0.89 BCI), shrub and edge species (-1.00 , -2.05 – 0.03 BCI), woodland species (-0.44 , -1.43 – 0.54 BCI), while there positive effect of percent developed area on grassland facultative species (0.43 , -0.63 – 1.52 BCI) and urban species (1.25 , -0.28 – 3.06 BCI; Fig. 1c). There was a moderate negative correlation between percent developed area and species richness of grassland obligates ($r = -0.52$, -0.57 to -0.48 BCI; Fig. 3f) and a moderate positive correlation with species richness of urban birds ($r = 0.65$, 0.41 to 0.81 BCI; Fig. 3r).

The effect of patch area of each site on the mean estimated occupancy probability varied between guilds. There was a positive effect of patch area on occupancy probability of grassland-obligate species (1.19 , 0.08 – 2.38 BCI), and negative effects on occupancy probability of shrub and edge species (-0.63 , -1.2 – 0.05 BCI) and urban species (-1.33 , -2.77 – 0.08 BCI; Fig 2a). Patch area had a moderate positive correlation with species richness of grassland obligates ($r = 0.59$, 0.55 to 0.74 BCI; Fig. 4c) and a weak negative correlation with species richness of woodland species ($r = -0.37$, -0.50 to -0.22 BCI; Fig. 4i) and urban species ($r = -0.43$, -0.59 to -0.26 BCI; Fig. 4k).

The effect of perimeter-to-area ratio on mean estimated occupancy probability varied between guilds. Higher values of perimeter to area ratio represent smaller core area and increased edge habitat. There was a positive effect of perimeter to area ratio on occupancy probability of woodland species (0.50 , -0.12 – 1.41 BCI) and negative effect on occupancy

probability of grassland obligates, grassland facultative, shrub and edge species, and urban species (Fig. 2b). Perimeter-to-area ratio had a weak negative correlation with species richness of grassland obligates ($r = -0.36$, -0.44 to -0.24 BCI; Fig. 4d) and a weak positive correlation with richness of woodland species ($r = 0.40$, 0.22 to 0.57 BCI; Fig. 4j).

3.4 Local-scale Covariates

Species richness of the whole avian assemblage did not significantly differ among the two habitat types (remnant prairie/ hayfield) ($t(35) = -1.5$, $p = 0.14$), but the occupancy probability and species richness of some guilds differed between the two habitat types (Fig. 6). The species richness of grassland obligates was significantly higher for remnant prairies than hayfields ($t(46) = 2.0$, $p = 0.05$; Fig. 7) and species richness of woodland species was significantly higher for hayfields than remnant prairies ($t(31) = -2.8$, $p = 0.009$; Fig. 7). The estimated occupancy probability of grassland obligate and grassland facultative species was slightly higher in remnant prairies than hayfields. The estimated occupancy probability of woodland and urban species was slightly lower in remnant prairies than hayfields (Fig. 6).

There was a negative effect of vegetation PC1 on grassland obligate (-0.38 , -0.95 to 0.17 BCI; Fig. 5) and grassland facultative (-0.21 , -0.44 to 0.00 BCI; Fig. 5) indicating a negative association with litter depth, higher litter on ground cover and lower bare ground cover. There was a slight negative effect of vegetation PC2 on grassland obligates (-0.35 , -0.99 to 0.32 BCI; Fig. 5) indicating a weak positive association with higher grass cover, shorter vegetation, and lower forb cover. The effect of proximity to trees on mean estimated occupancy probability also varied between guilds. As distance to nearest trees increased, occupancy probability of grassland

obligates increased (0.17, -0.7 to 1.33 BCI; Fig. 2c) and occupancy probability of woodland species decreased (-0.44, -0.93 to -0.02; Fig. 2c).

4. Discussion

Our application of multi-species occupancy models (MSOM) found support for the effects of landscape- and local-scale factors on guild-specific and species-specific occupancy and species richness of grassland bird assemblages and guilds. Overall, the landscape-scale factors (landcover, patch area, and perimeter-to-area ratio) were much stronger drivers of occupancy patterns of the avian community than the local-scale factors (habitat type, proximity to trees, and vegetation structure) in the fragmented Tallgrass prairies of Arkansas and Missouri. Our data also demonstrate the effect of landscape composition on species richness of different function groups (habitat guilds) and the avian assemblage.

4.1 Avian Assemblage Response

The landscape composition, area, and perimeter-to-edge ratio of sites had a strong effect on the composition of avian assemblage and species richness of the different habitat guilds. The species richness of the assemblage was higher for sites with higher forest- and developed- cover when compared to sites with high grassland cover in a 1000 m radius the around site. Similar patterns of high species richness of assemblage were observed for fragments with smaller area and high perimeter-to-area ratio. The higher species richness of assemblage in more heterogenous landscapes, smaller patches, and patches with increased edge effect was driven by higher occupancy of woodland and urban species (many of which are generalists) and lower occupancy of grassland obligate species (also habitat specialists). Similar influence of landscape

variables was reported in Pampas grasslands in Argentina where the richness and abundance of grassland obligate species was lower in smaller patches and patches surrounded by forest cover (Pretelli et al. 2018). In the prairie fragments in North Dakota, South Dakota, and Minnesota, USA, there was stronger influence of local variables than landscape variables on the grassland obligate and facultative species (Shahan et al. 2017). On the contrary, we found strong effects of landscape-scale variables on the occupancy and species richness of grassland obligates. This difference might be attributed to the difference in the radii at which landscape variables were collected, our study looked at landscape within 1-km radii and (Shahan et al. 2017) looked at landscape within 3-4 km around the patch.

Whether the habitat was a remnant prairie or a hayfield had little influence on overall species richness of the assemblage, however, the composition of the assemblage was quite different between the two habitat types. This underscores that species richness is not always the best index to reflect community-level dynamics (Lindenmayer et al. 2015). Even though species richness is comparable for remnant prairies and hayfields, the species composition was different. For our study, the avian assemblage in remnant prairies had more grassland obligate (also habitat specialists) and fewer woodland and urban species (also generalists) than that of agricultural lands (hayfields).

4.2 Landscape-scale Effects

The landscape matrix around a site had a strong influence on the occupancy and species richness of each guild. Grassland obligates had strong positive associations with percent grassland area around a site. This relationship has been shown by previous research with varying buffer radii (Ribic and Sample 2001, Hamer et al. 2006, Ribic et al. 2009, Lituma and Buehler

2020). Our classification of land cover as grassland did not distinguish between native prairie vegetation and fields used for agricultural purposes (hayfields, pastures or cropland). Although land used for agriculture might not provide high quality habitat and structural heterogeneity to grassland obligate and facultative species, they provide secondary habitats (Lituma and Buehler 2020). Conversely, we found that increased grassland cover had negative effects on occupancy of shrub and woodland species.

Occupancy of grassland obligates was negatively affected by increasing forest cover as shown in previous research (Cunningham and Johnson 2006, West et al. 2016). Increasing forest cover in the landscape increases the edge habitat and decreases the interior habitat available for grassland obligate species. Many of these grassland obligate species are area- or edge-sensitive species (Delisle and Savidge 1997, Winter et al. 2000, Jensen and Finck 2004). Increased forest cover in the landscape negatively affects their occupancy (West et al. 2016, Lituma and Buehler 2020), density (Murray et al. 2008), and reproductive success (Herkert 2002, Ribic et al. 2009). Afforestation and woody encroachment have been cited as one of the major threats to grassland birds in the US (Brennan and Kuvlesky Jr 2005, Askins et al. 2007). Increasing forest cover in the surrounding matrix led to increased occupancy of woodland species which can be explained by availability of resources and suitable habitat for woodland species which would otherwise be absent in expansive grassland.

Amount of developed area around a site had strong positive effects on occupancy of species in the urban and grassland facultative guild and negative effect on grassland obligate, shrub, and woodland guilds. Previous research has shown that urbanization promotes widespread generalist species and negatively impacts habitat specialists (Devictor et al. 2007) and urbanization negatively affects occupancy and density of grassland birds in Tallgrass prairie

fragments (McLaughlin et al. 2014). Increased man-made structure such as building, roads, utility poles or barns in the landscape provides habitat and resources for urban species such as House Finch (*Haemorhous mexicanus*) and Purple Martin (*Progne subis*) and non-native species such as European Starling (*Sturnus vulgaris*), Rock Pigeon (*Columba livia*) and Eurasian-collared Dove (*Streptopelia decaocto*). We also observed higher occupancy of species in the grassland facultative guild with increasing developed area in the landscape. There might be two possible explanation for this pattern. First, many grassland facultative species such as American Kestrels (*Falco sparverius*) and Eastern Kingbird (*Tyrannus tyrannus*) utilize anthropogenic structures like power lines and utility poles as perches and Barn Swallows (*Hirundo rustica*) and Cliff Swallows (*Petrochelidon pyrrhonota*) use barns and bridges, respectively, as nesting and roosting sites. Second, this pattern could also be a result of the way we classified land use in the surrounding landscape. We merged cells classified as open space and low intensity development class with medium and high intensity development. This resulted in merging land used for farmhouses or low-maintenance roads with highly urbanized land use. Low intensity developed areas such as rural areas would still provide suitable habitat to many grassland facultative species.

There were strong relationships between patch area and mean occupancy of several guilds. As the area of the fragment increased, the mean occupancy of grassland obligate species increased. The result highlights the importance of large prairie patches and negative effects of fragmentation on imperiled grassland obligate species. Previous studies have shown that patch area is an important factor for all the four grassland obligates included in our study (Johnson and Temple 1986, Herkert 1991, Helzer and Jelinski 1999, Winter and Faaborg 1999). In addition, we found that smaller fragments had higher occupancy of shrub and woodland species than

larger fragments which can be explained by increased edge exposure in small fragments than large fragments.

Our results demonstrated a strong effect of edge habitat on composition of the bird assemblage as well as on guild-specific occupancy probabilities. We examined edge effect through perimeter-to-area ratio, fragments with elongated shapes or indented perimeters have higher perimeter-to-area ratios than fragments of the same area with compact shapes and unbroken perimeters. In addition, small patches generally have higher perimeter-to-area ratios than large patch. Our results show that as perimeter-to-area ratio increased i.e. more edge exposed, occupancy of woodland species increased and occupancy of grassland obligates, grassland facultative and shrub species decreased. Previous studies in grasslands have shown that edge can have negative effect on occupancy and reproductive success of grassland obligate species due to edge-sensitivity, brood parasitism and nest predation (Helzer and Jelinski 1999, Herkert et al. 2003).

4.3 Local-scale Effects

We found that the guild-specific occupancy and species richness was significantly different between remnant prairies and hayfields. The occupancy of grassland obligate and facultative species was slightly higher in remnant prairies than hayfields. Studies in other parts of North American grasslands have shown that density of some grassland obligate species such as Dickcissel and Eastern Meadowlark is high in patches used for agricultural purposes (Ribic et al. 2009). Cost-sharing conservation approaches like Conservation Reserve Program (CRP) have been shown to benefit breeding birds and other wildlife populations (Johnson and Igl 1995). Using Breeding Bird Survey data to compare grassland bird population trends before and after

the onset of Farm Bill cost-share programs, (Herkert 2009) identified a positive change in abundance of many grassland bird species including: Grasshopper Sparrow (0.64%/year), Dickcissel (2.18%/year), and Field Sparrow (*Spizella pusilla*; 0.5%/year), though negative changes were documented for Eastern Kingbird (−2.14%/year) and Northern Bobwhite (*Colinus virginiana*; −0.09%/year) among others. Although CRP has benefitted grassland birds in agricultural landscapes by providing secondary habitats, (Rahmig et al. 2009) cautioned that these areas might have lower habitat value in the context of native prairies. Other working lands such as alfalfa hay fields are used by grassland birds, sometimes at great densities, but are considered ecological traps because reproductive success is extremely low due to intensive agricultural disturbance such as haying during the breeding season (Frawley and Best 1991, Perlut et al. 2006). Our application of MSOM can identify assemblage-level occupancy patterns, but it is unable to differentiate ecological traps (sinks) from high quality habitat that supports viable populations. To evaluate the effectiveness land-sharing conservation approaches such as CRP on community, population, and demographic dynamics of a species, abundance and reproductive success data should be assessed in addition to occupancy data.

Proximity to trees (distance to nearest trees in riparian buffer, windbreak tree lines or edge of a woodland) had a negative effect on occupancy on grassland obligates and positive effect on occupancy of grassland facultative, shrub and woodland guild. Grassland obligates are adapted to open, treeless landscapes and trees or woody vegetation reduces the amount of core area available to them for breeding and also increases edge effects (Helzer and Jelinski 1999, Herkert et al. 2003, Dias et al. 2013). Our results concur with those reported by previous studies that proximity to trees negatively affect grassland birds (Coppedge et al. 2001, Ribic and Sample 2001).

We found the effect of vegetation structure to be weak relative to the effects of landscape-scale factors on occupancy of different avian guilds. Grassland obligates and grassland facultative species had slightly higher preference for sites with lower litter ground cover, higher bare ground, and lower litter depth (indicated by vegetation PC1). Occupancy of grassland obligate species was also higher in sites with higher percent grass cover, lower percent forb cover and intermediate vegetation height (as indicated by vegetation PC2). Our results agree with previous research on species-specific vegetation structure requirements for grasshopper sparrows, which prefer bare ground, higher percent grass cover and intermediate vegetation height (Whitmore 1981, Dechant et al. 2002). However, our results for the other three grassland obligate species only partially agreed with results from previous research. Henslow's sparrow prefers taller live grasses, high litter depth, and standing dead vegetation (Zimmerman 1988, Herkert 1994, Winter and Faaborg 1999), dickcissel inhabit fragments of dense, tall vegetation and high forb cover (Temple 2002), and Eastern Meadowlark preferred higher grass cover and higher litter depth and litter on the ground (Granfors 1992). This could be due to differences in selection of location of vegetation sampling; previous research was focused on characterizing microhabitat requirements for nesting site locations, whereas we sampled vegetation for our point count locations. Nevertheless, previous studies have recommended management of tallgrass-prairie to generate a more heterogeneous mosaic of grassland types with heterogeneity in vegetation structure that may enhance the diversity of grassland species by mimicking grazing patterns prior to European settlement (Fuhlendorf and Engle 2001, Askins et al. 2007, Hovick et al. 2015). Such vegetation heterogeneity can be managed by burning discrete patches of prairie and then allowing free-ranging grazers (either bison or cattle) to selectively graze areas of burned and unburned prairie (Fuhlendorf and Engle 2001).

4.4 Conclusions and Conservation Implications

The primary finding of the study described herein is that landscape context matters. To reverse grassland bird population declines, conservation programs and managers should focus improving occupancy of target species across broad landscapes (Askins et al. 2007, Díaz and Concepción 2016). In the North American Great Plains more than 90% of pre-European prairie has already been converted to agriculture or urban land cover (Samson and Knopf 1994); promoting cost-sharing conservation practices on private lands should be a dominant strategy to conserve landscapes. Land managers should, however, maintain habitat quality to prevent private agricultural lands from becoming ecological traps for grassland birds by postponing haying until end of breeding season, promoting native vegetation, avoiding use of herbicides and pesticides and impeding encroachment of woody vegetation.

Patch area and edge have strong effects on grassland bird assemblages and occupancy of different guilds within a fragment. Conserving as much continuous grassland as possible should be a target especially for species that are known to be area- and edge-sensitive. Woody edges exert strong influence on grassland bird populations, reducing bird abundance, nest density and increasing rate of predation and parasitism (Johnson and Temple 1986, Johnson and Temple 1990, Winter et al. 2000, Bollinger and Gavin 2004). Fire- and grazing regime alone will not be sufficient to restore grass dominance in these ecosystems, land managers would need drastic measures such as mechanical removal of woody encroachment (Briggs et al. 2005).

Promoting vegetation heterogeneity by generating mosaics of grassland types will benefit grassland bird diversity. Different species and guilds have different habitat and resource requirement depending on their life history. Vegetation heterogeneity can be maintained by burning discrete patches of prairie and allowing selective grazing in burnt and unburnt prairie.

Literature Cited

- Andren, H. 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. *Oikos*:355-366.
- Askins, R. A., F. Chávez-Ramírez, B. C. Dale, C. A. Haas, J. R. Herkert, F. L. Knopf, and P. D. Vickery. 2007. Conservation of Grassland Birds in North America: Understanding Ecological Processes in Different Regions:" Report of the AOU Committee on Conservation". Ornithological Monographs:iii-46.
- Bajema, R. A., and S. L. Lima. 2001. Landscape-level analyses of Henslow's sparrow (*Ammodramus henslowii*) abundance in reclaimed coal mine grasslands. *The American Midland Naturalist* **145**:288-298.
- Bakker, K. K., D. E. Naugle, and K. F. Higgins. 2002. Incorporating landscape attributes into models for migratory grassland bird conservation. *Conservation Biology* **16**:1638-1646.
- Best, L. B., H. Campa III, K. E. Kemp, R. J. Robel, M. R. Ryan, J. A. Savidge, H. P. Weeks Jr, and S. R. Winterstein. 1997. Bird abundance and nesting in CRP fields and cropland in the Midwest: a regional approach. *Wildlife Society Bulletin*:864-877.
- Bollinger, E. K., and T. A. Gavin. 2004. Responses of nesting Bobolinks (*Dolichonyx oryzivorus*) to habitat edges. *The Auk* **121**:767-776.
- Brennan, L. A., and W. P. Kuvlesky Jr. 2005. North American grassland birds: an unfolding conservation crisis? *The Journal of Wildlife Management* **69**:1-13.
- Briggs, J. M., A. K. Knapp, J. M. Blair, J. L. Heisler, G. A. Hoch, M. S. Lett, and J. K. McCarron. 2005. An ecosystem in transition: causes and consequences of the conversion of mesic grassland to shrubland. *BioScience* **55**:243-254.
- Burger, L. D., L. W. Burger Jr, and J. Faaborg. 1994. Effects of prairie fragmentation on predation on artificial nests. *The Journal of Wildlife Management*:249-254.
- Burke, D. M., and E. Nol. 1998. Edge and fragment size effects on the vegetation of deciduous forests in Ontario, Canada. *Natural Areas Journal* **18**:45-53.
- Coppedge, B. R., D. M. Engle, S. D. Fuhlendorf, R. E. Masters, and M. S. Gregory. 2001. Landscape cover type and pattern dynamics in fragmented southern Great Plains grasslands, USA. *Landscape Ecology* **16**:677-690.
- Cunningham, M. A., and D. H. Johnson. 2006. Proximate and landscape factors influence grassland bird distributions. *Ecological Applications* **16**:1062-1075.
- Davis, S. K. 2004. Area sensitivity in grassland passerines: effects of patch size, patch shape, and vegetation structure on bird abundance and occurrence in southern Saskatchewan. *The Auk* **121**:1130-1145.

- Dechant, J. A., M. L. Sondreal, D. H. Johnson, L. D. Igl, C. M. Goldade, M. P. Nenneman, and B. R. Euliss. 2002. Effects of management practices on grassland birds: Grasshopper Sparrow.
- Delisle, J. M., and J. A. Savidge. 1997. Avian use and vegetation characteristics of Conservation Reserve Program fields. *The Journal of Wildlife Management*:318-325.
- Devictor, V., R. Julliard, D. Couvet, A. Lee, and F. Jiguet. 2007. Functional homogenization effect of urbanization on bird communities. *Conservation Biology* **21**:741-751.
- Dias, R. A., V. A. Bastazini, M. S. Gonçalves, F. C. Bonow, and S. C. Müller. 2013. Shifts in composition of avian communities related to temperate-grassland afforestation in southeastern South America. *Iheringia. Série Zoologia* **103**:12-19.
- Dorazio, R. M., and J. A. Royle. 2005. Estimating size and composition of biological communities by modeling the occurrence of species. *Journal of the American Statistical Association* **100**:389-398.
- Dunning, J. B., B. J. Danielson, and H. R. Pulliam. 1992. Ecological processes that affect populations in complex landscapes. *Oikos*:169-175.
- Díaz, M., and E. D. Concepción. 2016. Enhancing the effectiveness of CAP greening as a conservation tool: a plea for regional targeting considering landscape constraints. *Current Landscape Ecology Reports* **1**:168-177.
- Fahrig, L., and G. Merriam. 1985. Habitat patch connectivity and population survival: Ecological archives e066-008. *Ecology* **66**:1762-1768.
- Fisher, R. J., and S. K. Davis. 2010. From Wiens to Robel: a review of grassland □ bird habitat selection. *The Journal of Wildlife Management* **74**:265-273.
- Flather, C. H., and J. R. Sauer. 1996. Using landscape ecology to test hypotheses about large □ scale abundance patterns in migratory birds. *Ecology* **77**:28-35.
- Fletcher Jr, R. J. 2005. Multiple edge effects and their implications in fragmented landscapes. *Journal of Animal Ecology* **74**:342-352.
- Fletcher Jr, R. J., and R. R. Koford. 2002. Habitat and landscape associations of breeding birds in native and restored grasslands. *The Journal of Wildlife Management*:1011-1022.
- Forman, R. T. 1995. Some general principles of landscape and regional ecology. *Landscape Ecology* **10**:133-142.
- Frawley, B. J., and L. B. Best. 1991. Effects of mowing on breeding bird abundance and species composition in alfalfa fields. *Wildlife Society Bulletin (1973-2006)* **19**:135-142.
- Fuhlendorf, S. D., and D. M. Engle. 2001. Restoring heterogeneity on rangelands: ecosystem management based on evolutionary grazing patterns: we propose a paradigm that

- enhances heterogeneity instead of homogeneity to promote biological diversity and wildlife habitat on rangelands grazed by livestock. *BioScience* **51**:625-632.
- Gelman, A., and D. B. Rubin. 1992. Inference from iterative simulation using multiple sequences. *Statistical Science* **7**:457-472.
- Granfors, D. A. 1992. The impact of the Conservation Reserve Program on eastern meadowlark production and validation of the eastern meadowlark habitat suitability index model.
- Haddad, N. M., L. A. Brudvig, J. Clobert, K. F. Davies, A. Gonzalez, R. D. Holt, T. E. Lovejoy, J. O. Sexton, M. P. Austin, and C. D. Collins. 2015. Habitat fragmentation and its lasting impact on Earth's ecosystems. *Science Advances* **1**:e1500052.
- Hamer, T. L., C. H. Flather, and B. R. Noon. 2006. Factors associated with grassland bird species richness: the relative roles of grassland area, landscape structure, and prey. *Landscape Ecology* **21**:569-583.
- Helzer, C. J., and D. E. Jelinski. 1999. The relative importance of patch area and perimeter-area ratio to grassland breeding birds. *Ecological Applications* **9**:1448-1458.
- Herkert, J. R. 1991. An ecological study of the breeding birds of grassland habitats within Illinois. University of Illinois at Urbana-Champaign.
- Herkert, J. R. 1994. The effects of habitat fragmentation on midwestern grassland bird communities. *Ecological applications* **4**:461-471.
- Herkert, J. R. 2002. Effects of management practices on grassland birds: Henslow's Sparrow.
- Herkert, J. R. 2009. Response of bird populations to farmland set-aside programs. *Conservation Biology* **23**:1036-1040.
- Herkert, J. R., D. L. Reinking, D. A. Wiedenfeld, M. Winter, J. L. Zimmerman, W. E. Jensen, E. J. Finck, R. R. Koford, D. H. Wolfe, and S. K. Sherrod. 2003. Effects of prairie fragmentation on the nest success of breeding birds in the midcontinental United States. *Conservation Biology* **17**:587-594.
- Hinkle, D. E., W. Wiersma, and S. G. Jurs. 2003. Applied statistics for the behavioral sciences. Houghton Mifflin College Division.
- Hoekstra, J. M., T. M. Boucher, T. H. Ricketts, and C. Roberts. 2005. Confronting a biome crisis: global disparities of habitat loss and protection. *Ecology letters* **8**:23-29.
- Horn, D. J., R. R. Koford, and M. L. Braland. 2002. Effects of field size and landscape composition on grassland birds in south-central Iowa. *Journal of the Iowa Academy of Science: JIAS* **109**:1-7.

- Hovick, T. J., R. D. Elmore, S. D. Fuhlendorf, D. M. Engle, and R. G. Hamilton. 2015. Spatial heterogeneity increases diversity and stability in grassland bird communities. *Ecological Applications* **25**:662-672.
- Jacobs, R. B., F. R. Thompson III, R. R. Koford, F. A. La Sorte, H. D. Woodward, and J. A. Fitzgerald. 2012. Habitat and landscape effects on abundance of Missouri's grassland birds. *The Journal of Wildlife Management* **76**:372-381.
- Jensen, W. E., and E. J. Finck. 2004. Edge effects on nesting dickcissels (*Spiza americana*) in relation to edge type of remnant tallgrass prairie in Kansas. *The American Midland Naturalist* **151**:192-199.
- Johnson, D. H., and L. D. Igl. 1995. Contributions of the Conservation Reserve Program to populations of breeding birds in North Dakota. *The Wilson Bulletin*:709-718.
- Johnson, M. D. 2007. Measuring habitat quality: a review. *The Condor* **109**:489-504.
- Johnson, R., and S. Temple. 1986. Assessing habitat quality for birds nesting in fragmented tallgrass prairies.
- Johnson, R. G., and S. A. Temple. 1990. Nest predation and brood parasitism of tallgrass prairie birds. *The Journal of Wildlife Management*:106-111.
- Koper, N., and F. K. Schmiegelow. 2006. A multi-scaled analysis of avian response to habitat amount and fragmentation in the Canadian dry mixed-grass prairie. *Landscape Ecology* **21**:1045-1059.
- Leach, M. K., and T. J. Givnish. 1996. Ecological determinants of species loss in remnant prairies. *Science* **273**:1555-1558.
- Lindenmayer, D., W. Blanchard, P. Tennant, P. Barton, K. Ikin, A. Mortelliti, S. Okada, M. Crane, and D. Michael. 2015. Richness is not all: how changes in avian functional diversity reflect major landscape modification caused by pine plantations. *Diversity and Distributions* **21**:836-847.
- Lindenmayer, D. B., and J. Fischer. 2013. *Habitat fragmentation and landscape change: an ecological and conservation synthesis*. Island Press.
- Lituma, C. M., and D. A. Buehler. 2020. Cost-share conservation practices have mixed effects on priority grassland and shrubland breeding bird occupancy in the Central Hardwoods Bird Conservation Region, USA. *Biological Conservation* **244**:108510.
- McLaughlin, M. E., W. M. Janousek, J. P. McCarty, and L. L. Wolfenbarger. 2014. Effects of urbanization on site occupancy and density of grassland birds in tallgrass prairie fragments. *Journal of Field Ornithology* **85**:258-273.
- Murray, L. D., C. A. Ribic, and W. E. Thogmartin. 2008. Relationship of obligate grassland birds to landscape structure in Wisconsin. *The Journal of Wildlife Management* **72**:463-467.

- Naugle, D. E., K. F. Higgins, S. M. Nusser, and W. C. Johnson. 1999. Scale-dependent habitat use in three species of prairie wetland birds. *Landscape ecology* **14**:267-276.
- O'Leary, C. H., and D. W. Nyberg. 2000. Treelines between fields reduce the density of grassland birds. *Natural Areas Journal* **20**:243-249.
- Oksanen, J., F. G. Blanchet, M. Friendly, R. Kindt, P. Legendre, D. McGlinn, P. R. Minchin, R. O'Hara, G. Simpson, and P. Solymos. 2019. *vegan: Community Ecology Package*. R package version 2.5–6. 2019.
- Pereira, H. M., P. W. Leadley, V. Proença, R. Alkemade, J. P. Scharlemann, J. F. Fernandez-Manjarrés, M. B. Araújo, P. Balvanera, R. Biggs, and W. W. Cheung. 2010. Scenarios for global biodiversity in the 21st century. *Science* **330**:1496-1501.
- Perlut, N. G., A. M. Strong, T. M. Donovan, and N. J. Buckley. 2006. Grassland songbirds in a dynamic management landscape: behavioral responses and management strategies. *Ecological Applications* **16**:2235-2247.
- Plummer, M. 2003. JAGS: A program for analysis of Bayesian graphical models using Gibbs sampling. Pages 1-10 *in* Proceedings of the 3rd international workshop on distributed statistical computing. Vienna, Austria.
- Pretelli, M. G., J. P. Isacch, and D. A. Cardoni. 2018. Species-area relationships of specialist versus opportunistic pampas grassland birds depend on the surrounding landscape matrix. *Ardeola* **65**:3-23.
- Quamen, F. R., and D. E. Naugle. 2007. Benefits of the Conservation Reserve Program to Grassland Bird Populations in the Prairie Pothole Region of North Dakota and South Dakota. Final Report to the US Department of Agriculture Farm Service Agency RFA OS-IA-04000000-N34.
- Rahmig, C. J., W. E. Jensen, and K. A. With. 2009. Grassland bird responses to land management in the largest remaining tallgrass prairie. *Conservation Biology* **23**:420-432.
- Ralph, C. J., S. Droege, and J. R. Sauer. 1995. Managing and monitoring birds using point counts: standards and applications. In: Ralph, C. John; Sauer, John R.; Droege, Sam, technical editors. 1995. Monitoring bird populations by point counts. Gen. Tech. Rep. PSW-GTR-149. Albany, CA: US Department of Agriculture, Forest Service, Pacific Southwest Research Station: p. 161-168 **149**.
- Rands, M. R., W. M. Adams, L. Bennun, S. H. Butchart, A. Clements, D. Coomes, A. Entwistle, I. Hodge, V. Kapos, and J. P. Scharlemann. 2010. Biodiversity conservation: challenges beyond 2010. *Science* **329**:1298-1303.
- Renfrew, R. B., and C. A. Ribic. 2008. Multi-scale models of grassland passerine abundance in a fragmented system in Wisconsin. *Landscape Ecology* **23**:181-193.

- Ribic, C. A., R. R. Koford, J. R. Herkert, D. H. Johnson, N. D. Niemuth, D. E. Naugle, K. K. Bakker, D. W. Sample, and R. B. Renfrew. 2009. Area sensitivity in North American grassland birds: patterns and processes. *The Auk* **126**:233-244.
- Ribic, C. A., and D. W. Sample. 2001. Associations of grassland birds with landscape factors in southern Wisconsin. *The American Midland Naturalist* **146**:105-121.
- Robel, R., J. Briggs, A. Dayton, and L. Hulbert. 1970. Relationships between visual obstruction measurements and weight of grassland vegetation. *Rangeland Ecology & Management/Journal of Range Management Archives* **23**:295-297.
- Robinson, G. R., R. D. Holt, M. S. Gaines, S. P. Hamburg, M. L. Johnson, H. S. Fitch, and E. A. Martinko. 1992. Diverse and contrasting effects of habitat fragmentation. *Science* **257**:524-526.
- Rosenberg, K. V., A. M. Dokter, P. J. Blancher, J. R. Sauer, A. C. Smith, P. A. Smith, J. C. Stanton, A. Panjabi, L. Helft, and M. Parr. 2019. Decline of the North American avifauna. *Science* **366**:120-124.
- Russell, R. E., J. A. Royle, V. A. Saab, J. F. Lehmkuhl, W. M. Block, and J. R. Sauer. 2009. Modeling the effects of environmental disturbance on wildlife communities: avian responses to prescribed fire. *Ecological Applications* **19**:1253-1263.
- Samson, F., and F. Knopf. 1994. Prairie conservation in north america. *BioScience* **44**:418-421.
- Sauer, J. R., and W. A. Link. 2002. Hierarchical modeling of population stability and species group attributes from survey data. *Ecology* **83**:1743-1751.
- Sauer, J. R., and W. A. Link. 2011. Analysis of the North American breeding bird survey using hierarchical models. *The Auk* **128**:87-98.
- Shahan, J. L., B. J. Goodwin, and B. C. Rundquist. 2017. Grassland songbird occurrence on remnant prairie patches is primarily determined by landscape characteristics. *Landscape Ecology* **32**:971-988.
- Su, Y.-S., M. Yajima, M. Y.-S. Su, and J. SystemRequirements. 2015. Package 'R2jags'. R Package Version 0.03-08.
- Söderström, B., and T. Pärt. 2000. Influence of landscape scale on farmland birds breeding in semi-natural pastures. *Conservation Biology* **14**:522-533.
- Team, R. C. 2019. R: A Language and Environment for Statistical Computing (Version 3.5. 2, R Foundation for Statistical Computing, Vienna, Austria, 2018).
- Temple, S. A. 2002. Dickcissel: *Spiza americana*. Birds of North America, Incorporated.

- Vickery, P. D., P. L. Tubaro, J. Cardoso da Silva, B. G. Peterjohn, J. R. Herkert, and R. B. Cavalcanti. 1999. Conservation of grassland birds in the western hemisphere. *Studies in Avian Biology* **19**:2-26.
- West, A. S., P. D. Keyser, C. M. Lituma, D. A. Buehler, R. D. Applegate, and J. Morgan. 2016. Grasslands bird occupancy of native warm-season grass. *The Journal of Wildlife Management* **80**:1081-1090.
- Whitmore, R. C. 1981. Structural characteristics of grasshopper sparrow habitat. *The Journal of Wildlife Management* **45**:811-814.
- Wilcove, D. S., C. H. McLellan, and A. P. Dobson. 1986. Habitat fragmentation in the temperate zone. *Conservation Biology* **6**:237-256.
- Winter, M., and J. Faaborg. 1999. Patterns of area sensitivity in grassland-nesting birds. *Conservation Biology* **13**:1424-1436.
- Winter, M., D. H. Johnson, and J. Faaborg. 2000. Evidence for edge effects on multiple levels in tallgrass prairie. *The Condor* **102**:256-266.
- Winter, M., D. H. Johnson, and J. A. Shaffer. 2005. Variability in vegetation effects on density and nesting success of grassland birds. *The Journal of Wildlife Management* **69**:185-197.
- With, K. A., A. W. King, and W. E. Jensen. 2008. Remaining large grasslands may not be sufficient to prevent grassland bird declines. *Biological Conservation* **141**:3152-3167.
- Wright, C. K., B. Larson, T. J. Lark, and H. K. Gibbs. 2017. Recent grassland losses are concentrated around US ethanol refineries. *Environmental Research Letters* **12**:044001.
- Wright, C. K., and M. C. Wimberly. 2013. Recent land use change in the Western Corn Belt threatens grasslands and wetlands. *Proceedings of the National Academy of Sciences* **110**:4134-4139.
- Yahner, R. H. 1988. Changes in wildlife communities near edges. *Conservation Biology* **2**:333-339.
- Zimmerman, J. L. 1988. Breeding season habitat selection by the Henslow's Sparrow (*Ammodramus henslowii*) in Kansas. *The Wilson Bulletin*:17-24.
- Zipkin, E. F., A. DeWan, and J. Andrew Royle. 2009. Impacts of forest fragmentation on species richness: a hierarchical approach to community modelling. *Journal of Applied Ecology* **46**:815-822.
- Zschokke, S., C. Dolt, H.-P. Rusterholz, P. Oggier, B. Braschler, G. H. Thommen, E. Lřdin, A. Erhardt, and B. Baur. 2000. Short-term responses of plants and invertebrates to experimental small-scale grassland fragmentation. *Oecologia* **125**:559-572.

Figures and Tables

Table 1. Summary of species detected in remnant and degraded prairies of Arkansas and Missouri, USA. No. of sites column represents number of sites where the species was detected during point count surveys in 2019.

Common Name	Scientific Name	Species Code	No. Sites
Grassland Obligate Species			
Dickcissel	<i>Spiza americana</i>	DICK	60
Eastern Meadowlark	<i>Sturnella magna</i>	EAME	63
Grasshopper Sparrow [*]	<i>Ammodramus savannarum</i>	GRSP	3
Henslow's Sparrow ^{*†}	<i>Ammodramus henslowii</i>	HESP	18
Grassland Facultative Species			
American Kestrel	<i>Falco sparverius</i>	AMKE	5
Barn Swallow	<i>Hirundo rustica</i>	BARS	37
Brown-headed Cowbird	<i>Molothrus ater</i>	BHCO	26
Cliff Swallow	<i>Petrochelidon pyrrhonota</i>	CLSW	24
Common Yellowthroat	<i>Geothlypis trichas</i>	COYE	42
Eastern Bluebird	<i>Sialia sialis</i>	EABL	25
Eastern Kingbird	<i>Tyrannus tyrannus</i>	EAKI	12
Killdeer	<i>Charadrius vociferous</i>	KILL	8
Mourning Dove	<i>Zenaida macroura</i>	MODO	40
Northern Bobwhite ^{*†}	<i>Colinus virginianus</i>	NOBO	41
Red-Winged Blackbird	<i>Agelaius phoeniceus</i>	RWBL	38
Scissor-tailed Flycatcher	<i>Tyrannus forficatus</i>	STFL	31
Tree Swallow	<i>Tachycineta bicolor</i>	TRES	5
Turkey Vulture	<i>Cathartes aura</i>	TUVU	22
Shrub and Edge Species			
Bell's Vireo ^{*†}	<i>Vireo belli</i>	BEVI	18
Blue Grosbeak	<i>Passerina caerulea</i>	BLGR	11
Brown Thrasher	<i>Toxostoma rufum</i>	BRTH	17
Carolina Wren	<i>Thryothorus ludovicianus</i>	CARW	33
Common Grackle	<i>Quiscalus quiscula</i>	COGR	19
Eastern Towhee [*]	<i>Pipilo erythrophthalmus</i>	EATO	11
Field Sparrow	<i>Spizella pusilla</i>	FISP	27
Gray Catbird	<i>Dumetella carolinensis</i>	GRCA	1
Indigo Bunting	<i>Passerina cyanea</i>	INBU	53
Northern Cardinal	<i>Cardinalis cardinalis</i>	NOCA	56
Northern Mockingbird	<i>Mimus polyglottos</i>	NOMO	47
Painted Bunting [*]	<i>Passerina ciris</i>	PABU	19
Prairie Warbler	<i>Setophaga discolor</i>	PRAW	1
White-eyed Vireo	<i>Vireo griseus</i>	WEVI	7
Yellow-breasted Chat	<i>Icteria virens</i>	YBCH	25
Woodland Species			
American Crow	<i>Corvus brachyrhynchos</i>	AMCR	52
American Goldfinch	<i>Spinus tristis</i>	AMGO	25

Table 1 (contd.). Summary of species detected in remnant and degraded prairies of Arkansas and Missouri, USA. No. of sites column represents number of sites where the species was detected during point count surveys in 2019.

Common Name	Scientific Name	Species Code	No. Sites
American Robin	<i>Turdus migratorius</i>	AMRO	30
Blue-grey Gnatcatcher	<i>Polioptila caerulea</i>	BGGN	7
Blue Jay	<i>Cyanocitta cristata</i>	BLJA	33
Carolina Chickadee	<i>Poecile carolinensis</i>	CACH	8
Cooper's Hawk	<i>Accipiter cooperii</i>	COHA	1
Downy Woodpecker	<i>Picoides pubescens</i>	DOWO	7
Eastern Phoebe	<i>Sayornis phoebe</i>	EAPH	7
Eastern Wood-Pewee*	<i>Contopus virens</i>	EAWP	8
Fish crow	<i>Corvus ossifragus</i>	FICR	6
Great Crested Flycatcher	<i>Myiarchus crinitus</i>	GCFL	2
Mississippi Kite	<i>Ictinia mississippiensis</i>	MIKI	1
Northern Parula	<i>Setophagus americana</i>	NOPA	2
Pileated Woodpecker	<i>Dyrocopus pileatus</i>	PIWO	3
Red-bellied Woodpecker	<i>Melanerpes carolinus</i>	RBWO	25
Red-eyed vireo	<i>Vireo olivaceus</i>	REVI	3
Red-shouldered Hawk	<i>Buteo lineatus</i>	RSHA	6
Red-tailed Hawk	<i>Buteo jamaicensis</i>	RTHA	3
Ruby-throated Hummingbird	<i>Archilochus colubris</i>	RTHU	3
Summer Tanager	<i>Piranga rubra</i>	SUTA	4
Tufted Titmouse	<i>Baeolophus bicolor</i>	TUTI	17
Yellow-billed Cuckoo**†	<i>Coccyzus americanus</i>	YBCU	14
Urban Species			
Chimney Swift*	<i>Chaetura pelagica</i>	CHSW	7
Eurasian Collared-Dove	<i>Streptopelia decaocto</i>	ECDO	9
European Starling	<i>Sturnus vulgaris</i>	EUST	13
House Finch	<i>Haemorhous mexicanus</i>	HOFI	2
Purple Martin	<i>Progne subis</i>	PUMA	7
Rock Pigeon	<i>Columba livia</i>	ROPI	4

* Species of Conservation Concern in Arkansas

† Species of Concern in Missouri

Table 2. Land cover classification scheme using National Land Cover Database (NLCD).

Land cover	NLCD classification	Matrix element description
Grassland	Grassland/Herbaceous	Areas dominated by grammanoid or herbaceous vegetation, generally greater than 80% of total vegetation.
	Pasture/Hay	Areas of grasses, legumes, or grass-legume mixtures planted for livestock grazing or the production of seed or hay crops, typically on a perennial cycle
	Cultivated Crops	Areas used for the production of annual crops, such as corn, soybeans, vegetables, tobacco, and cotton, and also perennial woody crops such as orchards and vineyards. Crop vegetation accounts for greater than 20 percent of total vegetation. This class also includes all land being actively tilled.
Forest	Deciduous Forest	Areas dominated by trees generally greater than 5 meters tall, and greater than 20% of total vegetation cover
	Evergreen Forest	Areas dominated by trees generally greater than 5 meters tall, and greater than 20% of total vegetation cover. More than 75 percent of the tree species maintain their leaves all year. Canopy is never without green foliage.
	Mixed Forest	Areas dominated by trees generally greater than 5 meters tall, and greater than 20% of total vegetation cover.
Developed	Developed, Open Space	Includes areas with a mixture of some constructed materials, but mostly vegetation in the form of lawn grasses.
	Developed, Low Intensity	Includes areas with a mixture of constructed materials and vegetation. Impervious surfaces account for 20-49 percent of total cover. These areas most commonly include single-family housing units.
	Developed, Medium Intensity	Includes areas with a mixture of constructed materials and vegetation. Impervious surfaces account for 50-79 percent of the total cover. These areas most commonly include single-family housing units
	Developed, High Intensity	Includes highly developed areas where people reside or work in high numbers. Examples include apartment complexes, row houses and commercial/industrial. Impervious surfaces account for 80 to 100 percent of the total cover.

Table 3. Factor loadings and percentage of variance explained by the first two principal components (PC) axes for a) vegetation-specific variable and b) sample-specific variables expected to influence occupancy and detection, respectively, of avian assemblage in Tallgrass prairies of Arkansas and Missouri, USA. Bold figures indicate variables with highest loading.

Vegetation Covariates		
Principal Components	1	2
Eigen values	3.14	2.38
% of variation	44.89	33.96
Cumulative % of variation	44.89	78.85
Variables (Eigen Vectors)	PC1	PC2
Vegetation height	-0.16	0.69
Litter Depth	0.84	0.45
% Litter	0.91	0.37
% Bare	-0.91	-0.37
% Grass	0.60	-0.73
% Forbs	-0.61	0.69
% Dead	-0.13	0.64
Sampling Covariates		
Principal Components	1	2
Eigen values	1.98	1.11
% of variation	37.55	22.23
Cumulative % of variation	37.55	59.79
Variables (Eigen Vectors)	PC1	PC2
Julian Date	0.20	0.92
Minutes from sunrise	0.63	-0.13
Temperature	0.74	0.31
Windspeed	0.60	-0.38
Humidity	-0.73	0.13

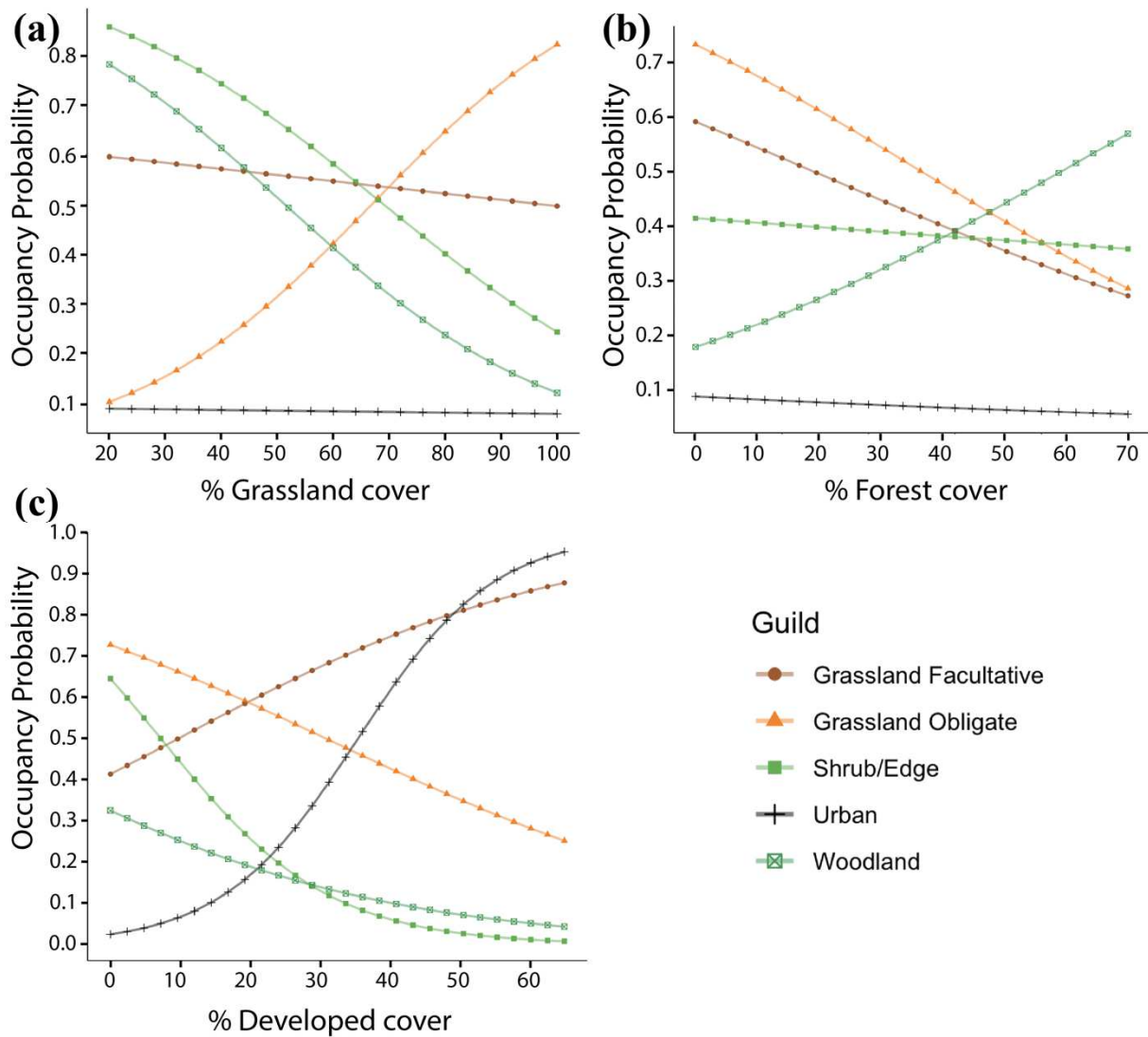


Figure 1. Relationship between guild-specific occupancy probability and (a) percent grassland cover (b) percent forest cover, and (c) percent developed cover within a 1000 m radius of a site in the fragmented Tallgrass prairie landscape in Arkansas and Missouri, USA.

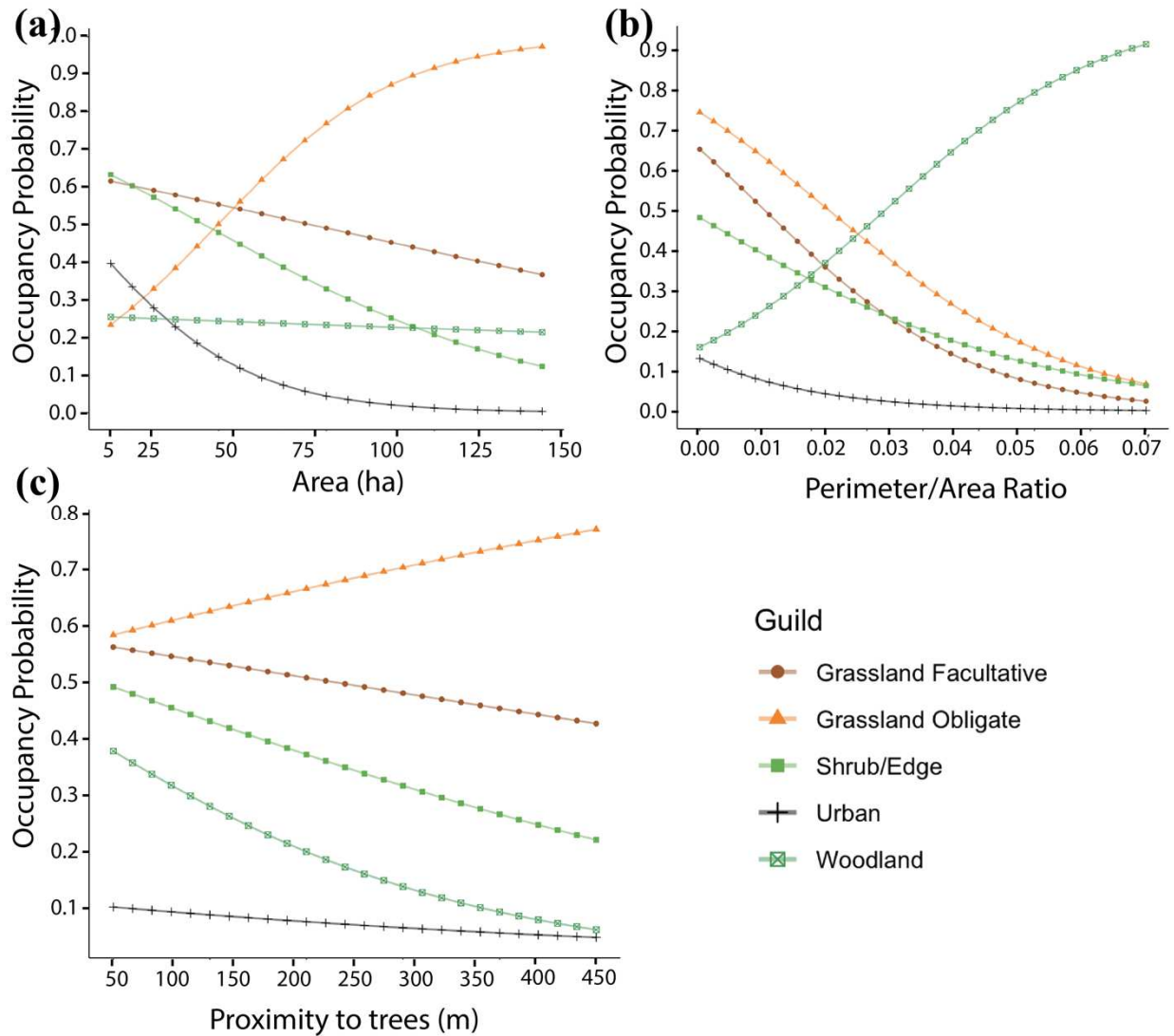


Figure 2. Relationship between guild-specific occupancy probability and (a) patch area (b) perimeter-to-area ratio, and (c) proximity to trees of a site in the fragmented Tallgrass prairie landscape in Arkansas and Missouri, USA.

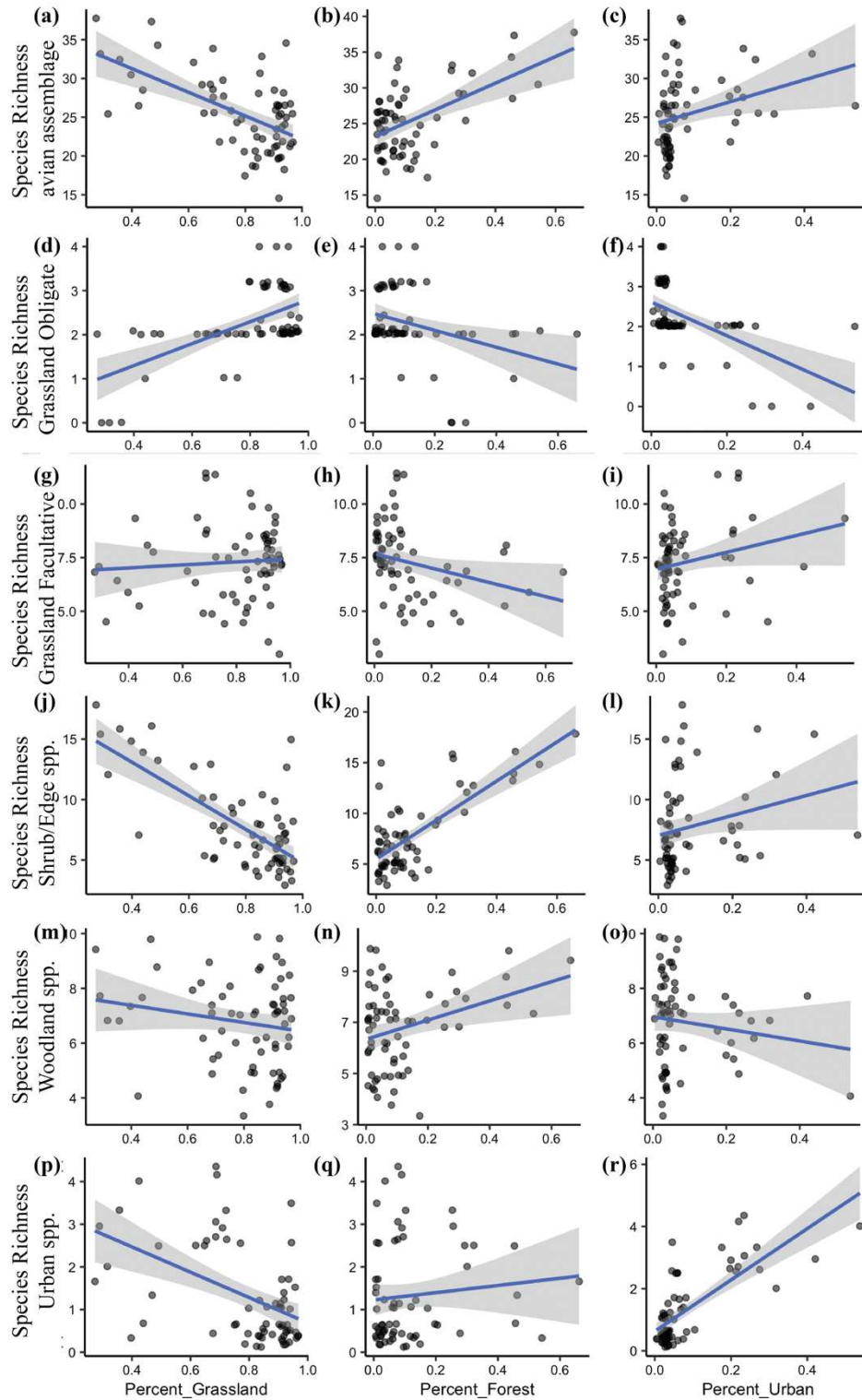


Figure 3. Effect of percent land cover type: grassland, forest or developed cover, on mean species richness of (a,b,c) whole avian assemblage, (d,e,f) grassland obligate species, (g,h,i) grassland facultative species, (j,k,l) shrub or edge species, (m,n,o) woodland species, and (p,q,r) urban species species

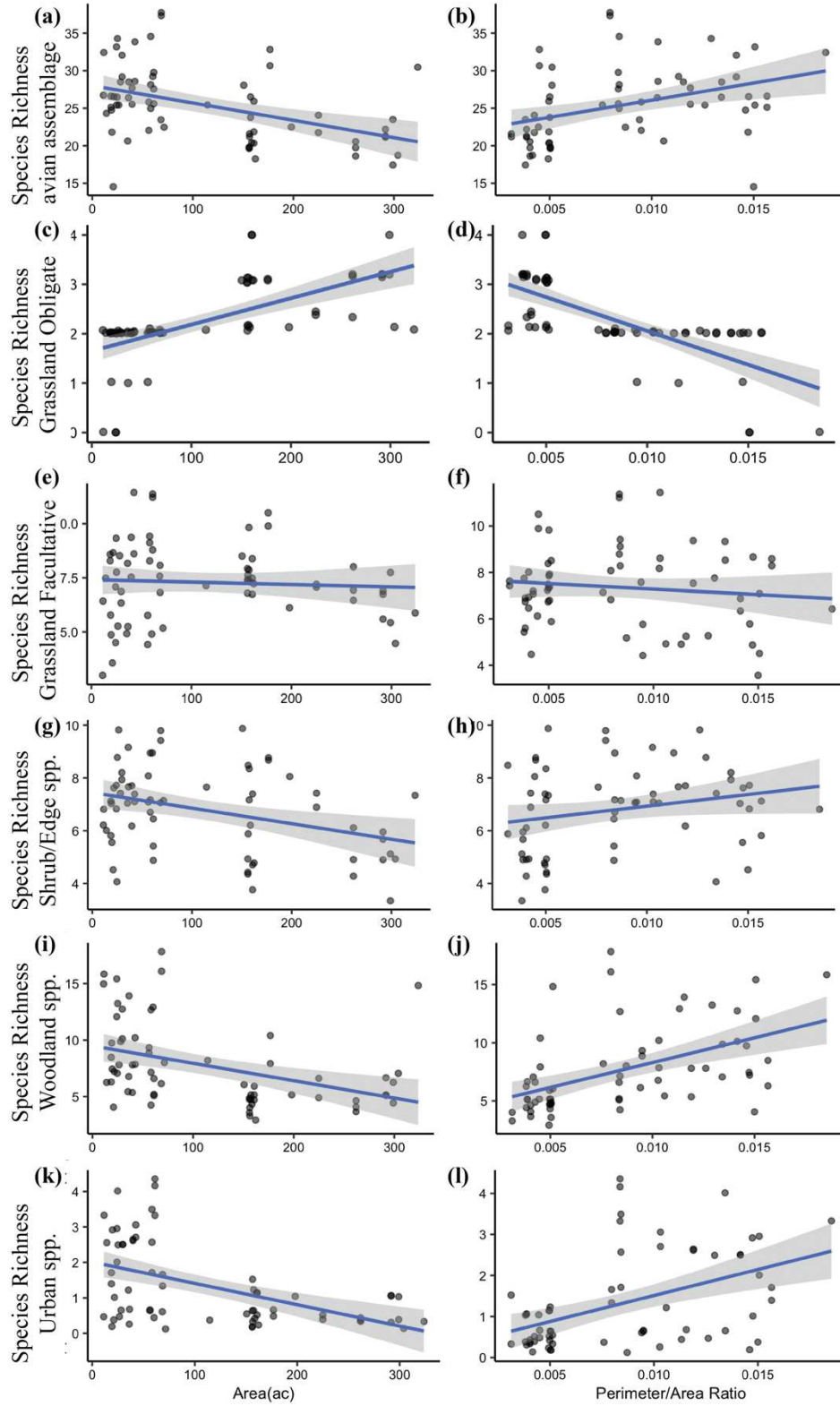


Figure 4. Effect of patch area and perimeter-to-area ratio on species richness of (a,b) whole avian assemblage, (c,d) grassland obligate species, (e,f) grassland facultative species, (g,h) shrub or edge species, (i,j) woodland species, and (k,l) urban species species.

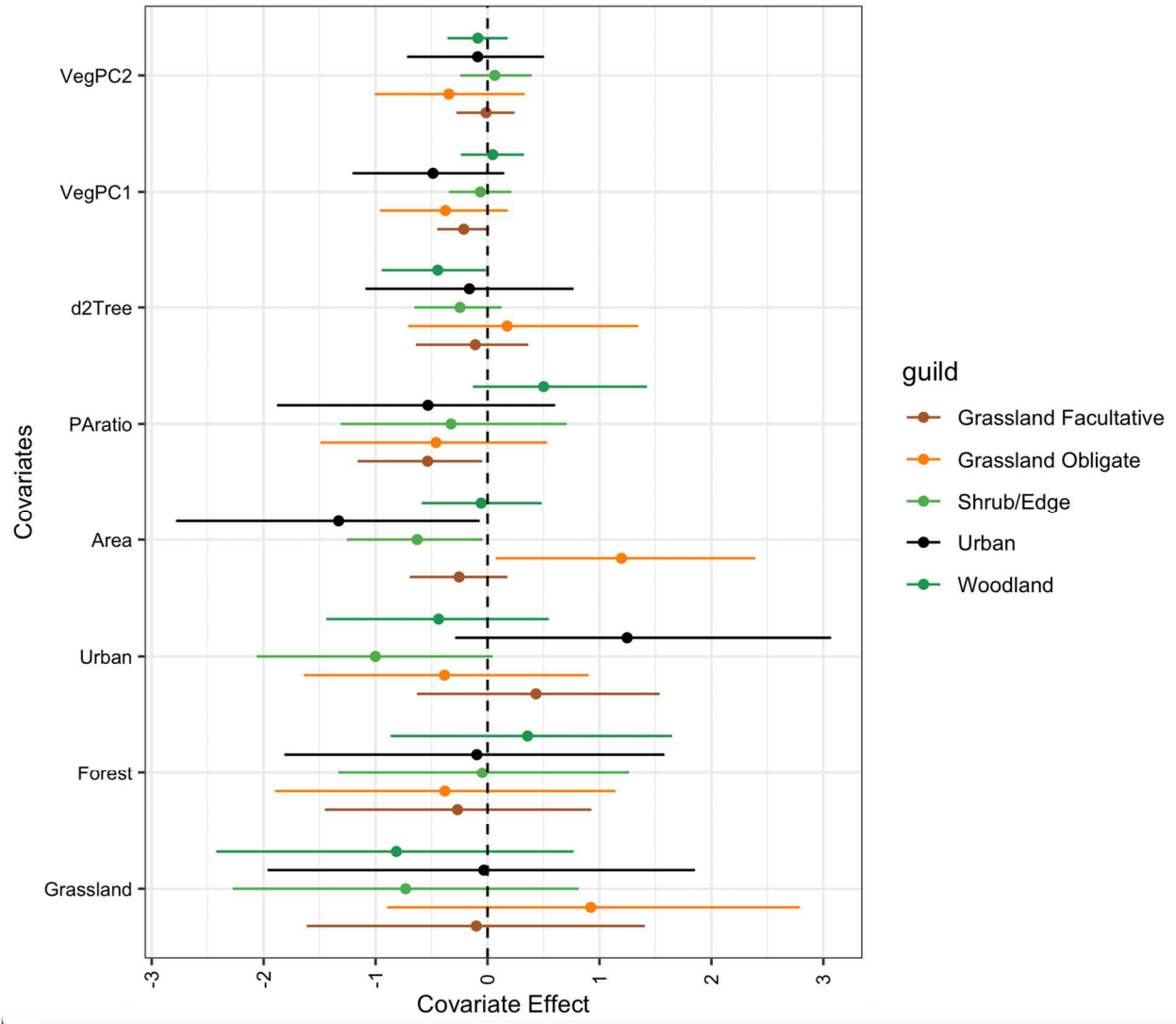


Figure 5. Estimates of alpha parameters with 95% Bayesian credible interval on effects of percent grassland cover, forest cover, and developed cover within 1000 m radius, patch area, perimeter-to-area ratio (PAratio), proximity to trees (d2Tree), and vegetation PC1 and PC2 on guild-specific occupancy probability.

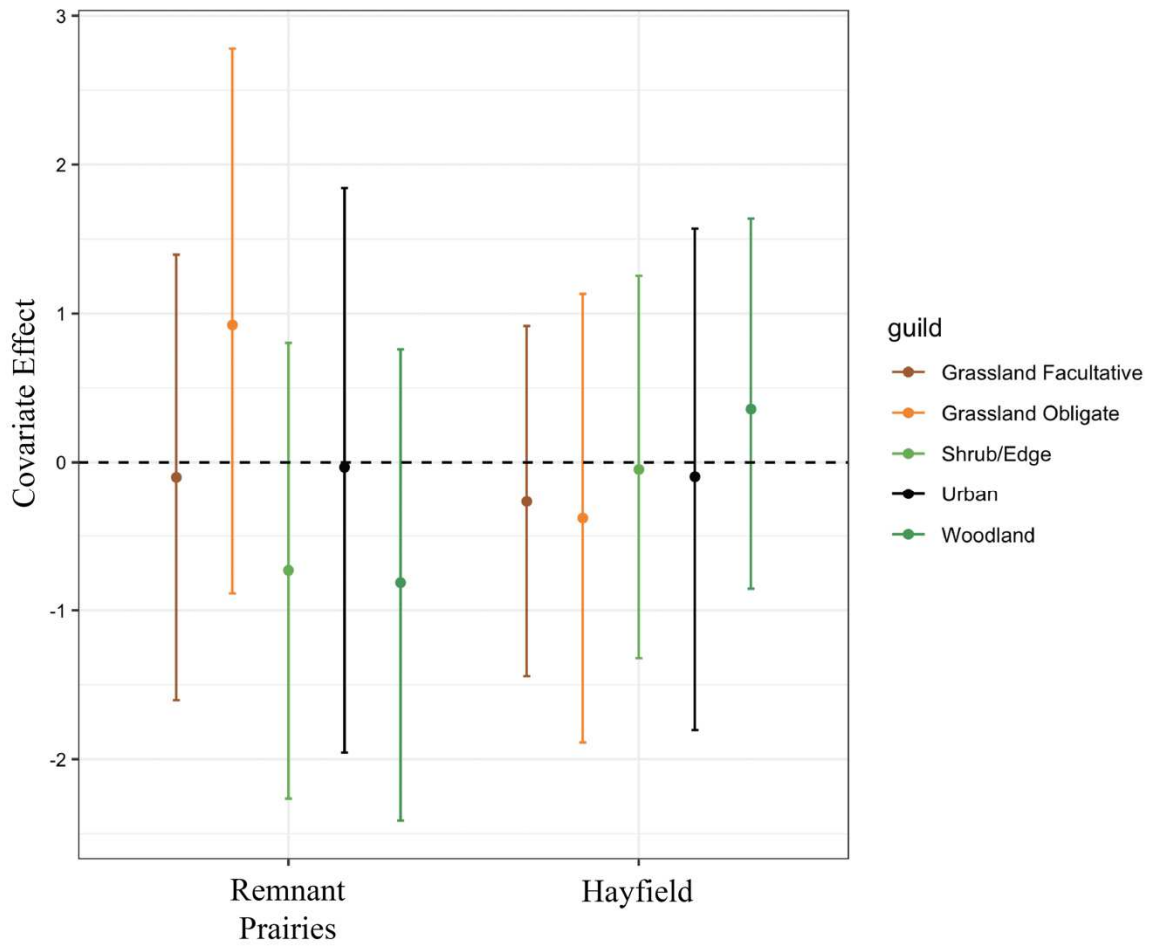


Figure 6. Effect of habitat type covariate on guild-specific occupancy probabilities of grassland birds in Tallgrass prairies of Arkansas and Missouri, USA.

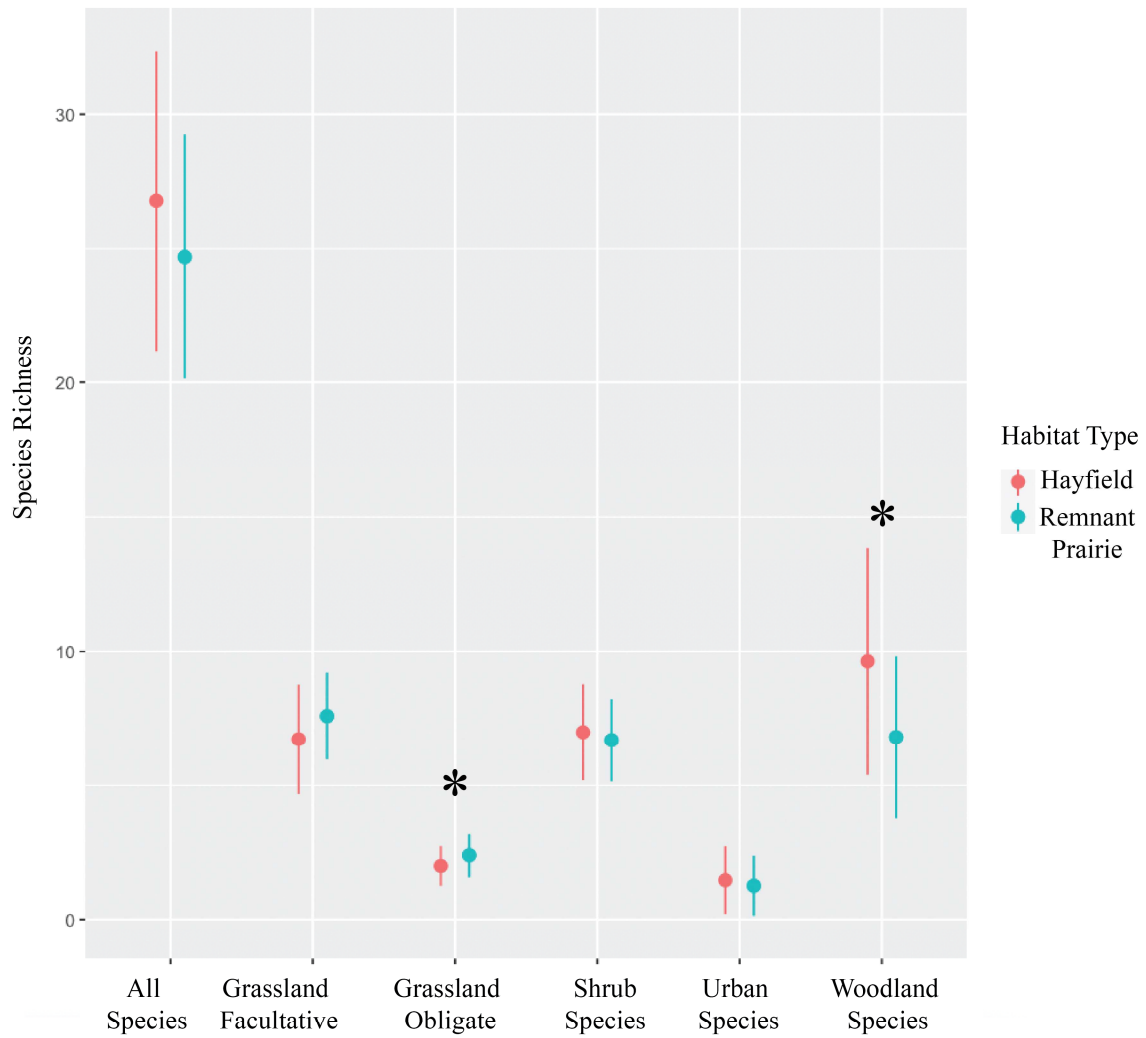


Figure 7. Estimated mean species richness of the whole avian assemblage and guilds in the two habitat types: remnant prairies and hayfields. Significant differences between guild-specific species richness between the two habitat types is indicated by an asterisk (*).

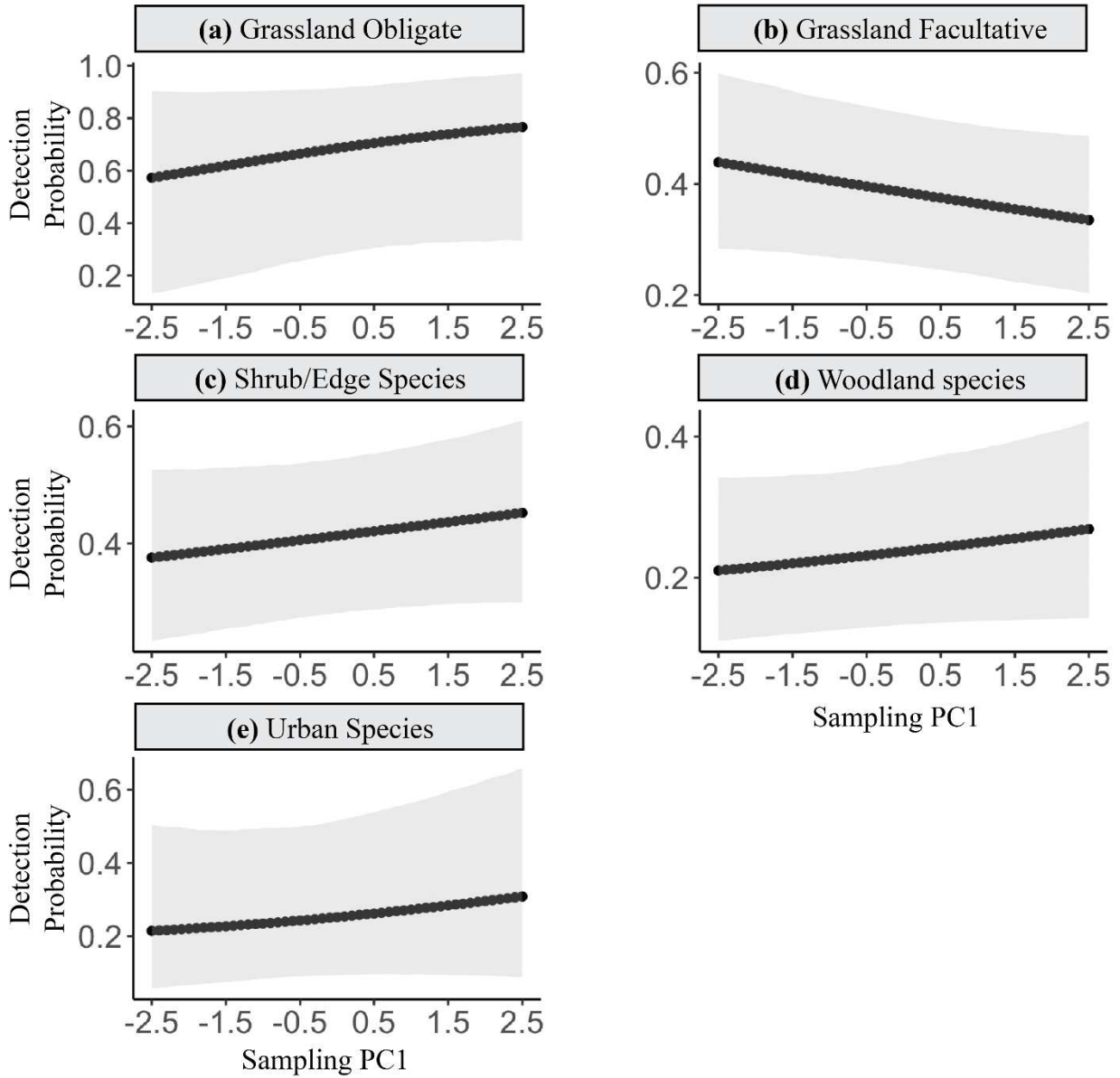


Figure 8. Effect of sampling PC1 on guild-specific detection probability. Sampling PC1 indicates environmental condition i.e. time since sunrise, increasing temperature and decreasing humidity. Detection probability of (a) Grassland Obligate, (b) Grassland Facultative, (c) Shrub and Edge species, (d) Woodland, and (e) Urban species as a response to sampling PC1.

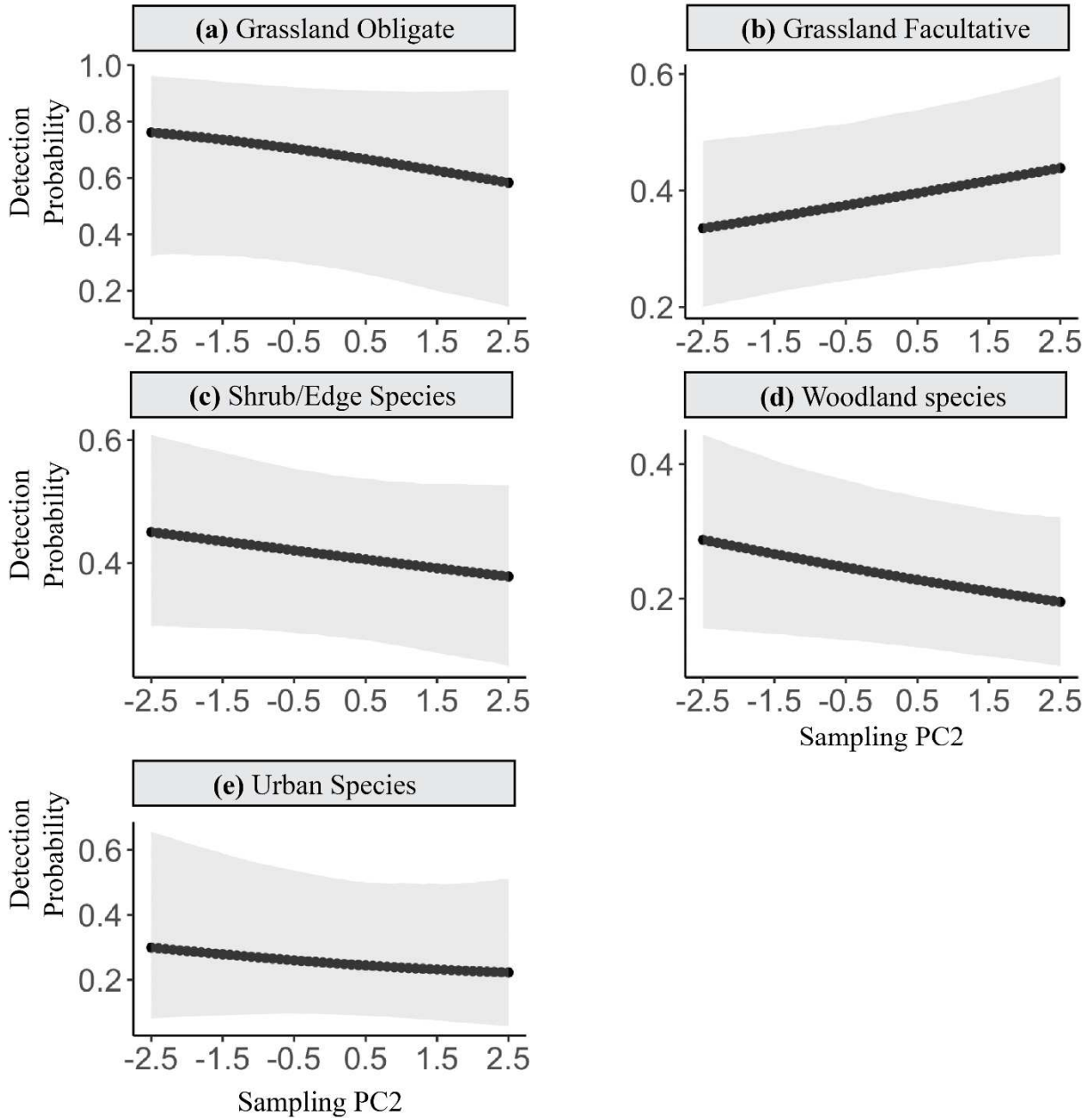


Figure 9. Effect of sampling PC2 on guild-specific detection probability. Sampling PC2 indicates Julian date. Detection probability of (a) Grassland Obligate, (b) Grassland Facultative, (c) Shrub and Edge species, (d) Woodland, and (e) Urban species as a response to sampling PC2.

Conclusion

Grasslands are one of the most imperiled ecosystems on the earth. Fragmented grasslands embedded within anthropogenically-modified landscape matrix have substantial effects on grassland bird populations mediated by factors operating at multiple spatial scales. In this thesis, I had examined the effect of local- and landscape-scale elements on composition of grassland avian assemblage and guild-level occupancy patterns in the fragmented Tallgrass prairies of Arkansas and Missouri, USA. We recommend habitat management strategies and landscape-level conservation plans based on our results.

Our application of multi-species occupancy models (MSOM) found support for the effects of landscape- and local-scale factors on guild-specific and species-specific occupancy and species richness of grassland bird assemblages and guilds. Overall, the landscape-scale factors (landcover, patch area, and perimeter-to-area ratio) were much stronger drivers of occupancy patterns of the avian community than the local-scale factors (habitat type, proximity to trees, and vegetation structure) in the fragmented Tallgrass prairies of Arkansas and Missouri. The avian assemblage richness was higher for heterogenous landscape, small patches, and patches with more edge habitat. The avian assemblage in these sites had a lower proportion of habitat specialists (grassland obligate) and higher proportion of habitat generalists. For grassland obligate species, high grassland cover, low forest cover, large patch area, less edge habitat, and low litter depth had strong positive effects on their occupancy and guild-level species richness at a site. For grassland facultative species, highly developed cover around a site, small patch size, high edge habitat, and low litter depth had strong positive effects on their occupancy and guild-level species richness at a site. For woodland species, low grassland cover and high forest cover around a site, small patch, and high edge habitat had strong positive effects on their occupancy

and guild-level species richness. Urban species had higher occupancy for sites with high developed type land cover within 1 km buffer and increased edge habitat. Collectively, our results indicate that 1) response to local- and landscape-scale factors varies between the guilds 2) habitat specialists are negatively affected by habitat fragmentation.

Conservation efforts should focus on conserving landscapes with large tracts of prairies and reduced edge habitat. Consequently, preventing further land development and woody encroachment in remaining large prairies is crucial to reversing the rapid declines that grassland birds are currently experiencing. We found that hayfields and other agricultural lands can provide secondary habitat to grassland birds. Hence, agricultural practices (such as haying) could be postponed until end of breeding season, promoting native vegetation, avoiding use of herbicides and pesticides and impeding encroachment of woody vegetation in these agricultural lands could help grassland bird populations. Different species and guilds have different habitat and resource requirement depending on their life history. Promoting vegetation heterogeneity within available habitat through burning discrete patches of prairie and allowing selective grazing in burnt and unburnt prairie will benefit grassland bird diversity.