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IDENTIFYING LANDSCAPE-LEVEL TRENDS IN PRAIRIE SONGBIRDS WITH FRAGMENTED HABITATS

by

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Bachelor of Science, Randolph-Macon Women's College, 2008

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This thesis submitted by Jessica Lynn Shahan in partial fulfillment of the requirements for the Degree of Master of Science from the University of North Dakota, has been read by the Faculty Advisory Committee under whom the work has been done and is hereby approved.

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ABSTRACT

Grassland songbirds are experiencing significant population declines due to habitat loss and degradation. This study investigated the relationship between landscape-level patterns and prairie-level patterns in presence/absence, richness, and diversity for seven individual species, the total grassland songbird community, and three community subgroups. Overall, grassland songbirds did respond to landscape-level variables, although the strength of the relationship and the variables involved differed by species and functional group.

CHAPTER I

INTRODUCTION: LANDSCAPE ECOLOGY AND ITS APPLICATIONS TOWARD GRASSLAND SONGBIRD CONSERVATION

Landscape ecology is key to understanding patterns and processes associated with both individual species and ecological communities. Landscape ecologists seek to decipher the associations between biological processes and the spatial relationships of landscape-level elements. This study uses bird abundances, landscape-scale, and local-scale measurements to identify changes in grassland songbird species occurrence and community structure based on differences in local prairie quality and the landscape composition and structure surrounding remnant native prairies.

Grassland Habitat Declines and the Impacts on Grassland Songbird Populations

Grassland songbirds live on one of the most threatened habitat types in the world (Hoekstra et al., 2005). In North America, more than 70% of the Great Plains has been converted to agriculture and other forms of development (Samson et al., 2004). This loss is especially dramatic in the northern plains, where the tallgrass prairie has declined by 99% from its historic range (Samson and Knopf, 1994). These declines impact the plants and animals that rely on grasslands, as illustrated by the grassland songbird community. Overall, grassland birds have seen the largest declines of any group of birds in North America, with 48% of grassland obligates listed as being of conservation concern and 55% showing significant population declines (North American Bird Conservation

Initiative, 2009). Analysis of the North American Breeding Bird Survey shows that 86% of grassland species showed negative or neutral population trends between 1999 and 2003 (Pardieck and Sauer, 2007). Even species considered common or abundant have been impacted, including Savannah Sparrows (*Passerculus sandwichensis*) and Western Meadowlarks (*Sturnella neglecta;* Igl and Johnson, 1997).

While it is clear that these declines are linked to habitat loss, a large part is also due to fragmentation and habitat degradation. Direct habitat loss leads to population declines by forcing individuals into smaller habitat patches and limiting resource availability. Multiple species (including Bobolinks [*Dolichonyx oryzivorus*], Clay-colored sparrows [*Spizella pallida*], Grasshopper Sparrows [*Ammodramus savannarum*], and Western Meadowlarks) demonstrate patch size preferences, although the type and magnitude of the effects varies between species and studies (Winter and Faaborg, 2000; Johnson and Igl, 2001; Davis, 2004; Davis et al., 2006, Ribic et al., 2009). Some variation may be due to different life history traits (preferred habitats or migratory status), but such variation does not alter the fact that direct habitat loss alters grassland songbird populations (Bender et al., 1998).

Some population declines result from habitat fragmentation and associated changes in habitat quality. Fletcher (2005) found that the probability of Bobolink occurrence increased with distance from the patch edge. Strong negative relationships have also been demonstrated between perimeter-area relationships and the abundances of several grassland bird species (Helzer and Jelinski, 1999), while smaller fragments have been found to support lower grassland songbird richness (Herkert, 1994). As the remaining prairies shrink in size, perimeter-area ratios increase and the distance to an edge from any given point on the prairie decreases. These smaller prairie fragments become less suitable for birds with strong edge-avoidance behaviors, and result in greater decreases in habitat availability than would be expected with direct area loss.

Fragmentation also changes population dynamics and predation rates. A review of existing studies by Stephens et al. (2003) found evidence for fragmentation effects on nesting success at several different spatial scales. At the same time, Herkert et al. (2003) identified increased nest predation rates with decreasing prairie fragment size. Higher incidence of nest parasitism by Brown-headed Cowbirds (*Molothrus ater*) has also been documented on smaller grassland fragments, with the probability of parasitism increasing with decreasing distance to the fragment edge (Johnson and Temple, 1990; Davis, 1994; Patten et al., 2006). As prairie patches decrease in size, breeding songbird are exposed to more nest predators and parasites, which reduce reproductive success. When combined with a smaller area of breeding habitat, the challenges to nest success put additional pressure on already threatened populations.

Even in those regions where agricultural conversion and fragmentation have not been as extensive, the grasslands that remain are often heavily invaded by exotic grass and forb species (Cully et al., 2003). With et al. (2008) found that populations of three common prairie songbirds (Dickcissel, Grasshopper Sparrow, and Eastern Meadowlark-*Sturnella magna*) were demographically non-viable at the regional scale based on fecundity estimates in one of the largest remaining tallgrass prairies. They concluded that much of the grassland in their study region was being degraded by current land use practices and was no longer of high enough quality to prevent further population declines (With et al., 2008). Therefore, remaining grassland fragments are no longer equal in quality to the historic grasslands that were present before extensive agricultural development.

Using Landscape Ecology to Promote Grassland Songbird Conservation

Future grassland songbird conservation efforts should include landscape information to augment our understanding of the habitat patch-based processes that are influencing populations, especially when considering highly mobile grassland songbirds. Daily foraging means birds are moving around the landscape, especially when feeding and nesting sites are separated (Hutto, 1985). Birds are also exposed to and use multiple landscapes and matrix elements as they move between their breeding and wintering grounds during migration (Moore et al., 1995; Rodewald and Brittingham, 2007). In North Dakota alone, more than half the grassland bird species are at least short-distance migrants (Igl and Johnson, 1997), meaning that a large portion of the grassland songbird community is exposed to the landscapes surrounding remnant prairies every year.

In areas where the landscape is full of grassland-like matrix elements, migrating grassland songbirds might be expected to display stronger responses. Migrating birds might find a matrix element with similar structure to the grasslands that they normally breed in and choose to either settle there for breeding or use it as a stop-over location. If the area has good resources, this could encourage additional breeding or ensure that the birds have enough energy to reach a given remnant prairie. If the area has poor resources or is routinely disturbed, such as might be seen in a hay field, the birds could be negatively impacted. With these potential influences, grassland songbird conservation will benefit from quantifying these landscape-scale effects.

Multiple studies have addressed the issue of landscape effects on grassland songbirds, and these studies demonstrate several commonalities. Many of the studies are species specific, focusing on anywhere from one (e.g. Bajema and Lima, 2001) to twelve species (e.g. Horn and Koford, 2006). Species are analyzed independently and measurements incorporated into the final models are population-oriented (population density: Bakker et al., 2002; Winter et al., 2006; relative abundance: Haire et al., 2000; Horn et al., 2002; Renfrew and Ribic, 2008; Jacobs et al., 2012; nest success: Grant et al., 2004; Patten et al., 2006). These results make it difficult to easily manage grasslands for multiple grassland songbird species at a time, which reduces their applicability in this time of limited conservation resources.

These studies also typically include only a few variables, the majority of which measure landscape composition elements (either specific matrix elements or generalized habitat categories). Many have emphasized woody cover (Coppedge et al., 2001; Grant et al., 2004; Cunningham and Johnson, 2006), while other studies have examined grasslands only (Bakker et al., 2002; Horn and Koford, 2006; Ribic et al., 2009). Of those studies using multiple matrix elements, landscape characterization is often based on percent cover rather than matrix element configuration (Bergin et al., 2000; Söderström and Pärt, 2000; Best et al., 2001; Ribic and Sample, 2001; Fletcher and Koford, 2002; Veech, 2006; Quamen, 2007). Fewer studies have looked at configuration via edge or connectivity measures (Fletcher and Koford, 2002; Hamer et al., 2006; Koper and Schmiegelow, 2006).

There is also variation in landscape definition, with the majority of studies using landscape radii of 2 km radius or less (Bergin et al., 2000; Bajema and Lima, 2001; Ribic and Sample, 2001; Grant et al., 2004; Jacobs et al., 2012), despite the high mobility of songbirds. While it is true that daily breeding or feeding territories may not be as large as 2 km, there is a hierarchical process by which migrating grassland songbirds narrow down and identify the specific locations in which they will spend their breeding seasons (Cody, 1981). Because of this, it is necessary to investigate larger spatial scales to include all factors that influence patch-level patterns of occurrence, abundance, richness, and diversity. It is also important to note that a study of prairie beetles found significant landscape effects out to 800 m (Fischer, 2006). If an organism so much smaller than the typical prairie songbird experiences effects to that extent, it seems logical that larger and more mobile songbirds are going to be impacted at even greater scales.

Earlier landscape studies have also delineated the landscape in different ways, which has implications for being able to separate true landscape-level effects from patch-level effects. A common method of landscape definition is to center the landscape on a point at the center of a point count or transect (Best et al., 2001; Coppedge et al., 2001; Bakker et al., 2002; Fletcher and Koford, 2002; Winter et al., 2006). Other studies have used landscapes centered on the mid-point of a breeding bird survey route (Hamer et al., 2006; Veech et al., 2006). These buffered-point studies may not be measuring their landscape data in a way that matches bird use. The point-based technique, while easy to apply, limits the landscape sampling area, particularly on very small grasslands (Fig. 1). For example, a 15 ha focal patch buffered with a 100 m radius buffer around a single central point might not include any area that is not part of the focal patch itself. As a result, most of the detected effects would actually be habitat-based, making it difficult to separate local habitat variability effects from landscape effects.

Some studies have tried to address these methodological issues by using a focal patch-based approach, where landscape buffers were applied starting at the edges of the study patch (Söderström and Pärt, 2000; Cunningham and Johnson, 2006; Renfrew and Ribic, 2008; Ribic et al., 2009), allowing for a clear separation between habitat and landscape-level measurements. There have also been studies that investigated spatial scales greater than 2 km (Koper and Schmeigelow, 2006; Veech et al., 2006; Quamen 2007). However, none of these studies have addressed all of the possible issues in one place. The focal patch studies are smaller in scale and may not extend far enough into the landscape to capture all of the potential influences that birds experience. Those studies that do have larger scales looked primarily at the composition of the landscape (such as percent grassland cover or tree cover) with less attention paid to how the components in the landscape are arranged. Their landscape measurements are typically at courser scales, compromising their ability to detect landscape effects that derive from finer-scale patterns.

This variability in existing methodologies and study designs has led to mixed conclusions regarding the influences of the landscape on grassland songbird populations. Many studies have identified landscape effects (Söderström and Pärt, 2000; Ribic and Sample, 2001; Bakker et al., 2002; Hamer et al., 2006; Winter et al., 2006; Renfrew and Ribic, 2008), but others have found little to no effect (Horn et al., 2002; Bajema and Lima, 2003; Koper and Schmeigelow, 2006; Jacobs et al., 2012). There are also studies that fall into a middle category, where combining models with both landscape and local variables created stronger models than either variable category separately (Fletcher and Koford, 2002; Cunningham and Johnson, 2006; Quamen, 2007). One review of landscape studies identified landscape effects in less than 80% of the bird-focused studies (Mazerolle and Villard, 1999). Another review found that bird studies were least likely to demonstrate landscape effects, even though birds were one of the most frequently studied taxa (Thornton et al., 2011).

Island Biogeography Theory and Evolving Applications for Terrestrial Systems

As discussed above, landscape ecology can provide new insights into population and community patterns. However, it is important to understand how the discipline has evolved from its early roots to where it stands today. In 1967, MacArthur and Wilson published a landmark theory describing patterns of species richness on island archipelagoes (MacArthur and Wilson, 1967). In this theory, the number of species present on an oceanic island is a function of the rate of immigration of new species onto the island from a mainland source and the rate of extinction of those species already on the island (MacArthur and Wilson, 1967). Where these two rates intersect represents the equilibrium number of species found on that island. (MacArthur and Wilson, 1967). The theory also states that islands of differing sizes and distances from a mainland will have different immigration and emigration rates and thus different equilibrium points (MacArthur and Wilson, 1967).

After the theory's publication, biologists saw clear applications toward terrestrial ecosystems. Early research saw habitat fragments as islands in a sea of inhospitable matrix (Freemark and Merriam, 1986; Blake and Karr, 1987; Robbins et al., 1989). In these studies, the landscape is viewed as a binary system where the fragments are the only habitat capable of sustaining the target species' life history requirements. The land surrounding the fragments (containing multiple matrix element types) cannot support the target species and has no impact on fragment-based dynamics (Haila, 2002). These studies typically focus on measures of fragment structure, including fragment area, perimeter-area ratios, and distance between fragments (Lynch and Whigham, 1984; Blake and Karr, 1987; Hamazaki, 1996; Bolger et al., 1997; Helzer and Jelinski, 1999; Magura et al., 2001; Hill and Curran, 2003).

While these studies have contributed significantly to our understanding of fragmented systems, it is important to consider fragment context. Landscape ecology provides the link to that context by examining patterns in the composition (total amount of area) and configuration (relative shapes and arrangement of separate patches) of secondary matrix elements and land uses surrounding fragments of interest. Different landscape elements can influence how species move between habitat fragments (Chardon et al., 2003; Marsh et al., 2005; Gillies and St. Clair, 2008). When taken together, these elements create an overall measure of connectivity in the landscape and can limit or support movement between suitable habitat patches (Taylor et al., 1993). Such connectivity variation results in richness and diversity variation even between fragments of similar size and shape.

Landscape supplementation and complementation can also alter richness and diversity. In a supplementation situation, alternative matrix elements may provide adequate substitute habitat that support populations at higher densities than expected given the resources of the habitat fragment, or they may represent sink habitats that remove individuals from the population (Dunning et al., 1992; Pickett and Rogers, 1995). At the same time, some matrix elements may have negative impacts on species by creating sinks that cause local extinctions and alter the number of individuals in the landscape (Ritchie, 1997). In complementation, meanwhile, nearby like habitat patches provide a critical resource threshold that allows a species to survive on an otherwise deficient habitat patch (Dunning et al., 1992; Choquenot and Ruscoe, 2003).

While resource availability is important for understanding landscape-level patterns, it is also important to understand how population dynamics play a role. Classic metapopulation theory classifies the landscape in a binary manner, with habitat patches suitable for breeding embedded in a matrix of unsuitable but permeable habitat (Levins, 1968). Within this network of suitable patches, some are occupied by breeding populations and others are waiting to be colonized (Hanski et al., 1995). All breeding populations are subject to potential extinctions that open habitat patches to subsequent colonization events from the patches with current breeding populations (Hanski et al., 1995). Therefore, individual movement through the landscape and the presence of suitable breeding habitat patches are of the utmost importance for species displaying metapopulation patterns.

For habitat specialists unable to locate the resources necessary for survival on non-breeding patches, metapopulation dynamics become important for predicting focal patch occupancy in highly fragmented landscapes. In these situations, small breeding habitat patches may be unable to support large populations. These small populations have greater risks from environmental or genetic stochasticity (Shaffer, 1981), and if there is not a breeding population nearby in the landscape the habitat patch may never be recolonized. At the same time, a small habitat fragment may support a population because of higher breeding patch density nearby. Landscape ecology studies should include data about focal habitats within the landscape to take any potential metapopulation dynamics into account.

Landscape ecology can contribute to biodiversity conservation by establishing an understanding of landscape-scale influences on richness and diversity. While some species may respond well to management based on the island biogeography principles of patch size and isolation (Samson, 1980), others have demonstrated landscape-context sensitivity (Andrén, 1994; Horn and Koford, 2006). As such, local-level management alone may not be sufficient, and multiple calls have been made for a realignment of management toward landscape scales (Wiens, 1994; Rodewald, 2003). While the landscape effects described above are occurring at a species-level, they can alter community-level richness and diversity by influencing species abundance and distribution. Increasing our understanding of how these two levels interact will improve management for individual species while allowing management techniques to address the needs of the entire community instead of patch sensitive species only.

Moving forward, it is important to recognize areas of landscape ecology that continue to be developed. We have made significant progress toward understanding landscape-level patterns associated with forest species and communities (Blake and Karr, 1987; Andrén, 1992; Freemark and Collins, 1992; McGarigal and McComb, 1995; Villard et al., 1999; Lee et al., 2002), but have paid less attention to grassland habitats. Since many forest species may be unable to survive in a non-forested area, forests lend themselves well to the idea of suitable habitat patch vs. inhospitable matrix. However, it may be unrealistic to extrapolate the lessons learned in this system to other habitat types, particularly grasslands. As grasslands around the world decline from agricultural conversion and development (Hoekstra et al., 2005), the species that depend on them are increasingly exposed to novel habitats. It is well understood that grassland species are sensitive to vegetation structure (Cody, 1985) and may be able to use habitats with similar structure that they encounter in the landscape. As such, it is important to understand the unique landscape patterns associated with grasslands and their dependent communities.

The Importance of a Community Approach to Landscape Ecology

While many studies have analyzed the patterns of individual species (e.g. Rotenberry and Knick, 1999; Naugle et al., 1999; Bajema and Lima, 2001; Renfrew and Ribic, 2008), community studies can add to our understanding of landscape-level properties. Communities can be loosely defined as a collection of species that share a common space, while physically defined communities are those collections of species that can be consistently found in a certain type of habitat (Morin, 2011). Each community consists of multiple functional groups containing at least two species that meet the defining characteristic of the functional group (such as habitat preference or feeding methods; Morin, 2011). Because communities are made of multiple species, each with their own requirements for food, shelter, and breeding resources, communities are potentially influenced by a wide range of variables. For physically-defined communities, landscape ecology can provide insight into factors influencing community composition.

Landscapes consist of multiple habitat types with distinct sets of resources. These resources dictate which species are found within the landscape and their relative abundances. Habitat complementation and supplementation can influence communities at a landscape scale by altering the available resources for birds living on a given habitat patch, and means that the presence of different habitat types in the landscape alters the potential species pool using the habitat patch from the species present if the patch was isolated.

While the landscape directly influences the species assemblage, interspecific processes (competition, territoriality, and predation) can also influence community structure. Competition occurs when resources on a habitat patch are scarce and can change both species occurrence and abundance. Intraspecific competition reduces population density through increased dispersal or mortality rates (Stiling et al., 1984; Matthysen, 2005), as conspecifics compete for identical resources. Meanwhile, interspecific competition between species with similar ecological niches can result in one species edging out another and limiting the overall richness of the community (Fraser, 1976; Bengtsson, 1989). Similarly, territorial species may lower overall richness by forcing less competitive species off the habitat patch (Downes and Bauwens, 2002; Parr, 2008). Finally, nest parasites and predatory species may have direct negative consequences on other species' populations (Schmidt and Whelan, 1999; Smith et al., 2002).

Metacommunity theory investigates questions related to sets of communities connected through the dispersal actions of interacting species (Leibold et al., 2004). This theory can provide a framework for understanding community-based patterns across multiple landscape scales. Habitat patch and landscape-level resources dictate which species are able to use the landscape, while species interactions can limit the number of species from that original pool that are actually present at a particular site. At the same time, resource configuration and composition may influence how species move through the landscape, resulting in differential patterns of patch colonization and altering the final richness and diversity levels observed on focal patches. This community approach to landscape ecology (considering all species instead of one or a small subset) takes these multiple interactions into account, helping to clarify differences between seemingly identical habitat patches.

Identifying Trends at the Landscape Level: Focal Patch Methods and Terminology

As scientists investigate the effects of landscape variables on grassland populations, metapopulations, communities, and metacommunities, it is important to measure processes at the appropriate scales. This means having a clear, biologically relevant definition of what constitutes habitat vs. landscape, as established using the focal patch approach.

The focal patch methodology uses landscapes centered on a specific patch of contiguous homogenous habitat, with the boundaries of the landscape starting at the edges of the patch and excluding the patch itself (Brennan et al., 2002; Fig. 1B). This ensures that landscape-level measurements are measuring processes in the landscape instead of those occurring on the focal patch (as is seen in studies where sampling points are buffered, as in Fig. 1A; e.g. Best et al., 2001; Coppedge et al., 2001; Bakker et al., 2002; Fletcher and Koford, 2002; Hamer et al., 2006; Veech et al., 2006; Winter et al., 2006. Focal patch methods ensure independence between landscape samples, allowing studies to include landscapes with a range of structures and secondary habitat types (Brennan et al., 2002).

Previous landscape-level research has used variable vocabulary, but focal patch studies lend themselves to a specific terminology. In this study, "habitat" is the focal patch on which sampling was performed and represents the scale at which the biological response (richness, diversity, or presence/absence) is measured. Focal patch (local) measurements are designed to assess differences in focal patch habitat quality that might influence biological response. This information is crucial for separating landscape effects from focal patch resource variation-related patterns. Uneven resource distribution alters how individuals within a community disperse themselves through the habitat patch, resulting in uneven local-scale distributions. These patterns must be taken into account even when focusing on landscape scales. In this study, local-level variables measured focal patch vegetation type and structure. These variables influence birds during habitat selection (Cody, 1981; Madden et al., 2000; Fisher and Davis, 2010) and help shape the community on each focal patch.

The "landscape" surrounds the focal patch. Landscape variables come in two varieties: those associated with the landscape as a single unit (aggregate landscape variables) and those associated with specific habitats within that unit (matrix elements). As discussed above, each of these aggregate or matrix element variables may be responsible for resource supplementation or complementation and should be taken into account when attempting to understand relationships between patch-level processes and their surrounding landscapes.

Multiple composition and configuration measurements can be made at the aggregate landscape level. Composition-based measurements are based on the number of different types of habitats and their relative amounts, and can be measured most simply using total richness (the number of different habitat types in the landscape; McGarigal et al., 2002). While useful, this measurement does not convey relative proportion information. Habitat evenness describes how proportional the relative amounts of each habitat type are, but excludes richness information (Rey-Benayas and Pope, 1995; Magurran, 2004). While both of these measures can be useful, incorporating both richness and evenness into a single index provides a consolidated picture of each landscape and allows for simpler comparisons between them. Diversity indices include both habitat richness and evenness (Magurran, 2004; Hendrickx et al., 2007).

In this study, I used total richness and the Shannon Diversity Index to quantify landscape composition. Total richness allowed the landscapes to be placed along a simple gradient of low to high number of habitats, then was refined by incorporating the evenness component of the Shannon Diversity Index. In this index, a diversity value is calculated by summing the proportional abundance of each habitat type, weighted by that proportion (Shannon and Weaver, 1949). This index increases with increasing habitat richness or as the relative habitat areas become more evenly distributed. Previous work has found that the index t is sensitive to rare habitat types (Magurran, 2004), but it has been used widely in landscape ecology (Weibull et al., 2000; Krauss et al., 2003; Oindo and Skidmore, 2003) and allows for cross-study comparisons.

While landscape composition is important, configuration-based measurements focus on patch arrangement within the landscape regardless of habitat type.

Configuration plays a role in individual movement through the landscape and can alter landscape suitability for species. Connectivity is strongly related to landscape configuration (Taylor, et al., 1993). Focal patch species assemblage is dictated by the birds/ ability to reach the patch, and certain patch configurations or shapes may help or hinder that process. Species' dispersal ability can be limited by hostile matrix elements or barriers like roads and rivers (Carr and Fahrig, 2001; Hayes and Sewlal, 2004). Meanwhile, corridors linking habitat patches allow movement between patches and potential colonizations (Haddad, 2000; Dunning et al., 1995). Patch shape may also influence movement by altering edge densities, particularly for edge sensitive species. Large, uniformly shaped patches have a lower perimeter-area ratio (with lower edge densities) than small, irregularly shaped patches (Helzer and Jelinski, 1999). Edge avoiders may not disperse well through a landscape with many small or irregularly shaped patches, while species that use edge habitat may not be able to find enough resources in landscapes with only a few large habitat patches.

Given the edge sensitivity of many grassland songbirds (DeLisle and Savidge, 1996; Jensen and Finck, 2004; Fletcher, 2005; Conover et al., 2011), I used configuration measurements that emphasize the amount of edge and their aggregate landscape-level distributions (total edge density, landscape contagion). These two measures have been described as redundant (Hargis et al., 1997), but contagion provides a rough corollary for connectivity by estimating aggregation of similar matrix elements within the landscape. Contagion is calculated by measuring the probability that two adjacent cells of a raster data set are the same matrix element type (McGarigal et al., 2002). Low contagion values indicate a higher probability that a patch of one habitat type is located next to a different habitat patch, while high values show a high concentration of similar matrix elements (O'Neill et al., 1988; Li and Reynolds, 1993). As such, measuring contagion provides insight into the ability of species (particularly edge sensitive species) to move between habitat patches. Total edge density, meanwhile, fails to take into account relative closeness of similar habitat patches. Instead, it is calculated simply as the total length of edge relative to the area of the habitat patch (McGarigal et al., 2002). It can be used to identify differences in landscapes based on patch shape, as landscapes with many small, irregular patches will have a higher edge density than landscapes with only a few large or rounded patches (Hargis et al., 1997).

Matrix element variables (non-focal patch habitats and land uses) also measure habitat composition (how much area they cover) or configuration (how they are arranged within the landscape), but each matrix element is measured independently of the others in the landscape. At this level, composition is a function of the amount of area covered by each matrix element rather than overall richness or diversity. Composition measures are important for grassland songbirds with minimum-threshold sensitivities (Grant et al., 2004). If a matrix element is commonly used by grassland songbirds, it is possible to estimate the amount of alternative habitat available for resource complementation and supplementation. If the matrix element decreases survival odds, composition may be a measure of population sinks or predator sources (Grant et al., 2006; Perlut et al., 2008).

Matrix element configuration is also important. By measuring the patch number, median area, and patch density, it is possible to understand how matrix elements are distributed. Matrix elements present as a single contiguous area may have different effects than matrix elements that are broken into smaller patches with more edges and less core area (Turner et al., 2001). Patch density was included to standardize patch number by landscape area. This metric is calculated by dividing the number of patches by the area of the total landscape extent, which varies between replicates in the focal patch approach (McGarigal et al., 2002).

Additional metrics were used to measure patch isolation and the amount of matrix element-specific edge. Isolation alters matrix element connectivity and changes grassland songbirds' patch use. When patches are farther apart, individuals with limited dispersal ability or facing many dispersal barriers (Moore et al., 2008) may be unable to reach new focal patches. In this study, I assessed patch isolation using median Euclidean nearest neighbor distance based on the straight line distance between patches of the same matrix element type (McGarigal et al., 2002). Matrix element edge density was included because of its ability to modify patch use (O'Leary and Nyberg, 2000) and predator or nest parasite occurrence (Johnson and Temple, 1990; Patten et al., 2006). This variable was measured at the aggregate landscape level but was also included at the matrix element scale because different edge types show different response signs or magnitudes. Dickcissels (*Spiza americana*), for example, have experienced different rates of nest parasitism based on their proximity to either wooded or cropland edges (Jensen and Finck, 2004). If this pattern holds true for other species or communities, including matrix element-specific information may help to clarify previously observed edge sensitivity trends.

Summary

As discussed above, grassland songbirds face significant declines and many efforts are being made to understand their causes. My study seeks to improve their conservation by addressing unanswered questions and clarifying conflicting results left by previous landscape-level studies. The focal patch methodology allows for a clearer identification of local verses landscape-level effects. Meanwhile, using larger and multiple scales makes it easier to isolate the extent of landscape effects and the scales at which individual variables are most strongly felt. When combined with a multi-model approach that identifies which variables have the strongest influences, these methods ensure that my study includes a more comprehensive collection of landscape measures. With this information, it will be possible to understand the relationship between landscape patterns and the richness and diversity of grassland songbird communities and the occurrence of individual species within that community. This will make it possible to improve conservation efforts and minimize future population declines.

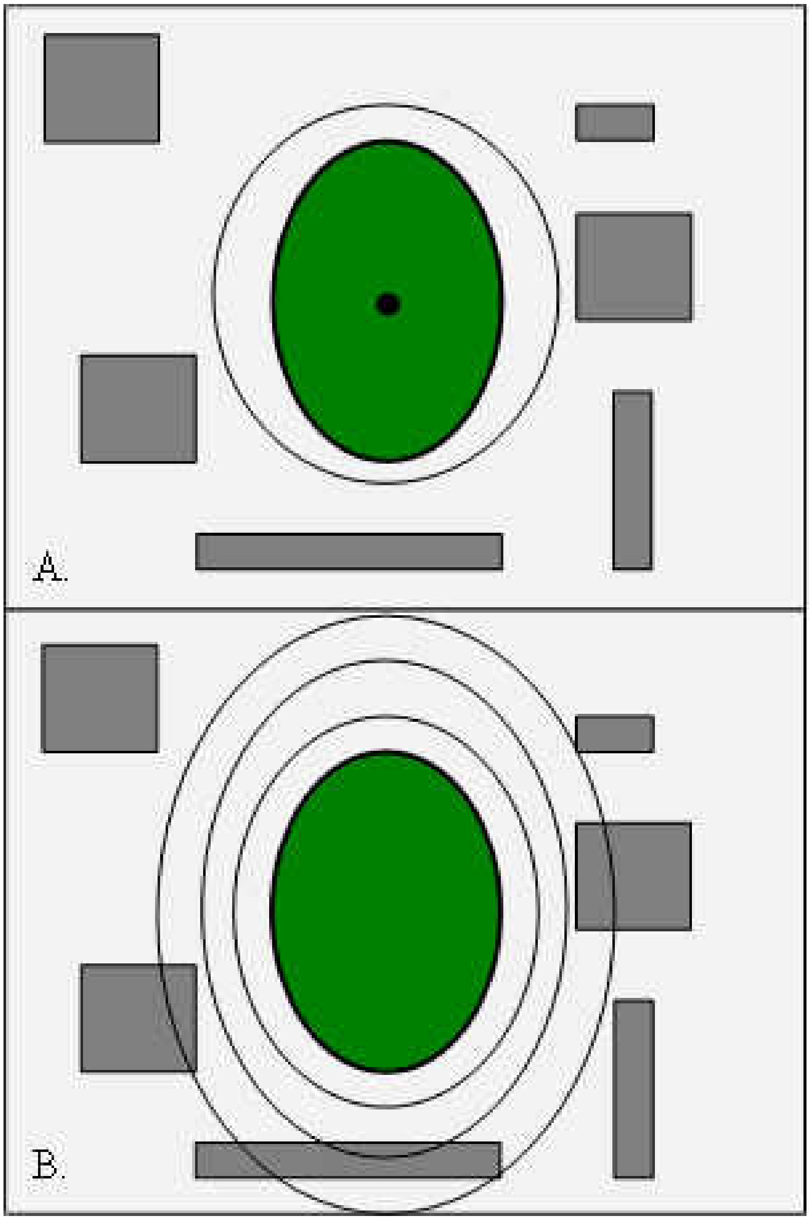


Figure 1. Previous buffered layouts vs. the current study design. Landscape A represents studies in which a point count (within the boundaries of a prairie) is buffered, whereas Landscape B shows a buffered focal patch in which more of the surrounding landscape is actually included in the sample.

CHAPTER II

PREDICTING GRASSLAND SONGBIRD OCCURRENCE FROM LANDSCAPE-LEVEL DATA AND LIFE HISTORY TRAITS

Introduction

Over the last century, North America's grasslands have experienced increasing pressures from agricultural expansion and increasing urbanization. The Great Plains have been heavily impacted with almost 70% of historic grassland range lost (Samson et al., 2004). This loss is especially dramatic in the northern plains, where less than 1% of the original tallgrass prairie remains (Samson and Knopf, 1994).

Such losses have not been without consequences for prairie species. North American grassland songbirds are experiencing the fastest population declines compared to any other group of birds on the continent (Samson and Knopf, 1994). From 1968 to 2008, 37% of grassland obligate species declined (Sauer and Link, 2011), while only 14 to 18% experienced population growth (Sauer et al., 2003; Pardieck and Sauer, 2007). Even common species like Savannah Sparrows (*Passerculus sandwichensis*) and Clay-colored Sparrows (*Spizella pallida*) have experienced declines in at least a part of their range (Igl and Johnson, 1997).

In the face of these declines, much research has been done to identify the forces acting at the habitat patch level upon grassland songbird populations. This includes the more obvious effects of habitat loss and fragmentation (Herkert, 1994; Bender et al., 1998; Helzer and Jelinski, 1999; Johnson and Igl, 2001; Davis, 2004; Fletcher, 2005) and less obvious effects on prairie fragment quality and vegetation structure (O'Leary and Nyberg, 2000; Cully et al., 2003; Davis, 2005; With et al., 2008). Multiple species have been identified as area or edge sensitive (DeLisle and Savidge, 1996; Winter et al., 2000; Jensen and Finck, 2004; Koper et al., 2009) and responsive to specific vegetation or structural features (Whitmore, 1981; Davis et al., 1999; Winter et al., 2005; Jacobs et al., 2012). All of this information has been integrated into management plans for individual species based on their specific requirements and sensitivities (Dechant et al., 1998; Dechant et al., 1999b) or for prairie songbirds as a group (Madden et al., 2000; Walk and Warner, 2000).

These details, while important, overlook the fact that prairie fragments do not exist in isolation. Instead, they are surrounded by a range of matrix elements present in differing amounts and configurations. These provide a variety of resources or threats to birds moving through the landscape, and each has the potential to influence which species make their way onto remnant prairie patches. Research has found that matrix elements are capable of providing secondary habitat (Johnson, 2000), altering predation or parasitism rates (Borgmann and Rodewald, 2004; Patten et al., 2006), and influencing dispersal ability (Haas, 1995). All of these factors can potentially impact the species found on prairie patches, but few studies have analyzed them (Rodewald, 2003). Despite the limited attention paid to matrix effects, one review of 104 landscape-level studies of multiple taxa found that the type of matrix surrounding focal patches influenced species richness or abundance 95% of the time (Prevedello and Vieira, 2010). Given these results, future efforts to manage remnant prairies must also include an understanding of the landscapes that they are embedded in.

However, landscape-level effects may not be identical across all songbirds. Each species has its own specialized suite of resources needed for foraging and reproduction, and these resources may dictate how that species responds to a particular element in the landscape. Similarly, individual species' dispersal patterns and avoidance behaviors can also influence their responses at the landscape level. These behaviors and needs may also influence the distances at which those landscape influences are manifest. This study seeks to identify landscape-level patterns in songbird occurrence arising from the species-specific behaviors and resource requirements described above. Understanding these relationships will make it possible to predict which species could occupy a given prairie remnant embedded in a specific type of landscape. Being able to identify a potential pool of species that should be present on a prairie is useful in discerning those remnant prairie patches with grassland songbird communities that are not as large or diverse as they should be, making it easier to identify prairies whose bird communities need additional management efforts.

At the same time, connecting landscape patterns to life history traits allows for extrapolation of trends to species with similar resource requirements (such as habitat guilds or functional groups). For example, if a particular species that uses ground nests shows avoidance behaviors in the presence of woody vegetation, it may be possible that other species of ground-nesting birds respond to woody vegetation in a similar fashion. Identifying such connections between species behaviors and life history traits would permit the development of management techniques that are suitable for more than a single target species and would make it easier to maximize conservation resources. These patterns could also be used to identify prairies on which particular groups of species are at risk or in need additional of management attention. A previous study found that it is possible to predict forest bird community responses to landscape changes using species' life history traits (Hansen and Urban, 1992), and it makes sense to try incorporating the same kinds of information into grassland songbird management.

Methods

The Focal Patch Approach

I used a focal-patch approach that differs from some of the previous landscape studies of songbirds (Fig. 1A; e.g. Ribic and Sample, 2001; Bakker et al., 2002; Kalinowski and Johnson, 2010). I defined the focal patch as the extent of the contiguous native prairie in a given area (Fig. 1B), allowing the analysis to separate effects that are truly the result of the surrounding landscape from those that derive from local characteristics surrounding the census unit. Through this method, each prairie patch and surrounding landscape represents an experimental unit in the analysis and replication occurs at the landscape level rather than the habitat level (Brennan et al., 2002). This is an important distinction because most prairie management techniques (such as grazing or prescribed burning) occur at the patch or management unit-level instead of being centered on a point or transect within the patch or management unit (Fig. 1A).

Most grassland songbirds migrate at least short distances every year (Igl and Johnson, 1997). As they return from their wintering grounds, the birds must identify prairie patches on which to establish breeding territories. This process is hierarchical, as birds are influenced by different factors at progressively smaller scales as they narrow their range of movement from large (migratory movements) to small (establishing nesting or feeding territories; Johnson, 1980; Hutto, 1985). As such, occupancy patterns may ultimately begin at larger scales and could be missed by studies at smaller scales. To capture this effect, I used a larger scale (4 km) than most of the previous landscape studies of grassland songbirds, which looked no farther than 2 km into the landscape (Jacobs et al., 2012; Bajema and Lima, 2001; Bergin et al., 2000; Ribic and Sample, 2001; Grant et al., 2004). Two kilometers may seem large, but a study of prairie-dwelling beetles found that landscape effects extended out to 800 m from the prairie boundary (Fischer, 2006). If beetle-sized organisms experience landscape effects at that scale, then larger and likely more vagile birds should be influenced at even greater distances.

Although I would have liked to use even larger buffers than 4 km, the amount of time needed to digitize larger buffered areas was prohibitive. Some studies have looked at larger scales than this one, but they either focused on species density and nest success (Koper and Schmeigelow, 2006), relied on buffered Breeding Bird Survey routes (Veech et al., 2006), or used a regional method of bird surveying rather than the focal patch methodology of this study (Horn et al., 2002; Horn and Koford, 2006; Quamen, 2007).

Site Selection

I selected native, unplowed prairie fragments located in western Minnesota and eastern North and South Dakota, owned and/or managed by The Nature Conservancy, Minnesota Department of Natural Resources, U.S. Fish & Wildlife Service, or the University of North Dakota. All sites were separated by a minimum of 8 km between prairie edges to ensure independent landscape data for each focal patch. Where potential sites were within 8 km of each other, I eliminated the prairie that was closest in size to already selected sites. If both sites were of similar size, I chose the one with the landscape that was least similar to those that had already been selected, based on proportions of woody vegetation, grass, agriculture, and open water. Prairies were also excluded if they were scheduled for burning or grazing management during the 2-year study period. From this narrowed list, I chose prairies to represent a wide range of fragment sizes and landscape compositions (ranging from agriculture dominated to grass dominated; see Appendix A: Landscape Maps). Through this selection process, I identified 29 separate sites (Fig. 2), ranging in size from approximately 7 to 1,181 ha, with a median of 67.5 ha (IQR= 36.7 – 237.9 ha; Table 1). Total landscape composition ranged from 0.3- 65% grass, (median= 8.1%, IQR= 5.7- 20.8%), 19.1- 97.7% agriculture (median = 68.2%, IQR= 59.8- 79.1%), and 0.5- 25.8 % woody vegetation (median = 2.1%, IQR= 1.5-5.5%).

Bird Counts

I conducted bird counts during the songbird breeding season, from mid- late May through mid-July (5/13/2010 – 7/15/2010, 5/15/2011 – 7/15/2011). These counts took place from dawn until approximately 10:30 to 11:00 am, at the time when the birds were most active and vocal and on days when the weather conditions were best for hearing and seeing birds (wind speeds less than 32 kph, minimal precipitation; Bibby et al., 1992). I sampled each site twice during each field season, except when weather conditions and flooding limited access. Seven sites were surveyed twice in 2010, and 26 sites were surveyed twice in 2011.

Each count used a linear transect that allowed sampling of significant portions of each prairie while minimizing the amount of time spent sampling (Gibbons et al., 1996; Anderson and Ohmart, 1981). Transect length was dictated by prairie fragment size. For the smallest fragments (7 – 40 ha), I used 400 m of transect, as this was the longest amount of transect that would fit on the smallest field site. I used 1,200 m of transect on the largest sites (≥ 161 ha), which was the longest amount of transect that could be surveyed in a single morning and still leave enough time to visit multiple sites per day. Sites between 41 and 161 ha were assigned 800 m of transect, both because that length represented a middle ground between the smallest and largest sites and because that length of transect fit well on the majority of the medium-sized fragments.

I placed each transect at least 100 m from the edge of the prairie, to avoid edge effects that might influence the bird community (Fletcher, 2005). In two cases, prairie fragments were shaped so that a standard-length transect would not fit and still be at least 100 m from the prairie's edges. For these two sites, I used shortened transects (700 m and 750 m) that extended as far as the shape of the prairie would allow. I plotted transects as a single straight line, unless the size of the prairie or the placement of wetlands prevented it. In these cases, I used multiple smaller transects that added up to the total transect length dictated by fragment area (Gates, 1981). Each of these smaller transects were placed at least 300 m apart to avoid double counting birds (Davis, 2004; Koper and Schmiegelow, 2006).

I walked each transect at a steady pace and recorded all birds seen or heard within 50 m on either side of the transect. I only recorded birds flying over the transect if they actually landed on the focal patch or were observed foraging aerially above it. For each bird that was sighted, I noted the species and distance from the beginning of the transect, as determined by a hand-held GPS unit accurate to 3 m (Garmin eTrex H Handheld

Navigator). I also noted birds seen using the prairie while I was on the way to or from the transect in case they represented species that were not seen along the transect.

Measuring Local Patch Characteristics

I used vegetation measurements to identify local differences in habitat quality that might influence bird occupancy on the prairie patch. I used a Robel pole to quantify vegetation height and structure (Robel et al., 1970) at points every 100 m along the transect starting at the beginning of the transect. For each Robel pole reading, I placed the pole 1 m to the right of the transect, to avoid the vegetation that had been disturbed by earlier movement along the transect and took measurements at each of the cardinal directions (determined by a hand-held GPS unit) around the Robel pole.

I also performed visual estimates to assess the relative percentages of grasses, forbs, trees, shrubs, and bare ground along each transect. I chose these characteristics because of their potential influence on the bird species assemblage due to variations in habitat selection, foraging or nesting resources, predation, and parasitism (Dion et al., 2000; Davis, 2004; Grant et al., 2004; Davis, 2005; Fisher and Davis, 2010). I applied a 5 m boundary to either side of the transect, so that cover types were estimated across a 10 m wide section of prairie. I chose this width because 10 m to either side was approximately the distance at which it became difficult to discern smaller forbs from taller grasses. It covered as large an area as possible without compromising accuracy in the estimates. The estimates were made along 100 m segments of the transect, then averaged over the length of the transect. These measurements were performed once during the study (2010), because the relative amount of each cover type was unlikely to change drastically between the two survey years.

In addition, I interpreted and digitized land cover from digital aerial photographs (land cover maps were created with Arc GIS 9.3 and 10.o (Environmental Systems Research Institute (ESRI), Redlands CA, 2010; 2011)), to calculate the percentages of four general cover types on each prairie: grass, woody vegetation, vegetated wetlands, and open water. This was done by digitizing each of the four land cover types separately, then merging them together to create a single digitized image. I measured the number of hectares of each cover type and converted the hectares into percentages of the total prairie area.

Landscape-level Data

I collected landscape-level data by interpreting and digitizing land cover from digital aerial photographs (Arc GIS 9.3 and 10.0: ESRI, 2010; 2011). The aerial photographs were obtained from the National Agriculture Imagery Program (NAIP), via the Minnesota Department of Natural Resources Data Deli (http://deli.dnr.state.mn.us), the North Dakota GIS Hub (http://www.nd.gov/gis), and the South Dakota Department of Environment and Natural Resources (http://www.sdgs.usd.edu). The most recent images available were from 2009 for Minnesota and North Dakota, and 2008 for South Dakota. Because these photographs were not taken the same year as the bird counts, I verified the aerial photographs through on-site visual confirmation. This was done by walking the outer perimeter of each prairie fragment to confirm the land uses touching the prairie, and then driving around each landscape to look at the areas visible from the road.

For each prairie fragment, I used GPS coordinates to locate the site on the aerial photograph, then digitized the prairie boundaries based on the extent of native undisturbed prairie. Multiple sites were surrounded by grasslands of other types (such as

Conservation Reserve Program (CRP), restored prairie, or reverted prairie) that could have the potential for different species responses than those seen on the undisturbed prairie itself (due to vegetation structure or plant species differences). I identified these alternative grasslands using existing site maps provided by the organization that owned/managed the site, and excluded them from the focal patch.

Once the focal patch was defined, I created a 4-km buffer around the field site starting at the edge of the prairie, to delineate the extent of the landscape for analysis. This distance was chosen because it provided larger landscape units than previously seen in most avian landscape studies (Ribic et al., 2009; Renfrew and Ribic, 2008; Bakker et al., 2002) and allowed me to extract detailed landscape information without being time prohibitive.

The area of the buffered landscapes varied from approximately 5,418 - 1,448 ha (median = 6,435.6 ha, IQR: 6,160.3 – 7,578.9 ha), and ranged from approximately 0.2 - 65% grassland habitats and 19 - 98% agricultural land. The outermost buffer of each landscape was separated from its closest neighboring landscape by a minimum of 1 km and a maximum of 79 km, with a median of 13 km (IQR: 4 – 31 km).

I digitized each landscape according to the matrix elements that were present. I defined habitat and land use categories using a land cover classification scheme (Table 2) adapted from a U.S. Geological Survey classification scheme specifically for use with remotely-sensed data (Anderson et al., 1976). I streamlined this scheme to eliminate matrix elements that were not present in my study area, and subdivided grassland categories to reflect both current (native grasslands, marginal grasslands) and historical uses (restored grassland, CRP) of the study area’s grasslands (Table 2).

I then subdivided each landscape using five different buffers (500 m, 1 km, 2 km, 3 km, and 4 km), resulting in five separate landscapes for all 29 field sites. For each landscape, I calculated the area of individual habitat polygons using GIS area calculation tools, and used the summary statistics tool to determine the total area covered by each habitat and land use. Finally, I converted the area values to percentages of the total landscape, to be able to make direct comparisons between landscapes of different sizes.

I converted each digitized aerial photograph to a raster image using ERDAS Imagine 2011 (Intergraph., 2011). I then used FRAGSTATS version 3.3 (McGarigal et al., 2002) to calculate structural measurements for each landscape as a whole and for each habitat type individually (Table 3). These variables were included to determine if the songbird communities were responding to the overall combination of the structures and habitats in the landscape or to the configuration of specific habitats within the landscape. The aggregate landscape variables were divided into those associated with the composition of the landscape (types of habitats present: Habitat Richness, Habitat Diversity) and with the configuration of those different habitat patches (how the patches of those habitats are arranged within the landscape:Total Edge Density, Contagion).

Measurements of the specific land cover types (matrix elements) focused on the structure and arrangement of each given habitat within the landscape without considering the other habitat types present. The number of patches and patch density were calculated to determine how many individual patches of each habitat there were and how close or far apart they were within the landscape. Euclidean nearest neighbor measurements were used to identify an average distance between those patches and provided a rough estimate of their distribution throughout the landscape. Finally, median patch area was used to assess how large those separate patches were, while edge density was used to calculate the amount of edge specific to that habitat type.

Data Analysis

Multiple Logistic Regression Analysis-Species Presence/Absence

In this study, I used multi-model analysis to identify the landscape features and scales that are most important for predicting the occurrence of songbird species that use native grasslands in North Dakota, South Dakota, and Minnesota. The landscape features and scales were then compared with species life history traits to identify possible mechanisms for these relationships, and common trends were identified across species with similar traits. With this information, it will be possible to use landscape-level information to identify remnant prairies on which songbird populations may need additional support because of the landscapes that they are surrounded by.

I used multiple-logistic regression to relate species presence/absence to landscape and habitat characteristics. I only analyzed species found on 11 to 20 sites of the 29 censused sites (Table 4; Appendix B) to ensure that there was enough variability in the data to allow the model-fitting algorithm to be successful. Nine species (American Goldfinch- *Carduelis tristis*, Barn Swallow- *Hirundo rustica*, Grasshopper Sparrow- *Ammodramus savannarum*, Le Conte's Sparrow- *Ammodramus leconteii*, Sedge Wren- *Cistothorus platensis*, Upland Sandpiper- *Bartramia longicauda*, Cliff Swallow- *Hirundo pyrrhonota*, Marsh Wren- *Cistothorus palustris*, and Western Meadowlark- *Sturnells neglecta*) fit this requirement, covering a wide variety of habitat requirements and guild associations.

For this analysis, I used multiple logistic regression in R 2.14.2 (R Development Core Team, 2012) to determine the relationship between the local and landscape data and species presence/absence. This was completed within a multi-model framework that was used to select the best-fitting models out of all the possible model combinations (Burnham and Anderson, 2002). Because of the size of the data set involved, I divided all variables into hypotheses based on the scale at which they were measured- local variables measured on each focal patch, aggregate landscape variables that measured composition and configuration of the landscape as a whole, and matrix element variables at 0.5, 1, 2, 3, and 4 km associated with the composition and configuration of specific matrix elements within the landscape (Fig. 3).

The local variable analysis consisted of a single step, in which one round of multi-model analysis was used to identify the local variables in the top models with the most statistical support (defined as those with ΔAICc < 2). This step allowed only the variables with the most statistical support to be incorporated into the final models and avoided creating models with a large number of predictor variables relative to the number of samples.

The aggregate landscape branch of the analysis focused on those variables associated with the diversity and structural complexity of the buffered landscapes and was conducted in two steps (Fig. 3). First, I identified the scales with the most statistical support for each variable, then used that pool of variables to determine the final set of landscape variables with the most statistical support. As with the local variables, I used ΔAICc < 2.

The third branch of the analysis (Fig. 3) focused on matrix element variables associated with the structure and amount of those individual matrix elements within the landscape (e.g. high density forest or restored prairie). Because of the large number of variables in this branch, I used multiple rounds of analysis to narrow the pool of variables. As with the aggregate landscape variables, the first round was used to identify the important scales for each variable (again with ΔAICc < 2). The most important variables were then identified for each matrix element, then for groupings of similar matrix elements (based on Level 1 classifications described in Table 2). I used the variables from this round to build final matrix element models consisting of the best supported variables from all matrix element types.

I then incorporated the top variables from the local, aggregate landscape, and matrix element analyses into a single analysis to produce the best models including both landscape and local features. This process was repeated for each of the nine target species identified above and resulted in a set of top models all with relatively similar levels of statistical support (ΔAICc < 2). Finally, I used the entire set of top models for each species to calculate the deviances associated with each specific variable to determine their relative importance. For each variable within a model, the variable deviance was weighted by that of the model itself. Those weighted deviances were then added across all models for each variable to assess the relative importance of that variable.

Results

Nine species were identified as having been found on between 11 and 20 field site (Table 4). Matrix element variables explained the most deviance for seven species while local variables explained the most deviance for two (Fig. 4). Within the matrix element variables, configuration explained more deviance for the same seven species described above, while the last two had the most deviance explained by composition matrix elements (Fig. 5). The majority of species (7 out of 9) had the largest amount of deviance at the highest scales (3 and 4 km), while the other two species had the most deviance at the smallest scale (0.5 km; Fig. 6).

Overall, the global models explained between 46% (Grasshopper Sparrow) and 71% (Western Meadowlark) of the deviance in the data. The American Goldfinch global model explained a similar amount of deviance to that of the Grasshopper Sparrow (47%), while the Barn Swallow global model had the second best fit of the species in the analysis at 61%. The other five species explained between 54% and 57% of the deviance in the data.

Western Meadowlark- (*Sturnella neglecta*; Grassland Obligate Functional Group)

Western Meadowlarks are strongly influenced by features in the landscape surrounding remnant prairies, and both aggregate landscape and individual matrix element structure are important, especially at the larger scales (Fig. 4, Fig. 6). The top models for this species explained between 55% and 66% of the deviance in the presence/absence data. These birds are most sensitive to the amount of edge in the landscape, based on the positive relationship with median patch size and the negative response to edge density and contagion (Fig. 7). As patch size increases, perimeter-area ratios decrease and meadowlarks are exposed to fewer edges, while increased contagion at the landscape level might indicate larger concentrations of edge habitat as individual patches become more aggregated. As such, meadowlarks might be avoiding movement through landscapes with high amounts of edge, resulting in smaller populations on prairies embedded in edge-filled landscapes. Previous patch-level research has identified Western Meadowlarks as both edge sensitive (Bock et al., 1999) and area sensitive (Helzer and Jelinski, 1999; Johnson and Igl, 2001), although area sensitivity may actually be a reflection of edge sensitivities (Bender et al., 1998; Johnson and Igl, 2001; Fletcher, 2005). This supports the landscape-level findings in that highly fragmented landscapes are more likely to have smaller prairies with higher proportions of edge.

Locally, the amount of high density forest within the boundaries of the prairie fragment decreased the probability of meadowlarks occurrence (Fig. 7). Previous studies have shown that greater amounts of woody vegetation are linked with increased predation rates and decreased nest success for grassland songbirds (Johnson and Temple, 1986; Johnson and Temple, 1990; Conover et al., 2011). As open-cup ground nesters (Ehrlich et al., 1988), meadowlarks might be more susceptible to attack from predators associated with woody vegetation than species using more highly camouflaged nests. On those remnant prairies surrounded by rural commercial lands or many edges, removing local woody vegetation might help make the remnant prairie more suitable for those meadowlarks that do manage to navigate the landscape.

Upland Sandpiper- (*Bartramia longicauda*; Grassland Obligate Functional Group)

The Upland Sandpiper models explained between 36% and 48% of the deviance in the presence/absence data and reflected the influence of the species' life history traits. The birds' ability to feed and nest on bare ground (Suart et al., 2011) would be restricted as increased visual obstruction and total grass cover limited access to the soil, but some shrubby cover may provide desirable nesting sites (Fig. 8; Dechant et al., 1999a).

Meanwhile, they are more likely to use larger prairie remnants that might provide more of these open areas and nesting sites (Fig. 8), resulting in the species' previously demonstrated area sensitivity (Vickery et al., 1994; Helzer and Jelinski, 1999).

The significant matrix element variables showed that maintaining grassland areas in the greater landscape around remnant prairies is important for Upland Sandpiper use, but not all grasslands are equal (Fig. 8). CRP grasslands appear to be beneficial but marginal grasslands do not. This may be indicative of area sensitivity, as most of the CRP fields were larger in size than the small patches of marginal grass typically found in smaller patches along roadsides and between agricultural fields. Upland Sandpipers are also susceptible to negative edge effects associated with woody vegetation (Fig. 8). This relationship has been seen previously (Grant et al., 2004) and may be the result of increased predation or nest parasitism risks for ground nesting birds (Johnson and Temple, 1986; Johnson and Temple, 1990; Conover et al., 2011).

Local patch variables that influence nesting and foraging abilities play the largest role in predicting which remnant prairies are used by Upland Sandpipers. At the landscape scale, there was strong evidence for hierarchical habitat selection as the amount of useable habitat was most important at the largest scale, while the configuration of specific matrix element types (with both positive and negative influences) was important at smaller scales (Fig. 8). Upland Sandpipers may be more sensitive to landscape composition than other species in this study because of its specific habitat requirements (Fig. 5). Not all grasslands provide both the bare ground and the dense vegetation that Upland Sandpipers need to nest and feed (Fritcher et al., 2004), so having greater proportions of grassland in the landscape increases the probability of finding enough sites to meet those requirements.

Grasshopper Sparrow- (*Ammodramus savannarum*; Grassland Obligate Functional Group)

The top models for the Grasshopper Sparrow explained between 19% and 34% of the deviance in the presence/absence data. This species was most sensitive to landscape edges (at both the matrix element and aggregate landscape level; Fig. 9), but responded differently to different types of edges. Edge sensitivity has been documented in this species by other studies (Delisle and Savidge, 1996; Helzer and Jelinski, 1999), including a well-documented negative relationship with shrubs (Whitmore, 1981; Grant et al., 2004; Sutter and Ritchison, 2005) that may reflect an increased rate of nest predation or brood parasitism in the landscape as a whole. Grassland edge responses, meanwhile, differed by grassland type and could indicate differential use of grassland types (Delisle and Savidge, 1996; Klute et al., 1997). Clustering patches at the aggregate landscape scale also created negative edge effects, although this effect was less significant than that of overall positive effects of landscape-level matrix element diversity and richness (Fig. 9).

These birds were least responsive to local habitat structure or quality (Fig. 4), but showed interesting trends when compared to previous research or effects seen at the landscape scale. They responded positively to visual obstruction and high density forest cover, which may indicate that Grasshopper Sparrows select remnant prairies with a greater woody vegetation and overall vegetation density. This does contradict previous studies (Madden et al., 2000; Sutter and Ritchison, 2005) and landscape-level patterns, but the species has been found to build nest on sites with higher tree cover than the rest of the territory (Sutter and Ritchison, 2005). The birds may prefer some woody vegetation at the local level, possibly leading to higher densities at specific locations within a given grassland and a greater probability of observation on the focal patch.

Le Conte's Sparrow- (*Ammodramus leconteii*; Grassland User Functional Group)

The top models for Le Conte's Sparrows explained between 37% and 54% of the deviance in the presence/absence data, and shows that these birds are highly influenced by the grassland components present in the landscape surrounding remnant prairies (Fig. 10). This species has been found to breed in both native prairie and CRP fields (Igl and Johnson, 1995; Igl and Johnson, 1999; Lowther, 2005), as reflected by the top models (Fig. 10). More grassland habitat in the landscape results in large populations present, an easier ability to move between prairie patches, and an increased probability of observing them on the focal prairie patch.

Interestingly, the species responded positively to CRP edge density, despite being classified as area sensitive (Johnson and Igl, 2001) and potentially edge avoiding. This may be indicative of more useable habitat in the landscape, even if the patches are irregularly shaped and have smaller core areas. At the same time, landscapes with high overall edge density (such as is seen with larger numbers of small or irregularly shaped patches) did not appear to support Le Conte's Sparrows, even if individual patches within the landscape may have supplied some temporary benefits.

Increased visual obstruction on the focal patch led to a decreased probability of occurrence. These birds appear to spend the majority of their time on the ground (Ehrlich et al., 1988; personal observations), and previous research has found that the species chooses nest sites with shorter, less dense vegetation than surrounding areas (Winter et al., 2005). As vegetation density increases, the birds will find it harder to locate nesting sites, resulting in prairie remnants that are not as suitable as those with less dense cover.

Overall, the presence of grassland matrix elements in the landscape is the most important factor in predicting Le Conte's Sparrow occurrence on remnant prairie fragments (Fig. 10). Increasing the number of grassland patches and the area of those patches in the landscape increases the probability of their presence on a given prairie patch. Meanwhile, increasing the edge density in the landscape as a whole will decrease the probability of occurrence. Le Conte's Sparrows are influenced by these landscape features at the largest scales (3 and 4 km; Fig. 6) but local vegetation structure is still important for ensuring that the focal patch is useable.

Sedge Wren- (*Cistothorus platensis*; Wetland User Functional Group)

The top models for this species explained between 36% and 55% of the deviance in the presence/absence data. They showed that Sedge Wrens appear to be most sensitive to matrix element variables that represent habitat availability (Fig. 4; Fig. 11). Increasing proportions of native grassland in the landscape may include to greater amounts of the wet meadows that the birds rely on and lead to a greater probability of occurrence (Fairbairn and Dinsmore, 2001; Riffell et al., 2001; Bakker et al., 2002). Similarly, more patches of open water may result in a higher occurrence of temporary wetlands available for use (Fairbairn and Dinsmore, 2001). At the same time, increased amounts of wetlands and associated emergent vegetation may mean less area available in the landscape for wet meadows and grasslands (Herkert et al., 2001). On the patch itself, additional cover types (open water and forbs) crowd out the wet meadow sedges and grasses that the birds prefer to forage on (Herkert et al., 2001) , making them less likely to occupy that particular remnant prairie patch.

At the aggregate landscape scale, matrix element richness patterns related to the strict habitat requirements of the species, as only a handful of matrix elements would meet their requirements in this study (wetland, CRP, pasture, native and restored prairie; Fig. 11). As richness increases, more non-suitable matrix elements are being added to the landscape that would make it harder for the birds to find the suitable resources that they need. Meanwhile, increasing aggregate landscape edge density reduced the probability of occurrence, most likely due to edge avoidance and area sensitivity responses (Bakker et al., 2002; Herkert, 1994). This indicates that Sedge Wrens are not as likely to be found on remnant prairies surrounded by landscapes with large amounts of edge habitat.

Marsh Wren- (*Cistothorus palustris*; Wetland User Functional Group)

The Marsh Wren top models explained between 40% and 53% of the deviance in the presence/absence data. These birds responded strongly to landscape composition (specifically water and wetland-related matrix elements, as would be expected from its wetland habitat associations; Fig. 12; Niesar, 1994; Kroodsma and Verner, 1997; Cunningham and Johnson, 2006; Spautz et al., 2006). Increasing the amount of habitat may not be enough, however, if the configuration of the habitat patches elevates levels of intraspecific and interspecific aggression (Verner, 1975; Picman and Picman, 1980; Picman, 1983; Picman and Belles-Isles, 1987). Minimum wetland area size does not appear to matter, as has been previously documented (Benoit and Askins, 2002), but wetlands containing large amounts of open water may lack suitable cover (Fairbairn and Dinsmore, 2001; Shriver et al., 2004).

Similarly, the configuration of different matrix elements within the landscape may limit the suitability of a given wetland for occupancy. Wetlands near CRP edges decreased the probability of occurrence, as did high amounts tree cover on the remnant prairie patch. Previous studies have identified the species as edge sensitive (Fairbairn and Dinsmore, 2001; Spautz et al., 2006), but this study is the first to single out CRP edges. The avoidance of woody vegetation has been documented (Cunningham and Johnson, 2006; Forcey et al., 2007), but they have also been observed using woody vegetation on grasslands (Niesar, 1994).

Interestingly, the species shows a clear example of hierarchical habitat selection. Landscape composition and the amount of habitat mattered at larger scales (2 km), when migrating birds would be searching for a region in which to settle down (Fig. 6). As the birds get closer to identifying a specific patch to settle on, configuration becomes more important (all three configuration variables were measured at 0.5 km; Fig. 6). In the future, presence/absence models might be better improved through a focal patch methodology centered on individual wetlands rather than prairie patches, as this reflects the actual primary habitat of the species.

Cliff Swallow- (*Hirundo pyrrhonota*; Grassland User Functional Group)

The top models for this species explained between 27% and 51% of the deviance in the presence/absence data, which is the lowest amount of deviance explained out of the nine species. Unlike most other species in this study, Cliff Swallows were most sensitive to local-level variables (Fig. 4). They were more likely to be found on larger prairie fragments (Fig. 13), which may reflect the species' open-space and aerial foraging preferences (Ehrlich et al., 1988; Brown and Brown, 1995). Larger colonies of Cliff

Swallows have occurred in landscapes that contain more water (Brown et al., 2002), and large areas of vegetated wetlands may not provide enough open water for foraging. Similarly, brush and high density forest on the prairie patch may also limit open foraging areas, although Brown et al. (2002) concluded that vegetation structure and diversity are not as important as how those vegetation types influence food availability.

At the landscape level, Cliff Swallows continue to show apparent structural preferences. They showed a strong probability of occurrence in landscapes with high matrix element richness and diversity, with aggregated yet evenly shaped patches (Fig. 13). This may provide a high variety of food resources while simultaneously ensuring enough space for aerial foraging. The important matrix elements also reflected foraging and food resource needs. A high density of monotypic hay fields reduced occurrence, possibly through decreased insect richness and abundance (Haddad et al., 2001). This pattern was also seen in Brown et al. (2002), although no direct insect measurements were made in that study or this one.

Barn Swallow- (*Hirundo rustica*; Human Functional Group)

The Barn Swallow models explained between 51% and 60% of the deviance in the presence/absence data, and showed that the swallows are sensitive to the structure of matrix elements within the landscape and their potential foraging opportunities (Fig. 4). Previous research has shown that the species preferentially uses edges that concentrate or increase prey availability (Evans et al., 2003), but row crop edges do not appear to serve this function and have been found to have very low insect productivity overall (Ambrosini et al., 2002; Evans et al., 2007). If a landscape has a large proportion of row crops, it may represent a food desert for these birds. Landscapes with large patches of marginal grassland show similar responses, possibly because of low grassland quality (to support insect populations) or because a lack of grazing animals reduces the ability to forage effectively (Evans et al., 2007; Henderson et al., 2010).

At the same time, landscapes with high matrix element richness had a higher probability of Barn Swallow occurrence (Fig. 14). This species is considered a generalist, being able to occur in a wide variety of habitats and to feed on many different types of prey (Turner, 2006). As such, matrix element richness may promote Barn Swallow occurrence if those matrix elements are open enough for the species' aerial foraging methods (Ehrlich et al., 1988; Brown and Brown, 1999). These birds have been found to forage up to 300 m from their colony sites (Turner, 2006), making it possible to conclude that Barn Swallows seen on the prairie fragments were from colonies located nearby. As such, those landscapes with high levels of matrix element richness and potentially higher insect abundance may be able to support swallow colonies better than landscapes with a limited number of matrix elements and foraging opportunities.

American Goldfinch- (*Carduelis tristis*; Tree Functional Group)

The American Goldfinch top models explained between 34% and 41% of the deviance in the presence/absence data. Unlike any other species in this study, American Goldfinches were sensitive to landscape level features only (Fig. 4). This is consistent with their status as an edge species (Herkert, 1994; Horn et al., 2002) that relies heavily on shrubs and trees for nesting and movement (Stokes, 1950; Middletown, 1979; McGraw and Middletown, 2009; personal observations). In the grass and agriculture-dominated landscapes of this study, trees and shrubs were found most reliably in the windbreaks built between fields, and when these features became more widely dispersed, the birds found it harder to move through the landscape to the remnant prairie patch (Fig. 15). When they are easily navigated, grasslands can provide greater proportions of the seed-bearing plants (grasses and forbs) that the birds prefer, which in turn leads to a greater probability of observing the species within that landscape (as has also been seen by Horn and Koford, 2006). Unfortunately, monotypic hayfields do not contain enough seeds for foraging (Ehrlich et al., 1988; McGraw and Middleton, 2009) and can actually reduce the probability of occurrence Fig. 15).

Having high levels of matrix element richness and diversity may make it easier for goldfinches to find suitable nesting sites and have enough foraging opportunities. At the same time, overall edge distribution should be even across the landscape rather than bunched in a smaller section. This would make it easier for the edge-loving species to move through the landscape and reach the foraging and nesting resources provided by the landscape.

Overall Trends in Landscape-Level Responses

Seven out of nine species responded most strongly to matrix element variables, while the two remaining species (Cliff Swallow and Upland Sandpiper) responded most strongly to local variables. There was no relationship between the dominant variable type and the species' functional group, although both species that responded to local variables were tied to grasslands. All three grassland obligate species responded most strongly to landscape variables at 4 km, and all of the other functional groups had at least one species respond at the 3 km or greater scale.

The type of variables that had the biggest effect also varied by functional group. Grassland obligate and user species both responded to edge density measurements, although the both the edge type and the response type differed between species with obligates responding to stark edges (shrubs, high density forest, rural commercial properties) and users responding to grassland-like edges (CRP). The wetland users, meanwhile, responded most strongly to patch density of water-based matrix elements.

Discussion

Evidence of Hierarchical Habitat Selection in Grassland Songbirds

This study illustrates a clear relationship between the landscape surrounding remnant prairies and the bird species that choose to use those prairies during the breeding season. As birds return in the spring to find new nesting grounds for the year, they first look for specific matrix elements at broad scales. These matrix elements can either be avoided, as Western Meadowlarks avoid rural commercial properties, or targeted, as is seen with Le Conte's Sparrows that choose regions with higher amounts of native prairie and CRP field. Once the migrating birds have selected a region they are going to settle in, focal-patch level characteristics become important, including the relationships with woody vegetation and vegetation structure that have been well documented previously (Whitmore, 1981; Davis et al., 1999; Winter et al., 2005; Jacobs et al., 2012). The only situations where this pattern does not hold true are for those species that have very specific requirements, such as Upland Sandpipers that are limited to a smaller range of prairies based on their need for bare ground and shorter vegetation.

The Importance of Edges

One of the striking patterns across the species in this study is the prevalence of responses to habitat edges. Every single species responded to at least one edge measurement, and three species (Grasshopper Sparrow, LeConte's Sparrow, Cliff

Swallow) responded to more than one edge variable, although the type and magnitude varied significantly between species. Overall, there were no clear relationships between functional guilds or life history traits and the kinds of edge effects identified. Interestingly, only two species responded to total edge density (LeConte's Sparrow and Sedge Wren), indicating that the specific edge type might be much more important than estimated by previous research (DeLisle and Savidge, 1996; Winter et al., 2000; Jensen and Finck, 2004; Koper et al., 2009).

Conclusions

This study has demonstrated that grassland birds do respond to characteristics of the landscape, including both the structure and composition of the landscape as a whole and the structure of individual sub-components. These responses vary according to each species' feeding and breeding requirements, but there are some commonalities between species with similar requirements. The study also showed that most grassland songbird species respond to the landscape at consistently larger scales than previously demonstrated (Jacobs et al., 2012; Bajema and Lima, 2001; Bergin et al., 2000; Ribic and Sample, 2001; Grant et al., 2004).

While it is true that songbird management can only occur on specific parcels of land (like the focal patch) rather than at the entire landscape scale, understanding the landscape context around the focal patch can help to identify songbird populations located in less-hospitable landscapes that may be in need of local habitat improvements that would provide population support. As such, future species management plans should include an understanding of the landscape context out to at least 4 km if not further. Efforts should also be made to include details about matrix element configuration and edge type rather than area only (particularly for those matrix elements that provide sharp contrasts to grassland structure). Plans targeted at species with very specific or limiting habitat requirements should also include information about the landscape composition, with specific attention being paid to matrix elements that either complement those requirements or make them harder to be met.

Table 1: Field Site Information.

This table describes the 29 field sites used in this study, their location, management agency, and area. SNA= Scientific and Natural Area, WMA= Wildlife Management Area, WPA= Waterfowl Production Area.

Field Site	County	Managed By	Remnant Prairie Size (ha)
Minnesota			
Agassiz Dunes SNA	Polk	MN DNR	141.4
Blazing Star Prairie	Clay	TNC	65.9
Bluestem Prairie SNA	Clay	TNC	1180.9
Clinton Prairie SNA	Big Stone	MN DNR	64.6
Compass Prairie SNA	Nobles	MN DNR	7.1
Frenchman’s Bluff SNA	Norman	MN DNR	15.1
Lundblad Prairie SNA	Murray	MN DNR	31.8
Malmberg Prairie SNA	Polk	MN DNR	32.8
Mentor Prairie WMA	Polk	MN DNR	40.4
Mound Springs Prairie SNA	Yellow Medicine	MN DNR	67.5
Pembina Trail Preserve SNA	Polk	TNC	677.8
Sandpiper Prairie SNA	Norman	MN DNR	129.4
Santee-Wombach Prairie SNA	Mahnomen	MN DNR	720.8
Zimmerman Prairie	Becker	TNC	33.1
South Dakota			
Berwald WMA	Roberts	SD FWS	223.7
Buffalo Lake WMA	Marshall	SD FWS	57.7
Horseshoe Lake WMA	Codington	SD FWS	252.1
Jensen WMA	Marshall	SD FWS	440.9
North Lamee WMA	Marshall	SD FWS	162.3
Olson WMA	Marshall	SD FWS	59.2
Overland WMA	Codington	SD FWS	154.9
Roe WMA	Codington	SD FWS	288.8

Table 1 cont.

Field Site	County	Managed By	Remnant Prairie Size (ha)
Rolstad WMA	Marshall	SD FWS	151.2
Wike WMA, East Pasture	Roberts	SD FWS	26.3
North Dakota			
Deep Valley WPA	Benson	ND FWS	89.9
Lone Tree WPA	Benson	ND FWS	53.4
Oakville Prairie	Grand Forks	UND	390.3
SBA WPA	Towner	ND FWS	64.3
Ziegler WPA	Ramsey	ND FWS	27.5

Table 2: GIS Classification Scheme adapted from Anderson et al., 1976. In this adaptation, grassland habitats are more specifically subdivided according to management history.

Level 1	Level 2	Matrix Element Characteristics
Agriculture	Small Grains & Row Crops (Row)	Actively plowed, planted, and harvested fields
	Pasture (Pas)	Grassland used for grazing cattle, horses, and other livestock
	Hay (Hay)	Grasslands that are cut and baled at least once a year, including road margins and similar fragments that are otherwise unused
Forested	High Density Forest (HDF)	Tree cover of 10% or more, of any tree species assemblage
	Savannah (Sav)	Mixed grassland and trees, with a tree cover of less than 10%
	Forested Riparian Buffer (FRB)	The area of land under influence of a stream or river, with more than 10% tree canopy cover
	Windbreaks (Win)	Rows of planted trees in a linear arrangement
	Shrubs (Bru)	Areas with greater than 10% shrub cover
Grassland	Native Grassland (Nat)	Unplowed prairie that retains at least a partial native prairie plant community
	Restored Grassland (Res)	Grasslands currently displaying a prairie plant community, which had been previously used for agricultural purposes and replanted with native species.
	Conservation Reserve Program (CRP)	Fields enrolled in the Conservation Reserve Program, previously agriculture but planted with prescribed grass seed mixes
	Herbaceous Riparian Buffer (HRB)	The area of land under influence of a stream or river, with less than 10% tree canopy cover
	Marginal Grassland (Mar)	Areas of grassland not actively managed or grazed, such as along fences and in between fields. Also fields that have been left to go fallow, but were not enrolled in the Conservation Reserve Program

Table 2 cont.

Level 1	Level 2	Matrix Element Characteristics
Water	Open Water (Wat)	Ponds, lakes, and portions of wetlands that do not contain emergent vegetation
	Wetlands (Wet)	Submerged or saturated areas covered in emergent vegetation at the time of study. Includes natural and man-made wetlands
Anthropogenic	Urban (Urb)	Land with a high proportion (80% or more) of impermeable surfaces, including roads, residential and commercial areas, and associated land features (parks, lawns, golf courses etc.)
	Rural Commercial (RC)	Land occupied by extensive buildings, paved areas, or bare ground, not adjacent to a town or city, including airports
	Rural Residential (RR)	Farm homesteads and associated outbuildings, lawns, and windbreaks
	Gravel Pit (Grav)	Areas where vegetation and topsoil have been removed to access gravel deposits
	Minor Road (Road)	Roads with 4 or more lanes
	Major Highway (Hwy)	Roads with 1 or 2 lanes, including rural paved and gravel roads
	Railroad (Rail)	Railroad tracks and associated gravel beds
Barren Land	Bare Ground (Bare)	Areas lacking in vegetative cover, not associated with mines, agriculture, residences, or commercial sites

Table 3: List of variables used in the three-pronged regression analysis framework. Local variables included vegetation measurements taken along the sampling transects and % cover variables measured using Arc-GIS. Total landscape variables were measured using FRAGSTATS, and were divided into composition and configuration classes. Matrix element variables, focusing on specific habitat types found within the overall landscape, were also divided into composition and configuration classes, with composition variables being measured using Arc GIS and configuration classes being measured with FRAGSTATS.

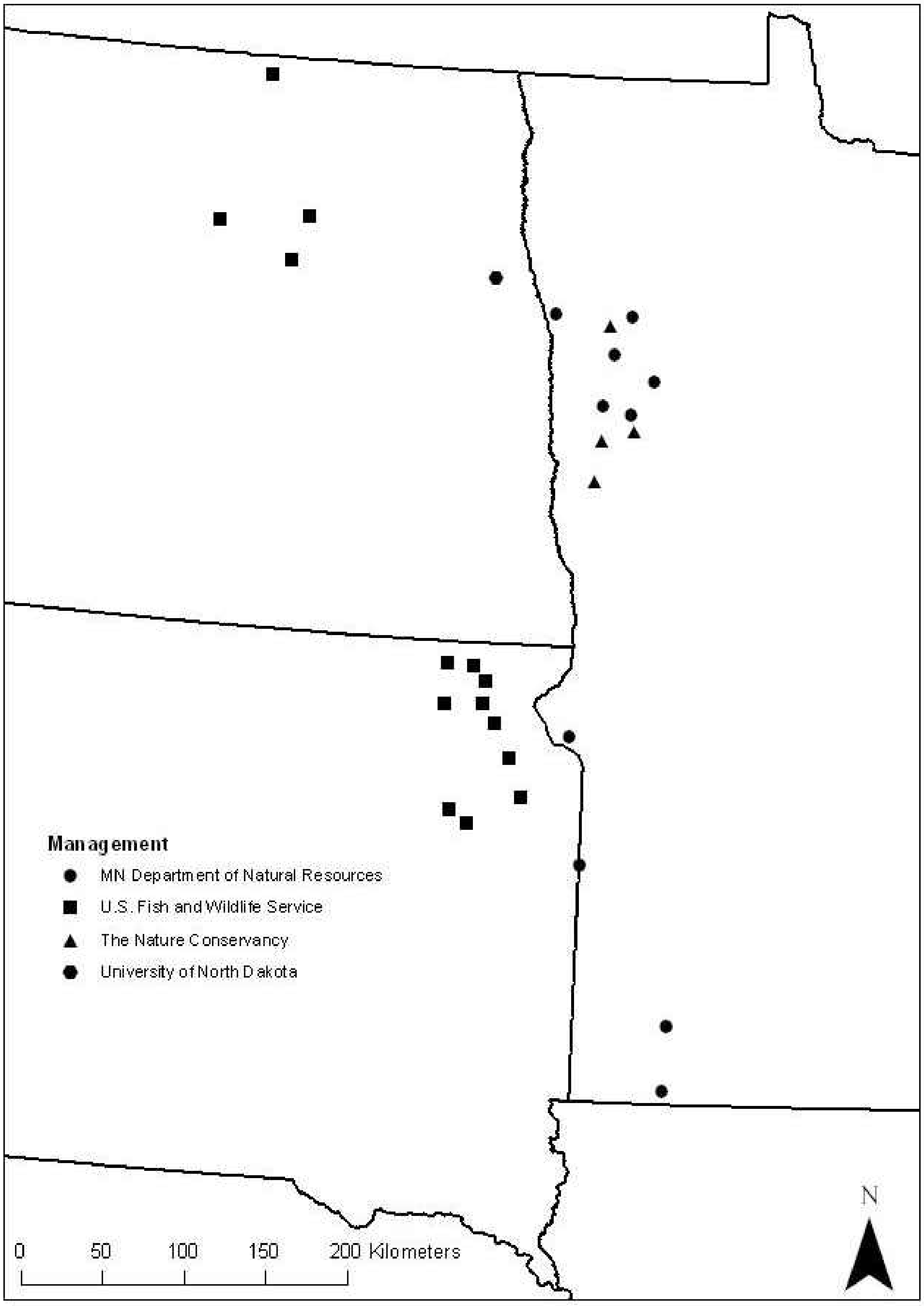
Variable Type	Units	Calculated With	Variable Name
Local Variables			
Transect Variables			
Forb Cover	%	Visual Estimate	Forb
Grass Cover	%	Visual Estimate	Grass
Shrub Cover	%	Visual Estimate	Brush
VOR	decimeter	Robel Pole	Robel
Patch Variables			
Patch Size	hectare	Arc GIS	Patch
Tree Cover	%	Arc GIS	HDF
Open Water	%	Arc GIS	Water
Wetland	%	Arc GIS	Wetland
Aggregate Landscape Variables			
Composition			
Matrix Element Richness	n/a	Fragstats	PR
Matrix Element Diversity	n/a	Fragstats	SHDI
Total Edge Density	meters/hectare	Fragstats	EDL
Configuration			
Contagion	%	Fragstats	Contag
Matrix Element Variables			
Area	%	Arc GIS	A
Number of Patches	n/a	Fragstats	NP
Median Patch Area	ha	Fragstats	MD
Patch Density	#/ 100 hectares	Fragstats	PD
Edge Density	meters/hectare	Fragstats	EDC
Euclidean Nearest Neighbor	meters	Fragstats	ENN

Table 4: Species observed on the focal patches. Each species is identified by common name, alpha code, scientific name, and guild. Guild status was determined based on feeding and breeding habitats (Ehrlich et al., 1988). Species used in the logistic regression analysis are identified by **.

Species	Scientific Name	Number of Sites
Grassland Obligates		29
Bobolink (BOBO)	*Dolichonyx oryzivorus*	28
Chestnut-collared Longspur (CCLO)	*Calcarius ornatus*	4
Dickcissel (DICK)	*Spiza americana*	7
Grasshopper Sparrow (GRSP)**	*Ammodramus savannarum*	12
Savannah Sparrow (SAVS)	*Passerculus sandwichensis*	26
Upland Sandpiper (UPSA)**	*Bartramia longicauda*	13
Western Meadowlark (WEME)**	*Sturnella neglecta*	19
Wilson's Snipe (WISN)	*Gallinago gallinago*	1
Grassland Users		29
Brown-headed Cowbird (BHCO)	*Molothrus ater*	21
Clay-colored Sparrow (CCSP)	*Spizella pallida*	27
Cliff Swallow (CLSW)**	*Hirundo pyrrhonota*	14
Eastern Kingbird (EAKI)	*Tyrannus tyrannus*	25
Field Sparrow (FISP)	*Spizella pusilla*	4
Killdeer (KILL)	*Charadrius vociferous*	1
LeConte's Sparrow (LCSP)**	*Ammodramus leconteii*	12
Vesper Sparrow (VESP)	*Pooecetes gramineus*	5
Western Kingbird (WEKI)	*Tyrannus verticalis*	1
Wetlands		27
Common Yellowthroat (COYE)	*Geothlypis trichas*	23
Marsh Wren (MAWR)**	*Cistothorus palustris*	14
Red-winged Blackbird (RWBL)	*Agelaius phoeniceus*	25
Sedge Wren (SEWR)**	*Cistothorus platensis*	13
Yellow-headed Blackbird (YHBL)	*Xanthocephalus xanthocephalus*	6

Table 4 cont.

Species	Scientific Name	Number of Sites
Tree		17
American Goldfinch (AMGO)**	*Carduelis tristis*	12
Black-billed Magpie (BBMA)	*Pica pica*	1
Orchard Oriole (OROR)	*Icterus spurius*	1
Tree Swallow (TRES)	*Tachycineta bicolor*	8
Yellow Warbler (YEWA)	*Dendroica petechia*	6
Shrub		11
Alder Flycatcher (ALFL)	*Empidonax alnorum*	1
Brown Thrasher (BRTH)	*Toxostoma rufum*	1
Gray Catbird (GRCA)	*Dumetella carolinensis*	4
Song Sparrow (SOSP)	*Melospiza melodia*	1
Willow Flycatcher (WIFL)	*Empidonax traillii*	8
Human		9
Barn Swallow (BARS)**	*Hirundo rustica*	12
Eastern Phoebe (EAPH)	*Sayornis phoebe*	1
Mourning Dove (MODO)	*Zenaida macroura*	1
Rock Pigeon (ROPI)	*Columba livia*	1
Generalist		20
American Robin (AMRO)	*Turdus migratorius*	7
Common Grackle (COGR)	*Quiscalus quiscula*	24



Jessica Shahan
Created: May 7, 2012
Source: MN Data Deli

Figure 2: Field sites in North Dakota, South Dakota, and Minnesota, n=29. These tallgrass and mixed-grass prairie sites are owned and managed by Then Nature Conservancy, U.S. Fish and Wildlife Service, and The University of North Dakota.

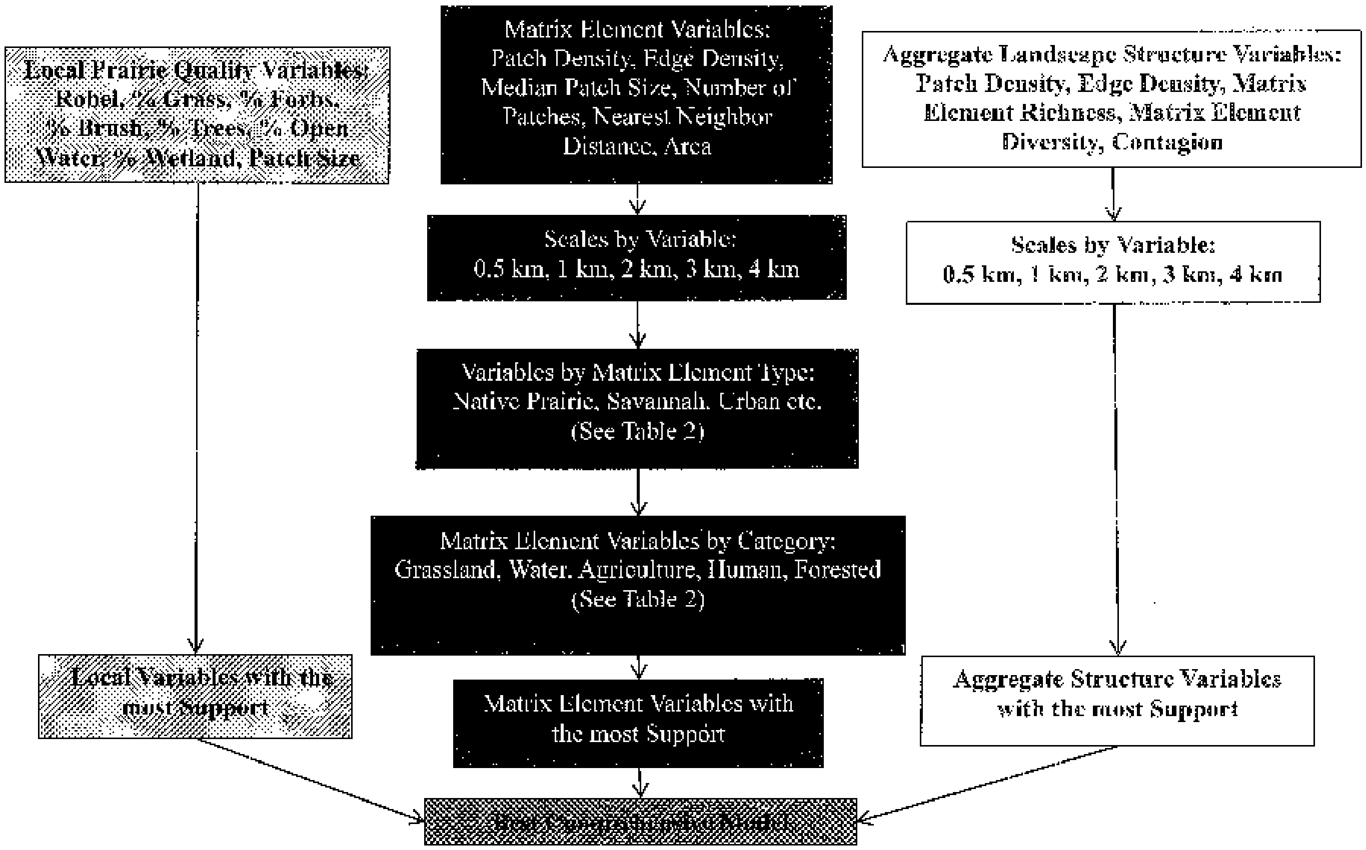


Figure 3: Species occurrence analysis schematic. Multiple rounds of multi-model analysis were used to identify the variables with the most statistical support at each level of measurement. For each round of analysis, variables appearing in the top models ($\Delta AIC < 2$) were retained and moved to the next round of analysis. This framework was repeated for each of nine species found on between 11 and 20 field sites (American Goldfinch- *Carduelis tristis*, Barn Swallow- *Hirundo rustica*, Grasshopper Sparrow- *Ammodramus savannarum*, Le Conte's Sparrow- *Ammodramus leconteii*, Sedge Wren- *Cistothorus platensis*, Upland Sandpiper- *Bartramia longicauda*, Cliff Swallow- *Hirundo pyrrhonota*, Marsh Wren- *Cistothorus palustris*, and Western Meadowlark- *Sturnella neglecta*)

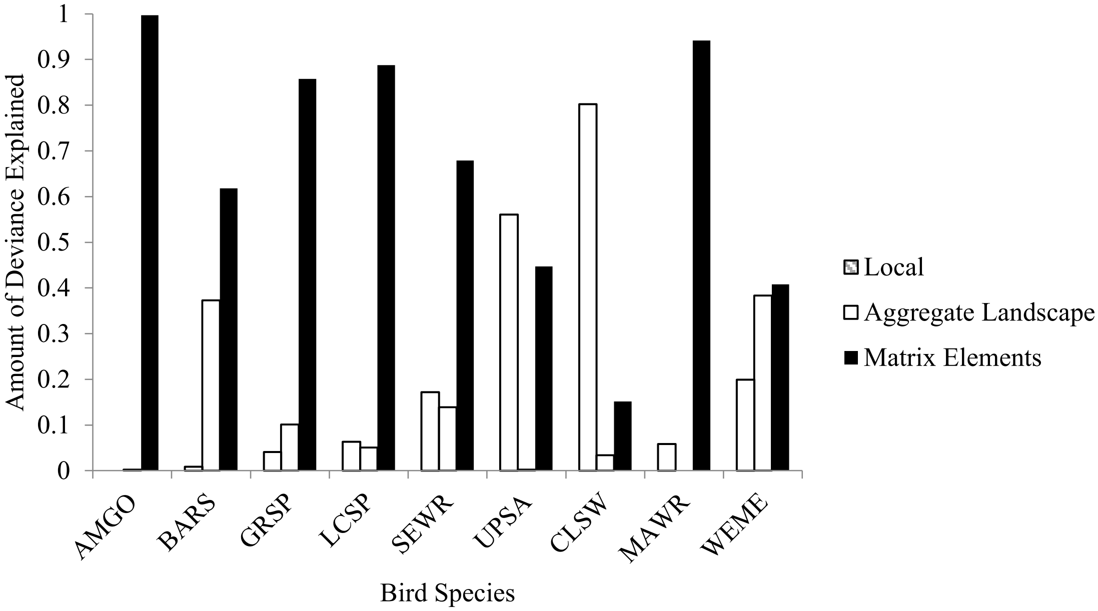


Figure 4: Amount of deviance in the top models explained by variables at the local, aggregate landscape, and matrix element levels. Matrix element variables explained the most deviance for seven species (American Goldfinch: AMGO, Barn Swallow: BARS, Grasshopper Sparrow: GRSP, Le Conte's Sparrow: LCSP, Sedge Wren: SEWR, Marsh Wren: MAWR, and Western Meadowlark: WEME), while local variables explained the most for two species (Upland Sandpiper: UPSA, Cliff Swallow: CLSW).

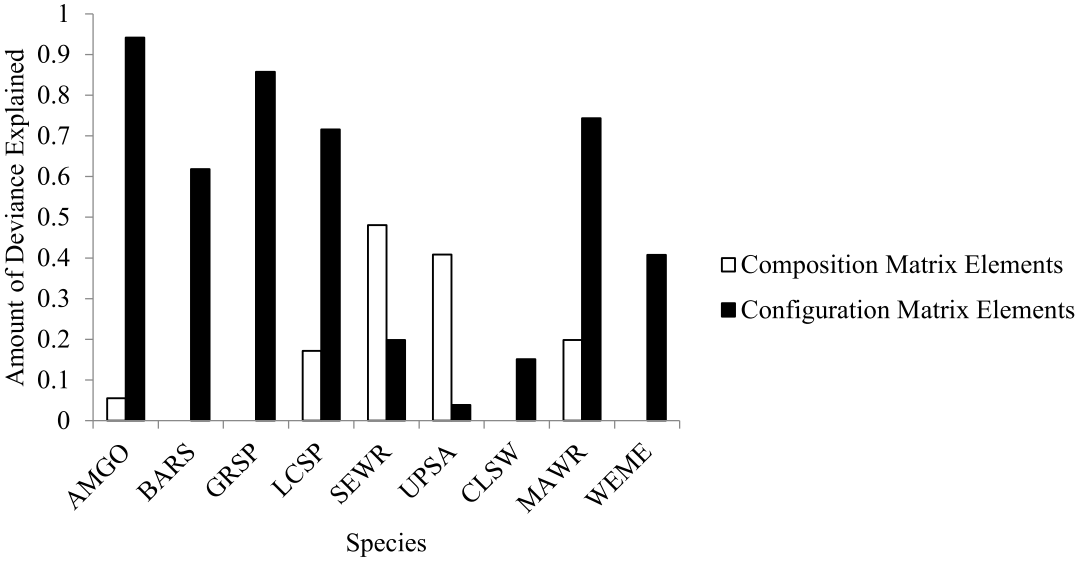


Figure 5: Configuration matrix element variables explained the most deviance for seven species (American Goldfinch: AMGO, Barn Swallow: BARS, Grasshopper Sparrow: GRSP, Le Conte's Sparrow: LCSP, Cliff Swallow: CLSW, Marsh Wren: MAWR, and Western Meadowlark: WEME), with three of those species (BARS, CLSW, WEME) showing no composition variables. Composition matrix element variables did explain the most deviance for two species (Sedge Wren: SEWR, Upland Sandpiper: UPSA).

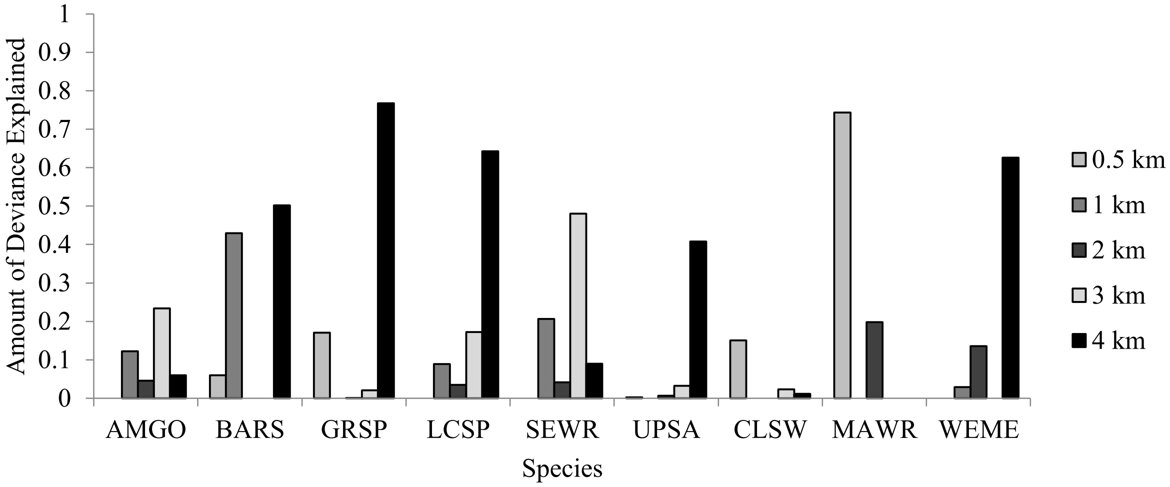


Figure 6: Amount of deviance explained by each scale by the nine species used in the logistic regression analysis (American Goldfinch: AMGO, Barn Swallow: BARS, Grasshopper Sparrow: GRSP, Le Conte's Sparrow: LCSP, Sedge Wren: SEWR, Upland Sandpiper: UPSA, Cliff Swallow: CLSW, Marsh Wren: MAWR, and Western Meadowlark: WEME). Landscape-level responses were seen for all nine species, and reached 4 km for all but the MAWR.

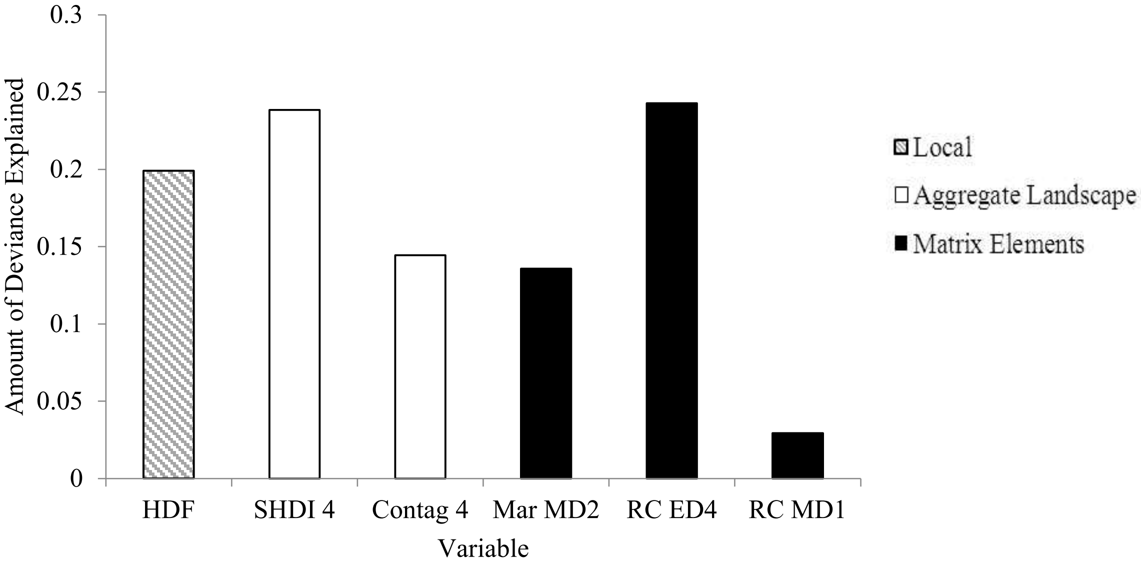


Figure 7: Western Meadowlark deviance summary, based on weighted deviances from each of the top models with $\Delta AIC<2$. They were most responsive to matrix elements (Marginal Grassland Median Patch Size 2km: MarMD2, Rural Commercial Edge Density 4 km: RCED4, and Rural Commercial Median Patch Size 1 km: RCMD1). They were moderately responsive to aggregate landscape variables (Shannon Diversity 4 km: SHDI4, Contagion 4km: Contag4), and least responsive to local variables (High Density Forest: HDF). This species was more likely to be found in landscapes with a higher diversity of matrix elements (SHDI4), lower levels of edge density (RCED4), and evenly distributed patches (Contag4) at the largest scales, and bigger patches of grassland habitat at medium scales (MarMD2).

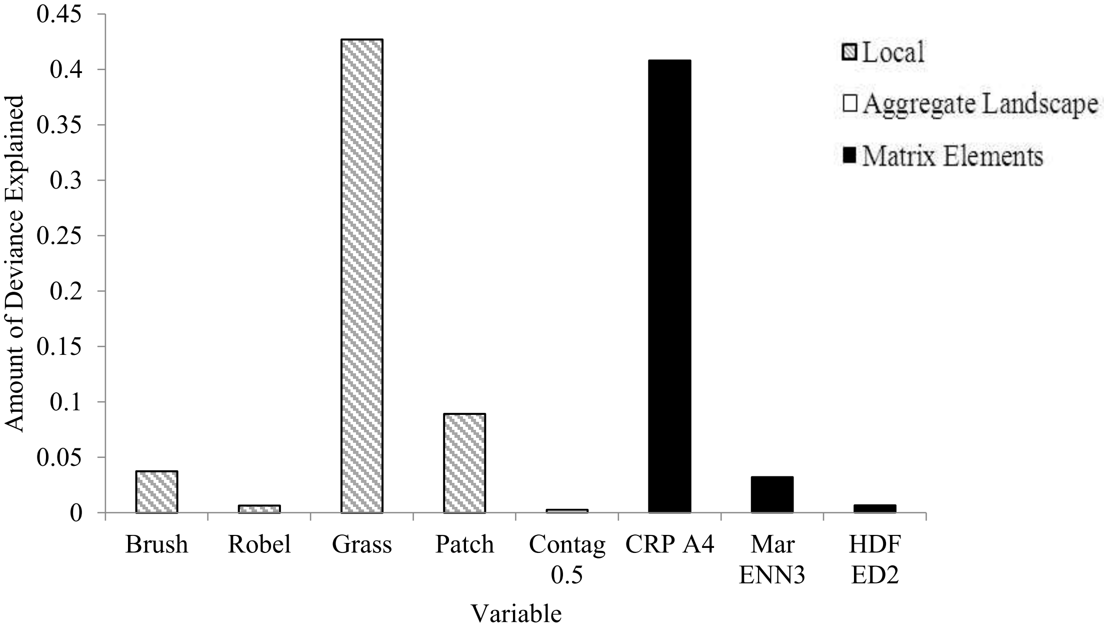


Figure 8: Upland Sandpiper top model deviances, based on weighted deviances from each of the top models with ΔAIC<2. Overall, the species was more responsive to local variables (% Brush Cover: Brush, Vegetation Height: Robel, % Grass Cover: Grass, and Patch Size: Patch), and could be found on larger remnant prairies with less vegetation and shorter vegetation. They were also more likely to be found on prairies embedded in landscapes with higher amounts of CRP (CRP Area 4km: CRPA4) and lower amounts of high density forest (High Density Forest Edge Density 2 km: HDFED2). Upland Sandpipers were somewhat responsive to landscape contagion at 0.5 km (Contag0.5) and distance between patches of marginal grassland at 3 km (MarENN3).

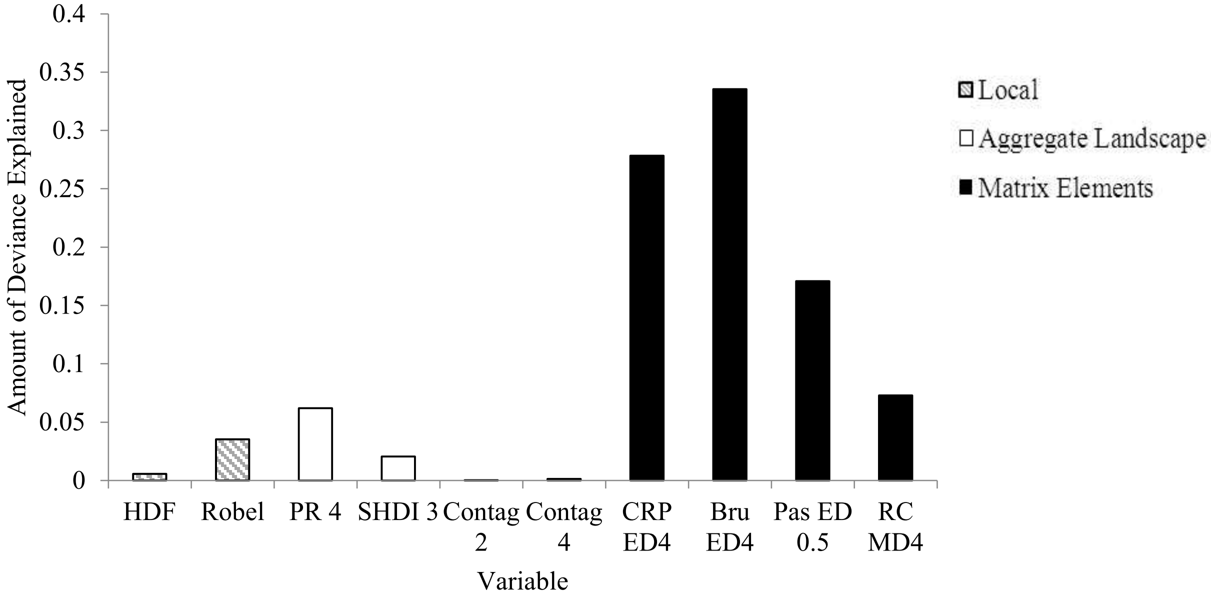


Figure 9: Grasshopper Sparrow top model deviances, based on weighted deviances from each of the top models with ΔAIC<2. These sparrows were more likely to be found on patches with taller, denser vegetation and greater proportions of high density forest (vegetation height: Robel, % High Density Forest Cover: HDF), embedded in landscapes with few CRP and brush edges and more pasture edges (CRP Edge Density 4 km: CRPED4, Brush Edge Density 4km: BruED4, Pasture Edge Density 0.5 km: PasED0.5), as well as greater levels of matrix element richness and diversity at larger scales (Matrix Element Richness 4 km: PR4, Matrix Element Diversity 3 km: SHDI3). Grasshopper Sparrows were also responsive to the aggregation of patches at 2 and 4 km (Contagion 2 km, Contagion 4 km: Contag2, Contag4) and the median patch size of Rural Commercial property at 4 km (RCMD4)

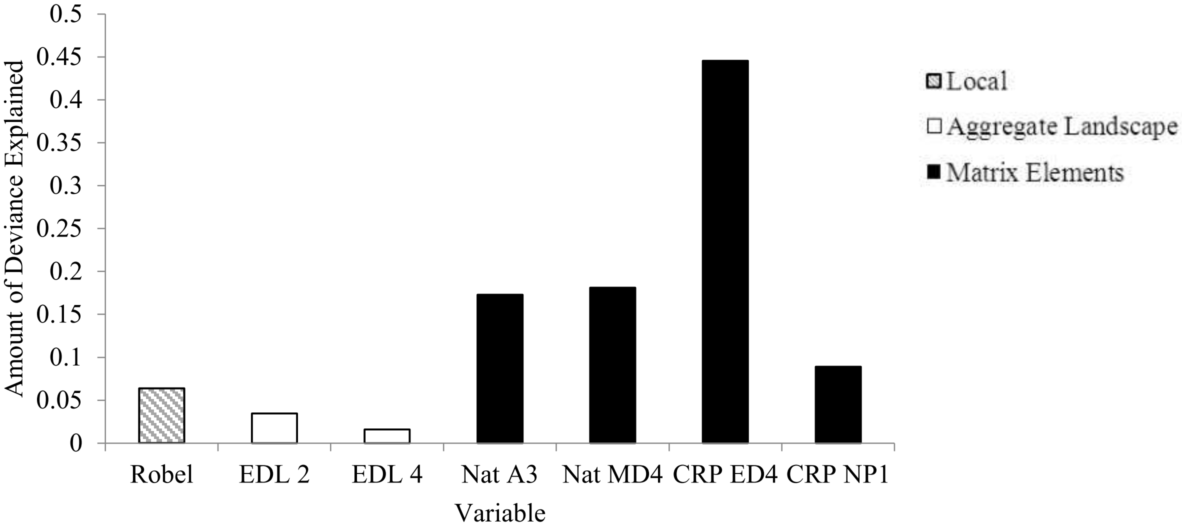


Figure 10: Le Conte's Sparrow deviances from the top models, based on weighted deviances from each of the top models with ΔAIC<2. Le Conte's Sparrows responded most strongly to matrix element variables (total native prairie area at 3 km: NatA3, median patch size of native prairie at 4 km: NatMD4, CRP edge density at 4 km: CRPED4, and the number of CRP patches at 1 km: CRPNP1) and were more likely to be found on prairies surrounded by landscapes with high amounts of native prairie and lower amounts of CRP and overall edge density (landscape-level edge density at 2 km and 4 km: EDL2, EDL4). Le Conte's Sparrows also responded to the height and density of vegetation on the prairie fragment itself (Robel).

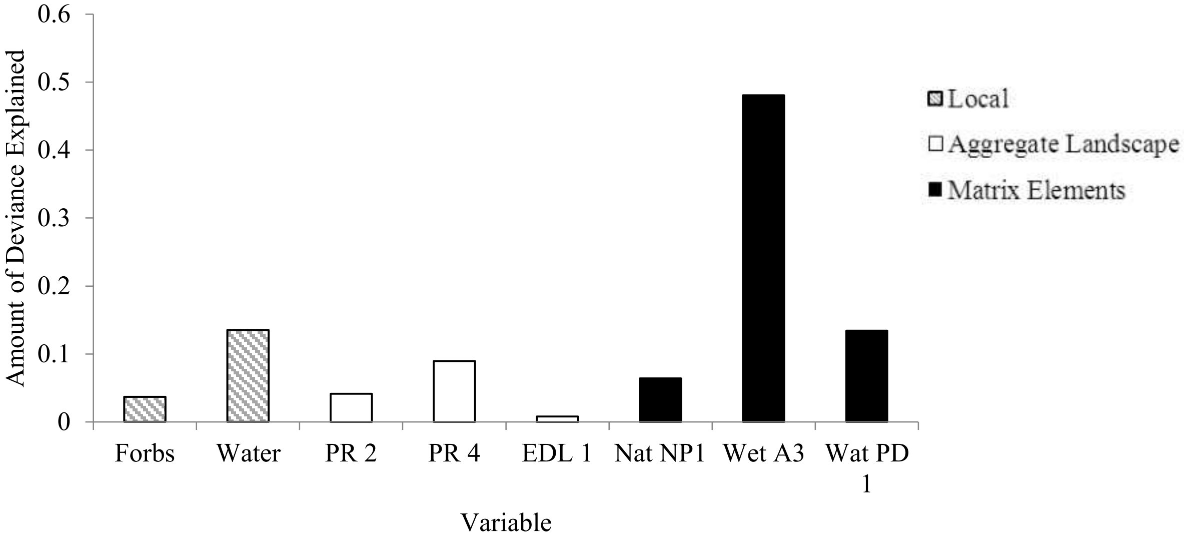


Figure 11: Sedge Wren deviances across the top models, based on weighted deviances from each of the top models with ΔAIC<2. There were equal numbers of matrix element (number of patches of native prairie at 1 km: NatNP1, total wetland area at 3 km: WetA3, and patch density of open water at 1 km: WatPD1) and total landscape variables (matrix element richness at 2 and 4 km: PR2, PR4, and total edge density at 1 km: EDL1), but the species was more likely to be found in landscapes with many native prairie patches, smaller wetlands, and higher matrix element diversity at medium scales. They also responded to percent forb cover (Forbs) and percent open water cover (Water) on the prairie patch itself.

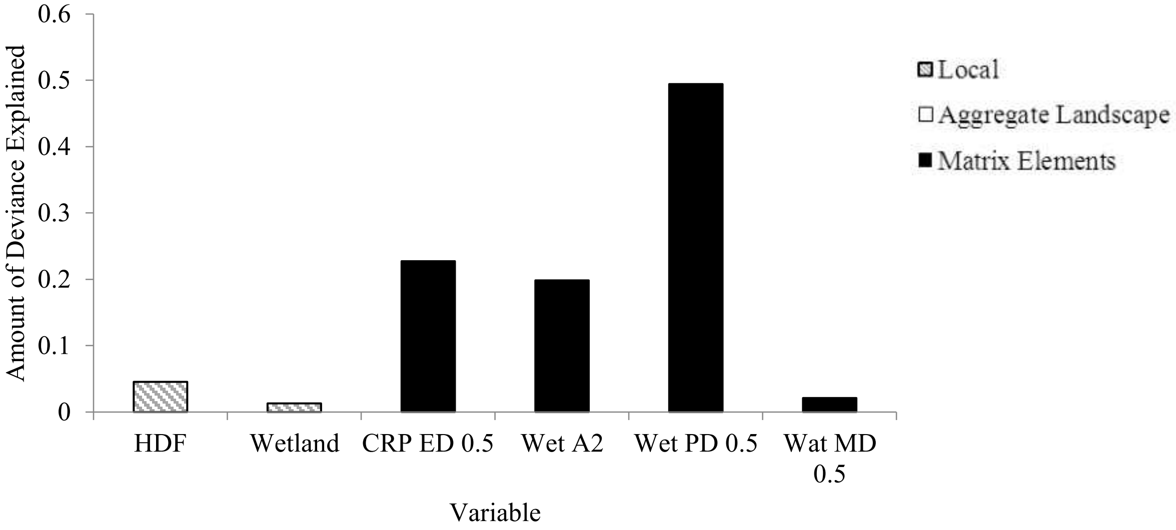


Figure 12: Deviance summaries for the Marsh Wren top models, based on weighted deviances from each of the top models with ΔAIC<2. At the local level, the wrens responded to percent high density forest cover (HDF) and percent wetland cover (Wetland). They also responded to CRP edge density at 0.5 km (CRPED0.5), wetland area at 2 km (WetA2), wetland patch density at 0.5 km (WetPD0.5), and open water median patch size at 0.5 km (WatMD0.5). These birds were more likely to be found on remnant prairies surrounded by landscapes with larger wetland patches but lower wetland density, and on those prairies with more wetland patches and high density forest.

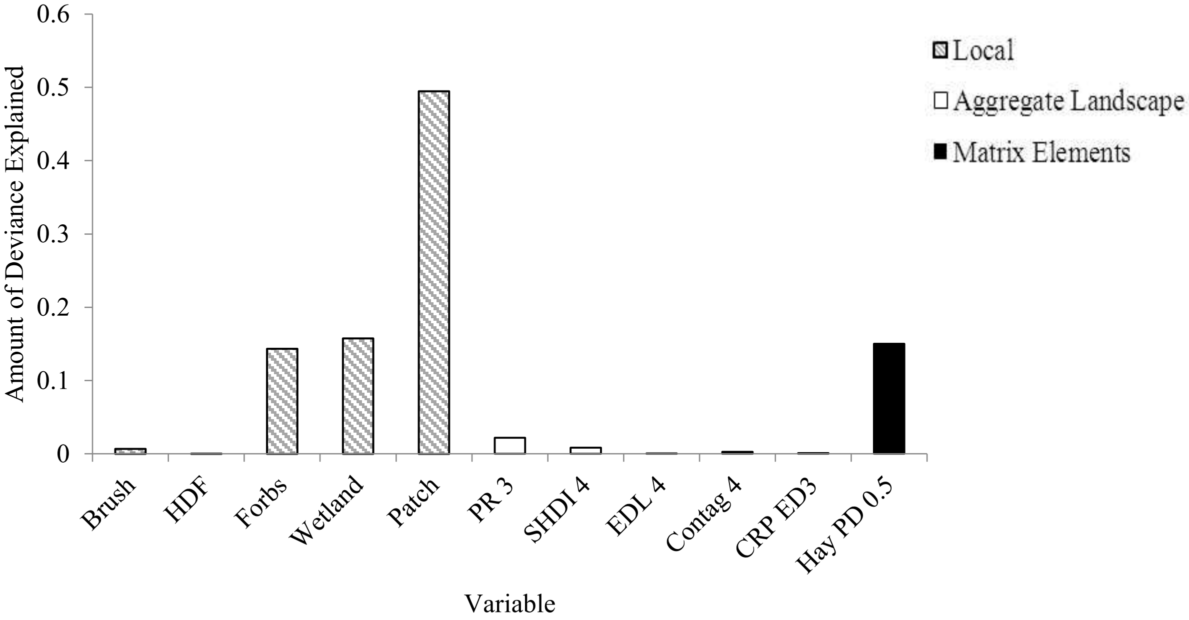


Figure 13: Cliff Swallow deviances across all top models, based on weighted deviances from each of the top models with ΔAIC<2. They responded to a variety of local variables, including percent brush cover (Brush), percent high density forest cover (HDF), percent forb cover (Forbs), percent wetland cover (Wetland), and remnant prairie patch size (Patch). At the aggregate landscape level, the responded to matrix element richness at 3 km (PR3), matrix element diversity at 4 km (SHDI4), total edge density at 4 km (EDL4), and landscape contagion at 4 km (Contag4). At the matrix element level, they responded to CRP edge density at 3 km (CRPED3) and hay field patch density at 0.5 km (HayPD0.5). Overall, the species was more likely to be found on larger remnant prairies with less wetlands, forbs, or woody vegetation, surrounded by landscapes with high hay field patch density at small scales.

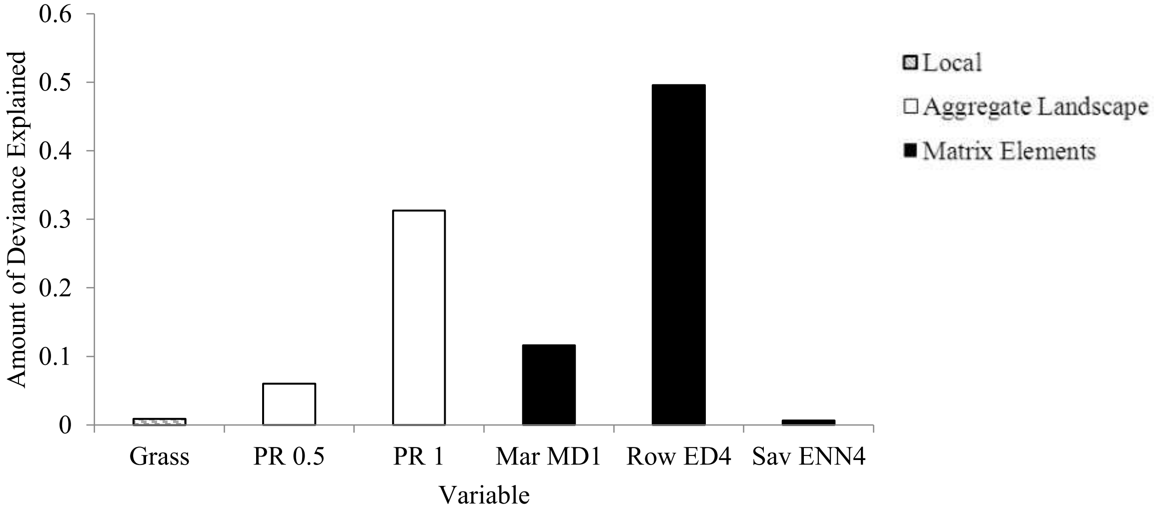


Figure 14: Amount of deviance explained by the top models for Barn Swallows, based on weighted deviances from each of the top models with ΔAIC<2. At the local level, Barn Swallows responded to the percent cover of grass (Grass), while they responded to aggregate landscape matrix element richness at 0.5 and 1 km (PR0.5 and PR1). Matrix element variables included median patch size of marginal grassland at 1 km (MarMD1), row crop edge density at 4 km (RowED4), and the distance between savannah patches at 4 km (SavENN4). Landscape-level variables were most important, with species occurrence being more likely in landscapes with high row

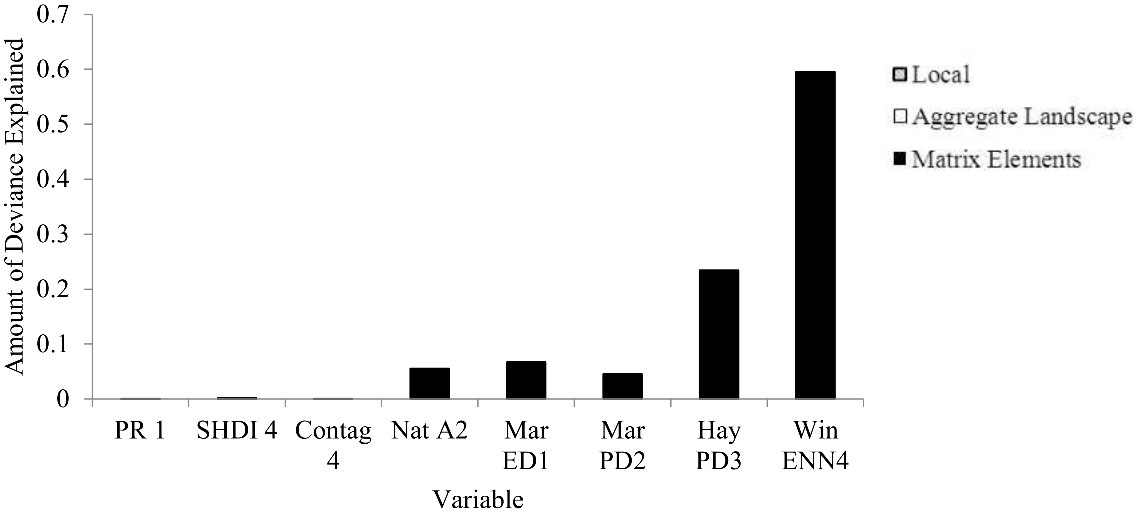


Figure 15: American Goldfinch top model deviances, based on weighted deviances from each of the top models with ΔAIC<2. Goldfinches responded to landscape-level variables only. They were more likely to be found in landscapes with higher amounts of native prairie (NatA2), hay field patch density (HayPD3), and marginal grassland edge (MarED1) and patch density (MarPD2). Occurrence decreased, meanwhile, as windbreak density (WinENN4) increased. They also responded to aggregate landscape variables including matrix element richness at 1 km (PR1), matrix element diversity at 4 km (SHDI4), and landscape contagion at 4 km (Contag4).

CHAPTER III

IDENTIFYING LANDSCAPE-LEVEL PATTERNS IN GRASSLAND SONGBIRD COMMUNITY RICHNESS AND DIVERSITY

Introduction

Worldwide, grasslands are among the most endangered habitats (Hoekstra et al., 2005). In the northern Great Plains more than 70% of the prairie has been lost (Samson et al., 2004). More than 99% of tallgrass prairie has been lost to agriculture or urban expansion and mixed grass prairie has also declined, though not to the same degree (Samson and Knopf, 1994). These extensive grassland losses have been accompanied by major declines in the grassland-breeding songbird populations. Sauer and Link's (2011) analysis of Breeding Bird Survey data from 1968 to 2008 found that grassland obligate species declined by 37%, while Pardieck and Sauer (2007) found that only 14% of grassland species had positive population trends (the lowest percentage for any habitat-associated group of species).

Many studies have investigated local mechanisms that might explain these declines, including patch size (Winter and Faaborg, 1999; Johnson and Igl, 2001; Davis et al., 2006), grassland perimeter-area ratios (Helzer and Jelinski, 1999; Davis, 2004), edge effects (Jensen and Finck, 2004; Fletcher, 2005; Patten et al., 2006), and the vegetation quality of prairie remnants (Herkert, 1994; Cully et al., 2003; Davis, 2004). Fewer studies have looked beyond the edges of the prairie remnants into the landscape that the prairie patch is embedded in. Landscape context is an important consideration given the high levels of mobility exhibited by many bird species. While species may move around the habitat patch daily in search of resources, they also make annual migratory movements that expose them to the landscape, especially those species that breed in the northern Great Plains and migrate at least short distances every year (Igl and Johnson, 1997).

Landscape context has the ability to influence patch selection, both during the identification of breeding habitat and their ability to survive successfully at that location. As birds return to the northern prairie during spring migration, they are forced to make a series of hierarchical decisions that direct them from broad landscape scales during migration to small habitat patches when they reach their breeding grounds (Cody, 1981). At the largest scales, regions with differing habitat structures or food availability may experience variable amounts of migration leading to differences in the species that reach individual habitat patches (Buler et al., 2007; Rodewald and Brittingham, 2007). Meanwhile, the success of individual species within a community on a particular habitat patch can be boosted through landscape supplementation or complementation processes (Dunning et al., 1995; Haddad, 2000; Carr and Fahrig, 2001; Hayes and Sewlal, 2004) or repressed through variations in predation or nest parasitism rates driven by landscape effects (Johnson and Temple, 1986; Johnson and Temple, 1990; Conover et al., 2011). These factors all have the potential to alter the songbird community from what would be predicted based on local-level data alone, making landscape context equally important to patch characteristics.

Does Landscape Context Influence Grassland Songbirds?

Previous attempts to quantify the effects of the landscape on grassland songbirds have yielded ambivalent results with varied effects and strengths of those effects depending on the landscape variables and species studied (Söderström and Pärt, 2000; Ribic and Sample, 2001; Bakker et al., 2002; Hamer et al., 2006; Winter et al., 2006; Renfew and Ribic, 2008). Part of this variability may be related to the methods used to define landscape versus local features.

Most of these previous studies have used buffered point count locations (Fig. 16a; Best et al., 2001; Fletcher and Koford, 2002), buffered transects (Fig. 16b; Bakker et al., 2002; Winter et al., 2006) or Breeding Bird Survey routes (Fig. 16c; Coppedge et al., 2001; Hamer et al., 2006; Veech, 2006). Buffered-point or transect methods may conflate local effects (measured with the first few buffers) with true landscape effects, particularly in the case of sampling on larger prairie patches (Fig. 16a, 16b). In those studies that rely on Breeding Bird Survey routes, sampling routes pass through multiple types of habitats and land uses (Fig. 1c). These routes, based on human transportation systems, may not clearly differentiate between distinct habitat patches or distinguish between areas of habitat use and non-use along the route. In contrast, the focal patch approach (Brennan et al., 2002) clearly delineates between the habitat patch (the sampling unit) and the landscape context assessed by buffering from the boundaries of the focal patch. To my knowledge, there are very few studies of songbird response to landscape context have used this approach, and none of them focus specifically on grassland songbirds.

Many previous studies have also focused solely on the relative amounts of land cover types within the landscape, either using only grassland habitats (Bakker et al., 2002) or including other matrix elements like wetlands, woody vegetation, or agriculture (Söderström and Pärt, 2000; Cunningham and Johnson, 2006; Horn and Koford, 2006; Winter et al., 2006; Ribic et al., 2009). Fewer studies have included information about how land cover elements are arranged within the landscape, such as measurements of the distance between the habitat patch and target landscape features (Bajema and Lima, 2001; Ribic and Sample, 2001) or edge density (Fletcher and Koford, 2002; Jacobs et al., 2012).

Another feature of the previous landscape studies described above is that most of them use a species-by-species methodology relating specific landscape variables to the population density, relative abundance, or nest success of individual species even in studies where multiple species are surveyed (Bakker et al., 2002; Grant et al., 2004; Patten et al., 2006; Winter et al., 2006; Renfrew and Ribic, 2008; Jacobs et al., 2012). While these results provide insight into how the landscape influences individual species, they may not be the most useful tool for grassland songbird conservation. Each study can provide information about conservation techniques for the small number of focal species in that study but such results cannot be extended to all of the birds that use remnant prairies. Given the extent of grassland songbird declines, it would be more efficient to find management techniques that apply to all species present rather small subsets.

A few landscape studies have used community-based measures of richness and diversity (Pearson, 1993; Jones et al., 2000; Fletcher and Koford, 2002; Hamer et al., 2006; Koper and Schmiegelow, 2006), but only three have targeted grassland songbirds

(Fletcher and Koford, 2002; Hamer et al., 2006; Koper and Schmiegelow, 2006). Of those landscape studies that have researched grassland songbirds as communities, two found that species richness is indeed influenced by landscape level variables (Fletcher and Koford, 2002; Hamer et al., 2006). In both of these studies, adding landscape metrics to models of local variables increased the goodness of fit of the final models, indicating that grassland species richness is a function of processes occurring at multiple scales (Fletcher and Koford, 2002; Hamer et al., 2006).

Finally, it is important to consider the scale at which landscape variables are measured. Previous studies have typically used buffers with a radius of 2 km or less (Bergin et al., 2000; Bajema and Lima, 2001; Ribic and Sample, 2001; Bakker et al., 2002; Fletcher and Koford, 2002; Grant et al., 2004; Cunningham and Johnson, 2006; Renfrew and Ribic, 2008; Ribic et al., 2009; Jacobs et al., 2012). A few studies used larger buffers, but they concentrated on landscape composition (Koper and Schmiegelow, 2006; Quamen, 2007) or conducted a regional-level analysis that did not center on a specific focal patch (Veech, 2006). Given the potential ways that landscape context can influence bird communities, it seems reasonable to expect those communities to respond at greater landscape distances than 2 km. A focal patch study of grassland beetle communities found landscape effects past 800 m (Fischer, 2006) suggesting that larger, more vagile birds should experience landscape effects at larger scales. This is especially important when considering communities made of species with different movement patterns. The existing community-based landscape studies only extended 1 km into the landscape (Fletcher and Koford, 2002; Hamer et al., 2006; Koper and Schmiegelow, 2006). Given that previous individual species-based landscape studies have identified effects at scales larger than 1 km (Bergin et al., 2000; Quamen, 2007; Renfrew and Ribic, 2008), it seems necessary to investigate landscape effects on the grassland songbird community at those greater scales and to emphasize the focal patch approach that will ensure the identification of true landscape-level patterns. For my study, I chose a distance of 4 km, because it provided larger landscape units than previously seen in most avian landscape studies (examples of smaller landscape scales: Ribic et al., 2009; Renfrew and Ribic, 2008; Bakker et al., 2002), while allowing me to extract detailed landscape information.

It is also important to consider functional groups when studying grassland songbird communities. These groups are subsets of the total community that have shared life history characteristics (such as food or nesting preferences), that might cause them to respond differently to landscape features that another group with different life history characteristics. Previous research has found distinct differences in the landscape patterns between groups of specialist and generalists in both mid-Atlantic and southeastern U.S. forest-breeding birds (Jones et al., 2000; Mitchell et al., 2006), and it makes sense that the same differences might be seen in grassland songbirds. Understanding how functional group characteristics interact with landscape-level patterns to alter community richness and diversity is the next step in developing effective management techniques to limit further population losses.

A Focus on Richness and Diversity

Total richness provides a good first look at the songbird community by asking how many species are present but is sensitive to sampling effort (Magurran, 2004). Richness indices correct richness estimates for sampling effort allowing for site-to-site comparisons. Margalef's Index is one of the most popular richness indices (Magurran, 2004), but is still sensitive to sampling effort in that increased effort leads to higher index values (Gaston, 1996) and does not incorporate relative species evenness (Magurran, 2004). Diversity (or heterogeneity) indices incorporate species evenness by including variation in both the number of species and the number of individuals per species (Magurran, 2004). The Shannon-Wiener Index is a very popular diversity index (Magurran, 2004) and its use provides ample opportunity for comparison to landscape studies of other taxa or future grassland songbird studies. My study will use both richness and diversity to measure grassland songbird communities, as richness provides a direct measure of the species present while diversity quantifies relative proportions of species in the community and standardizes for sampling effort.

Study Goals

This study seeks to identify the influence of landscape context on grassland songbird community richness and diversity through a focal patch methodology that will determine 1) if landscape context (that is the composition and configuration of matrix elements) influences the richness and/or diversity of grassland songbird communities and 2) at what scale (distance from remnant prairie patch boundaries) are those effects are manifest. I will also compare any landscape context effects on the total songbird community versus effects on specific guilds.

Methods

Site Selection

I selected unplowed remnant prairies located in western Minnesota and eastern North and South Dakota (owned and/or managed by The Nature Conservancy, Minnesota

Department of Natural Resources, U.S. Fish & Wildlife Service, or the University of North Dakota) as focal sampling patches. All sites were separated by a minimum of 8 km to ensure independent landscape data for each focal patch. Where two potential sites were within 8 km of each other, I chose the site that maximized the range of patch sizes in the study or, if there was little difference in patch sizes, the site that maximized the variation in landscape composition. Remnant prairies were excluded if they were scheduled for burning or grazing management during the 2-year study period (2010-2011). From this narrowed list, I chose sites that represented a wide range of remnant prairie sizes and landscape compositions (ranging from agriculture dominated to grass dominated; see Appendix A: Landscape Maps). Through this process, I identified 29 separate sites (Fig. 2), ranging in size from approximately 7 - 1,181 ha (Median= 67.5 ha, IQR= 36.7 – 237.9 ha; Table 1). Landscape composition ranged from 0.3- 65% grass, (median= 8.1%, IQR= 5.7- 20.8%), 19.1- 97.7% agriculture (median = 68.2%, IQR= 59.8- 79.1%), and 0.5- 25.8% woody vegetation (median = 2.1%, IQR= 1.5-5.5%).

Bird Counts

I conducted bird counts during the songbird breeding season, between mid to late May and mid-July (5/31 to 7/15 in 2010 and 5/15 to 7/15 in 2011). Counts ran from dawn until mid-morning, when the birds were most active and vocal and on days when the weather conditions were most conducive to hearing and seeing birds (wind speeds less than 32kph, minimal precipitation; Bibby et al., 1992). I sampled each site twice during each field season, except when weather conditions and flooding limited access. As a result, only seven sites were surveyed twice in 2010, and 26 sites were surveyed twice in 2011.

Each count was based on a linear transect (instead of point counts) as linear transects provided a way to sample significant portions of each focal patch while minimizing the time spent sampling (Gibbons et al., 1996; Anderson and Ohmart, 1981). Transect length was dictated by remnant prairie size. For the smallest fragments (7 – 40 ha), I used the longest amount of transect that would fit on the smallest field site- 400 m. I used 1,200 m of transect on the largest sites (>161 ha). This represented the longest amount of transect that could be surveyed in a single morning and still leave enough time to visit multiple sites on that same day. Sites between 41 and 161 ha were assigned 800 m of transect, both because that length represented a middle ground between the smallest and largest sites and because that transect length fit well on the majority of the medium-sized fragments.

Each transect was at least 100 m from the edge of the focal patch to avoid edge effects that might influence the bird community (Fletcher, 2005). In two cases, prairie fragments were shaped so that a standard-length transect would not fit and still be at least 100 m from the prairie's edges. For these two sites, shortened transects (700 and 750 m) were used which extended as far as the shape of the prairie would allow. I plotted transects as a single straight line unless the size of the remnant or wetland placement prevented it. In these cases, I used multiple smaller transects that added up to the total transect length dictated by fragment area (Gates, 1981). These smaller transects were placed at least 300 m apart to avoid double counting birds (Davis, 2004; Koper and Schmiegelow, 2006).

I walked each transect at a steady pace and recorded all birds seen or heard within 50 m on either side. Birds flying over the transect were only recorded if they actually landed on the focal patch. For each bird sighting, I recorded the species and distance from the beginning of the transect, as determined by a hand-held GPS unit (accurate to 3 m; Garmin eTrex H Handheld Navigator). I also noted birds seen using the focal patch while on the way to or from the transect in case they were species not seen on the transect.

Measuring Local Patch Characteristics

I measured local prairie characteristics in the afternoons after the optimal bird sampling period had ended. The vegetation measurements were used to identify local differences in habitat quality that might influence the bird community. I used a Robel pole to quantify vegetation height and structure (Robel et al., 1970) every 100 m along the bird sampling transect (starting at the beginning of the transect). For each Robel pole reading, I placed the pole 1 m to the right of the transect, to avoid the vegetation disturbed by earlier sampling. I took measurements at each of the cardinal directions around the Robel pole, as determined by a hand-held GPS unit.

I also visually estimated the relative percentages of grasses, forbs, trees, shrubs, and bare ground along each transect. These characteristics were chosen because of their potential to alter birds' habitat selection, foraging or nesting resources, and predation and parasitism rates (Dion et al., 2000; Davis, 2004; Grant et al., 2004; Davis, 2005; Fisher and Davis, 2010). I applied a 5 m boundary to either side of the transect, so that cover types were estimated across a 10 m wide section of prairie. I chose this width because 5 m was approximately the distance at which it became difficult to discern smaller forbs from taller grasses and provided as large a sample as possible without compromising estimate accuracy. I made estimates along 100 m segments of the transect then averaged over the length of the transect. I measured relative percentages once during the study (2010), because the values were unlikely to change drastically between the two survey years.

I used aerial photographs (using Arc GIS 9.3 and 10.0: Environmental Systems Research Institute (ESRI), Redlands CA, 2010; 2011) to quantify percentages of four general land cover types on each remnant prairie- grass, woody vegetation, vegetated wetlands, and open water. This was done to determine amounts of each cover type present on the focal patch that might have an influence on the bird community (see above) but were not included in the vegetation estimation buffer. I digitized each cover type and calculated the percent area that it covered on the prairie remnant.

Landscape-level Data

I collected landscape-level data using digitized aerial photographs in Arc GIS 9.3 and 10.0 (ESRI, 2010; 2011). The photographs were obtained from the National Agriculture Imagery Program (NAIP), via the Minnesota Department of Natural Resources Data Deli (http://deli.dnr.state.mn.us), the North Dakota GIS Hub (http://www.nd.gov/gis), and the South Dakota Department of Environment and Natural Resources (http://www.sdgs.usd.edu). The most recent images available were from 2009 for Minnesota and North Dakota, and 2008 for South Dakota. Because these photographs were not taken the same year as the bird counts, I verified the aerial photographs by driving around each landscape and visually confirming that the matrix elements on the photographs were still accurate. This was done by walking the outer perimeter of each prairie fragment to confirm the land uses touching the prairie, and then driving around each landscape to look at the areas visible from the road.

For each remnant prairie, I used GPS coordinates to locate the site on the aerial photograph and digitized the focal patch boundaries based on the extent of native undisturbed prairie. Where remnant prairies included restored areas (historically disturbed by agriculture and other land uses but replanted with native prairie grasses as part of the Conservation Reserve Program (CRP) or private restoration projects), the restored areas were classified as being in the landscape instead of part of the focal patch. The location and extent of the restored areas versus original prairie was confirmed with site managers, conservation agents, or other individuals familiar with the area.

Once the focal patch boundaries were established, I created a 4 km buffer starting at the edges of the remnant prairie to delineate the extent of the landscape for analysis. Buffered landscape areas varied from 5418 ha - 11,448 ha (median = 6,435.6 ha, IQR: 6,160.3 – 7,578.9 ha). Landscape composition ranged from approximately 0.2 - 65% grassland habitats and 19 - 98% agricultural land. Each landscape was separated from its closest neighboring landscape by a minimum of 1 km and a maximum of 79 km, with a median of 13 km (IQR: 4 – 31 km; See Fig. 2).

I defined matrix element categories using a land cover classification scheme adapted from a U.S. Geological Survey classification scheme for remotely-sensed data (Anderson et al., 1976), and streamlined this scheme to eliminate matrix elements that were not present in my study area, and subdivided grassland categories to reflect both current and historical grassland uses (Table 2).

I subdivided each digitized landscape using five different buffers: 0.5 km, 1 km, 2 km, 3 km, and 4 km. This resulted in five separate landscapes for each focal patch in the study. I calculated the area of individual habitat polygons in each landscape using

Arc-GIS (Arc GIS 9.3 and 10.0: Environmental Systems Research Institute (ESRI), Redlands CA, 2010; 2011) area calculation tools, and used the summary statistics tool to determine the total area covered by each matrix element and converted the resulting area values to percentages of the aggregate landscape to facilitate direct comparisons between landscapes of different sizes.

I converted each digitized landscape to a raster image using ERDAS Imagine 2011 (Intergraph, 2011), then used FRAGSTATS 3.3 (McGarigal et al., 2002) to calculate structural measurements for each landscape as a whole and for each matrix element individually (Table 3). Both aggregate landscape and matrix element variables were included to determine if the songbird communities were responding to the overall combination of matrix elements or to the configuration of matrix elements within the landscape. Aggregate landscape variables were divided into those associated with the composition of the landscape (Habitat Richness, Habitat Diversity, and Total Edge Density) and with the configuration of those matrix elements as a whole (Contagion). Measurements of the specific matrix elements focused on the structure and arrangement of each matrix element type (Patch Density, Edge Density, Number of Patches, Median Patch Area, and Euclidean Nearest Neighbor Distance).

Data Analysis

Bird Community Indices

I identified 38 species across all the focal patches in this study (Table 4). I examined the bird count data both at a community level (all of the species identified on each prairie) and at a habitat guild level (subsets of species with similar habitat requirements). I included a guild-level analysis because groups of species with shared requirements might have different responses to the same landscape features or respond at differing scales. For both the community and guild analyses, I calculated Margalef's Richness and Shannon Diversity indices (Magurran, 2004) using the count data collected on the transect only. Total richness was calculated using all of the species seen on the prairie remnant, including on the prairie and on the way to or from the transect. Indices for each survey year were calculated and averaged for the analysis.

For the guild analysis, I classified species into seven functional groups (Table 4) using their feeding and breeding requirements (Ehrlich et al., 1988). Grassland obligates were those species that feed and breed in grasslands, while grassland users either feed or breed in grasslands but perform the other activity in an additional habitat type. Wetland, tree, and shrub guilds require these specific habitats for both feeding and breeding. The human associated guild nests on man-made structures (bridges, eaves etc.) and are generally associated with human development. Finally, the habitat generalist guild includes species with a wide range of breeding locations, food sources, and foraging requirements. Of the seven total guilds, only the grassland obligates, grassland users, and wetland users were found on enough remnant prairies to conduct an accurate analysis (Table 4). For each of these three guilds, I calculated the Margalef's richness and Shannon diversity of each site.

Multiple Linear Regression Analysis - Bird Community Richness and Diversity

I used a multi-model approach to select the supported multiple regression models relating local and landscape variables to either total richness, Margalef's Richness, or Shannon Diversity (Burnham and Anderson, 2002). The analysis followed a series of progressive steps designed to identify the variables with the most support at each stage (see Fig. 3). I used this process because the final data set involved 150 variables after all the local variables and the landscape variables (both overall landscape measures and measures for each matrix element at each of the five scales investigated) were included. This approach allowed only the variables and scales with the most statistical support to be incorporated into the final models and avoided creating models with a large number of predictor variables relative to the number of samples. At each step, I kept only those variables with the strongest support (ΔAICc < 2). All statistical analyses were completed using R 2.14.2 (R Development Core Team, 2012).

I divided all variables into hypotheses according to the scale at which they were measured- local variables measured on each focal patch, aggregate landscape variables that measured composition and configuration of the overall landscape, and matrix element variables associated with the composition and configuration of specific habitat types within the landscape. The analysis of the local variables consisted of a single step, in which one round of multi-model analysis was used to identify local variables with the most statistical support. The landscape branch of the analysis focused on variables measured across all the matrix elements and was conducted in two steps. First, for each variable I identified the scales with the most statistical support for a relationship with the bird community measures. I then used that narrowed pool of variables to determine the final set of landscape variables with the most statistical support.

The third branch of analysis focused on variables associated with the structure and amount of individual matrix elements (e.g. high density forest or restored prairie). Because of the large number of variables, I used multiple rounds of analysis to narrow the pool of variables. As with the aggregate landscape analysis, the first round was used to identify the significant scales for each variable. The most significant variables were then identified for each matrix element, then for groupings of similar matrix elements (based on Level 1 classifications described in Table 2). I used the variables from this round to build final models consisting of the best supported variables from all matrix element types.

Lastly, I incorporated the most significant variables from the local, aggregate landscape, and matrix element analyses into a single analysis to produce the best models including landscape and local features. I repeated this analysis for each of the three community measurements (total richness, Margalef's richness, and Shannon diversity) for the entire bird community and for the subsets of the community consisting of the grassland obligates guild, grassland users guild, and wetland users guild separately (resulting in 12 groups of top models).

Results

Overall, landscape-level variables did influence the richness and diversity of the total community and the three functional groups (Appendix C). Landscape-level variables explained the most variance for the total community and all three functional groups (grassland obligates, grassland users, and wetland users) for both the Margalef's richness and Shannon diversity analyses. Matrix elements made up the largest part of this variance for all of the groups, although the strength of that importance varied between groups. Each group responded to a variety of habitat types, but there were a few consistent habitats across groups, including hay fields, high density forest, and urban areas. All three of these habitat types had consistently negative impacts on both richness and diversity. The configuration of those habitats in the landscape was more important than the amount of each one. (Fig. 17)

While typically explaining small amounts of variance, landscape composition variables were present in all three functional groups, but not the total community. The grassland obligates and grassland users had the highest amounts of variance associated with composition-related variables in the diversity and richness models respectively. Importantly, these composition-related variables included at least one grassland habitat for each group (native prairie, total grass in the landscape, and total prairie in the landscape), although grassland users showed a much broader range of composition variables than the other two functional groups. (Fig. 18)

Aggregate landscape variables were present in the diversity models for all four groups, but only in the richness models for the grassland obligate group. Grassland obligates showed the largest amount of aggregate landscape-related variance for both diversity and richness, and was the only group to consistently include total edge density variables. The models for all four groups also included landscape-level habitat diversity and contagion. Landscape-level edge density showed a mostly negative relationship with both richness and diversity (positive at 3 km only), while habitat diversity was positive for all groups except grassland obligates. Contagion showed mixed effects, but was mostly negative (positive only for the grassland users).

Model Fit

In looking across the total community and the three functional groups, most of the global models shows fairly good model fit. For the total community, the total richness model had the best fit (r^2=0.76), followed by the Shannon diversity model (r^2=0.72), and then finally the Margelef's richness model (r^2=0.44). Like the total community, the grassland obligate functional group's total richness model had the best fit (r^2=0.91), but the Margelf's richness model had the next best fit (r^2=0.87), followed by Shannon diversity (r^2=0.71). For the grassland users and wetland users, the Margelef's richness models both showed the best fit (r^2=0.77 and r^2= 0.83 respectively). The other two models for the grassland users also fit fairly well (total richness r^2=0.74, Shannon diversity r^2=0.60). The wetland users showed fairly equal amounts of fit between the total richness and Shannon diversity models (total richness r^2=0.61, Shannon diversity r^2=0.69).

Scales

Overall, landscape effects were seen out to 4 km for the total community and the three functional groups. Individual functional groups had different overall patterns of variance across scales (see Functional Group Results), but most could be generalized as higher at closer distances (0.5 and 1 km) and farther (3 and 4 km) distances than they were at a middle distance (2 km) from the boundaries of the focal patch. The only exception to this was the diversity model for the total community, which was slightly higher across the middle distances than the close or far distances (although these differences were very slight). (Fig. 19)

In looking at only aggregate landscape variables, it was clear that larger scales were more important than smaller scales for all four groups. All four groups had the largest amount of aggregate-landscape variance explained by variables at 3 and 4 km. The only smaller variable was seen at 1 km in the grassland obligates diversity model. The matrix element scale trends were less similar, but both the grassland obligates and grassland users showed the greatest and second greatest amount of variance at the largest scale (4 km) and smaller scales (0.5, 1 and 2 km) respectively in their richness and diversity models. The wetland users showed the greatest amount of matrix element variance at smaller scales (1 and 2 km) than the grassland obligates and grassland users. The total community, meanwhile, showed no clear trends in scale at the matrix element level.

Description of Functional Group Models

Grassland Obligates

Grassland obligates responded to landscape-level variables only, and did not respond to any local-scale variables. They responded most strongly to matrix element variables, which included all LCL1 habitat classes (broad classifications- grassland, forest, agricultural, water, human.), although forested habitat variables were found only in the richness models. Agricultural land uses consistently explained more variance than grassland habitats in both the richness and diversity models, while water habitats and human-related land uses were more important in the richness models than the diversity models. Edge related variables (including those at the aggregated landscape level) explained the most variance in both the richness and diversity models, and at the matrix element level were agriculture and grassland edges. Grassland obligates showed very consistent patterns in scale across both richness and diversity (across all variables), with the most variance explained at 4 km, followed by 0.5 km, then 1 km, 3 km, and 2 km. (Table 5)

Grassland Users

This group responded to all three levels of landscape analysis, with matrix elements consistently explaining the most variance, followed by local variables, and then aggregated landscape variables (in the diversity models only). All five LC L1 habitat classes were found in the grassland users models, with forested habitats and water showing up in both analyses, human habitats and grasslands appearing in the richness models only, and agriculture showing up in the diversity models only. Individual habitat types that appeared in both sets of models included hay fields, pasture, open water, and windbreaks. Grassland users responded very strongly to the median patch size, distance between habitat patches, and the overall area of these habitats. At the local level, they responded most strongly to the size of the remnant prairie patch, the height of the vegetation, and the percent forb cover. In terms of scales, grassland users had the most variance explained at 4 km, for both the richness and diversity models. The rest of the variance was explained at the 1 and 2 km scale for the richness models and 2 and 3 km for the diversity models. (Table 5)

Wetland Users

Wetland users responded to all three levels of analysis, with matrix elements explaining more variance than local variables. Aggregate landscape variables explained the least amount of variance and were found in the diversity models only. Within the matrix elements, all LCL1 classes were represented except the forested habitats. In the richness models, woody vegetation explained the most variance, followed by human-related land uses, agriculture, and grasslands. In the diversity models, water habitats explained the largest amount of variance, then agriculture, grasslands, and forested habitats. Within these habitat types, edge density and patch density explained the largest amount of variance for richness, while median patch size explained over half of the variance for diversity. This group showed different trends in scales between the two analysis types. For richness, the most variance was explained at 2 km, followed by 3 km, 0.5 km, and 1 km. For diversity, the most variance was explained at 1 km, then 3 km, then 2 km, and finally 4 km. (Table 5)

Discussion

Does the Landscape Influence Grassland Songbird Richness and Diversity?

I found landscape-level variables did influence grassland songbird community richness and diversity for both the overall community and individual functional groups. In fact, landscape variables were always at least as important as local variables. Some previous studies have seen more impacts from local-level variables (Horn et al., 2002; Koper and Schmiegelow, 2006) most likely due to the study design based on buffered transects or points and not using a focal patch method. Using a focal patch design I was able to clearly evaluate the relative effects of landscape variables versus local variables, allowing for a better identification of their importance for bird communities.

Within the aggregate landscape variables, total edge density explained the most variance by far and had an overall negative effect. Many other studies have found multiple species of grassland birds sensitive to edges or edge density (DeLisle and Savidge, 1996; Bajema and Lima, 2001; Davis, 2004; Fletcher, 2005). A large proportion of edges in the landscape (no matter what kind they are) may make landscapes less suitable for species with strong edge avoidance behaviors, as they may be reluctant to move through the matrix to reach isolated prairie remnants or to forage in the landscape for resources that the prairie is unable to provide. It may also make the prairie more vulnerable to nest parasites and predators that have affinities for edge habitat (Winter et al., 2000; Jensen and Finck, 2004).

Contagion and habitat diversity (both aggregate landscape variables) also explained some of the variance in the top models. Contagion had a mostly negative effect, which indicates that landscapes with large numbers of highly aggregated patches have a negative influence on grassland songbird richness and diversity, possibly due to greater overall edge density and edge effect exposure. Habitat diversity, meanwhile, had an overall positive effect on richness and diversity as has been seen in the literature (Pearson, 1993; Pino et al., 2000; Santos et al., 2008). Through resource complementation and supplementation, populations on isolated habitat fragments are bolstered (Dunning et al., 1992), leading to higher levels of both richness and diversity.

Matrix element landscape variables explained more variation than any other variable type. Based on these results, it is possible to conclude that individual components in the landscape matter more for predicting songbird richness and diversity than the arrangement of the landscape as a whole. Within these matrix elements, the configuration of specific habitat types was more important than the amount of those habitat types. Given that most studies only include composition-based variables, further attention needs to be paid to configuration (see Introduction).

The one clear pattern seen in the composition-related variables was that amount of grass habitat was present in the top models for all richness and diversity measurements (representing all groups except the total community), and showed mostly positive effects. This category included all of the available grass-based habitats in the landscape, including the obvious CRP, restored prairie, native prairie patches as well as the less obvious pastures, hay fields, and fallow, unused areas. These findings show that even less-than-pristine habitats are important for grassland songbirds, especially for those birds living on small remnant prairies where habitat supplementation may be necessary to maintain populations. Previous research has found that grassland songbirds will nest and forage in non-native grasslands (McMaster and Davis, 2001; Riffell et al., 2008), and these additional populations in the landscape have the ability to boost focal patch richness and diversity. Overall sensitivity to landscape variables differs based on patch size and amount of grassland in the landscape (Horn and Koford, 2006; Renfrew and Ribic, 2008), indicating that these additional grassland habitats and their songbird populations may help to mediate negative landscape or local effects.

These findings clearly show that the total organization of the landscape and the amount of different habitats are important, but not as important as the configuration of individual habitat types. Other studies have been able to strengthen their local-based models by adding landscape variables (Haire et al., 2000; Fletcher and Koford, 2002; Hamer et al., 2006), but my study shows that it may be just as important to consider landscape variables as primary drivers of diversity and richness patterns that are at least as important as local factors. As such, landscape studies in the future should utilize a focal patch approach (Brennan et al., 2002) to ensure that landscape effects can be detected separately from local habitat effects. These studies should measure the total configuration of all the patches in the landscape and both composition and configuration of specific habitat types.

At What Scales Are Landscape Effects Felt?

Landscape-level effects extended out to at least 4 km for at least one community measure across the total community and functional groups. This distance is twice as far as previous landscape studies with similar methods have identified and four times the distance identified by previous focal patch studies (Bergin et al., 2000; Bajema and Lima, 2001; Ribic and Sample, 2001; Bakker et al., 2002; Fletcher and Koford, 2002; Grant et al., 2004; Cunningham and Johnson, 2006; Renfrew and Ribic, 2008; Ribic et al., 2009; Jacobs et al., 2012). Since this study did not include any pieces of the remnant prairie in the buffered landscapes, it was possible to measure more of the actual landscape than the non-focal patch studies discussed above. This extended distance allowed for the identification of effects that would simply not have been measured by those studies. This study also included a larger range of measured variables than previous landscape studies (including focal patch studies), making it more likely for the analysis to identify significant variables that might not have been included before.

At the aggregate landscape level, more variance was explained at 3 and 4 km than smaller scales for both Margalef's richness and Shannon diversity. Patterns were less clear cut for the matrix element variables, but there were large amounts of variance explained at the larger scales for at least two community groups. These results may reflect hierarchical patterns of habitat selection (Buler et al., 2007; Rodewald and Brittingham, 2007) or landscape-level pressures from predators (Richmond et al., 2011) that were not measured directly in this study, but demonstrate that future studies should investigate scales out to at least 4 km if not larger (to identify the actual distance at which landscape variables stop having an impact). Including this information will help to reveal landscape features that have the potential to alter grassland songbird communities, making it easier to identify communities that need additional management support. While broad-scale landscape management is not realistic in most of the prairie region, it may be possible to target specific landscape features that have disproportionate influences or restrict landscape-level management to the scales at which it will be most useful.

Do Individual Functional Groups Respond to the Landscape Differently Than the Total Community?

Grassland Obligates

Grassland obligates (species that both feed and breed on grasslands) did not respond to any local variables, indicating that prairie quality is not driving their patterns of richness or diversity. These obligates might be forced to use any available prairies, including those of lower quality, in areas where grasslands are rare (Horn and Koford, 2006; Renfrew and Ribic, 2008). Even in regions where grasslands are common, alternative grasslands (CRP, pasture etc.) may have fewer nesting or food resources than native prairies (McIntyre and Thompson, 2003; Fondell and Ball, 2004), forcing obligates to use whatever prairies are available to meet their needs and effectively canceling out any detectable local-scale patterns.

At the aggregate landscape level, obligates responded to habitat diversity and the total amount of edge. This result shows that the overall configuration of the landscape is important for these species, most likely based on their known sensitivity to and avoidance of edges (DeLisle and Savidge, 1996; O'Leary and Nyberg, 2000; Fletcher and Koford, 2003; Bollinger and Gavin, 2004; Jensen and Finck, 2004). Landscape diversity impacted grassland obligates possibly through the increase in other types of grasslands in the landscape, as these species have been shown to have increased abundance in landscapes with higher proportions of grassland habitat (Ribic and Sample, 2001; Veech, 2006; Ribic et al., 2009). When looking at individual matrix elements, the presence of native prairie habitat was less important than agricultural land uses. Hay fields showed negative relationships with both focal patch richness and diversity, most likely related to increased predation, nest parasitism, harvest-related mortality, or edge effects (Bollinger et al., 1990; Fletcher and Koford, 2003; Bollinger and Gavin, 2004; Renfrew et al., 2005). Pastures, on the other hand, may provide replacement habitat if the grazing load is not too heavy (Johnson et al., 2011) and their edges may not be distinguishable from remnant prairies under these circumstances.

Across all landscape measurements, the most variance was explained by the largest scales (3 and 4 km), with the next largest amount explained by the smallest scales (1 and 0.5 km). This may reflect hierarchical patterns of habitat selection, in which birds returning from their wintering grounds assess potential habitat at progressively smaller scales to identify where they will set up their breeding territories (Wiens, 1973; Hutto, 1985). Overall, grassland obligates species appear to be sensitive to landscape context, responding to the proportion of habitat edge and the amount of grassland present, indicating that the most successful grassland obligate communities are those found on remnant prairies embedded in landscapes with a large proportion of grassland habitats and a minimum amount of edges. If landscape-level management efforts are to be incorporated, they should take place at a distance of 3 to 4 km from the prairie remnant in the best case scenario or within 1 km in the second best scenario.

Grassland Users

Grassland users (species that use both grasslands and other habitats to complete their life cycles) were more responsive to local variables than grassland obligates. These local variables indicate the importance of vegetation structure for grassland users when they choose where to breed and forage. Numerous studies have demonstrated the role of vegetation characteristics in habitat selection (Herkert, 1994; Patterson and Best, 1996; Madden et al., 2000; McCoy et al., 2001; Davis, 2004; Davis, 2005), and this study conforms to these finding as higher percentages of forb cover increased grassland user richness and diversity while greater Robel measurements decreased richness and diversity. Forb cover may provide additional food resources for foraging birds (either through increased seeds and fruits or increased structural diversity that leads to higher diversity and abundance of arthropod prey; McIntyre and Thompson, 2003; Flanders et al., 2006), while Robel height may be indicative of very dense monotypic stands of invasive grasses with fewer nesting or feeding resources (personal observations; McCoy et al., 2001).

At the same time, grassland users responded more strongly to individual habitats within the landscape than to the configuration or composition of the landscape as a whole. At the aggregated landscape level, increased habitat diversity led to increased grassland user richness and diversity, while there was a greater variety of habitats represented by composition variables than was seen with the grassland users. As the number and proportions of habitats increases, the amount of alternative foraging and nesting resources also increases. Barn swallows, for example, require human structures for nesting but forage in open spaces (Ehrlich et al., 1988). Having a higher proportion of human development in the landscape would increase the probability of there being barn swallow populations present in the landscape to be seen using native prairie remnants.

The matrix element variables were also related to grassland users' use of alternative habitats, and to movement between habitat patches and predator avoidance. Grassland users responded strongly to the availability of alternative habitats, including those provided by hay fields and pastures (especially those alternative habitats that are structurally diverse; Bollinger, 1990; Davis et al., 1999; Temple et al., 1999; Ribic and Sample, 2001; Fondell and Ball, 2004; Powell, 2006; Sliwinski, 2010; Johnson et al., 2011). As the amount of these habitats declines or the distance between individual patches increases, those resources may become harder for grassland users to access from remnant prairies, resulting in decreases in local richness and diversity. Meanwhile, limiting the availability of travel corridors (windbreaks) between remnant prairies and alternative habitat patches can also have a negative impact on grassland user richness and diversity (Jobin et al., 2001). Finally, grassland users responded negatively to habitats that increased the probability of predation or nest parasitism in the landscape, such as savannah (grasslands with some tree cover). This effect has been well studied in grassland obligate species of conservation concern (Johnson and Temple, 1990; Bergin et al., 2000; Jensen and Finck, 2004; Patten et al., 2006) and there is no reason to think that grassland users nesting in similar locations would not experience the same predation and parasitism pressures.

In terms of scales, grassland users experienced aggregate landscape effects at the largest scales (3 and 4 km) and matrix element effects out to the largest scales (3 and

4 km), with a smaller peak at the small to medium scales (1 and 2 km). This pattern lines up with that seen in the total community and grassland obligates, except that the smaller peak has shifted slightly away from the edges of the remnant prairie. This may be indicative of the fact that grassland users, by definition, need additional habitat types in the landscape matrix in order to survive. When this scale information is combined with that about matrix element and aggregate landscape effects, it seems clear that grassland users on remnant prairies are strongly impacted by the surrounding landscape. As such, it is important to consider these alternative habitats and scales when investigating population trends or implementing management plans. Management efforts may be better if they are focused on an individual species' specific nesting and feeding requirements rather than trying to manage this group as a whole.

Wetland Users

Wetland users (species that use wetlands for at least part of their life cycle) were more responsive to local variables than grassland obligates or users. Wetland users responded to a greater number of local variables based primarily on vegetation characteristics. Previous research has found positive trends between dense wet meadow vegetation, structural diversity, and wetland bird abundance (Riffell et al., 2001), and this study corroborates those findings as percent brush cover and Robel height both had positive relationships with richness and diversity. If the remnant prairies surrounding embedded wetlands contain similar features, wetland users may be able to utilize some of those grasslands in addition to the wetland itself, making it more likely for these birds to be counted along sampling transects.

Within the individual matrix elements, wetland users responded most strongly to grass, woody, and water-related habitats. Wetland users responded positively to percent grassland cover, which increased the amount of wetlands available (particularly in the South Dakota field sites; personal observation), which has been linked to higher levels of wetland bird abundance and richness (Fairbairn and Dinsmore, 2001; Riffell et al., 2001). Woody vegetation, meanwhile, showed a consistent negative relationship with richness and diversity. This relationship has been well documented in grassland species and wetland birds living in wetlands embedded in grasslands (Naugle et al., 1999b; Naugle et al., 2001; Alsfeld et al., 2010). Edge density of woody vegetation was also significant, and is consistent with other studies investigating grassland birds that have found sensitivities to woody vegetation (Coppedge et al., 2001; Grant et al., 2004; Cunningham and Johnson, 2006) and habitat edges (Johnson and Temple, 1990; Davis, 1994; O'Leary and Nyberg, 2000; Herkert et al., 2003; Stephens et al., 2003; Fletcher, 2005; Patten et al., 2006). Windbreaks consistently appeared in the top models, which relates to the above edge sensitivities in that windbreaks consist almost entirely of edges. They have also been found to serve as corridors for nest parasites and predators (Haas, 1997) that might limit richness or diversity for multiple functional groups. Finally, wetlands with open water increased landscape-level wetland community diversity through the creation of wetland edge habitat. This habitat is essential for wetland edge species like red-winged blackbirds (Fairbairn and Dinsmore, 2001), which might not be able to use fully vegetation wetlands.

The most interesting wetland user pattern was associated with the scale of landscape responses, which extended out to 4 km but were primarily smaller. Landscape composition variables in particular only extended out to 1 km, indicating that wetland users respond to landscape variables at relatively small scales compared to other birds on remnant prairies. Previous work has found that wetland birds are sensitive to both the local-scale vegetation features within prairie pothole wetlands and to landscape level variables beyond the edges of the wetlands under study (Naugle et al., 1999a; Fairbairn and Dinsmore, 2001; Tozer et al., 2010). Given that this study did not directly measure the quality or structure of wetlands on the remnant prairies, it is possible that the variables classified as local could actually be considered landscape variables for this particular subgroup of the prairie songbird community.

If this is the case, then the local variables found in the top models may be those that make it easier for wetland users to utilize grassland areas, making it more likely for them to be observed on transects that did not directly sample focal patch wetlands. As a result, future focal patch studies may be able to gain a clearer picture if they measure wetland quality. Based on the results of this study, however, wetland users are best supported by landscapes with a high proportion of wetland area, lower amounts of woody vegetation, and remnant prairie vegetation structure that mimics the densities found within the wetlands themselves.

Are There Specific Habitat Types That Have Consistent Effects Across Functional Groups?

While there were many differences in the effects of specific habitats on the total community and the three functional groups, there were some habitat types that showed identical trends between the total community and at least two of the three functional groups. Hay fields showed consistently negative effects on the total community and both grass-related functional groups. Previous studies have shown hay fields to have negative impacts on nesting grassland songbirds (Dale et al., 1997; Green et al., 1997). The primary causes of this effect appear to be mortalities that result from early hay cutting that destroy nests, kill incubating birds, and expose remaining nests to higher predation rates (Bollinger et al., 1990; Green et al., 1997; Grüebler et al., 2008). Given these results, landscapes that contain higher proportions of hay-based habitat may serve as population sinks (Perlut et al., 2006; Perlut et al., 2008) that limit the songbird populations available to use remnant prairies embedded within them.

High density forest also had negative impacts on grassland birds, across all four community groups that were studied. As with the hay fields described above, the relationship with woody vegetation has been well documented in previous studies (O'Leary and Nyberg, 2000; Coppedge et al., 2001; Chapman et al., 2004; Grant et al., 2004). While not all of these studies have focused specifically on high density forest patches, it stands to reason that the effects of woody vegetation might be increased as the density of woody vegetation within a patch increases. High density forest may also alter the bird species present by limiting their predator avoidance options and causing them to seek other nesting sites (Lima and Valone, 1991). In addition, the forest habitat represents a potential corridor through which predators and nest parasites (including species adapted to forests that grassland birds may not have experience avoiding) can move through the landscape to reach grassland birds on remnant prairie patches (Burger et al., 1994). In landscapes where grassland bird populations are already vulnerable from habitat loss, adding the extra pressure of increased predation and parasitism to reduced abundance and diversity can have greatly magnified negative impacts.

Not surprisingly, urban habitats also had a negative impact on the total community, grassland obligates, and wetland users. Both of these functional groups are ill-adapted to a landscape that is composed primarily of buildings and pavement, so it makes sense that urban areas would have little to offer such species. Previous studies have documented differences in grassland bird use along urban gradients, with more grassland birds present in less urbanized areas (Bock et al., 1999; Chapman and Reich, 2007). At the same time, urbanization may add features to the landscape, such as edges or novel tree and shrub species, which invite new bird species to the area and change the structure of the grassland bird community without significantly altering richness or diversity (Lancaster and Rees, 1979; Kalinowski and Johnson, 2010).

Based on these results, it seems clear that songbird populations on remnant prairie fragments embedded in landscapes with high proportions of these three habitat types should be monitored closely to ensure that richness and diversity are not overly impacted. In these situations, site managers might want to focus their efforts on local patch characteristics that influence these sensitive subgroups in order to make sure that the patches are of sufficient local quality to support the songbirds that manage to travel to them.

Conclusions

Using a focal patch methodology that accurately defines the local and landscape scales, this study has found that the grassland songbird community on remnant prairies is influenced by the surrounding landscape in addition to local level variables. These landscape-level patterns were seen out to 4 km, indicating a need to look even farther into the landscape to identify the actual limit of the landscape's impact. There were differences between the total community and the three largest functional groups within that total. Grassland obligates appear to be dependent on grasslands of any quality. Both the composition and configuration of the landscape was important for this group, although grasslands and edges explained the most variance compared to other variable types. Grassland users were not as dependent on grasslands and responded to the quality of the remnant prairie. They also responded to a more diverse group of habitats than obligates when looking at both composition and configuration. Wetland users were most sensitive to prairie vegetation structure and responded to the landscape at primarily smaller scales than the other groups. Across all groups, landscapes with high density forest, hay, and urban areas may be at the greatest risk for decreased community richness and diversity.

These results should be used to help identify remnant prairies that are in need of additional management efforts to support robust and healthy grassland songbird communities. If there are smaller or irregularly shaped prairies embedded in landscapes with high proportions of woody vegetation or hay fields, or within 4 km of an urban area, land managers may want to perform local-level assessments to ensure that the prairie itself is of good enough quality to support a robust population.

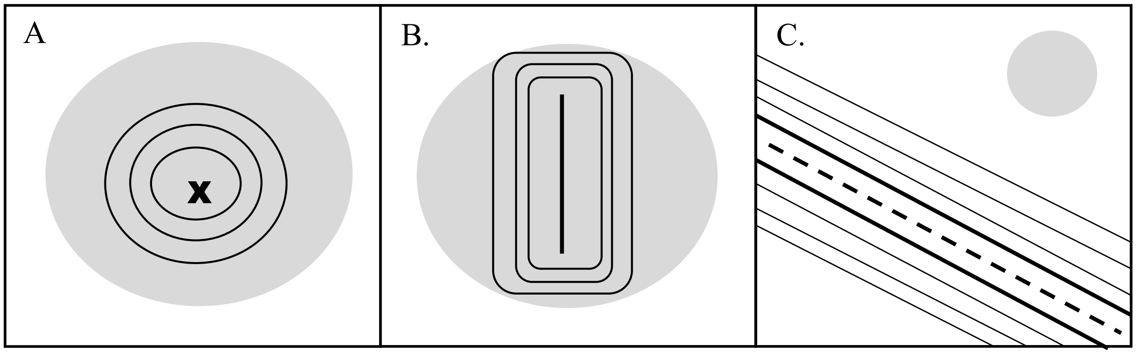


Figure 16: Various methods for landscape surveys on remnant grasslands (gray shaded area). Panels A and B illustrate buffered (solid lines) point counts (x) and transects (solid line) respectively. Panel C illustrates a Breeding Bird Survey route (road way) with buffers (solid lines).

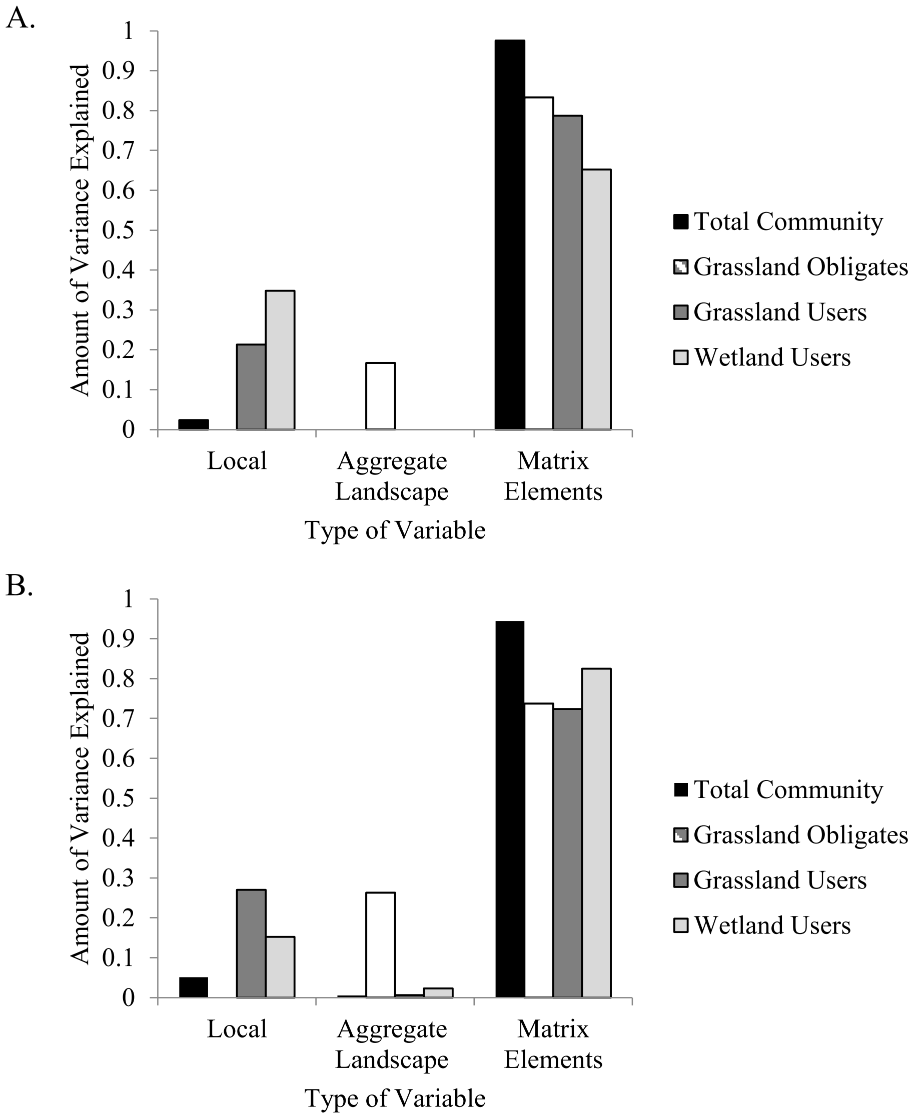
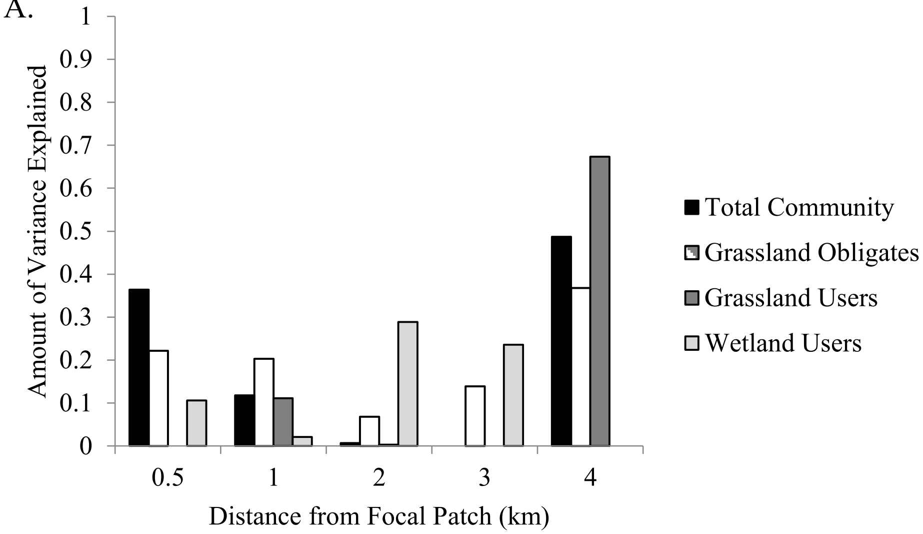


Figure 17: Amount of variance explained by each variable type for the top model sets of each community group. Matrix element variables consistently explained more variance than either local or total landscape variables.
A. Margalef's richness
B. Shannon diversity

A.



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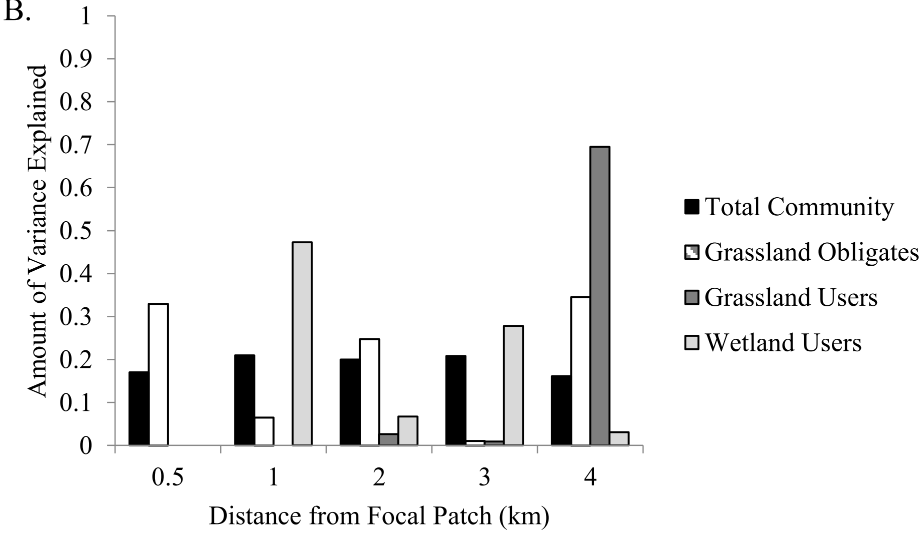


Figure 18: Amount of variance explained at each scale by both matrix element and aggregate landscape variables. Landscape effects reached out to 4 km for all community groups.
A. Margalef's richness
B. Shannon diversity

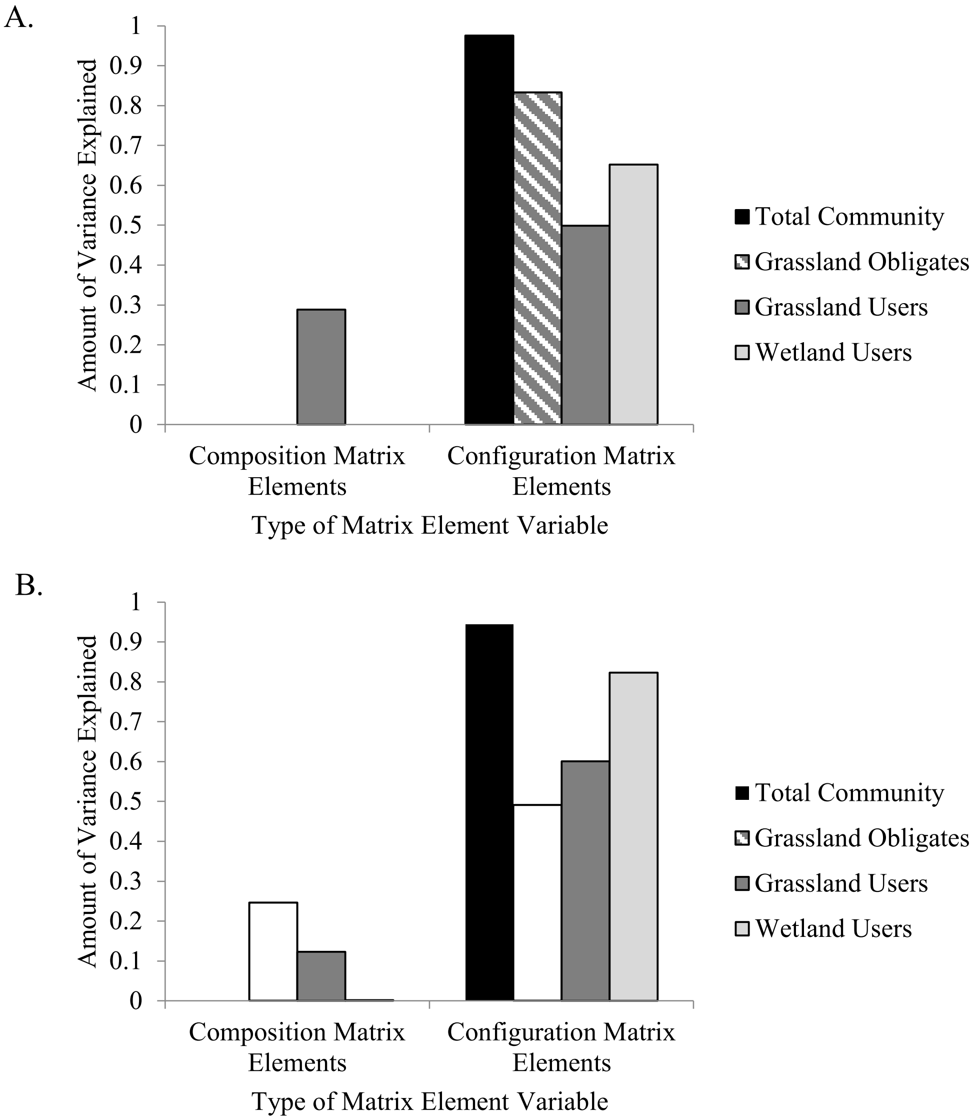


Figure 19: Amount of variance explained by composition and configuration matrix element variables. Configuration consistently explained the greatest amount of variance.
A. Margalef's richness
B. Shannon diversity

CHAPTER IV

CONCLUSIONS

This research has shown that the landscape does play a role in how grassland songbirds distribute themselves between remnant prairie fragments. It is also possible to use the focal patch methodology to identify patterns of richness, diversity, and occupancy for the total community, functional group subsets, and individual species. Finally, this research has demonstrated that landscape responses extend at least 4 km into the landscape for all functional groups and eight of nine species included in the analyses. Interestingly, those landscape responses included both composition and configuration, although specific responses differed depending on the community subset or species being considered.

These results have interesting implications for the future management of grassland songbird communities and populations. To begin with, it is possible to identify individual prairie patches that are surrounded by less hospitable landscapes, including those landscapes with large amounts of matrix element edge or with less-supportive matrix elements like hay fields (a sink habitat) or high density forest (which might cause birds to leave the overall area of the prairie fragment through avoidance behaviors). In those locations, efforts can be made to improve local habitat to support the birds that are already using the prairie. These could include selective burning, grazing, or targeted forb and sedge plantings that encourage greater richness, diversity, and individual species occurrence.

While the land managers and owners of prairie fragments can implement such management techniques for habitat-improvement, efforts should also be made to create partnerships or agreements with land owners to promote landscapes that support grassland songbirds. Where individual species are being targeted, landscape features that support grassland occupancy can be protected while landscape features that limit occupancy could be mitigated.

For example, Upland Sandpiper management programs could encourage the enrollment of more Conservation Reserve Program (CRP) fields in the landscape at 4 km from the prairie patch or provided added incentive to maintain those CRP fields already in existence at those scales. Le Conte's Sparrow management could work on maintaining large patches of native prairie at larger scales and preventing existing patches from being broken into smaller fragments by development. Finally, when focusing on Western Meadowlarks, efforts could concentrate on rural commercial properties. Where new properties are established, conservation agencies can work with project planners to minimize the amount of rural commercial edge by altering the shape of the new construction.

In some regions, it may not be feasible to use a species by species approach, so prairie managers can implement landscape-level strategies that encourage richness and diversity of specific target or functional groups like grassland obligates, grassland users, and wetland users. In cooperation with neighboring land owners, they can work to protect windbreaks that serve as movement corridors for wetland users and grassland users, which could make it easier for various species to move through the landscape to reach prairie patches. Similarly, herbaceous riparian buffers could be protected for grassland obligates by educating farmers about their importance and reducing the number of fields that are plowed all the way to the edges of waterways. At the same time, grassland obligates and grassland users could be targeted by increasing the amount of pasture and pasture edge in the landscape at multiple scales within the landscape. Where pastures only occur at larger scales, it might be worth incorporating additional pastures at smaller scales.

While matrix elements that promote richness and diversity can be protected or encouraged, it is also possible to make the landscape more attractive by removing those features that are related to limited species richness and diversity. With prairies that have limited wetland user diversity, this functional group could be encouraged by removing high density forest within 2 km of the prairie's boundaries. Aggregate landscape total edge density could be modified by changing the shapes of matrix element patches so that they become more rounded (to create more core area and less edge). Where patches of marginal grassland have appeared, they could be replanted with native grassland species to make them more appealing to birds migrating through the region.

The landscape-level approach to conservation could also be used to stretch limited funding and management resources. When patches of native prairie become available for purchase or conservation easement, landscape-level analysis can be used to identify which of a set of prairie patches would support the greatest richness and diversity or are most hospitable for a particular target species. For example, in a situation where a conservation agency must choose between two prairies of equal area and vegetation quality, a landscape analysis could show that Prairie A is mostly surrounded by high density forest while Prairie B is surrounded by patches of restored prairie. If the conservation priority is to support wetland users, funds would best spent on protecting Prairie B.

These techniques could also be used to identify which of a set of prairie patches would be best for specific species reintroduction sites. For example, Upland Sandpipers should be reintroduced to a prairie embedded in the landscape with less high density forest edge or greater amounts of CRP, as opposed to a prairie surrounded by a landscape with many small patches of matrix elements clustered together in close proximity to the prairie boundaries. Grasshopper Sparrows, meanwhile, might do better being reintroduced to prairies surrounded by landscapes with large rounded patches of matrix element, instead of prairies embedded in landscapes with very high edge density measurements.

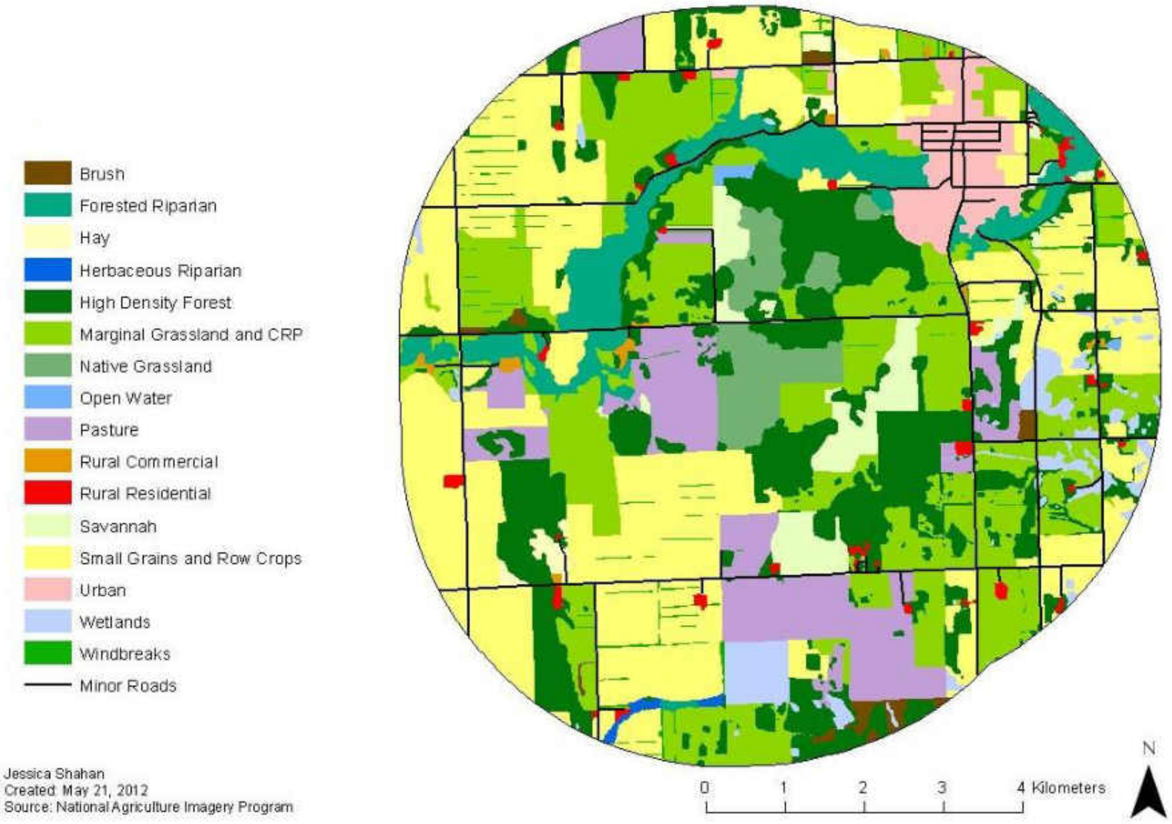
In the future, more landscape-level studies should be conducted to further refine the general trends that were identified in this study and to understand their underlying mechanisms. To begin with, these future studies should extend farther into the landscape than 4 km, to identify the true extent at which birds begin to respond to landscape-level variables. This will also help to clarify the point at which birds begin responding to configuration variables as they make movement decisions during migration, instead of using more general habitat availability cues.

In these studies, it would also be revealing to take measurements on the matrix elements themselves, particularly those that have strong positive or negative effects and have traditionally been considered useful to migrating grassland birds, such as CRP, herbaceous riparian buffers, and pastures. Pastures in particular are of great interest, as both the number of patches and edge density of this matrix element had positive effects in the top models for both the grassland obligate and grassland user functional groups. The positive relationship with pasture edge density was opposite of the trend seen with grassland obligate diversity and the aggregate landscape total edge density, so there may be some features of pasture edges that grassland birds are able to utilize.

Finally, the geographic range of these studies could be increased to include enough occupied patches to be able to perform presence/absence analyses for some of the more rare species seen in this study (Wilson's snipe, Chestnut-collared Longspur). While this might increase the difficulty of sampling, it would be worth it to see what landscape features are related to the distribution of less-than-common species within the grassland songbird community, particularly where those species are experiencing significant population declines.

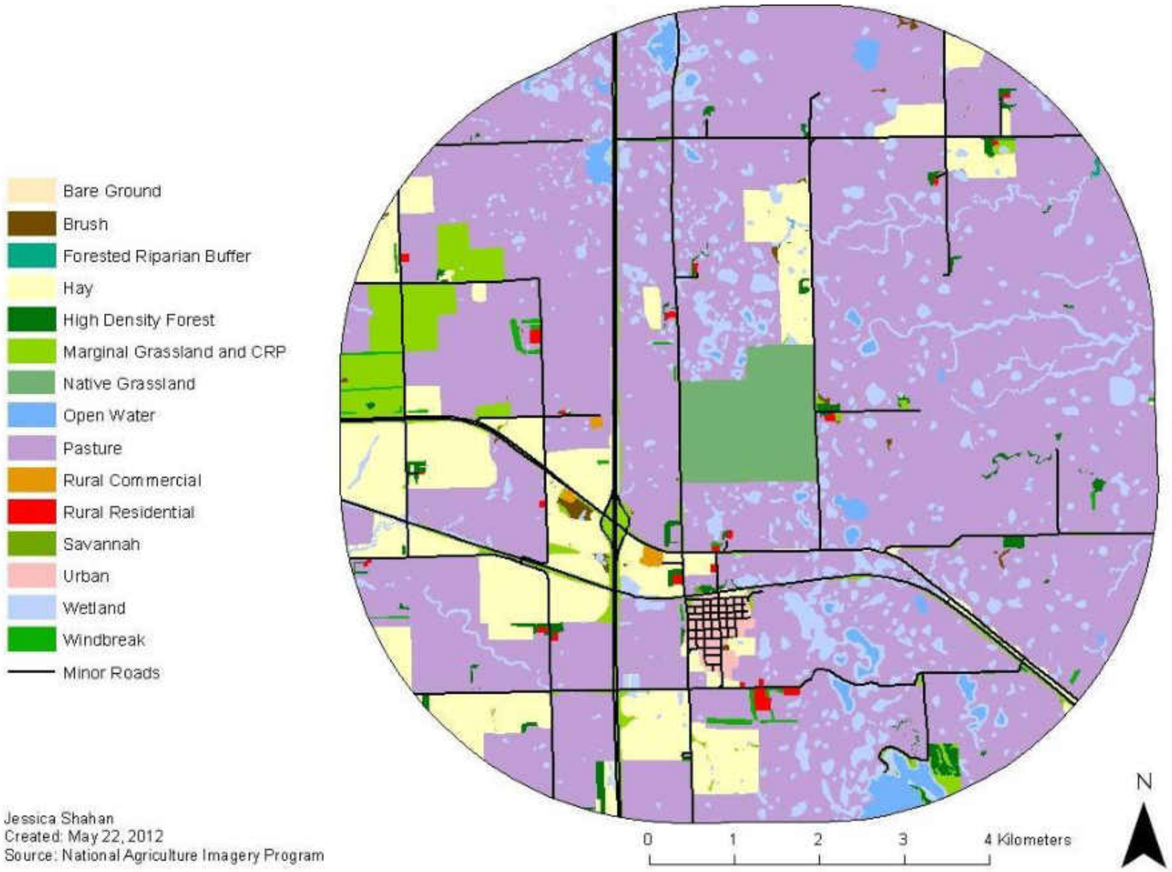
APPENDICES

Appendix A
Digitized Maps of Sampling Sites and 4 km Buffer Zones



Jessica Shahan
Created: May 21, 2012
Source: National Agriculture Imagery Program

Figure 20: Agassiz Dunes Scientific and Natural Area, Polk Co. Minnesota. Managed by Minnesota Department of Natural Resources. 141.4 ha, 12 bird species observed.



Jessica Shahan
Created: May 22, 2012
Source: National Agriculture Imagery Program

Figure 21: Berwald Wildlife Management Area, Roberts Co. South Dakota. Managed by South Dakota Fish and Wildlife Service. 223.7 ha, 14 bird species observed.

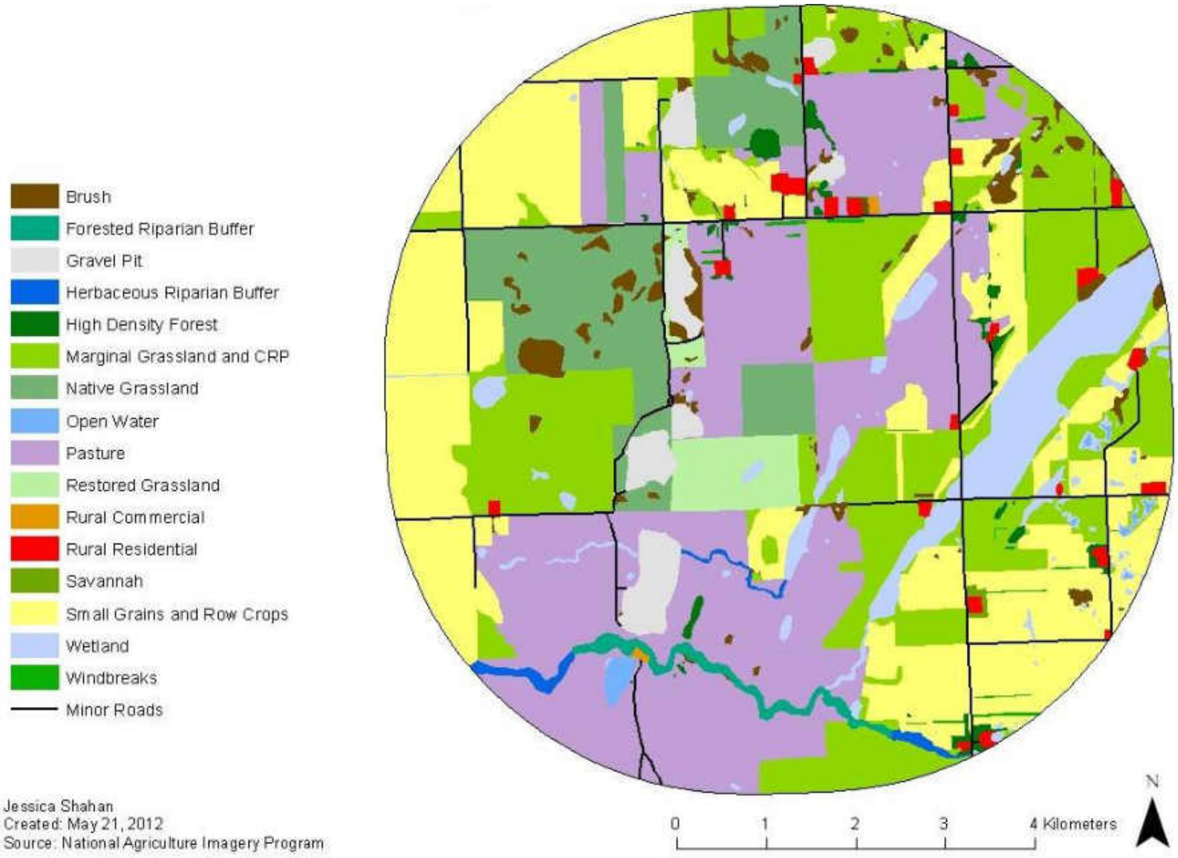


Figure 22: Blazing Star Prairie, Clay Co. Minnesota. Managed by The Nature Conservancy. 65.9 ha, 15 bird species observed.

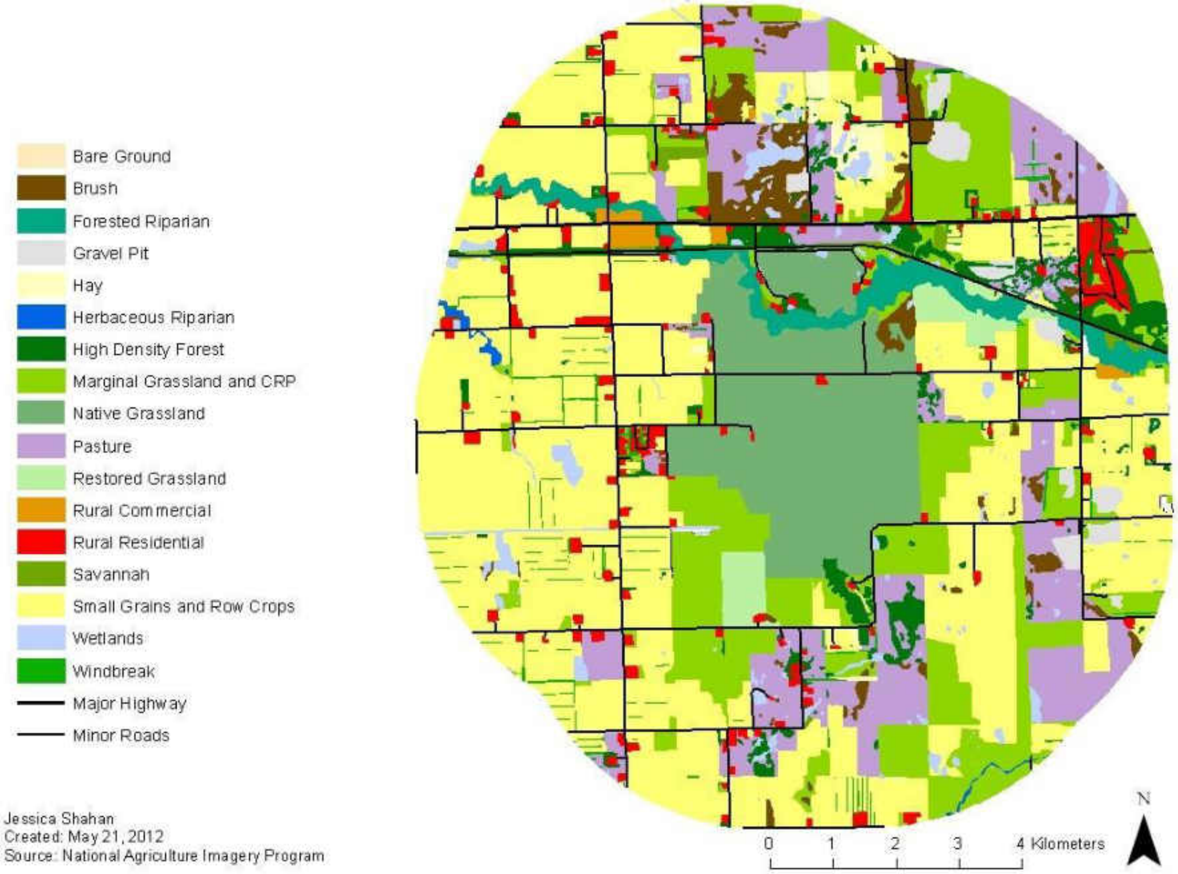
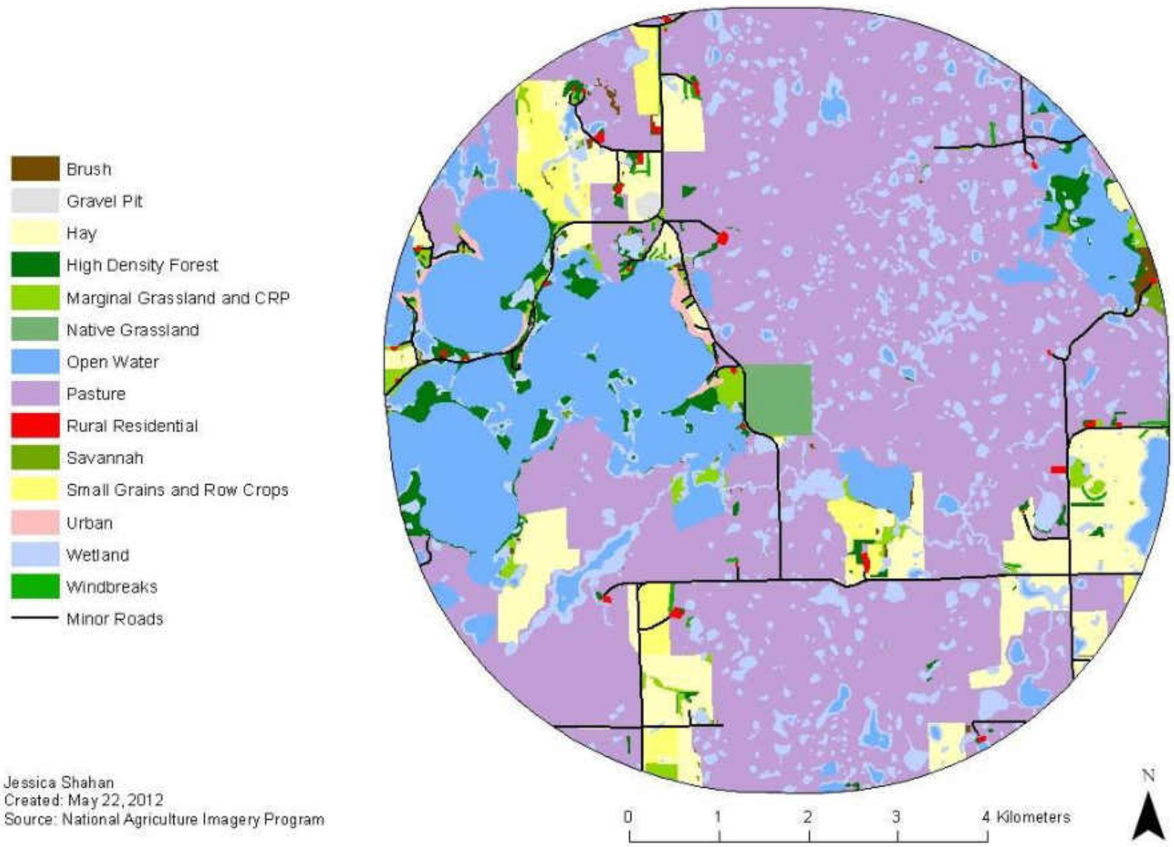


Figure 23: Bluestem Prairie Scientific and Natural Area, Clay Co. Minnesota. Managed by The Nature Conservancy. 1180.9 ha, 16 bird species observed.



Jessica Shahan
Created: May 22, 2012
Source: National Agriculture Imagery Program

Figure 24: Buffalo Lake Wildlife Management Area, Marshall Co. South Dakota. Managed by South Dakota Fish and Wildlife Service. 57.7 ha, 13 bird species observed.

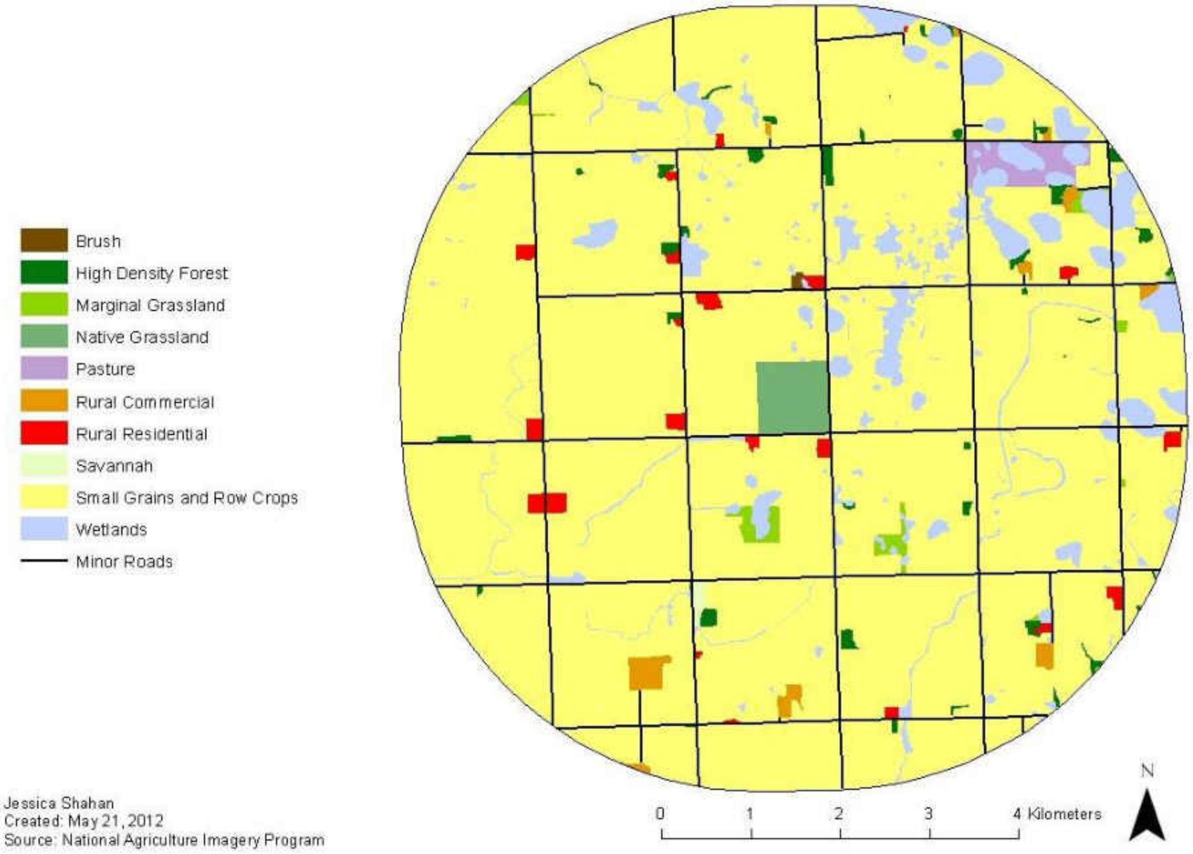
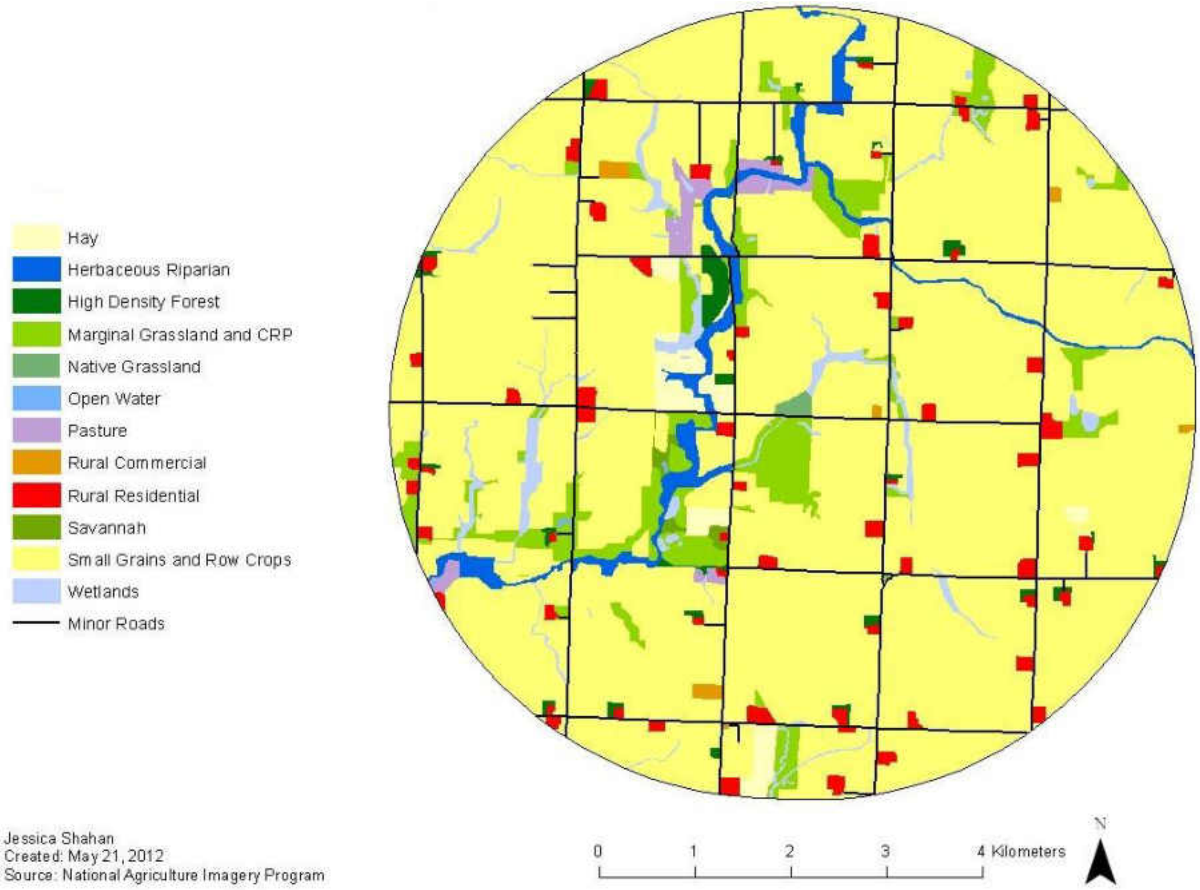


Figure 25: Clinton Prairie Scientific and Natural Area, Big Stone Co. Minnesota. Managed by Minnesota Department of Natural Resources. 64.6 ha, 12 bird species observed.



Jessica Shahan
Created: May 21, 2012
Source: National Agriculture Imagery Program

Figure 26: Compass Prairie Scientific and Natural Area, Nobles Co. Minnesota. Managed by Minnesota Department of Natural Resources. 7.1 ha, 11 bird species observed.

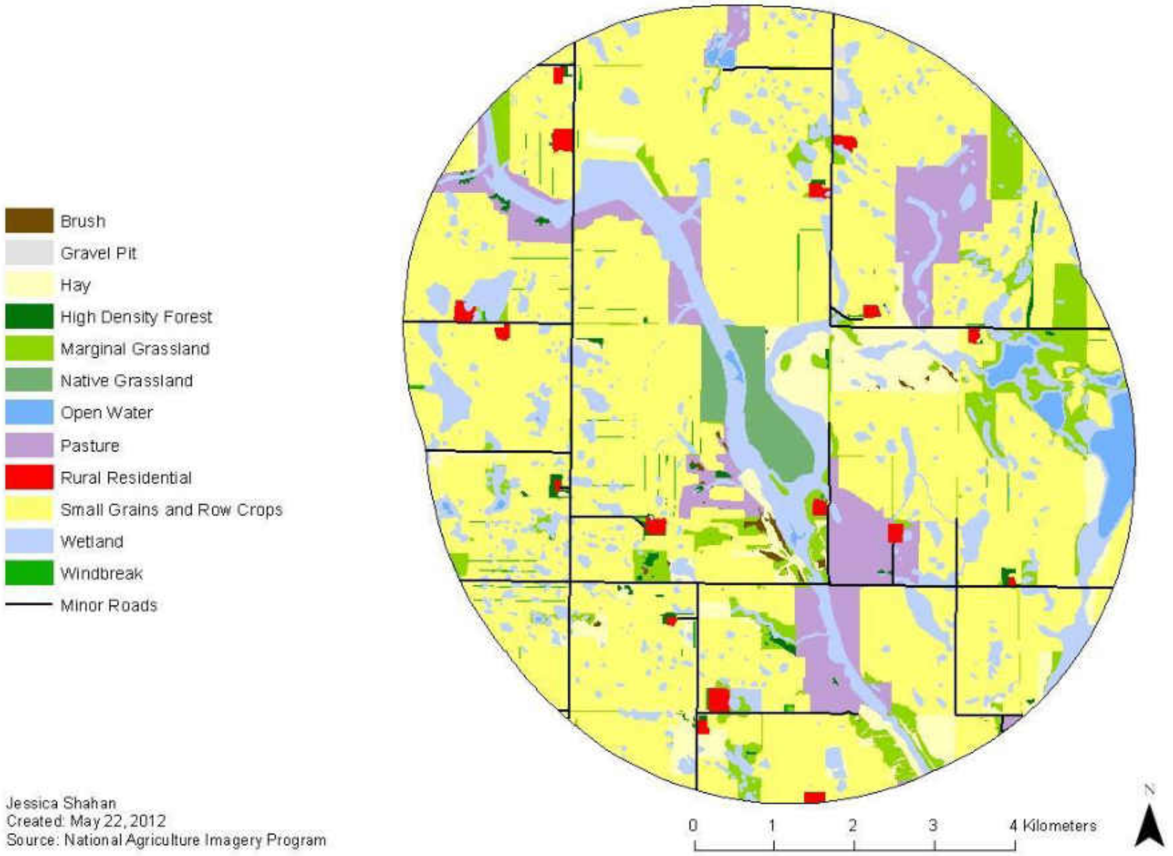
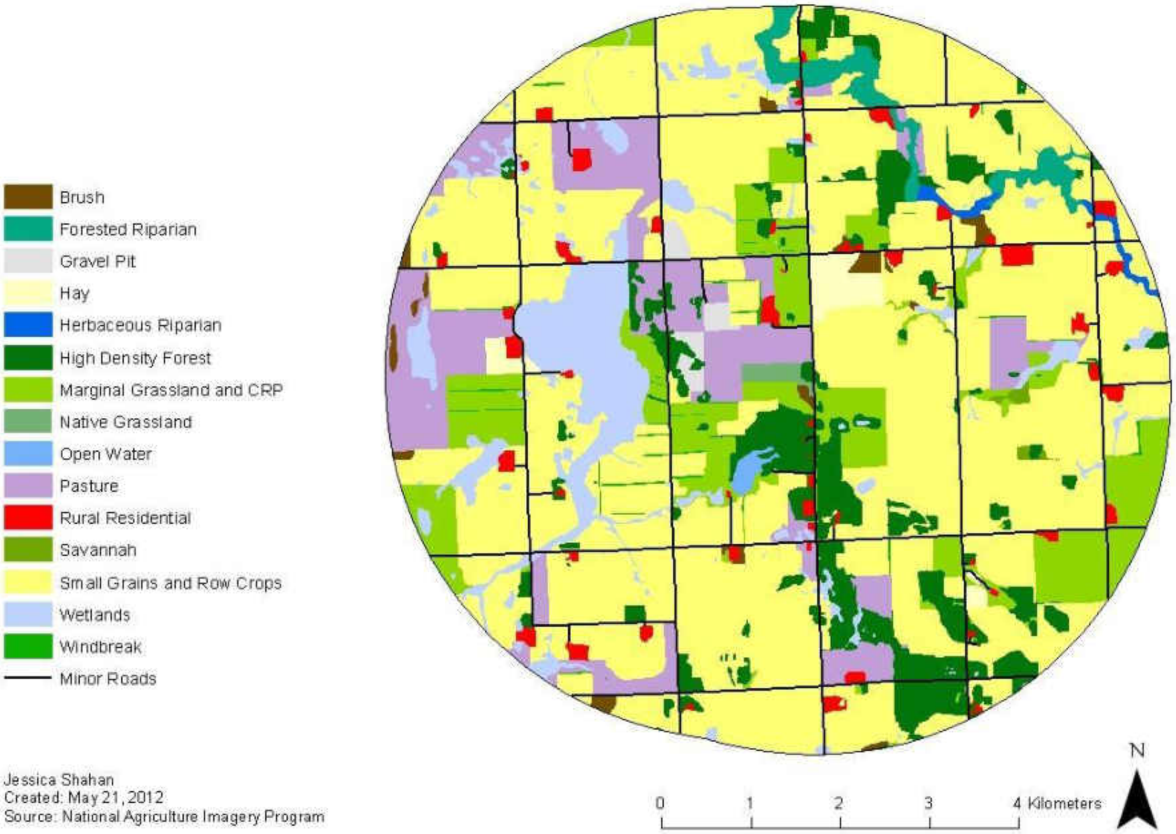


Figure 27: Deep Valley Waterfowl Production Area, Benson Co. North Dakota. Managed by North Dakota Fish and Wildlife Service. 89.9 ha, 14 bird species observed.



Jessica Shahan
Created: May 21, 2012
Source: National Agriculture Imagery Program

Figure 28: Frenchman's Bluff Scientific and Natural Area, Norman Co. Minnesota. Managed by Minnesota Department of Natural Resources. 15.1 ha, 14 bird species observed.

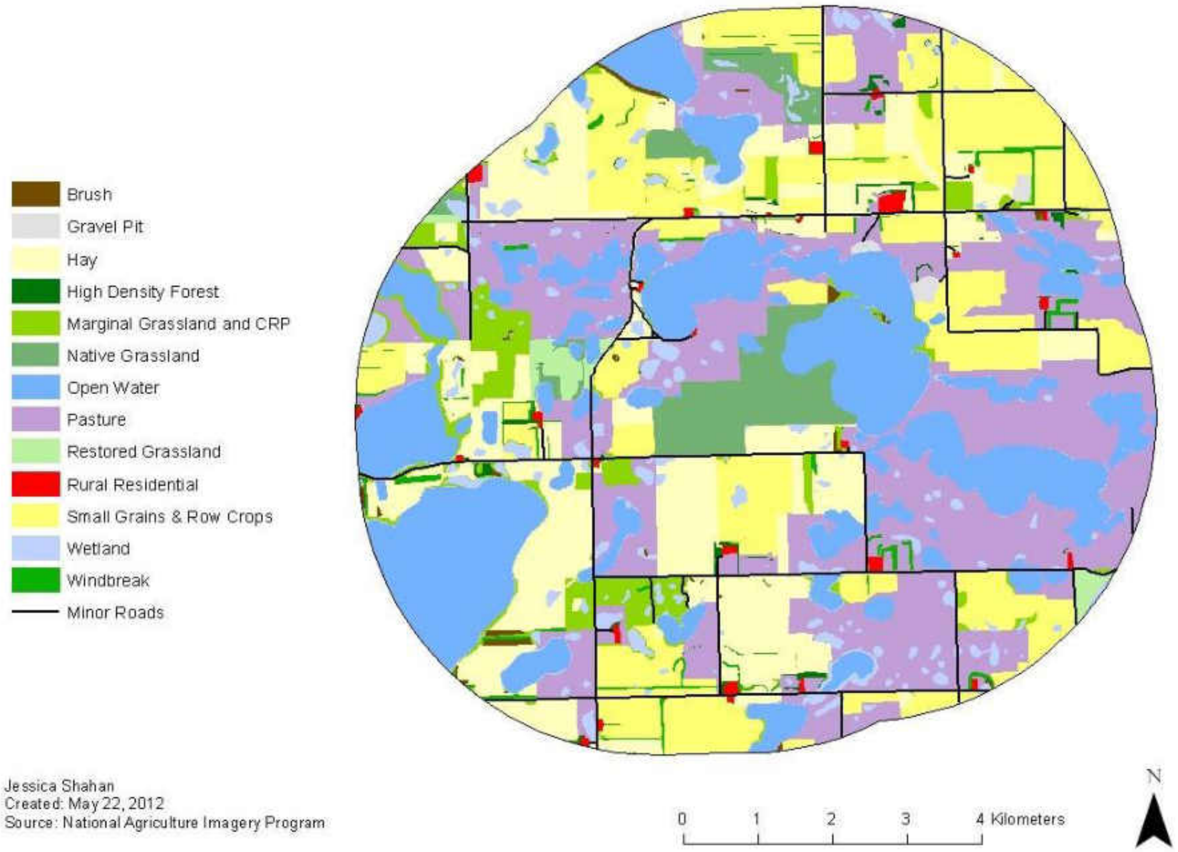
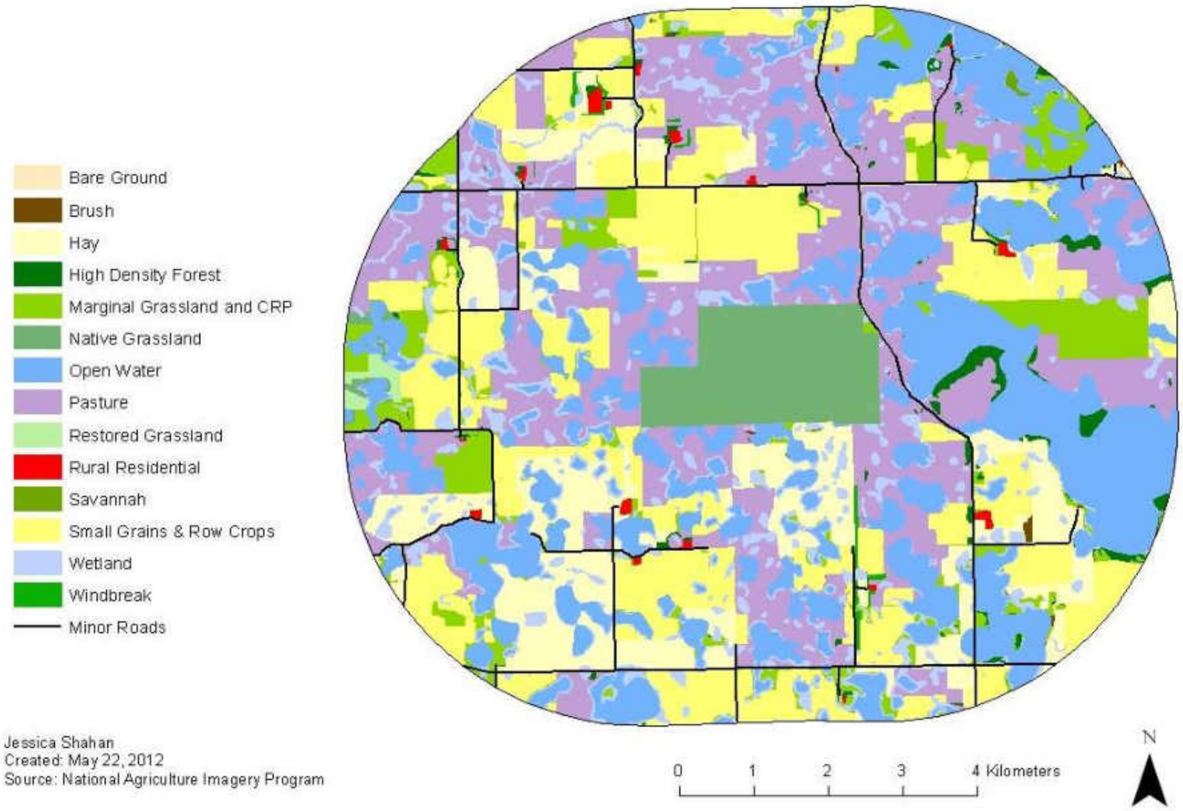


Figure 29: Horseshoe Lake Wildlife Management Area, Codington Co. South Dakota. Managed by South Dakota Fish and Wildlife Service. 252.1 ha, 10 bird species observed.



Jessica Shahan
Created: May 22, 2012
Source: National Agriculture Imagery Program

Figure 30: Jensen Wildlife Management Area, Marshall Co. South Dakota. Managed by South Dakota Fish and Wildlife Service. 440.9 ha, 12 bird species observed.

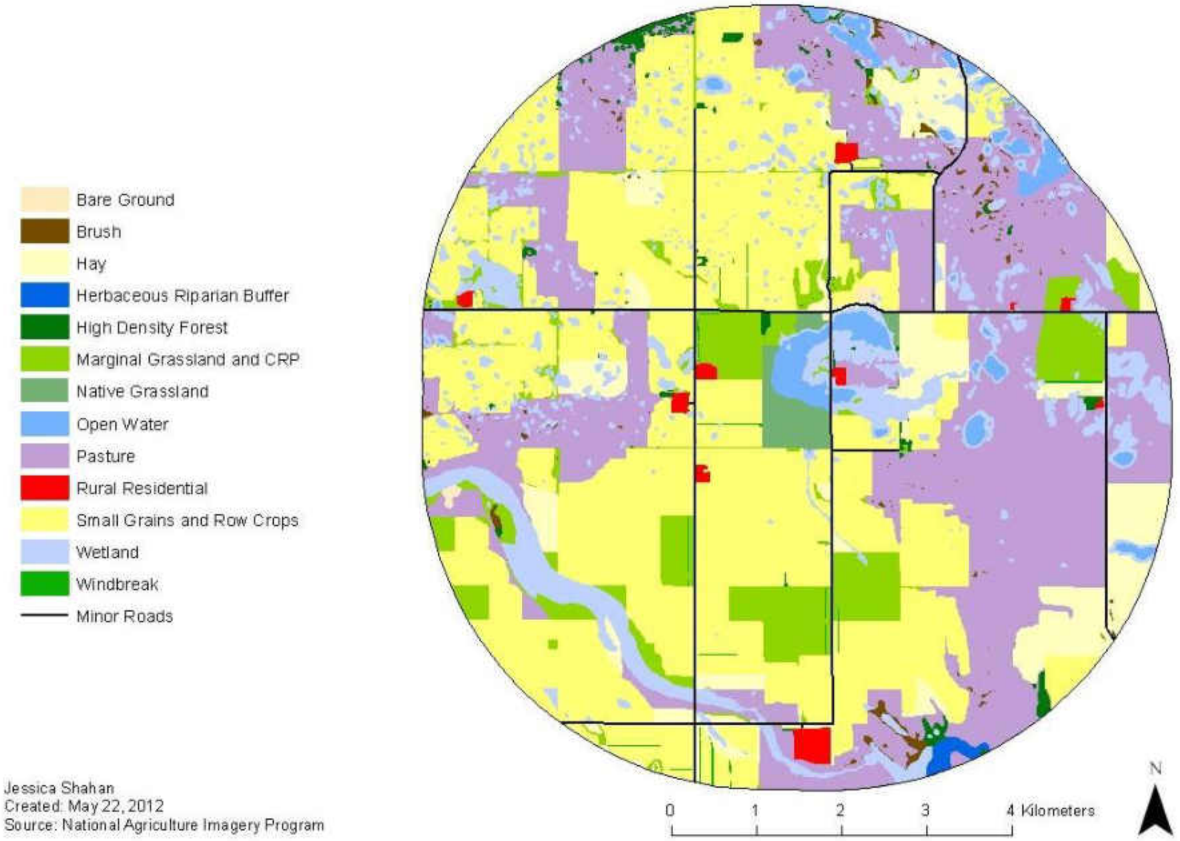
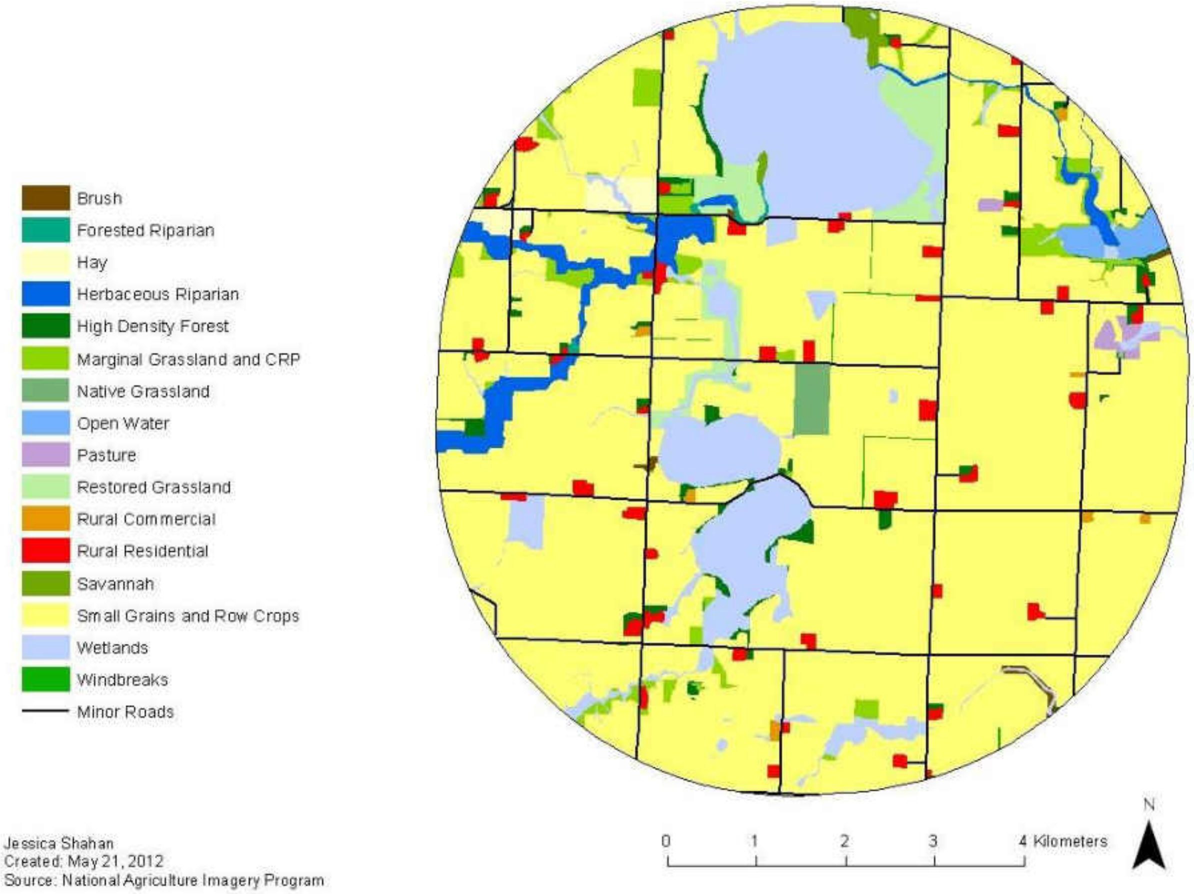
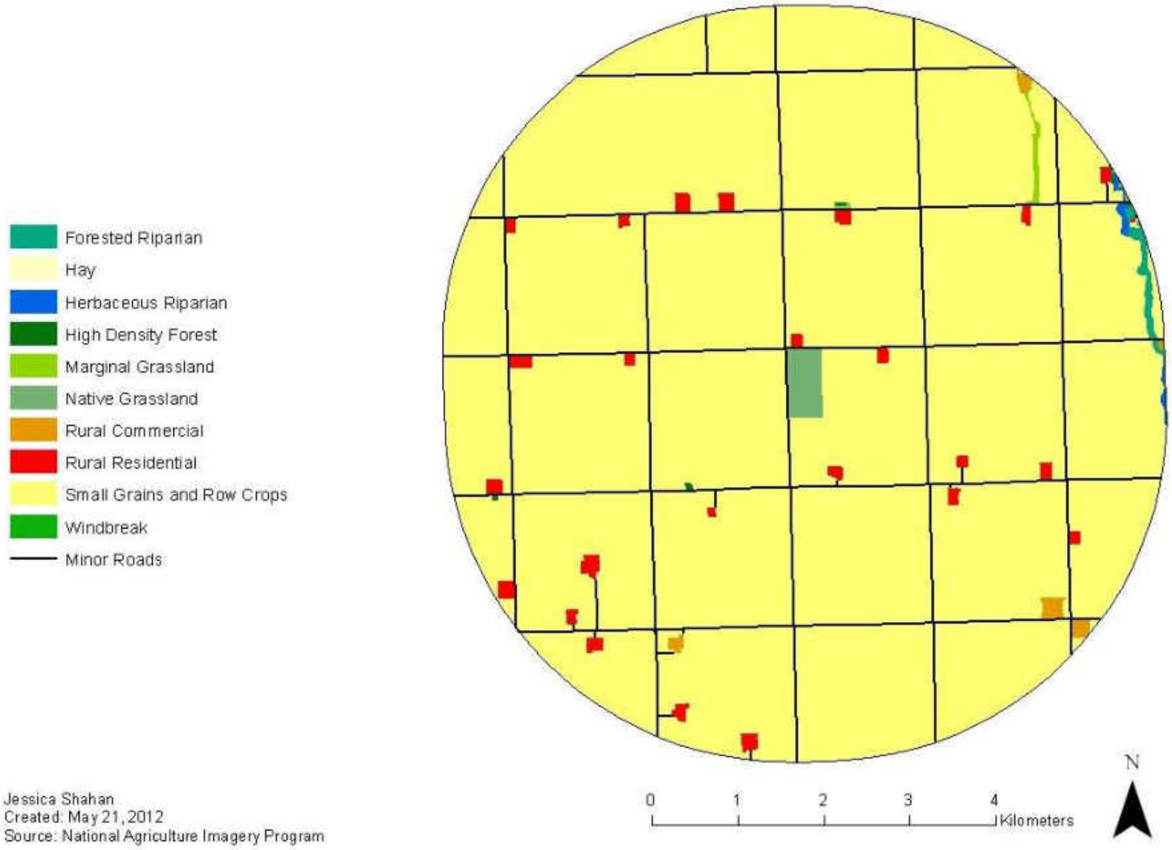


Figure 31: Lone Tree Waterfowl Production Area, Benson Co. North Dakota. Managed by North Dakota Fish and Wildlife Service. 53.4 ha, 12 bird species observed.



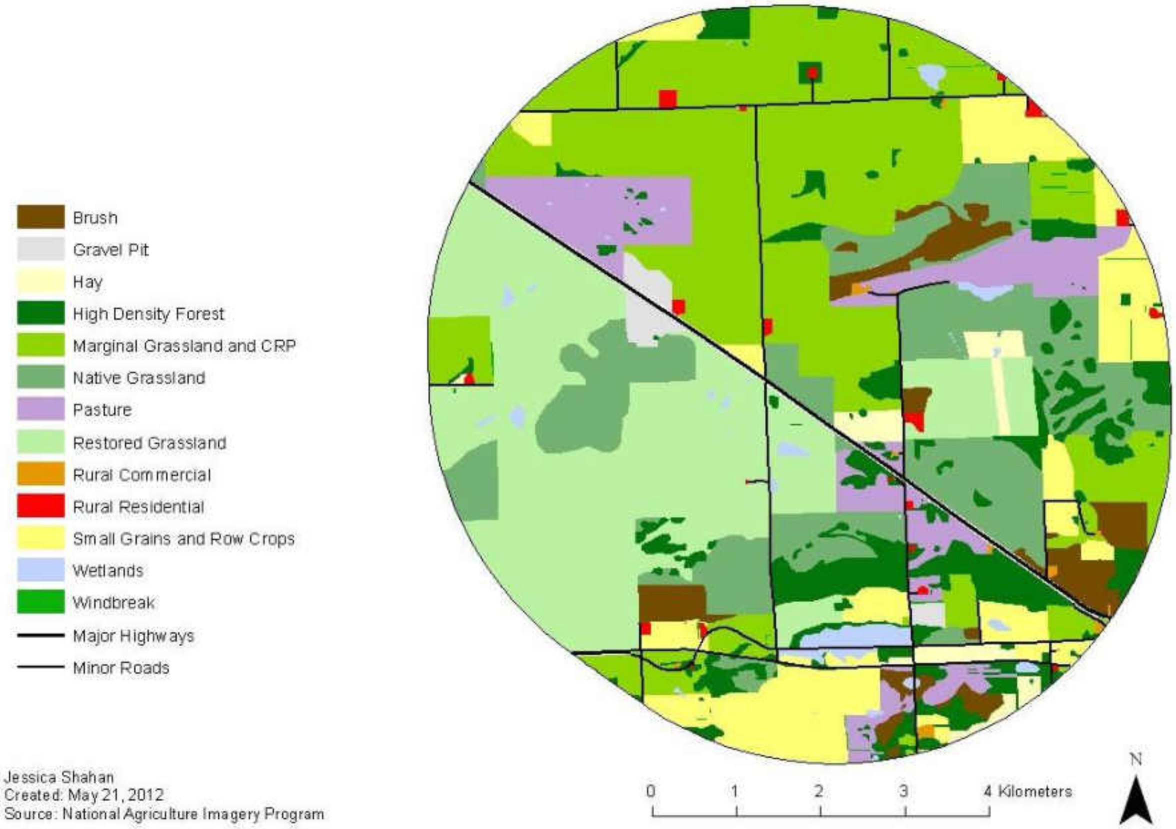
Jessica Shahan
Created: May 21, 2012
Source: National Agriculture Imagery Program

Figure 32: Lundblad Prairie Scientific and Natural Area, Murray Co. Minnesota. Managed by Minnesota Department of Natural Resources. 31.8 ha, 12 bird species observed.



Jessica Shahan
Created: May 21, 2012
Source: National Agriculture Imagery Program

Figure 33: Malmberg Prairie Scientific and Natural Area, Polk Co. Minnesota. Managed by Minnesota Department of Natural Resources. 32.8 ha, 14 bird species observed.



Jessica Shahan
Created: May 21, 2012
Source: National Agriculture Imagery Program

Figure 34: Mentor Prairie Wildlife Management Area, Polk Co. Minnesota. Managed by Minnesota Department of Natural Resources. 40.4 ha, 15 bird species observed.

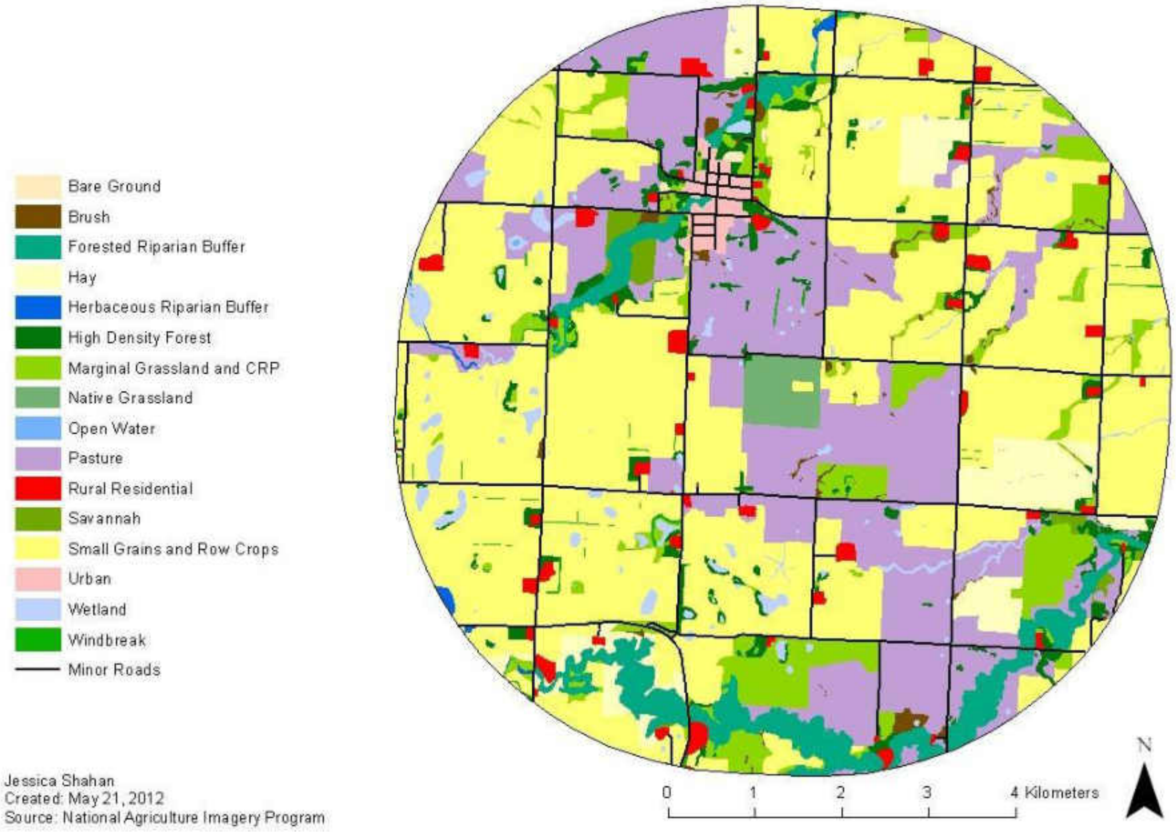


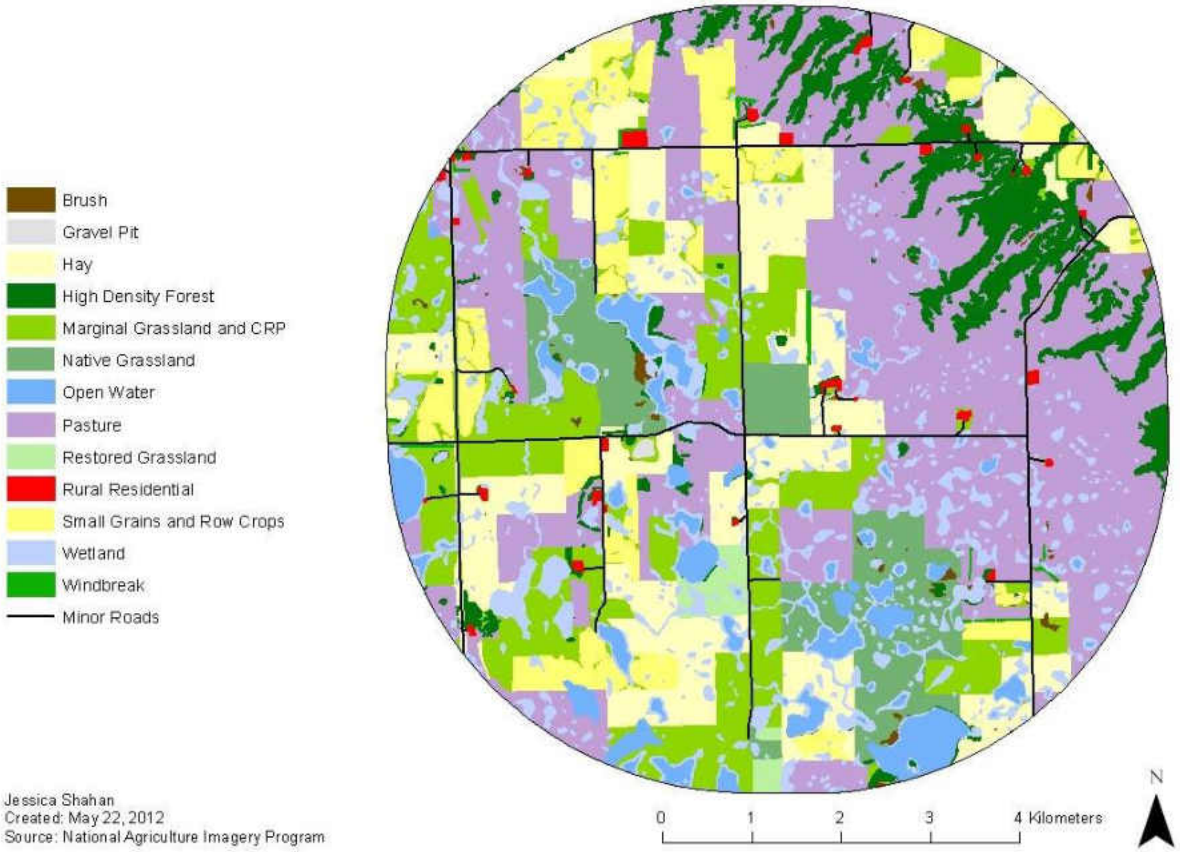
Figure 35: Mound Springs Prairie Scientific and Natural Area, Yellow Medicine Co. Minnesota. Managed by Minnesota Department of Natural Resources. 67.5 ha, 13 bird species observed.

Jessica Shahan
Created: May 22, 2012
Source: National Agriculture Imagery Program

Figure 36: North Lamee Wildlife Management Area, Marshall Co. South Dakota. Managed by South Dakota Fish and Wildlife Service. 162.3 ha, 16 bird species observed.

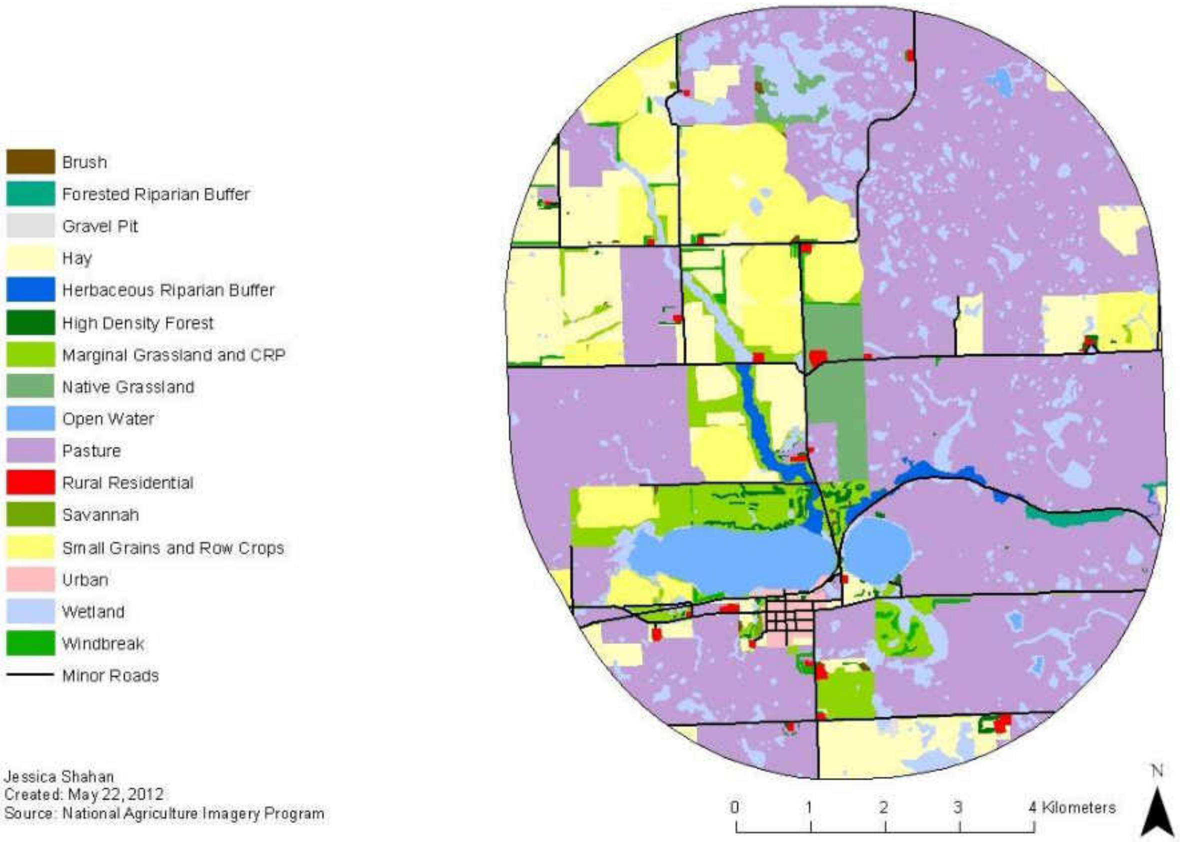
Jessica Shahan
Created: May 22, 2012
Source: National Agriculture Imagery Program

Figure 37: Oakville Prairie, Grand Forks Co., North Dakota. Managed by University of North Dakota. 390.3 ha, 11 bird species observed.



Jessica Shahan
Created: May 22, 2012
Source: National Agriculture Imagery Program

Figure 38: Olson Wildlife Management Area, Marshall Co., South Dakota. Managed by South Dakota Fish and Wildlife Service. 59.2 ha, 15 bird species observed.

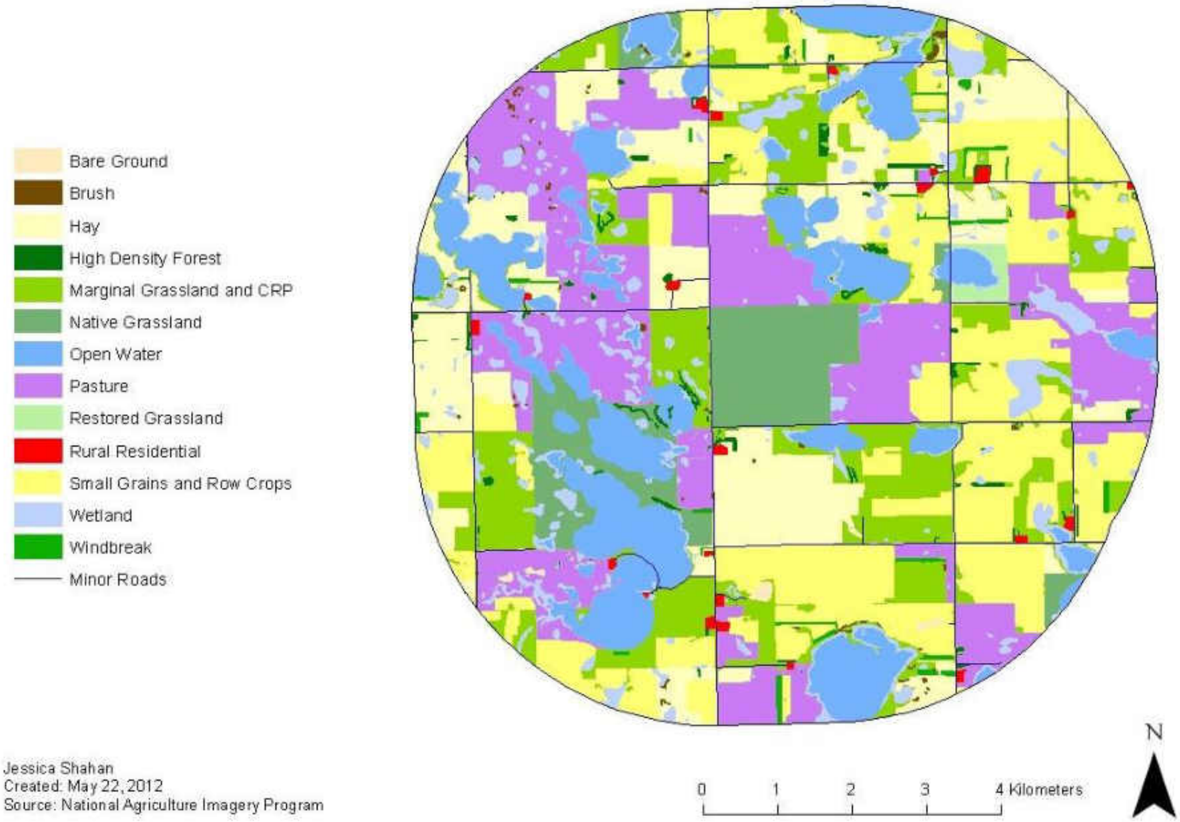


Jessica Shahan
Created: May 22, 2012
Source: National Agriculture Imagery Program

Figure 39: Overland Wildlife Management Area, Codington Co., South Dakota. Managed by South Dakota Fish and Wildlife Service. 154.9 ha, 15 bird species observed.

Jessica Shahan
Created: May 21, 2012
Source: National Agriculture Imagery Program

Figure 40: Pembina Trail Preserve Scientific and Natural Area, Polk Co. Minnesota. Managed by The Nature Conservancy. 677.8 ha, 17 bird species observed.



Jessica Shahan
Created: May 22, 2012
Source: National Agriculture Imagery Program

Figure 41: Roe Wildlife Management Area, Codington Co., South Dakota. Managed by South Dakota Fish and Wildlife Service. 288.8 ha, 16 bird species observed.

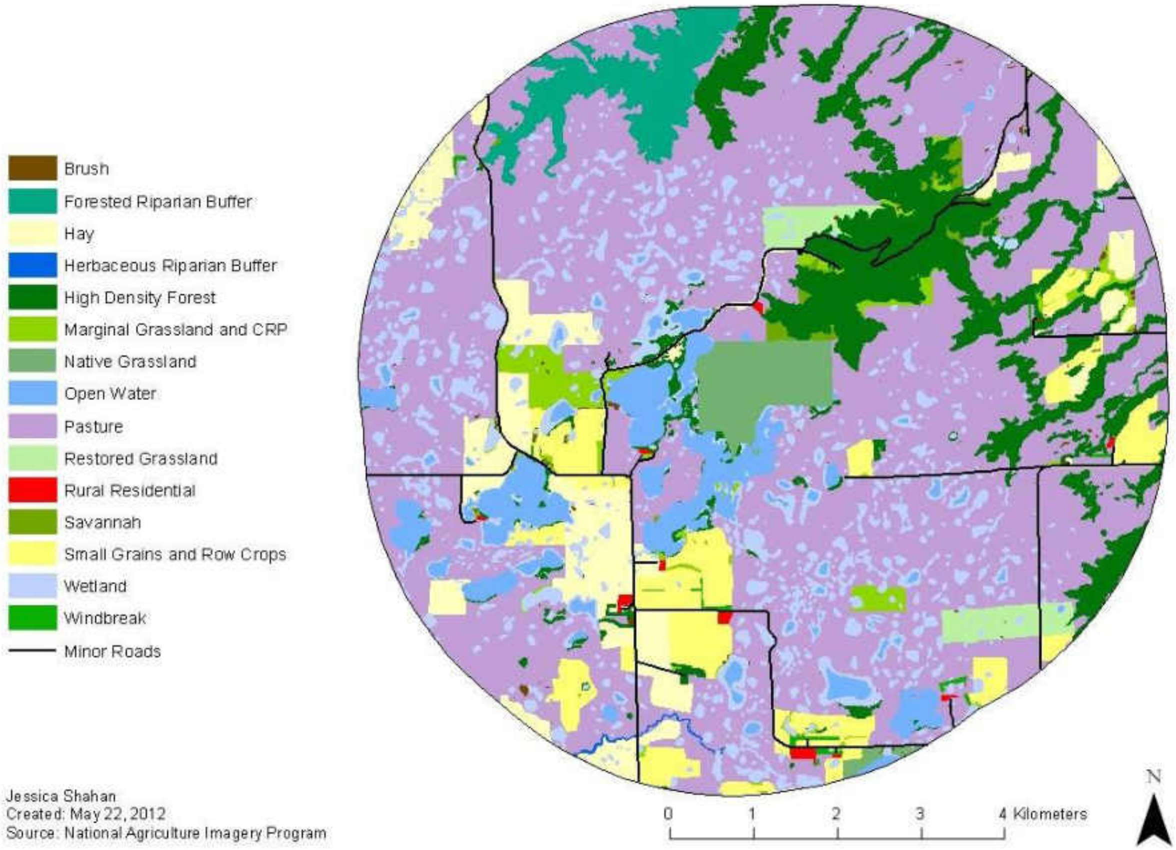


Figure 42: Rolstad Wildlife Management Area, Marshall Co., South Dakota. Managed by South Dakota Fish and Wildlife Service. 151.2 ha, 11 bird species observed.

Jessica Shahan
Created: May 21, 2012
Source: National Agriculture Imagery Program

Figure 43: Sandpiper Prairie Scientific and Natural Area, Norman Co. Minnesota. Managed by Minnesota Department of Natural Resources. 129.4 ha, 15 bird species observed.

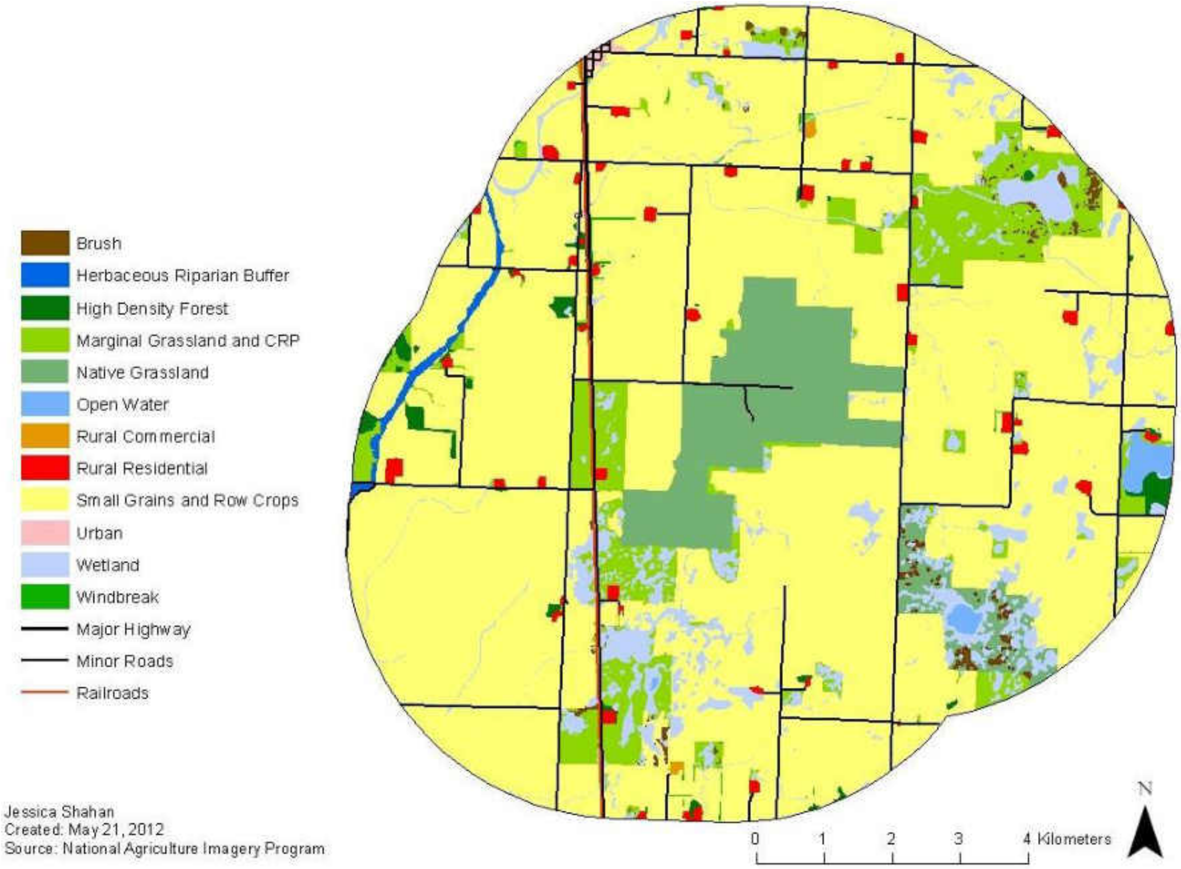
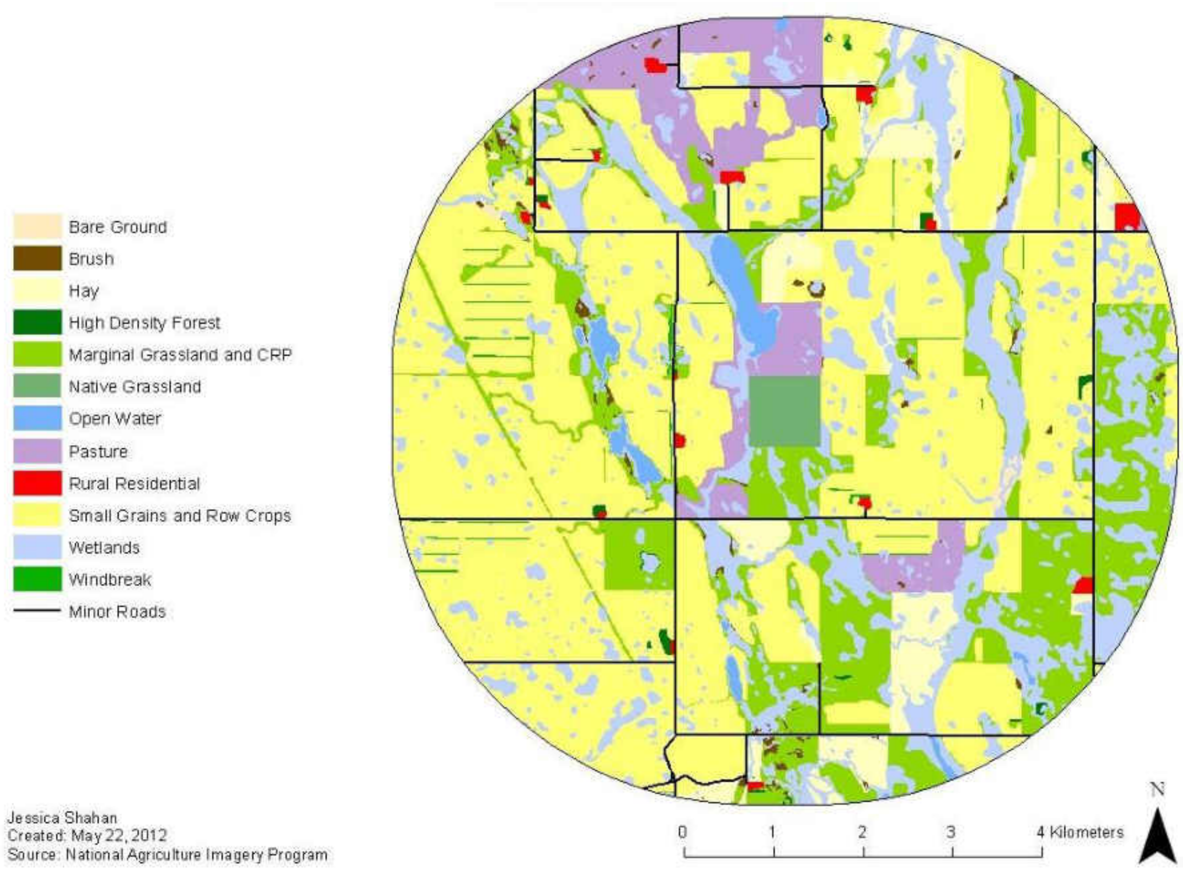


Figure 44: Santee-Wambach Prairie Scientific and Natural Area, Mahnomen Co. Minnesota. Managed by Minnesota Department of Natural Resources. 720.8 ha, 19 bird species observed.



Jessica Shahan
Created: May 22, 2012
Source: National Agriculture Imagery Program

Figure 45: SBA Waterfowl Production Area, Towner Co. North Dakota. Managed by North Dakota Fish and Wildlife Service. 64.3 ha, 12 bird species observed.

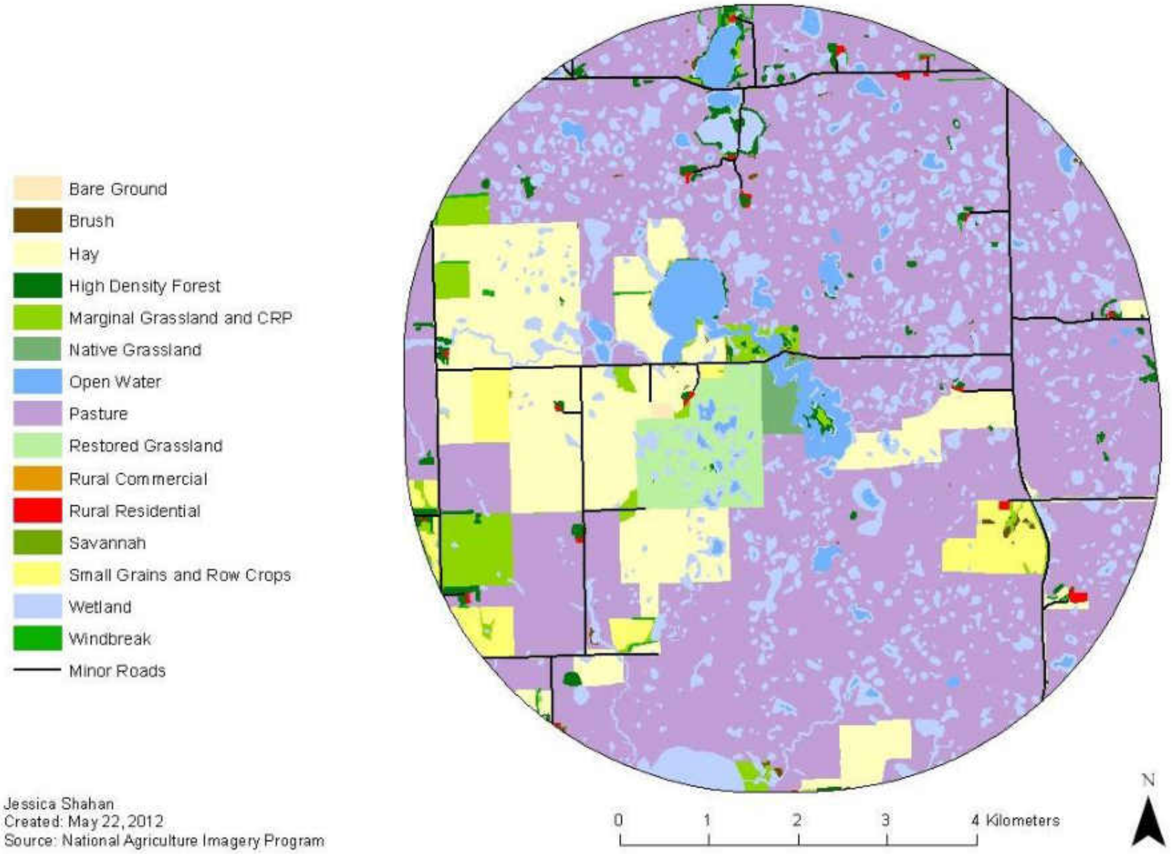


Figure 46: Wike Wildlife Management Area- East Pasture, Roberts Co., South Dakota. Managed by South Dakota Fish and Wildlife Service. 26.3 ha, 12 bird species observed.

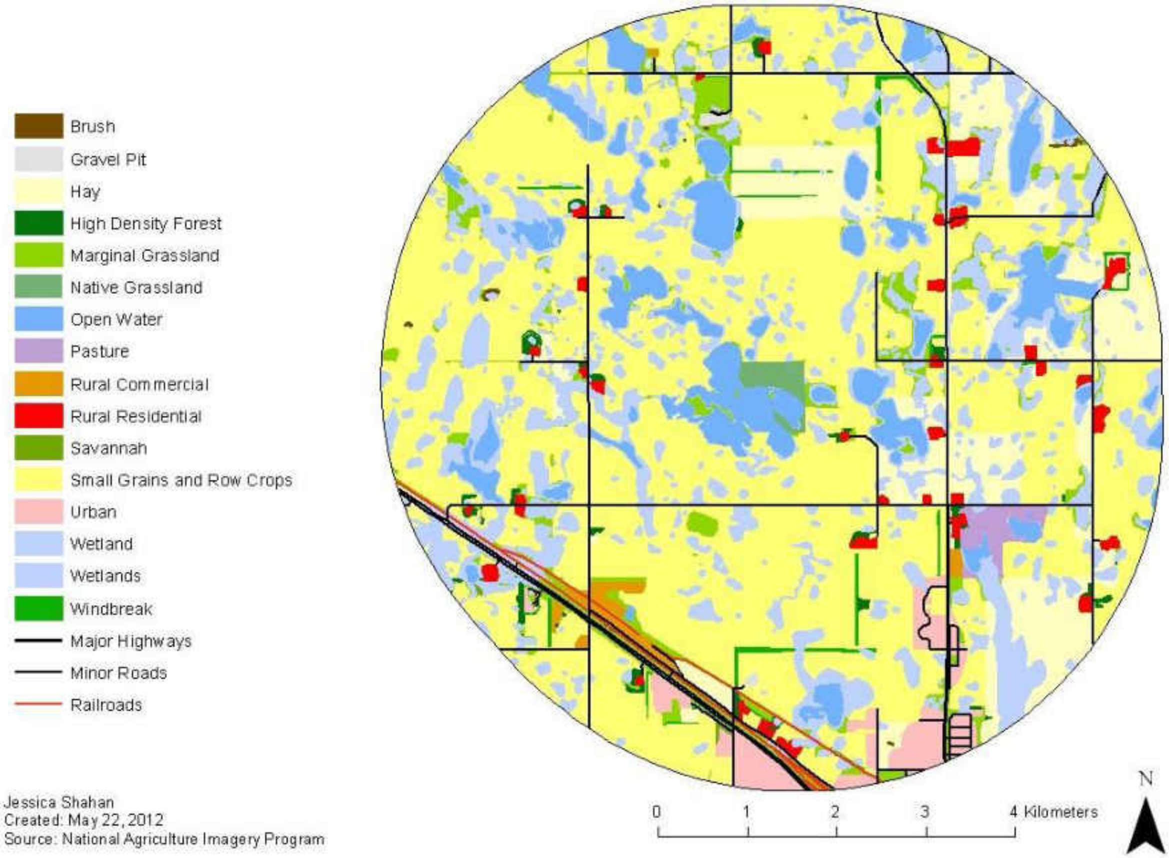


Figure 47: Ziegler Waterfowl Production Area, Ramsey Co. North Dakota. Managed by North Dakota Fish and Wildlife Service. 27.5 ha, 10 bird species observed.

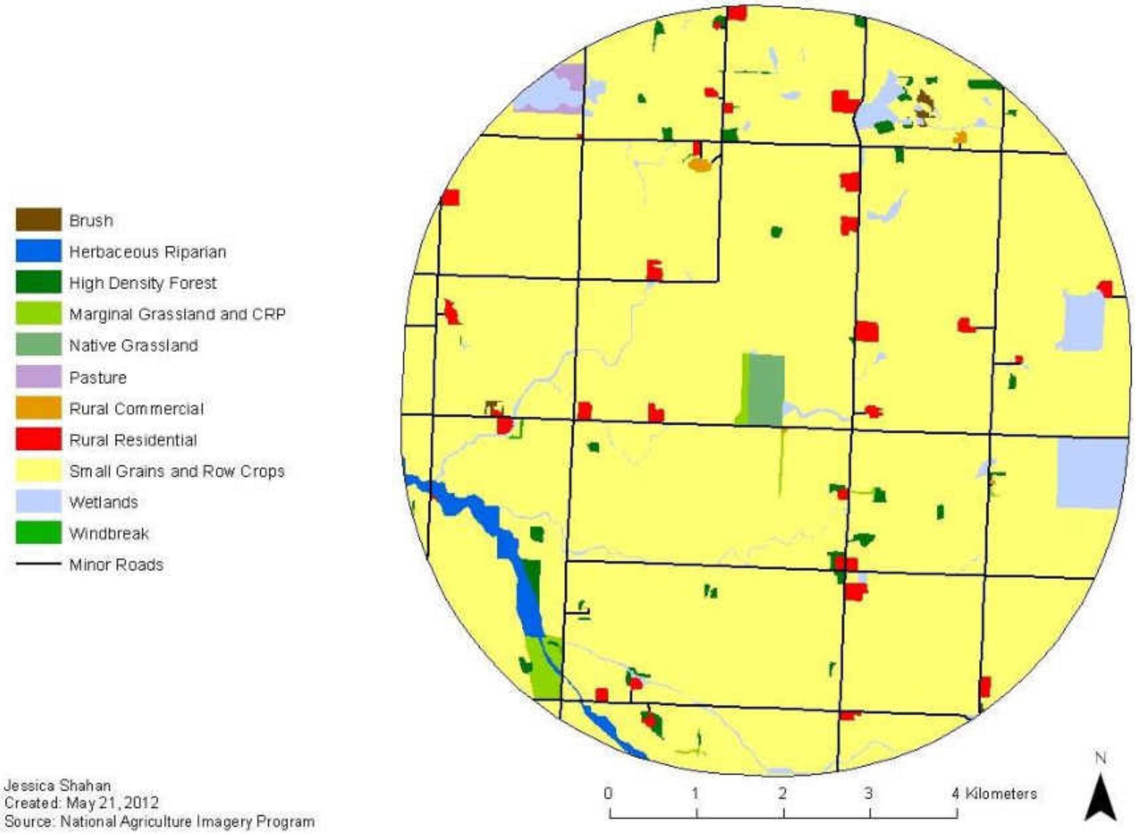


Figure 48: Zimmerman Prairie, Becker Co. Minnesota. Managed by The Nature Conservancy. 33.1 ha, 14 bird species observed.

Appendix B
Presence/Absence Models for Seven Grassland Songbird Species

Table 5: American Goldfinch (*Carduelis tristis*) presence/absence model results. A. shows model averaged results (deviance= 18.46), while B. shows the individual models with the best support.

A.

	Coefficient	Standard Error	95% CI
Intercept	-1.61	3.25	-8.17- 4.95
Contag4	-0.0069	0.034	-0.0755- 0.062
HayPD3	-2.44	2.30	-7.07 – 2.18
MarED1	-0.013	0.034	-0.081 – 0.055
MarPD2	-0.104	0.353	-0.805 – 0.597
NatA1	0.036	0.105	-0.176 – 0.248
PR1	0.021	0.104	-0.189 – 0.231
SHDI4	0.165	0.709	-1.26 – 1.59
WinENN4	0.0079	0.0042	-0.0007 – 0.0165

B.

Model	Deviance	ΔAIC	Model Weight
HayPD3 + WinENN4	15.01	0.00	0.22
MarED1+ WinENN4	13.53	1.48	0.11
MarPD2 + WinENN4	13.53	1.48	0.11
HayPD3 + NatA1 + WinENN4	16.15	1.57	0.10
HayPD3 + SHDI4 + WinENN4	16.14	1.57	0.10
NatA1 + WinENN4	13.21	1.79	0.09
HayPD3 + MarED1 + WinENN4	15.89	1.82	0.09
HayPD3 + PR1 + WinENN4	15.87	1.84	0.09
Contag4 + HayPD3 + WinENN4	15.86	1.85	0.09

Table 6: Barn Swallow (*Hirundo rustica*) presence/absence model results. A. shows model averaged results (deviance= 23.97), while B. shows the individual models with the best support.

A.

	Coefficient	Standard Error	95% CI
Intercept	26.60	1.42	-2.56 -55.7
Grass	0.0069	0.0277	-0.049 – 0.0629
MarMD1	-1.08	1.24	-3.61 – 1.44
PR1	-2.36	1.16	-4.75 – 0.0285
PR0.5	0.336	0.505	-0.675 – 1.35
RowED4	-0.168	0.089	-0.35 – 0.0147
SavENN4	0.0001	0.00054	-0.00099 – 0.0012

B.

Model	Deviance	ΔAIC	Model Weight
MarMD1 + PR1 + RowED4	21.22	0.00	0.32
MarMD1 + PR1 + PR0.5 + RowED4	23.43	0.64	0.23
PR1 + PR0.5 + RowED4	20.16	0.97	0.20
MarMD1 + PR1 + RowED4 + SavENN4	22.21	1.86	0.13
Grass + MarMD1 + PR1 + RowED4	22.14	1.93	0.12

Table 7: Grasshopper Sparrow (*Ammodramus savannarum*) presence/absence model results. A. shows model averaged results (deviance= 18.30), while B. shows the individual models with the best support.

A.

	Coefficient	Standard Error	95% CI
Intercept	-1.22	5.19	-11.6 – 9.11
BruED4	-0.252	0.24	-0.737 – 0.232
Contag2	-0.0081	0.034	-0.071 – 0.055
CRPED4	-0.125	0.142	-0.41 – 0.159
HDF	0.0317	0.161	-0.291 – 0.354
PasED0.5	0.0192	0.029	-0.087 – 0.077
PR4	0.154	0.268	-0.381 – 0.689
RCMD4	-0.17	0.365	-0.9 – 0.559
Robel	0.196	0.539	-0.879 – 1.27
SHDI3	0.138	0.54	-0.936 – 1.21

B.

Model	Deviance	ΔAIC	Model Weight
BruED4 + PasED0.5	11.51	0.00	0.10
BruED4 + CRPED4 + PR4 + RCMD4	16.35	0.80	0.07
BruED4 + PasED0.5 + Robel	13.34	0.87	0.07
BruED4 + CRPED4 + RCMD4	13.31	0.91	0.07
BruED4 + HDF + PasED0.5	13.26	0.95	0.06
BruED4 + CRPED4 + PasED0.5	13.18	1.03	0.06
CRPED4 + RCMD4	10.41	1.09	0.06
BruED4 + CRPED4 + PR4	13.02	1.19	0.06
BruED4 + PR4 + Robel	12.99	1.21	0.06

Table 7 cont.

Model	Deviance	ΔAIC	Model Weight
BruED4 + PasED0.5 + PR4	12.89	1.33	0.05
BruED4 + PasED0.5 + PR4 + Robel	15.62	1.53	0.05
BruED4 + Contag2 + CRPED4	12.56	1.65	0.05
CRPED4	7.32	1.68	0.04
BruED4 + CRPED4 + SHDI3	12.48	1.74	0.04
CRPED4 + SHDI3	9.75	1.75	0.04
Contag2 + CRPED4	9.71	1.79	0.04
CRPED4 + PR4 + RCMD4	12.30	1.91	0.04
BruED4 + PR4 + RCMD4	12.27	1.94	0.04

Table 8: Le Conte's Sparrow (*Ammodramus leconteii*) presence/absence model results. A. shows model averaged results (deviance= 22.12), while B. shows the individual models with the best support.

A.

	Coefficient	Standard Error	95% CI
Intercept	-0.691	2.31	-5.34 – 3.95
CRPED4	0.189	0.17	-0.151 – 0.529
CRPNP1	0.050	0.132	-0.211 – 0.312
EDL2	-0.0133	0.027	-0.067 – 0.041
EDL4	-0.0078	0.022	-0.051 – 0.036
NatA3	0.286	0.382	-0.483 – 1.06
NatMD4	0.0153	0.014	-0.012 – 0.043
Robel	-0.349	0.759	-1.86 – 1.16

B.

Model	Deviance	ΔAIC	Model Weight
CRPED4 + EDl2 + NatMD4	19.33	0.00	0.17
CRPED4 + EDl2 + NatA3 + NatMD4	21.20	1.07	0.10
CRPED4 + EDL4 + Nat MD4	18.21	1.12	0.10
CRPED4 + Nat MD4	15.33	1.30	0.09
NatA3 + Robel	15.30	1.33	0.09
CRPNP1 + NatA3 + NatMD4	17.89	1.45	0.08
CRPED4 + NatA3 + NatMD4	17.79	1.54	0.08
CRPNP1 + NatA3	15.04	1.59	0.08
CRPED4 + EDL4 + NatA3 + NatMD4	20.54	1.73	0.07
NatA3 + NatMD4 + Robel	17.59	1.74	0.07
CRPED4 + Robel	14.68	1.94	0.07

Table 9: Sedge Wren (*Cistothorus platensis*) presence/absence model results. A. shows model averaged results (deviance= 22.39), while B. shows the individual models with the best support.

A.

	Coefficient	Standard Error	95% CI
Intercept	9.32	10.7	-12.20 – 30.90
EDL1	0.011	0.026	-0.039 – 0.62
Forbs	-0.046	0.089	-0.225 – 0.133
NatNP1	0.177	0.41	-0.636 – 0.991
PR2	1.87	1.43	-1.04 – 4.78
PR4	-2.04	1.58	-5.23 – 1.16
Water	-0.44	0.28	-1.01 – 0.13
WatPD1	3.68	2.79	-1.96 – 9.32
WetA3	-0.69	0.399	-1.51 – 0.134

B.

Model	Deviance	ΔAIC	Model Weight
PR2 + PR4 + Water + WatPD1 +WetA3	19.42	0.00	0.48
Forbs + PR2 + PR4 + Water + WatPD1 +WetA3	22.13	0.80	0.32
EDL1 + NatNP1 + Water + WetA3	14.40	1.81	0.19

Table 10: Upland Sandpiper (*Bartramia longicauda*) presence/absence model results. A. shows model averaged results (deviance= 21.34), while B. shows the individual models with the best support.

A.

	Coefficient	Standard Error	95% CI
Intercept	7.97	10.600	-13.10 – 29.10
Brush	0.032	0.119	-0.207 – 0.272
Contag0.5	-0.053	0.142	-0.335 – 0.228
CRPA4	0.195	0.128	-0.062 – 0.453
Grass	-0.087	0.046	-0.180 – 0.006
HDFED2	-0.006	0.026	-0.058 – 0.046
MarENN3	0.0005	0.002	-0.002 – 0.004
Patch	0.0015	0.003	-0.005 – 0.008
Robel	-0.087	0.378	-0.848 – 0.675

B.

Model	Deviance	ΔAIC	Model Weight
CRPA4 + Grass	14.49	0.00	0.26
Contag0.5 + Grass + MarENN3 + Patch	19.03	1.11	0.15
Brush + CRPA4 + Grass	15.87	1.33	0.13
CRPA4 + Grass + Patch	15.77	1.43	0.13
CRPA4 + Grass + MarENN3	15.72	1.49	0.12
CRPA4 + Grass + HDFED2	15.45	1.75	0.11
CRPA4 + Grass + Robel	15.41	1.79	0.11

Table 11: Cliff Swallow (*Hirundo pyrrhonota*) presence/absence model results. A. shows model averaged results (deviance= 23.03), while B. shows the individual models with the best support.

A.

	Coefficient	Standard Error	95% CI
Intercept	1.97	4.36	-6.75 – 10.7
Brush	-0.026	0.116	-0.275 – 0.206
Contag4	0.0058	0.031	-0.056 – 0.067
CRPED3	-0.0043	0.031	-0.066 – 0.058
EDL4	-0.0008	0.006	-0.012 – 0.011
Forbs	-0.0669	0.073	-0.214 – 0.079
HayPD0.5	-0.728	1.35	-3.43 – 1.98
HDF	-0.0605	0.29	-0.649 – 0.528
Patch	0.0085	0.006	-0.003 – 0.019
PR3	-0.0798	0.206	-0.492 – 0.332
SHDI4	0.0089	0.812	-1.61 – 1.62
Wetland	-0.073	0.082	-2.238 – 0.091

B.

Model	Deviance	ΔAIC	Model Weight
Patch + Wetland	12.80	0.00	0.09
Forbs + Patch + Wetland	15.25	0.26	0.08
Forbs + HayPD0.5 + Patch + Wetland	18.06	0.39	0.07
Forbs + HayPD0.5 + Patch	14.91	0.60	0.06
Forbs + Patch + PR3 + Wetland	17.47	0.98	0.05
Contag4 + Forbs + Patch + Wetland	17.43	1.02	0.05
Patch	9.20	1.10	0.05

Table 11 cont.

Model	Deviance	ΔAIC	Model Weight
Forbs + Patch + SHDI4 + Wetland	17.27	1.17	0.05
HDF + Patch + Wetland	14.33	1.18	0.05
Brush + Patch + Wetland	14.24	1.27	0.05
Forbs + HayPD0.5 + Patch + PR3 + Wetland	20.36	1.29	0.05
Patch + PR3 + Wetland	14.09	1.42	0.04
Forbs + HayPD0.5 + Patch + PR3	16.79	1.66	0.04
Forbs + HayPD0.5	11.01	1.79	0.04
HDF + Patch	11.01	1.80	0.04
Forbs + Patch	11.00	1.81	0.04
EDL4 + Forbs + Patch + Wetland	11.00	1.89	0.03
HayPD0.5 + Patch + Wetland	16.56	1.93	0.03
Brush + Patch	13.58	1.96	0.03
Forbs + HayPD0.5 + PR3 + SHDI4	10.84	1.96	0.03
CRPED3 + Forbs + HayPD0.5 + Patch + Wetland	16.49	1.96	0.03

Table 12: Marsh Wren (*Cistothorus palustris*) presence/absence model results. A. shows model averaged results (deviance= 21.96), while B. shows the individual models with the best support.

A.

	Coefficient	Standard Error	95% CI
Intercept	0.954	1.270	-1.64 – 3.55
CRPED0.5	-0.204	0.114	-0.439 – 0.032
HDF	0.243	0.523	-0.812 – 1.300
WatMD0.5	-0.108	0.246	-0.604 -0.388
WetA2	0.441	0.257	-0.089 – 0.970
Wetland	0.025	0.044	-0.063 – 0.113
WetPD0.5	-0.343	0.182	-0.716 -0.031

B.

Model	Deviance	ΔAIC	Model Weight
CRPED0.5 + WetA2 + WetPD0.5	16.18	0.00	0.23
CRPED0.5 + HDF + WetA2 + WetPD0.5	18.86	0.27	0.20
CRPED0.5 + WatMD0.5 + WetA2 + WetPD0.5	18.79	0.34	0.19
CRPED0.5 + WetA2 + Wetland + WetPD0.5	18.56	0.57	0.17
CRPED0.5 + HDF + WetA2 + Wetland + WetPD0.5	21.14	1.19	0.12
CRPED0.5 + WatMD0.5 + WetA2 + Wetland + WetPD0.5	20.54	1.79	0.09

Table 13: Western Meadowlark (*Sturnella neglecta*) presence/absence model results. A. shows model averaged results (deviance=26.44), while B. shows the individual models with the best support.

A.

	Coefficient	Standard Error	95% CI
Intercept	6.00	12.10	-17.9 – 29.9
Contag4	-0.089	0.126	-0.34 – 0.162
HDF	-1.22	0.655	-2.57 – 0.13
MarMD2	-0.490	0.654	-1.80 – 0.82
RCED4	-2.51	2.010	-6.55 – 1.54
RCMD1	0.155	0.545	-0.951 – 1.26
SHDI4	2.37	2.560	-2.73- 7.47

B.

Model	Deviance	ΔAIC	Model Weight
HDF + RCED4 + SHDI4	21.93	0.00	0.18
HDF + MarMD2 + RCED4+ SHDI4	24.76	0.12	0.17
Contag4 + HDF + RCED4	21.29	0.64	0.13
HDF + MarMD2 + SHDI4	21.19	0.74	0.13
Contag4 + HDF + MarMD2 + RCED4	23.89	0.99	0.11
HDF + RCED4 + RCMD1 + SHDI4	23.71	1.17	0.10
Contag4 + HDF + RCED4 + RCMD1	23.47	1.41	0.09
Contag4 + HDF + MarMD2	120.39	1.54	0.08

Appendix C
Model-Averaged Results for Community and Functional Group Analysis

Table 14: Richness and Diversity results for the Total Community

	Total Richness (adjusted r^2=0.76)			Margelef's Richness(adjusted r^2=0.44)			Shannon Diversity (adjusted r^2=0.72)		
	Coefficient	Standard Error	95% CI	Coefficient	Standard Error	95% CI	Coefficient	Standard Error	95% CI
Intercept	9.12	0.537	8.01-10.20	2.13	0.073	1.98-2.29	1.82	0.08	1.66- 1.98
BruENN3	-	-	-	-	-	-	-0.0002	0.00007	-0.0003- -0.00006
BruNP0.5	-	-	-	0.031	0.007	0.015- 0.046	-	-	-
Brush	-	-	-	0.005	0.009	-0.012- 0.022	0.001	0.005	-0.008-0.01
FRBNP2	-	-	-	0.126	0.033	0.056-0.019	-	-	-
HayENN0.5	-	-	-	-0.0003	0.0001	-0.0005- -0.0007	-0.0004	0.0001	-0.0006- 0.0001
Hay MD4	-0.199	0.042	-0.29- -0.11	-0.005	0.007	-0.02- 0.0096	-0.011	0.01	-0.031- 0.0095
HDFMD1	-	-	-	-0.047	0.012	-0.073- -0.002	-	-	-
HDFNP4	-	-	-	-0.004	0.0006	-0.005- -0.003	-	-	-
Nat MD4	0.018	0.004	0.01-0.027	-	-	-	-	-	-
Nat NP1	0.356	0.136	0.073-0.64	-	-	-	-	-	-
PasMD0.5	-	-	-	0.002	0.001	0.0005- 0.0044	-	-	-
PasMD2	-	-	-	-	-	-	-0.006	0.005	-0.016- 0.004
Patch	0.004	0.001	0.002-0.006	-	-	-	0.0001	0.00013	-0.0002- 0.0004

Table 14 cont.

	Total Richness (adjusted r^2=0.76)			Margelef's Richness(adjusted r^2=0.44)			Shannon Diversity (adjusted r^2=0.72)		
	Coefficient	Standard Error	95% CI	Coefficient	Standard Error	95% CI	Coefficient	Standard Error	95% CI
RCArea4	-1.08	1.39	-3.85-1.68	-	-	-	-	-	-
RCED4	-0.504	0.524	-1.55-0.54	-	-	-	-	-	-
RRPD0.5	-	-	-	-0.096	0.034	-0.17- -0.025	-	-	-
SavNP4	-1.110	0.333	-1.79 - -0.4	-	-	-	-	-	-
SavPD4	75.4	24.8	23.8-127	-	-	-	-	-	-
SHDI4	-	-	-	-	-	-	0.008	0.003	-0.061- 0.076
UrbNP1	-	-	-	-0.109	0.028	-0.167- -0.0515	-	-	-
UrbPD1	-	-	-	-	-	-	-1.44	0.044	-2.34- -0.054
WetMD0.5	-	-	-	-	-	-	-0.02	0.035	-0.09- 0.049
WetNP0.5	-	-	-	-	-	-	0.001	0.0012	-0.001- 0.003

Table 15: Richness and Diversity results for the grassland obligates functional group

	Total Richness (adjusted r^2=0.91)			Margelef's Richness (adjusted r^2=0.87)			Shannon Diversity (adjusted r^2=0.71)		
	Coefficient	Standard Error	95% CI	Coefficient	Standard Error	95% CI	Coefficient	Standard Error	95% CI
Intercept	2.51	0.499	1.51- 3.51	0.451	0.181	0.0089- 0.811	4.03	2.68	-1.34- 9,4
BruENN2	-0.00018	0.00019	-0.0006- 0.0002	-	-	-	-	-	-
Contag2	-0.0018	0.0056	-0.013- 0.0093	-	-	-	-	-	-
Contag3	-	-	-	-	-	-	-0.003	0.027	-0.086- 0.025
Contag4	-	-	-	-	-	-	-0.0009	0.003	-0.0083- 0.0064
EDL1	-	-	-	-	-	-	-0.00025	0.001	-0.0023- 0.0018
EDL3	-	-	-	0.0094	0.01	-.011- 0.029	-0.0004	0.0016	-0.0036- 0.0028
EDL4	-	-	-	-0.012	0.011	-0.034- 0.0097	-0.0059	0.0029	-0.0118- 0.00004
HayED2	-0.028	0.0087	-0.046- -0.010	-0.0053	0.008	-.021- 0.011	-0.0006	0.0028	-0.0063- 0.0049
HDFPD0.5	-0.134	0.034	-0.205- -0.063	-	-	-	-	-	-
HRBENN4	-	-	-	0.0001	0.00009	-0.0001- 0.0003	0.000007	0.00003	-0.00005- 0.00007
HRBNP3	-	-	-	0.018	0.021	-0.023- 0.059	-	-	-
MarED3	-	-	-	-0.0006	0.0015	-0.0035- 0.002	-	-	-
MarMD0.5	-	-	-	-	-	-	-0.0025	0.0046	-0.012- 0.0067

Table 15 cont.

	Total Richness (adjusted r^2=0.91)			Margelef's Richness (adjusted r^2=0.87)			Shannon Diversity (adjusted r^2=0.71)		
	Coefficient	Standard Error	95% CI	Coefficient	Standard Error	95% CI	Coefficient	Standard Error	95% CI
NatArea2	-	-	-	-	-	-	0.026	0.011	-0.047- -0.0051
PasED0.5	0.026	0.0035	0.018- 0.033	0.0024	0.0022	-0.002- 0.007	0.0095	0.0019	0.0055- 0.013
PasNP3	0.001	0.004	-0.007- 0.196	-	-	-	-	-	-
RCED3	-0.066	0.134	-0.328- 0.196	-	-	-	-	-	-
RCMD2	0.017	0.041	-0.063- 0.098	-	-	-	-	-	-
RowMD1	0.007	0.002	0.003- 0.013	-	-	-	-	-	-
RRENN3	-	-	-	0.0003	0.00012	0.00005- 0.0006	-	-	-
RRPD0.5	-	-	-	-0.052	0.034	-0.122- 0.017	-	-	-
SHDI2	0.041	0.113	-0.185- 0.266	-	-	-	-	-	-
SHDI4	-	-	-	-	-	-	-0.359	0.502	-1.36- 0.646
UrbNP1	-	-	-	-	-	-	-0.0316	0037	-0.106- 0.0426
WatMD1	0.005	0.003	-0.0005- 0.011	0.002	0.0007	0.0005- 0.004	0.00026	0.0008	-0.0013- 0.0019
WetMD1	-	-	-	0.0082	0.0028	0.0022- 0.014	-	-	-
WetNP4	-	-	-	-	-	-	-0.0004	0.0002	-0.0009- -0.00002
WetPD2	-0.064	0.016	-0.097- -0.031	-	-	-	-	-	-
WinNP3	0.011	0.004	0.003-0.019	-	-	-	-	-	-

Table 16: Richness and Diversity results for the grassland users functional group

	Total Richness (adjusted r^2=0.74)			Margelef's Richness (adjusted r^2=0.77)			Shannon Diversity (adjusted r^2=0.60)		
	Coefficient	Standard Error	95% CI	Coefficient	Standard Error	95% CI	Coefficient	Standard Error	95% CI
WinPD4	-	-	-	0.22	0.079	0.056- 0.383	-	-	-
Intercept	2.05	0.204	1.842-2.251	0.7489	0.1190	0.6299- 0.8678	0.1955	1.0679	-0.8724- 1.2635
Contag3	-	-	-	-	-	-	0.0192	0.0225	-0.0033- 0.0417
Forbs	-	-	-	0.0043	0.0022	0.0021- 0.0066	0.0038	0.0030	0.0007- 0.0068
HayED2	-	-	-	-	-	-	-0.006	0.0044	-0.0104- -0.0016
HayENN4	-0.00095	0.00028	-0.0012-0.0006	-	-	-	-0.00035	0.00011	-0.00047- 0.00025
HDFMD1	-0.085	0.036	-0.122- -0.0485	-	-	-	-	-	-
NatA0.5	0.195	0.046	0.149-0.241	-	-	-	-	-	-
NatNP2	-	-	-	-0.0481	0.02556	-0.0737- -0.0225	-	-	-
PasNP1	0.0572	0.0187	0.0385-0.0759	-	-	-	-	-	-
PasNP3	-	-	-	-	-	-	0.0048	0.0026	0.0022- 0.0075
Patch	-	-	-	-	-	-	0.0003	0.0001	0.0003- 0.0005
RCA4	-	-	-	0.395	0.1596	0.2354-0.5546	-	-	-
RCPD4	-	-	-	-1.786	0.436	-2.222- -1.3499	-	-	-

Table 16 cont.

	Total Richness (adjusted r^2=0.74)			Margelef's Richness (adjusted r^2=0.77)			Shannon Diversity (adjusted r^2=0.60)		
	Coefficient	Standard Error	95% CI	Coefficient	Standard Error	95% CI	Coefficient	Standard Error	95% CI
Robel	-	-	-	-0.0769	0.0352	-0.112- -0.0417	-0.0609	0.0466	-0.1074- -0.0143
RowA4	-	-	-	-	-	-	-0.0026	0.0014	-0.0041--0.0012
RRMD1	-	-	-	-0.0668	0.0188	-0.0858- -0.0479	-	-	-
SavMD4	-0.091	0.037	-0.127- -0.054	-0.0403	0.0106	-0.0509- -0.0296	-	-	-
SHDI4	-	-	-	-	-	-	0.7300	0.4236	0.3064- 1.1536
TG4	-	-	-	0.0069	0.0028	0.0041- 0.0096	-	-	-
WatA4	-	-	-	-0.0139	0.0041	-0.0181- -0.0098	-0.0163	0.0051	-0.0214- 0.0112
WatED4	-	-	-	-	-	-	-0.0142	0.0044	-0.0185- 0.0099
WatENN3	0.0002	0.0001	0.0001-0.0003	-	-	-	-	-	-
WinMD4	0.2433	0.137	0.1063- 0.3803	-	-	-	0.1889	0.0551	0.1339- 0.244

Table 17: Richness and Diversity results for the wetland users functional group

	Total Richness (adjusted r^2=0.74)			Margelef's Richness (adjusted r^2=0.77)			Shannon Diversity (adjusted r^2=0.60)		
	Coefficient	Standard Error	95% CI	Coefficient	Standard Error	95% CI	Coefficient	Standard Error	95% CI
Intercept	2.73	0.325	2.05- 3.41	0.57	0.17	0.228- 0.911	0.904	0.307	0.294- 1.51
Brush	0.102	0.0204	0.0598- 0.145	-	-	-	0.0011	0.0045	-0.0078- 0.0101
BruED3	-	-	-	0.0207	0.0117	-0.0028- 0.0443	-	-	-
Contag4	-	-	-	-	-	-	-0.0016	0.0035	-0.0086- 0.0053
CRPPD0.5	-	-	-	-0.115	0.0779	-0.227- -0.0399	-	-	-
FRBED3	0.284	0.0824	0.114-0.453	-	-	-	-	-	-
Grass	-0.0178	0.0042	-0.0266- 0.0091	-0.0017	0.0022	-0.0061- 0.0027	-	-	-
HDFED2	-	-	-	-0.0087	0.0027	-0.0144- 0.0031	-0.0015	0.0035	-0.0085- 0.0054
MarA0.5	0.155	0.0297	0.0937-0.217	-	-	-	-	-	-
NatMD3	-	-	-	-	-	-	-0.0009	0.0004	-0.0018- -0.0002
PasENN0.5	-	-	-	0.0005	0.0002	0.00007- 0.00097	-	-	-
PasENN1	-	-	-	-	-	-	-0.00088	0.00017	-0.0012- -0.00052
PasMD3	-	-	-	-	-	-	-0.0034	0.0012	-0.0058- -0.0009
RCNP3	-	-	-	-0.087	0.0588	-0.204- 0.0303	-	-	-

Table 17 cont.

	Total Richness (adjusted r^2=0.74)			Margelef's Richness (adjusted r^2=0.77)			Shannon Diversity (adjusted r^2=0.60)		
	Coefficient	Standard Error	95% CI	Coefficient	Standard Error	95% CI	Coefficient	Standard Error	95% CI
RCPD3	-	-	-	2.99	2.06	-1.12- 7.1	-	-	-
ResED4	-	-	-	-	-	-	0.0032	0.0077	-0.0121- 0.0185
Robel	0.363	0.104	0.146-0.58	0.053	0.0628	-0.0714-0.178	-	-	-
SHDI4	-	-	-	-	-	-	0.0221	0.0565	-0.0904- 0.135
Tfor1	-0.0738	0.0208	-0.117- -0.0307	-	-	-	-	-	-
Tpr1	-	-	-	-	-	-	0.0006	0.0015	-0.0023- 0.0036
UrbMD2	-0.0203	0.0227	-0.0659- 0.0252	-	-	-	-	-	-
UrbPD1	-4.22	1.04	-6.38- -2.07	-	-	-	-	-	-
Water	-	-	-	-0.0122	0.005	-0.0222- -0.0022	0.0098	0.0057	-0.0212- 0.0016
WatMD1	-	-	-	-	-	-	0.0052	0.0011	0.003-0.0075
Wetland	-	-	-	0.0072	0.0021	0.0028- 0.0117	-	-	-
WetMD2	-	-	-	-	-	-	-0.0049	0.0174	-0.0673- 0.0417
WinMD1	-	-	-	-0.007	0.021	-0.049- 0.035	-0.0128	0.0277	-0.0673- 0.0417
WinPD2	-1.12	0.200	-1.54- -0.705	-	-	-	-	-	-

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