ABSTRACT

Niche and Neutral Factors Affecting Bird Community Assembly at Multiple Spatial Scales

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Neutral theory suggests communities are assembled based on demographic stochasticity and dispersal distance, while niche theory suggests that communities are assembled based on habitat requirements and interspecific interactions. The relative importance of niche and neutral processes in community assembly has received much attention. I hypothesized that niche processes were more important than neutral processes in structuring bird communities in central Texas. I sampled birds at 262 – 323 study sites during the summer breeding season in 2008, 2009, and 2010. To account for niche processes, environmental variables were measured at three spatial extents around each site using remotely-sensed landcover data at two spatial resolutions (10 meter and 30 meter resolution landcover maps). I also included niche variables representing interspecific interactions (avian nest predator abundance and the abundance of a brood parasite). Spatial eigenvectors were used to account for dispersal-based neutral processes. I used multiple regression and variance partitioning to determine the factors most important for bird assemblages in three different guild groupings (habitat, migratory, and trophic). Both niche and neutral variables were important for most guilds in all years. For most guilds, niche variables accounted for more of the variation in community composition than did spatial variables, suggesting that niche processes were more important than were neutral processes in structuring these assemblages. However, for a few guilds (permanent residents, short-distance migrants, and herbivores) in some years, spatial variables accounted for more of the variation in community composition than did niche variables, suggesting that neutral processes may play a dominant role in structuring some bird assemblages. Some of these results varied from year to year, suggesting the relative importance of niche and neutral processes may fluctuate temporally in bird communities. I also investigated the importance of environmental variables measured at multiple spatial extents on bird community composition. Overall, environmental variables measured at a small spatial extent around each study site explained more of the variation in community composition than did environmental variables measured at a medium and large spatial extent. Understanding the factors that are important for bird community assembly has important conservation implications and can inform management decisions for guild-level assemblages.

Niche and Neutral Factors Affecting Bird Community Assembly at Multiple Spatial Scales

by

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A Dissertation

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DEDICATION

Dedicated to my parents
Harry and Mary Carter

Thank you for encouraging me to believe anything is possible

CHAPTER ONE

Introduction

Stephen P. Hubbell's unified neutral theory of biodiversity and biogeography (2001) has created considerable controversy in the field of ecology. The theory proposes that the assembly of communities is a *neutral* process, meaning that individuals are *ecologically equivalent* in their response to the processes that drive community assembly. Hubbell posits that *ecological drift* (demographic stochasticity) is more important than biotic interactions in the assembly and processes of ecological communities, and that individuals are neutral in that they exhibit the same probability of experiencing birth, death, and dispersal. Neutrality in the theory is defined at the level of the individual, not the species (Hubbell 2001). An abundant species will have an advantage over a rare species in becoming established as a species, but given individuals of each species exhibit the same chance of establishment.

An important aspect of neutral theory is its contribution to the long-standing debate about community assembly processes. The *niche-assembly* perspective suggests communities are assembled on the basis of niche partitioning of limited resources, whereas the *dispersal-assembly* perspective suggests that communities are nonequilibrium groups of species assembled by random events of dispersal, ecological drift, and extinction (Hubbell 2001). Neutral theory favors the latter of these two perspectives, although it does recognize the importance of both ideas. Though niches do play a role in community assembly, neutral theory predicts that ecological drift is the dominant process of assembly (Hubbell 2001).

Among other predictions, neutral theory predicts that the similarity between communities should decrease with the geographic distance between the communities (Hubbell 2001). This idea, called distance decay in similarity, is also predicted from niche-assembly theory, and there are numerous studies that agree that community similarity decreases with distance (Nekola and White 1999, Palmer 2005, Steinitz et al. 2006, La Sorte and McKinney 2007). But under niche-assembly rules, it is assumed that the distance decay in similarity among communities is related to variation in environmental variables (Hubbell 2001). Neutral theory, in contrast, maintains that distance decay is the result of ecological drift (demographic stochasticity) and limited dispersal distance even in homogeneous landscapes (Hubbell 2001). Numerous studies indicating that bird diversity is significantly related to environmental conditions (e.g., Schulte and Niemi 1998, Laiolo 2003) suggest that niche factors play a large role in bird community assembly.

The specific prediction regarding community similarity and geographic distance can be reframed as a question of the relative importance of niche and neutral variables in community assembly. To what degree do the ideas of neutral theory explain bird community composition? And to what degree do environmental variables and interspecific interactions explain community composition? To answer these questions, I investigated the relationship between bird community composition and niche variables (environmental and interspecific interaction variables) and neutral variables (spatial predictors) in a multi-scale landscape-level study in central Texas.

Background

The results of several studies testing various aspects of neutral theory are varied. Some studies have found support for predictions of neutral theory (Volkov et al. 2003, Burns 2006), but others have not completely supported neutral theory (McGill 2003, Palmer 2005). In a meta-analysis investigating variation in community composition, Cottenie (2005) found that environmental variables were most important in explaining community composition, but that neutral processes were also important in explaining some of the variation for some communities. Hubbell (2001) uses a study by Nekola and White (1999) as support for neutral theory as it relates to distance decay in similarity in a plant community, though another study of a neotropical forest community (Palmer 2005) did not find strong evidence to support neutral theory. One study (Graves and Rahbek 2005) addressed community assemblage and distance decay among bird communities across South America and found that ecoregion distribution and habitat selection played key roles in avian community assembly (contrary to neutral theory which says that distance is the most important factor). Graves and Rahbek (2005), however, focused on a continental scale where large-scale changes in the ecosystem would be reflected in the analysis as habitat diversity. Steinitz et al. (2006) observed that both geographic distance and environmental variables explained variation in bird community similarity across a regional rainfall gradient, though these authors were not testing neutral theory *per se*. One assumption of neutral theory is that neutral processes will occur across homogeneous land areas (Hubbell 2001), and some studies of neutral theory in vagile communities to date have not adhered to this condition in their research design. In a novel approach, I tested neutral predictions in a bird community across a relatively homogeneous land area, a part of the Oaks and Prairies Bird Conservation Region (North American Bird Conservation Initiative, U.S. 2002) in central Texas.

Importance

Understanding the factors that influence community assembly has important conservation implications. Conservation efforts focused on a species of interest would be warranted if communities were assembled based on random interactions. However, if communities are assembled on the basis of interspecific interactions, conservation efforts focused on the community level would be best (Green and Sadedin 2005). Understanding the assembly of communities has important management implications as well. If communities are primarily structured based on ecological drift and dispersal limitation as predicted by neutral theory, reserve locations for conserving bird diversity should focus on areas that contain the species compositions of interest. If communities are primarily structured based on environmental differences, reserve locations for conserving bird diversity should focus on areas with a diversity of suitable habitat types (Legendre et al. 2005). Many bird species are sensitive to broad-scale habitat loss due to urbanization and changes in land use. Climate change also has contributed to changes in migratory patterns and species distributions. The landscape-level focus of my study provides information about bird community composition as it relates to neutral processes, environmental variables and interspecific interactions, at broad spatial extents. Understanding the important variables for bird community composition can inform management of birds in an ever-changing environment.

Guild Level Analyses

To investigate these questions, I subdivided birds into habitat, migratory and trophic guilds. Subdivision into guilds was designed to better understand the role of niche and neutral factors on specific groups of birds. Habitat guilds group species with similar habitat preferences, and these bird assemblages may be influenced by different niche and neutral variables. For example, my study area was in a historically prairie landscape with patchily distributed woodlands. Grassland birds may be less influenced by measured landscape variables, as the overall grassland habitat is abundant. Thus, neutral variables, such as dispersal limitation, may be important in structuring grassland bird assemblages. Woodland habitat, however, is less abundant and patchily distributed. Thus, woodland bird assemblages may be more influenced by specific landscape variables representing suitable habitat.

All birds included in my study were summer residents. However, migratory guilds grouped birds based on their fall and spring migration habits. Birds were either categorized as permanent residents, short-distance migrants, or neotropical (long-distance) migrants. Variation in migratory status among birds is an interesting characteristic when considering factors that influence community assembly. Permanent residents remain on summer breeding grounds year-round, but short distance and neotropical migrants form bird assemblages anew each breeding season. Thus, the influence of niche and neutral factors may differ between these groups.

One prediction of neutral theory is that neutral processes operate within the same broad trophic level (Hubbell 2001), and so grouping birds based on trophic guild (carnivores, herbivores, omnivores) was an important component to adequately testing neutral processes. The variation in diet among broad trophic guilds may also affect the variables important for bird community assembly. Thus, a guild-level analysis enabled me to investigate niche and neutral processes across a wide range of bird characteristics.

Landcover Data

Investigating environmental variables in my study required the use of remotely-sensed data. Much of the land area of my study was privately owned, and I conducted point counts along public roads. Therefore, access to the landscape surrounding my study sites was limited. Also, collecting vegetation data in the field is very labor intensive, and is limited to what can be sampled in the immediate area around a study site. So the use of remotely-sensed data for measuring environmental variables is essential. I used two sources of remotely-sensed data: a 10-meter resolution classified map (obtained from Texas Parks and Wildlife) and a 30-meter resolution classified map that I produced myself. The production of my own classified map for my study area was a challenging and time-consuming endeavor, but it was deemed important so that the landcover information would be representative of the years during which I sampled the bird community. Creating my own classified map also allowed me to specify cover types specifically relevant for the bird species in my study area.

Hypotheses

Neutral theory predicts that community assembly is related to dispersal distance and ecological drift (demographic stochasticity, Hubbell 2001). A neutral hypothesis regarding bird assemblage composition is that composition is more related to spatial variables (indicative of neutral processes) than environmental or interspecific interaction variables. Alternatively, niche assembly theory (species sorting) proposes that communities are organized based on habitat requirements and competition for limited resources. Niche theory, therefore, predicts that bird community composition is more related to environmental and/or interspecific interaction variables than to spatial variables. Environmental variables are known to affect bird abundance, which in turn influences community composition. Metrics of landscape composition and structure (Miller et al. 1997, Brennan and Schnell 2005) as well as measures of plant productivity (Hurlbert and Haskell 2003, Seto et al. 2004) have been shown to influence bird richness or abundance.

Interspecific interactions among bird species also may influence breeding habitat selection and therefore community similarity. I investigated the influences of two types of interactions (predation by avian nest predators and brood parasitism) on community similarity. The presence of some avian nest predators may impact nest survival (Rodewald and Yahner 2001). The presence of a brood parasite, such as the Brown-headed Cowbird (*Molothrus ater*), influences the distribution and abundance of host species (Woodworth 1999, Jewell and Arcese 2008). I used the abundance of avian nest predators and the abundance of Brown-headed Cowbirds as indices of the potential for nest predation and brood parasitism. Nest predators such as the American Crow (*Corvus brachyrhynchos*) and the Blue Jay (*Cyanocitta cristata*) were included.

Neutral theory predicts that ecological drift and limited dispersal is the main influence on community composition (Hubbell 2001), but alternative ideas suggest that community composition is better predicted by environmental variables and interspecific interactions (Chesson 2000). It is likely that these conditions affect community composition to some degree. My study was designed to identify the relative influence of neutral and niche variables on community composition. While I predicted that both neutral and niche variables would be important in bird community composition, I predicted that community composition would be more related to environmental variables and interspecific interactions (niche variables) than to spatial (neutral) variables.

In addition to examining the effects of the above factors on community composition, I also investigated effects on bird community composition from environmental conditions within different spatial extents. An understanding of spatial scale is essential in any ecological study. Scale consists of two components: *extent* and *grain*. Extent refers to the overall size of the area being observed, whereas grain refers to resolution, the size of the smallest unit for which observations are made (Wiens 1989). Studies of bird distributions or communities have shown the importance of measuring environmental variables at more than one spatial scale (Bossenbroek et al. 2004, Coreau and Martin 2007). My study investigated environmental variables measured at different resolutions and at three ecologically relevant extents centered on each study site. The smallest extent was used to measure variables within a radius calculated from the mean area per breeding pair for birds included in my study. The medium extent was used to measure variables within a radius equal to the median dispersal distance averaged over all species in the overall community. The large extent was used to measure variables within a radius equal to the maximum dispersal distance averaged over all species in the overall community. Bird abundances in a community may be more related to landscape variables measured at a spatial extent larger than the territory size of the bird species in a community than to variables measured within territory-sized areas (Brennan and Schnell

2007, Renfrew and Ribic 2008). I predicted that the spatial extent at which environmental variables were measured would be important in bird community composition. Specifically, I predicted that environmental variables measured at medium and large spatial extents would account for a greater portion of the variation in bird community composition than would environmental variables measured at a small spatial extent.

CHAPTER TWO

Materials and Methods

Study Area

My study area was located in the defined Oaks and Prairies Bird Conservation Region (BCR) (Figure 1). These BCRs are defined areas in North America with similar vegetation, wildlife, soils, temperatures and precipitation. Developed in 1998 by a team from the United States, Canada, and Mexico, BCRs were delineated from the hierarchical system designed by the Commission for Environmental Cooperation (CEC, http://www.cec.org) to reflect bird distributions and life-history requirements (North American Bird Conservation Initiative, U.S. 2002). The Oaks and Prairies BCR extends from central Texas north into Oklahoma. My study area consisted of a large area (~47,490 km^2) of the central portion of the BCR. I chose this area, in part, because it is a relatively homogeneous area without a large environmental gradient.

Study sites were randomly located along local, neighborhood, and rural roads (defined according to Census Feature Class Codes, U.S. Census Bureau 2009) using a Geographic Information System (GIS, ArcGIS ver 10.0). Study sites were situated at least 2.5 km apart, and were located outside of city limits. I sampled over 300 sites in each of three years, but included 262 sites in 2008, 299 sites in 2009, and 323 sites in 2010 in the final analyses. Some sites were removed each year due to questionable bird identifications, missing data, geographic location, uncorrected geographic coordinates, data outliers, or excessive noise (noise lasting >45 seconds that hinders the ability to hear bird sounds).

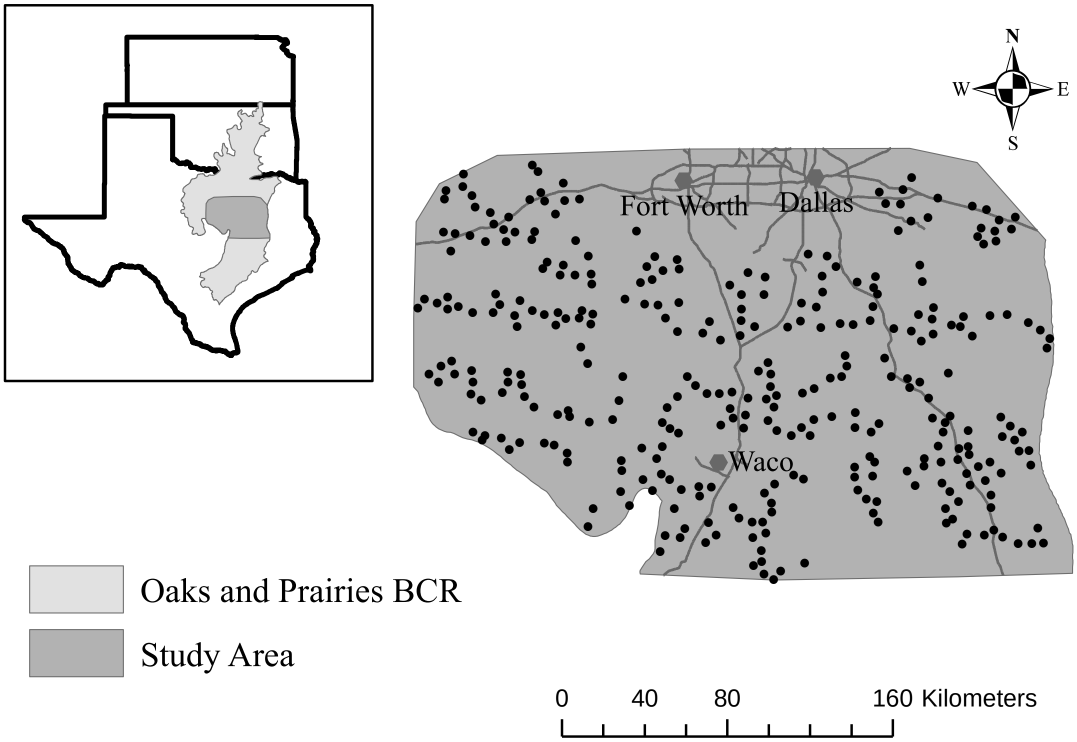


Figure 8. The study area included the central portion (dark gray) of the Oaks and Prairies BCR (light gray). The 323 study sites from the 2010 field season are shown in the enlarged study area.

Bird Data Collection

Roadside Point Counts

For this study, I used a point count method of sampling birds that involves standing in a location (point) for a set length of time and recording all birds seen or heard during that time interval (Johnson 1995). I conducted roadside point counts at each of the study sites once per field season for three consecutive summers (2008-2010) to sample birds in my study area.

Roadside surveys have often been used to census bird communities. The North American Breeding Bird Survey (BBS) of the U.S. Geological Survey (2001) has conducted roadside surveys throughout the continental United States and Canada since 1966, and BBS data have been used in many rigorous studies (e.g., Sauer et al. 2003, Schmidt and Ostfeld 2008). However, roadside surveys may not accurately reflect bird data in areas far away from roads (Keller and Fuller 1995). Also, according to a study by Forman et al. (2002) traffic noise may negatively influence distribution of birds near roads, but these results were most pronounced for areas with heavy traffic. Bird distribution was not significantly influenced by areas with light traffic (Forman et al. 2002). Traffic noise also may hinder the ability of an observer to hear bird vocalizations. To avoid potential biases, only local, neighborhood, and rural roads were used in this study to minimize potential traffic noise on these low traffic streets. However, to control for the effect of roads, the number of cars passing the study site during each point count was recorded as an index of traffic volume and used as a covariate in the analyses. Potential biases in roadside data can thus be addressed in a rigorous way, and using roadside surveys has the important advantage of enabling me to sample thoroughly a large study area without requiring admittance to private property.

Sites were grouped in clusters based on proximity, and one cluster (of approximately 10 sites) was sampled on a single morning. The order in which the groups were sampled was randomized to avoid time-of-season biases. The counts were conducted between late May and July 1 each year to correspond with the occurrence of summer resident species in Central Texas. These dates also corresponded to the North American BBS guidelines (2001) for Central Texas. For each subsequent year, the same sites were sampled in the same order whenever possible. Some site locations varied, and some sites were sampled in some years that were not sampled in the other years.

At each point count location, visual and audio detection of birds lasted 15 minutes (Su et al. 2004) with this period subdivided into 5 back-to-back 3-minute intervals. All birds seen or heard within an unlimited distance during this period were recorded. Counts were conducted beginning 30 minutes prior to sunrise and ending within 5 hours of the start time, which corresponded to BBS guidelines. These sampling techniques were not adequate for the following groups of species: crepuscular and nocturnal species (O'Connor et al. 2000); diurnal raptors (Hansen et al. 2011); vultures (which behave like raptors in terms of soaring); and waterfowl, waders, and shorebirds (wetland habitat not well-sampled by roadside point count method) and these species were excluded from my analyses. After each point count, I also recorded wind speed and temperature. I used a handheld GPS (Global Positioning System) with 1-3 m accuracy to acquire geographic coordinates for each study site.

Bird species included in the study were those species that occurred at least twice during the sampling season in any year of the study. I chose to include relatively rare species, though removing those that occurred only once to minimize statistical bias, so that the full variation within the bird assemblage was represented (Poos and Jackson 2012). I used this inclusive bird assemblage to calculate the spatial extents described below, but I found that I needed to remove very rare species (those occurring at <3% of sites) from the subsequent community composition value due to constraints of the ordination technique.

Guild Membership

Birds were assigned to habitat, migratory, and trophic guilds for analysis. Subdividing the bird species into guilds allowed me to determine if neutral or niche processes were more or less important for subsets of bird assemblages based on habitat requirements, migratory status, or diet type. Habitat and migratory guild membership was based on guild assignments used in the Breeding Bird Surveys (BBS). Trophic guild membership was based on diet information from the literature (Ehrlich et al. (1988) or the Birds of North America species accounts).

Avian Nest Predators and a Brood Parasite

Avian nest predators consisted of birds known to take eggs or young birds as a regular part of their diet: American Crow (*Corvus brachyrhynchos*), and Blue Jay (*Cyanocitta cristata*) were common nest predators in my study area. Brown-headed Cowbirds (*Molothrus ater*) are obligate brood parasites, and they occurred regularly in my study area. These species were included in the study to represent interspecific interactions.

Audio Recordings

I used a digital voice recorder to record bird songs and calls in the field to better identify unknown species. The use of a recorder was deemed important during the first field season because I was an inexperienced birder, but I continued to use a recorder in all three field seasons. I turned on the recorder during a point count when I heard a song/call I was unfamiliar with or wanted to verify later. I also typically turned on the recorder when there was a lot of bird activity so I would not miss some species songs/calls. I did not record the entire 15 minute point count for any site, but I did record some portion of the count (typically about 30 seconds to several minutes) for most of the study sites in all three years. After the field season, I used the recordings to verify, correct, or identify questionable species in the field.

Detection Bias and Adjusted Abundances

Abundance estimates of bird populations from point count data are susceptible to detection biases arising from differences in the habitats among point count locations, the time of year during which the counts are conducted, and observer abilities (Simons et al. 2007). For reliable estimates of abundance, one should correct for such biases (Royle et al. 2007). I computed detection probabilities for each species in our study area using the Royle repeated counts method (Royle 2004) in Presence software (Hines 2006). The repeated counts method uses temporally replicated point count data to estimate the population size across multiple sites. Since I was interested in a site-specific estimate of abundance for each species, I used the detection probabilities generated by the repeated count method to calculate a site-specific abundance estimate. I computed a detection probability for the entire study area for each species and year separately. I used these detection probabilities to adjust the observed counts of species at each site by dividing the counts for a species by the detection probability for that species (Lancia et al. 2005). This calculation yielded an index of a species' abundance at a site that was adjusted for detection bias, referred to as adjusted abundances, hereafter.

Landcover Maps

Remotely sensed data has the advantage of covering a large area and allowing information to be collected from a distance. Classified landcover maps assign each pixel a landcover type and are created from remotely sensed satellite imagery or aerial photographs. Classified landcover maps are often used to characterize landscape features in ecological studies of birds (Rhodes et al. 2015, Zuckerberg et al. 2016, Ikin et al. 2014).

10 Meter Resolution Landcover Map

I downloaded parts of the Texas Ecological Mapping System produced by the Texas Parks and Wildlife Department (Elliott et al. 2009-2014) representing small scale landcover. This map is a 10 meter spatial resolution land cover map classified from Landsat satellite imagery and using ancillary information such as soil surveys, Digital Elevation Models, and National Agriculture Imagery Program (NAIP) photographs to assign vegetation types. The representative years for the map include 2009 – 2014. The state was subdivided into six phases (corresponding to satellite scene data) for classification.

My study area was contained within three phases of the map, and so I downloaded these three phases of the mapping system. The sections were subset to match the boundaries of my defined study area from the BCR, that were then mosaicked together to form a single 10 meter resolution map. This resultant map originally contained 51 specific land cover classes defined by the Texas Parks and Wildlife Department. In order to meet variable limitations for the subsequent data analyses, I reclassified the map into a smaller number of classes, combining land cover classes with similar vegetation, and reduced the number of classes to 11 (Table 1, Figure 2).

Table 3. Combined landcover classes derived from the 10 m resolution Texas Ecological Mapping System. *The five most common landcover classes were used to calculate class-level environmental variables at the small spatial extent.

Landcover	Description
Agriculture*	cropland where fields are fallow some portion of the year
Grassland*	grasslands or pasture/hay/cover crop fields dominated by native, non-native, or introduced grasses or herbaceous cover, but woody species may be present; includes floodplain/riparian vegetation
Forest/Shrubland*	both deciduous and evergreen forest or shrubland, >25% woody cover; includes floodplain/riparian vegetation
Savanna Grassland*	grasslands with native and non-native species, as well as woody species such as oak, mesquite and juniper
Urban Low*	low intensity development, <70% impervious cover
Water	permanent open water such as reservoirs, rivers, ponds, etc.
Urban High	high intensity development, >70% impervious cover
Barren	little or no vegetation year-round
Cliff	slopes >100%
Marsh	herbaceous vegetation on floodplains, flatwoods soils, bogs, or along small streams, or wet herbaceous vegetation not associated with a specific flood plain or riparian area
Swamp	floodplain or riparian areas dominated by baldcypress and shrubs, or wet, forested wetlands not associated with a specific floodplain or riparian area

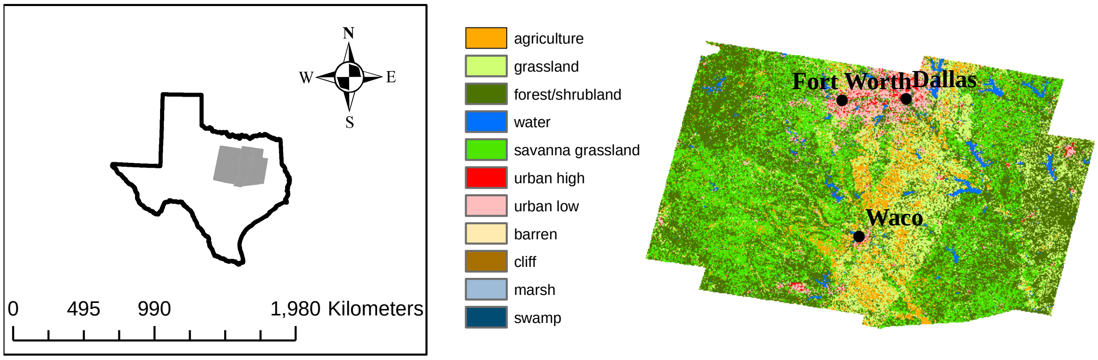


Figure 9. Texas Ecological Mapping System 10 m classified map of the central Texas study area. The classified map shown includes 11 total landcover classes.

30 Meter Resolution Landcover Map

Next, I then developed a medium-scale landcover map using satellite imagery with a 30 m spatial based 2009 information, representing the middle portion of my bird data collection. The process of converting a satellite image into a landcover map by assigning each pixel to a specific landcover type is called classification. A number of steps are involved in creating a reliable landcover map, and the process is time-consuming. Below is a detailed explanation of the steps I took to create the final 30 m resolution landcover map.

Image processing. Satellite imagery was obtained from the satellite Landsat 4-5 Thematic Mapper (US Geological Survey, www.glovis.usgs.gov). Landsat 4-5 TM images consist of 7 spectral bands (blue, green, red, near infrared, shortwave infrared 1, thermal, and shortwave infrared 2). The images have a spatial resolution of 30 m for all bands except band 6 (thermal) which has a resolution of 120 m. All 7 spectral bands were stacked resulting in images with 30 m spatial resolution. Landsat imagery is available in different scenes categorized using the Worldwide Reference System (WRS) based on path and row boundaries. I downloaded 7 scenes from both winter (January) and summer (June/July) satellite imagery in 2009. These 7 scenes (from both seasons) contained the entirety of my study area in central Texas. Cloud-free images were chosen when possible. For one summer image, I combined subsets of images from June and July to create a mostly cloud-free image. Preprocessing of the images included calculating new reflectance values to normalize the sun angle between all images. These new reflectance images were subsequently used in creating winter and summer images of my study area.

The next step in preprocessing was to combine (mosaic) the images into a single large image that encompassed my entire study area. This step was challenging because the colors of the images did not match initially (due to variations in conditions when the imagery was collected), and the seams were visible if I tried to mosaic the images. The full extent of all 7 scenes that included my study area was much larger than the study area itself. Consequently, I used subsets of the images so that it would be easier to color-match the images when mosaicking into a single scene. I used the Mosaic Express tool in ERDAS IMAGINE 2010 software (ERDAS 2009) to combine the scenes to produce one image for winter and one image for summer (Figure 3). The process of mosaicking the images was iterative, as I tried numerous settings to produce the best match between the different images. Settings in Mosaic Express included using histogram matching (matches the histogram values to a specified scene in the mosaic), defining the active area (removes the background area so only the scene of interest is included), using the most nadir seamline (diagonal line between overlapping areas of each image such that equal amounts of the overlapping area are from each image), and feathering to 60,000 m (a technique that smooths the appearance of the colors between images out to a set distance). I then used Principal Components Analysis (PCA) on all 14 channels of the winter and summer images to reduce the information in the multiple bands of the image to a smaller number of uncorrelated principal components. I retained the top 5 channels, representing the most spectral variation in the image, for classification. This PCA image of the combined winter and summer images (Figure 3) was the image classified into a landcover map.

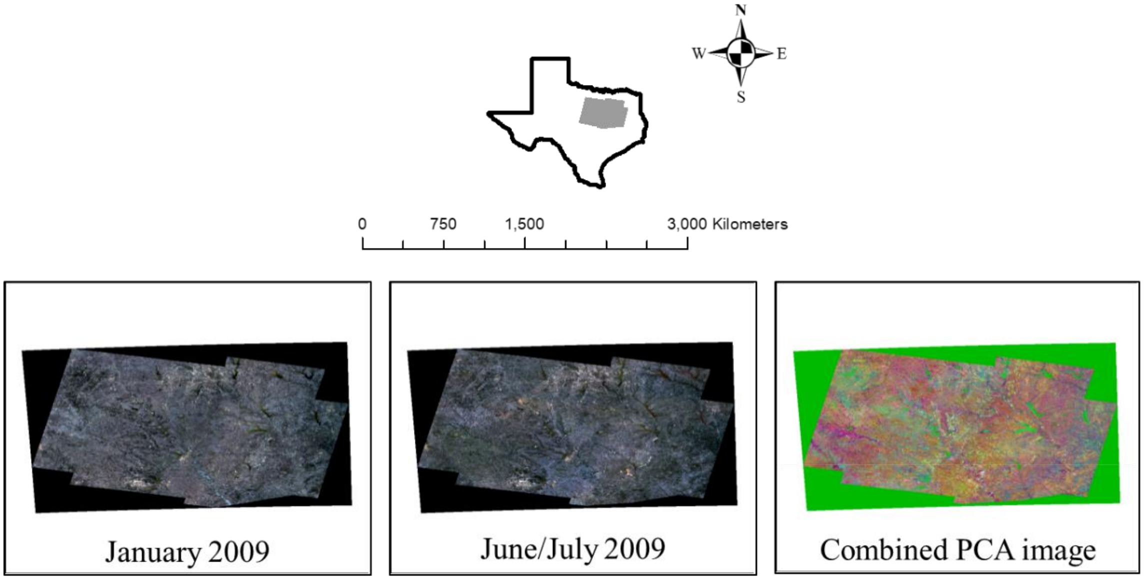


Figure 10. Scenes from satellite imagery were mosaicked together to produce satellite images that covered my study area for winter (January 2009) and summer (June/July 2009). The single PCA image was produced using both winter and summer satellite images. The top five bands of the PCA image were subsequently classified into a 30 m resolution landcover map.

Ground truth data. Existing landcover types verified in person in an area are known as ground truth data. Ground truth data are used both to define landcover types during the classification process (as training data) and to assess the accuracy of the final classification. I collected ground truth data at my road-side study sites by identifying basic vegetation or cover types for the areas surrounding the sites (Table 2). In the field, I recorded landcover information for the area on each side of the road along which study sites were located. Study site locations served as ground truth points (GTPs), and I chose a single landcover type for each GTP. Because the resulting map would have a spatial resolution of 30 m, I tried to identify areas larger than 30 m of a single, well-defined, cover type. If a single cover type was not present in a large enough area or the view of the area was occluded by a tall hedge row, I used the information from the other side of the road for the GTP. If the landcover on both sides of the road was difficult to define, I did not use that site as a GTP. If more than one landcover type was present at a study site, then only one was assigned to that site so that the GTP represented only one cover type. Occasionally, ground truth information was collected away from a study site. This was often true for cover types less likely to occur at the study sites (such as developed area and water). The majority of the GTPs were identified the 2010 field season, but some were identified during the 2008 and 2009 field seasons. Some GTPs were revisited in 2011 to verify or correct the ground truth information. All GTPs were at least 1000 m apart (and usually more than 2-3 km apart) to avoid spatial autocorrelation.

In order to facilitate the subsequent classification (described below), I subdivided my study area into smaller ecoregions based on the Level III Terrestrial Ecoregions from the Commission for Environmental Cooperation (CEC, http://www.cec.org). The three ecoregions included in my study area were the Cross Timbers, the Texas Blackland Praires, and the East Central Texas Plains ecoregions (Figure 4).

Table 4. Landcover classes for the 30 m classified satellite image. The six most common cover types were included in the analysis of the data.

Landcover	Description
Agriculture	row crops
Grassland	mostly open cover, grasses or herbaceous cover, <15% woody cover, includes pastures/hay fields
Medium-density woodland/shrubland	semi-open cover, containing grasses as well as trees/shrubs, 15-80% woody cover
Woodland	mostly closed cover, dominated by trees or woody shrubs, >80% woody cover
Water	open water, both intermittent and perenial; reservoirs, rivers, stock tanks, etc.
Developed	built up areas, includes low- and high-density development
Roads	primary roads (due to variable number constraints, this class was not included in the final analyses)

Approximately 10% of the GTPs were used as training data to inform the classification, and the remaining 90% were used for accuracy testing. I used a stratified random design to choose the training data by assigning random numbers to the GTPs, sorting the numbers smallest to largest, and choosing the top 10% of the GTPs for each landcover class and within each ecoregion. Training data requires a sufficient number of pixels in order to provide enough variation to accurately represent each landcover type. So if the randomly chosen training GTP did not represent an area large enough to be useful for informing the classification, I used the next GTP in the list as the training point. I used 40 GTPs for training data, and 328 GTPs for accuracy testing.

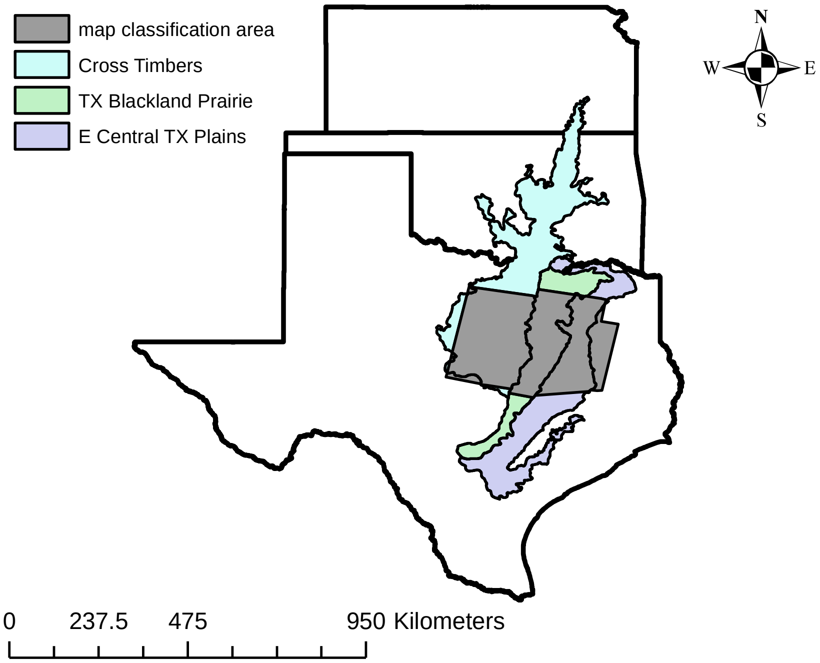


Figure 11. The land area for the classification was subdivided into level III terrestrial ecoregions to facilitate the classification. The land area classified is shown in dark gray, and included parts of the Cross Timbers, Texas Blackland Prairies, and East Central Texas Plains ecoregions.

Image classification. Next, the PCA winter/summer image was classified such that each image pixel was assigned a specific landcover type. I used a hybrid classification method (Richards and Jia 2006) with ERDAS IMAGINE 2010 software (ERDAS 2009). Hybrid classification uses both unsupervised classification (allowing the software to organize the pixels into classes of similar spectral values) and supervised classification (pixels are assigned specific landcover types based on known classes) to produce a final classified image.

As mentioned previously, I subdivided the study area into three ecoregions within the broader Oaks and Prairies BCR (Cross Timbers, Texas Blackland Prairies, and East

Central Texas Plains ecoregions). Subdividing into ecoregions allowed me to better classify the variation in my study area. Even though my study area was relatively homogeneous (within the same BCR), there was variation in rainfall and vegetation across the area. For example, grasslands in the eastern part of the study area may appear greener than their more xeric counterparts in the western part of the study area. So landcover types were spectrally more similar within ecoregions than across the entire study area. By initially performing classifications within ecoregions, this variation could be accounted for and landcover types appropriately assigned across the study area.

I first used the unsupervised classification method to produce spectral classes for each ecoregion. I instructed the software to produce 20 classes for each ecoregion based on similarity in spectral signatures among the pixels. Richards and Jia (2006) suggest using 2-3 spectral classes per cover type in unsupervised classification. I started with 9 cover types (reduced to 6 cover types in the final map), and so 20 classes were an appropriate start. I also experimented with 15 and 30 classes, but found 20 classes produced a comparable number of final classes when classes with similar spectral signatures were merged. The unsupervised classification method produced 20 spectral classes for each of three ecoregions, resulting in 60 total spectral classes.

I then used my training data to create spectral signature files (spectral classes) for the landcover types in each ecoregion. To create signature files from the training data, I located each training GTP on the combined winter/summer PCA image based on field notes about the location of the landcover in the area. I then allowed the software to select pixels with similar spectral signatures in the area so that I had a larger area represented as the cover type of interest. I used the winter and summer images separately to verify that the selected pixels were the same landcover type intended by the GTP. In some cases, I revisited the sites in the field to make sure the area included in the image was representative of the landcover type of interest. Bare ground was removed as a landcover type, as it was difficult to get a representative area large enough to be useful in classification. There was not a lot of bare ground in my study area, and so I usually collected ground truth information on bare areas such as those in the middle of a dirt road. However, the dirt roads were too narrow to classify well in a 30 m resolution image such that I was unable to create a spectral signature file that adequately represented bare ground in the study area. A very small amount of the combined winter/summer PCA image (<1%) was covered by clouds and cloud shadows (clouds were only present in the summer satellite image, but appeared in the combined winter/summer PCA image as well) and so I created signature files for clouds and cloud shadows as well. The resulting training spectral classes (40) of known landcover types and cloud/cloud shadow spectral classes (4) were combined with the unsupervised spectral classes (60) and used in a supervised classification using a maximum likelihood algorithm. The supervised classification assigned each of the pixels in the combined winter/summer PCA image into 104 spectral classes.

I then used spectral separability to determine which classes were unique and which could be merged to improve classification efficacy. This was done by cross-comparing the separability of each individual spectral class using the divergence separability index (ranges from 0-1). Initially, divergence values less than 0.05 were deemed inseparable. Within each ecoregion, classes with divergence values less than 0.05 were merged. This method helped to identify the unsupervised training classes when they could be merged with training classes of known landcover types. The 0.05 threshold proved to be too conservative, however, as it still left a number of unsupervised classes unmerged. To resolve this issue, I then raised the threshold value to 0.06. Again, classes with divergence values less than 0.06 were merged within ecoregions. There were some instances where classes with divergence values less than 0.06 were not merged. If two training classes with different cover types had divergence values below the 0.06 threshold, or when two unsupervised classes with divergence values less than 0.06 were clearly different landcovers (based on other information) they were not merged. After some iterations trying to merge or remove classes to produce the best classification, I ran a supervised classification again using a final reduced number of classes, resulting in a map with 63 spectral classes. Many of the unsupervised classes had merged with training classes during this process, and so most of the 63 classes could easily be assigned a landcover type. But if not, I assigned landcover types to the unsupervised classes. To help identify these cover types, I used Digital Orthophoto Quarter Quadrangles (DOQQs, 1 m resolution imagery available from www.tnris.org). Some of my initial landcover classes were combined at this point, as they were not easily distinguishable based on spectral signature. Open and mostly open cover were combined into a single grassland cover type. And mostly closed and closed cover were combined into a single wooded cover type. There were still obvious problem areas in the classified map at this point, particularly classes that clearly represented more than one cover type in a single class. Some examples included wooded areas that classified as water, and areas of vegetation that classified as developed area. There was also some difficulty in distinguishing grassland and agriculture in some areas. So further refinement of the image was necessary.

Refining the classification. To refine the classification, I used the Knowledge Engineer tool in the ERDAS IMAGINE 2010 software (ERDAS 2009) to derive a rule-based system to distinguish vegetated and non-vegetated cover types. For vegetation, changes in phenology helped to differentiate pasture grasses and seasonal agriculture. And variation in reflectance of growing vegetation helped to distinguish herbaceous cover, medium-density woody cover, and woodland cover types. I used a vegetation index (Normalized Difference Vegetation Index, NDVI) to distinguish types of growing vegetation from one another and from non-vegetation where possible. NDVI values range from -1 to +1, with higher values indicating dense vegetation (more visible light absorbed by chlorophyll and more near infrared light reflected). NDVI values were calculated for both the winter and summer satellite imagery, as well as the amplitude between winter and summer images, which can help distinguish seasonal variation in vegetation. I used DOQQ images (1 m resolution photographs where cover types are more easily recognizable) to identify areas of known cover types. I then sampled NDVI values from these areas to generate typical ranges of NDVI values and amplitude for the various cover types in my study area. I then incorporated this information into the Knowledge Engineer to establish a series of if/then statements to refine the cover types in the classification. I also incorporated a city polygon layer (2009 and one subset from 2011), a water polygon layer (2009, subdivided into intermittent and perennial water bodies), a perennial rivers/streams layer (2009) and a primary roads layer (2006, all layers available from www.tnris.org). These layers were rasterized and included in the Knowledge Engineer to help distinguish water, developed area, and roads.

To further distinguish mis-classed pixels when NDVI variability was minimal, I used variability in PCA bands. If certain cover types varied sufficiently when looking at PCA values, I incorporated that information into the Knowledge Engineer.

Finally, I addressed the part of my map affected by cloud cover. To classify the cloud/could shadow areas of the map, I first did an unsupervised classification on the winter satellite imagery. I then used the classified image to assign the unsupervised classes of the winter image. I incorporated this information into the Knowledge Engineer to assign the cloud and cloud shadow pixels with the appropriate land cover class. The completed map consisted of 7 landcover classes (see Table 3, Figure 5).

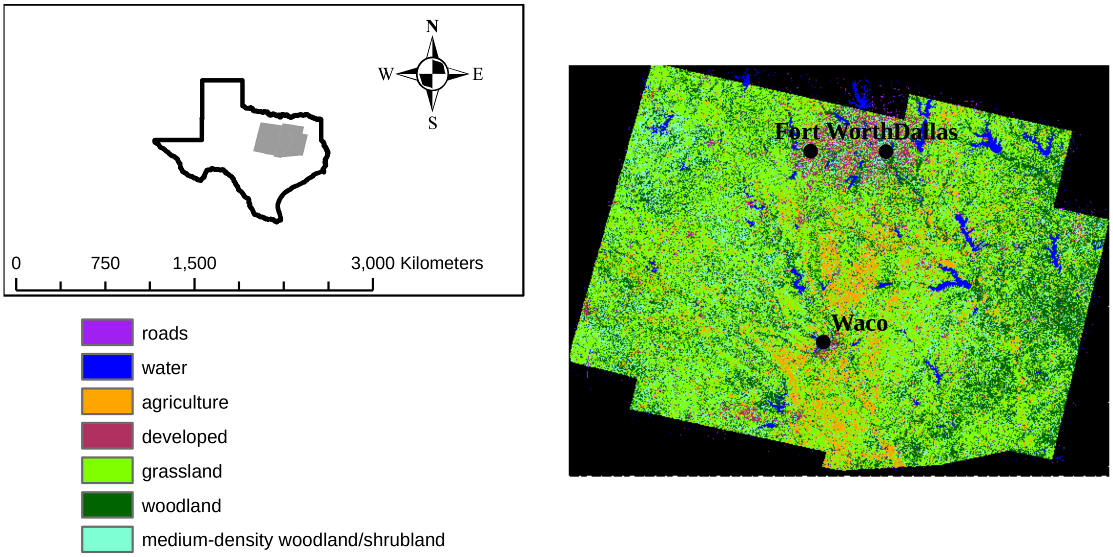


Figure 12. The final classified 30 m resolution landcover map consisted of 7 cover classes (agriculture, grassland, medium-density woodland/shrubland, woodland, water, developed area, and roads).

Accuracy assessment. An accuracy assessment of the classified map was necessary to determine how well my classified map reflected the actual landcover of my study area. Six of the seven final landcover classes were included in the accuracy assessment (primary roads were based on external information from the Texas Department of Transportation and were assumed correct). I generated an overall map accuracy value (number of correctly identified GTPs out of total number of GTPs) as well as a producer's/user's accuracy for each cover type. The producer's accuracy is the number of correctly classed pixels out of the total number of ground truth pixels of a specific cover type, while the user's accuracy is the number of correctly classed pixels out of the total number of pixels classified as the specific cover type in the map. I also calculated a Kappa statistic, which calculates the amount of agreement in my map classes versus the amount to be expected by chance. To calculate map accuracy, I had to first determine what pixels on my map were represented by my GTPs. Most of my GTP coordinates were taken along roadsides because that is where I sampled study sites (and most bordered private property), though the GTPs indicated broad areas on either side of the road. To account for road bias when assessing the accuracy of the map, I applied the following rule: If the cover type observed in the field was present within 3 pixels (or 90 m) of the GTP on the classified map, and +/- 45 degrees of the original compass direction, it was determined correct. If more specific information about the location of the land cover of interest was available, then that information was used even if different from the general rule. For example, if I observed a body of water near a roadside study site, I used a distance measurer to estimate the distance to the body of water and a compass to indicate the compass bearing. I then used this information when determining if the GTP was accurately classed on the map. For developed area, I usually did take the GTP coordinate on the developed cover (this was often an area where I could drive into a parking lot of a developed area). In these cases, the GTP was assumed correctly classed only if a developed class was within 1 pixel of the GTP.

Spatial Extents

For spatial analysis, digital circles of three different spatial extents were generated in a GIS that were centered on the sampling point of each study site. The size of each spatial extent was determined from estimates of biologically important variables for all the bird species included in the study. The small spatial extent (153 m radius) was based on the breeding pair density information obtained from studies included in the Birds of North America species accounts (Table 2, Appendix). I used density information as a proxy for area of daily use by breeding pairs. Home range information is not readily available for most species, and territory size is not a useful measure of daily use as it may not be well-defined for some species, or too small to indicate a daily use area (in the case of colonial breeders). I used only density information that was obtained from the breeding season. Studies performed in the breeding season presented information as pairs/unit area, breeding males/unit area, territories/unit area, or nests/unit area. Studies including density information outside of the breeding season, or that presented information as individuals/unit area were not included. If it was unclear the study was conducted during the breeding season from the BNA accounts, then I clarified the information about the study from the original literature if possible. Only studies that took place in North America were included. If density information meeting these requirements was not available, then the species or species group was not included in the calculation of the small spatial extent. A midpoint was taken if a study presented a range of values, and a midpoint was taken if a study presented density info for the same location across multiple years. If, however, a study presented density information for multiple habitats, each estimate was included for that species. A midpoint was then taken of the density estimates for all the habitats/studies available for each species. Density information was converted to the amount of circular area associated with one breeding pair, and a radius was generated from this circle. Then a mean radius was calculated to serve as the radius for the small extent of my study. This small spatial extent was used for all three years of the study. Mahon et al. (2016) used a similar spatial extent as representative of the core area used by birds in their study. Landscape variables measured in the small spatial extent were calculated from the 10 meter resolution landcover map (Figure 6).

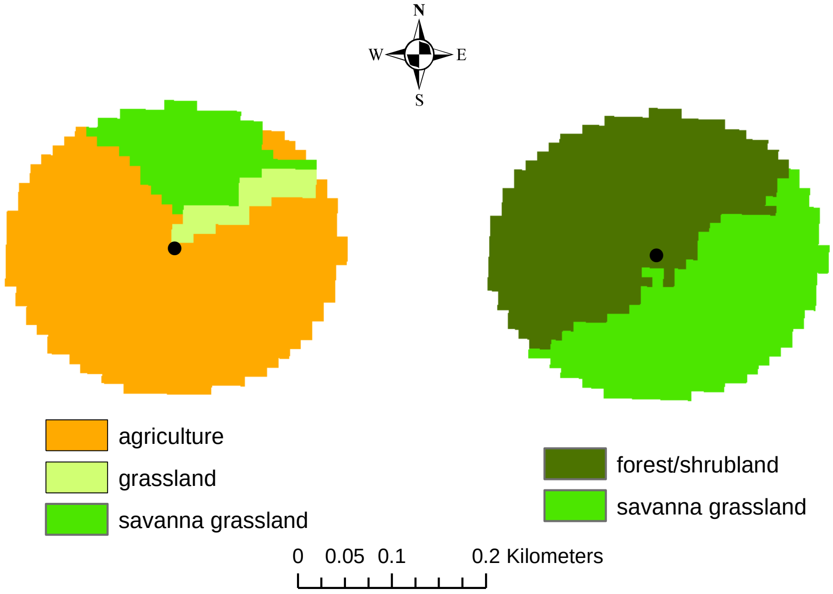


Figure 13. Examples of study sites measured at the small spatial extent (153 m radius). Data from the small spatial extent was taken from the 10 m landcover map. The sites shown here represent an agricultural site and a mixed woodland/savanna grassland site.

The medium and large spatial extents were calculated using an equation estimating the median and maximum dispersal distances for bird species in the study (Sutherland et al. 2000). The equation estimates median and maximum dispersal distances based on body mass and diet type (Table 1, Appendix). Two different equations were used: one for carnivores and another for omnivores/herbivores. To classify each species according to trophic group, I obtained diet information from the literature (Ehrlich et al. (1988) or the Birds of North America species accounts). When available, I used percentages of food taken as a way to classify species as either carnivores (>90% animal matter), omnivores (10-90% animal matter), or herbivores (<10% animal matter). Food intake over the entire year was considered when classifying each species into a trophic level. The body mass estimates for species in my study were taken from Dunning (2008). I took a mean body mass for males and females (where both were given for the same study), and in cases where multiple studies of the same species were presented, I took a mean mass of the body mass information provided by the different studies. The mean median dispersal distance was used as the radius for the medium spatial extent (1.8 km) and the mean maximum dispersal distance was used as the radius for the large spatial extent (23.1 km). The medium and large spatial extents were used for all three years of the study. Landscape variables measured in the medium and large spatial extents were calculated from the 30 meter resolution landcover map (Figure 7).

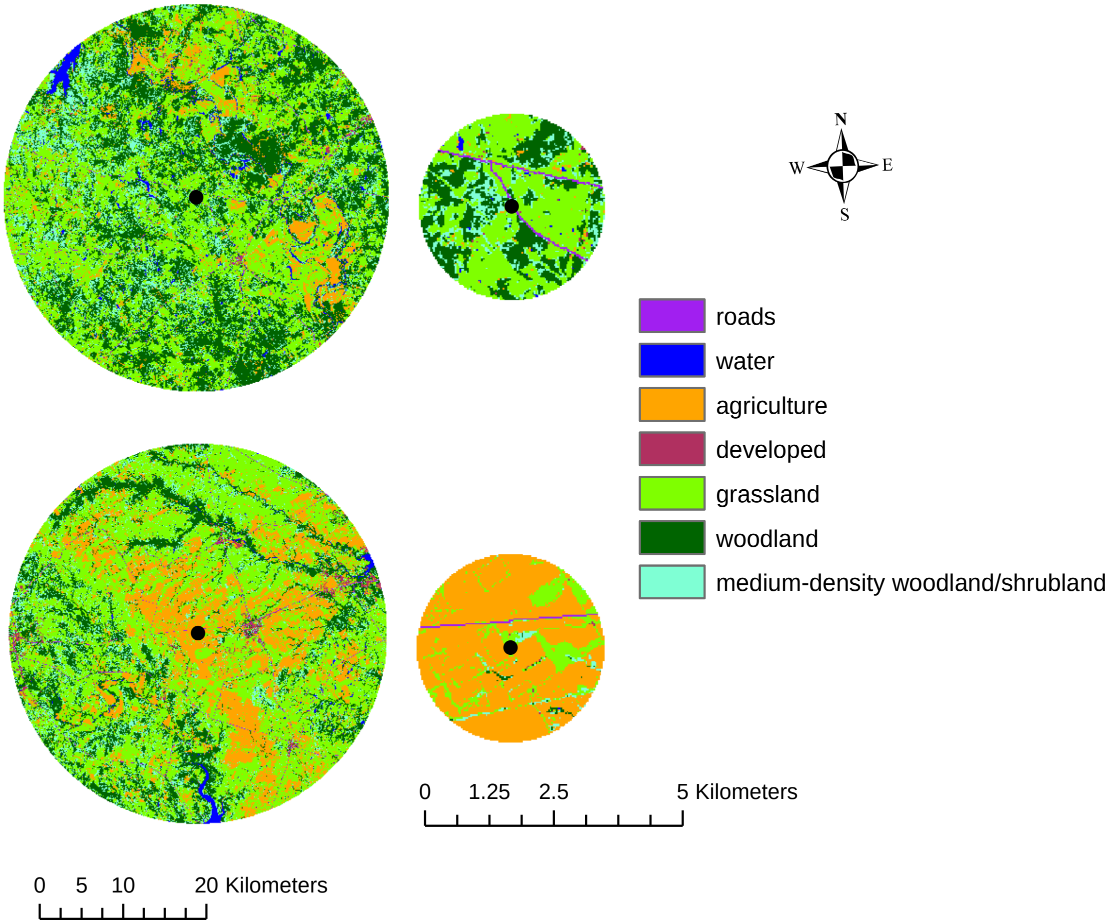


Figure 14. Examples of study sites measured at the medium (1.8 km radius) and the large (23.1 km radius) spatial extents. Note scale bars, as medium and large circles are not shown at comparable scales. Data for the medium and large spatial extents were measured from the 30 m resolution landcover map.

Niche Variables

Landscape Variables

I chose landscape variables that represented aspects of both landscape composition and configuration. Composition variables quantified the amount of each land use type within each scene (the circular area enclosed by each spatial extent for each site), and configuration variables accounted for the spatial arrangement of the different land use types within each scene. Specific variables were chosen with reference to their potential influence on bird community composition.

A total of 12 variables (Table 3) were calculated at the small spatial extent, and a total of 26 variables (Table 4) were calculated at the medium and large spatial extents. I limited the number of landscape variables to 26 so as not to overfit the subsequent PCA (see below). I followed a conservative rule-of-thumb recommending no more than 10 sample units per 1 variable (Osborne and Costello 2004). The smallest number of sites I sampled in any one year was 262 (2008), and so I limited the number of landscape variables measured to 26 for all three years.

Table 3. Landscape variables calculated at the small spatial extent measured from the 10-meter resolution landcover map. The 12 variables include % cover and patch density for 5 cover types, and total edge length and patch richness.

Main Landcover Types	Variable Description
agriculture	% cover (for main cover types)
forest/shrubland	patch density (for main cover types)
grassland	total edge length (for all cover types)
savanna grassland	patch richness - includes the 5 main cover types plus water, high-intensity urban, barren, cliff, march and swamp
low intensity urban	

Small extent variables. FRAGSTATS software (Spatial Pattern Analysis Program for Categorical Maps, version 4.2, McGarigal et al. 2012) was used to calculate total of 12 variables (see Table 3) from the 10-m resolution landcover data at the small spatial extent. These variables included 12 composition variables: percent cover and patch density (a measure of fragmentation) for agriculture, grassland, forest/shrubland, savanna grassland, and low-density urban area; and total edge length (for all cover types in the

Table 4. Landscape variables calculated at the medium and large spatial extents measured from the 30-meter resolution landcover map. A total of 26 variables were calculated.

Landcover Types	Variable Description
cropland	for cropland, grassland, woodland, and medium-density woodland/shrubland:
developed area	% cover
grassland	total edge length
woodland	mean patch area
medium-density woodland/shrubland	mean nearest neighbor distance
water	contagion
	Simpson's evenness index
	edge length between grassland and woodland
	edge length between cropland and woodland
	edge length between grassland and medium-density woodland/shrubland
	edge length between cropland and medium-density woodland/shrubland
	mean NDVI
	coefficient of variation of NDVI

measured scene) and patch richness. The percent cover of land cover types has been shown to influence bird richness or abundance (Renfrew and Ribic 2008, Reinkensmeyer et al. 2007, Chapman and Reich 2007). Edge density, which reflects the degree of habitat fragmentation, has also been found to be important to bird richness or abundance (Brennan and Schnell 2005, Fletcher and Koford 2002, Miller et al. 1997). Additional variables were not measured at the small spatial extent because the small size of the spatial extent meant that several variables (such as nearest neighbor distance or mean patch size) did not vary much across study sites.

Medium and large extent variables. A total of 26 variables (see Table 4) were calculated from the 30-meter resolution cover map at the medium and large spatial extents. I used FRAGSTATS software to quantify 24 of the landscape variables. Composition variables included percent cover (for grassland, shrubland, woodland, cropland, developed area, and water), mean patch area (for grassland, shrubland, woodland, and cropland), and total edge length (for grassland, shrubland, woodland, and cropland). Mean patch area, which reflects habitat fragmentation and/or the amount of suitable habitat, has been shown to be important to bird richness or abundance (Coppedge et al. 2001). I derived the length between high-contrast edges (grassland and woodland, grassland and shrubland, cropland and woodland, and cropland and shrubland) from information obtained from FRAGSTATS. I also calculated Simpson's Evenness Index (a measure of how evenly distributed are the cover types at each study site) as a diversity measure. Configuration variables included the nearest neighbor distance (for grassland, shrubland, woodland, and cropland) and Contagion (a measure of the spatial aggregation or clumpiness of landuse/cover types in the digital data).

Additional variables assessed at the medium and large extents included the mean and coefficient of variation of the Normalized Difference Vegetation Index (NDVI). This spectral index is often used as a surrogate for plant productivity (Jenson 2000). Measures of primary productivity have been shown to be important for bird richness or abundance (Hurlbert and Haskell 2003, Seto et al. 2004). NDVI values, in particular, have been shown to perform as well as classified landcover maps in the formation of bird-habitat models (Sheeren et al. 2014). From the spectral data, NDVI values were calculated for the study area.

$$\text{NDVI} = (NIR - red)/(NIR + red)$$

Where NIR and red refer to the near infrared and red bands of multispectral satellite imagery.

Principal components analysis. Similar to the spectral data from the satellite imagery, PCA was used to reduce the information in the landscape variables into a smaller number of principal components (PCs). PCA calculations for these data were performed using SAM 4.0 software, and separate PCA analyses were performed for landscape variables measured at small, medium, and large extents for each of the three study years (9 total PCAs). Assumptions of PCA (linearity and normality) were assessed and variables were transformed where necessary. In some cases, landscape variables were removed if transformations did not improve the linearity assumption. As PCA is sensitive to outliers, some sites were removed from the analyses. To determine if outliers were likely to impact the PCA results, I ran the PCA with and without outliers and then compared the results. If PCA variable loadings were similar for the group of sites with and without outliers, then no sites were removed. If variable loadings differed, I determined the outlying site or sites most likely responsible for the difference, and removed the site/sites from the analyses for that study year.

Interspecific Interactions

Niche-assembly theory suggests a community is assembled based on both habitat variables as well as interspecific interactions (Chesson 2000). Many types of interspecific interactions in my bird assemblage (competition, predation) were not feasible for us to measure and include in my study. However, I did calculate two interspecific interaction variables that were included as niche variables. I used the adjusted abundance of nest predators (Blue Jay and American Crow) and the adjusted abundance of a brood parasite (Brown-headed Cowbirds) as interspecific interaction variables. Other predatory birds, such as diurnal raptors, were not well sampled by my method, or were not present at enough sites to include in the analysis.

Neutral Variables

Spatial Eigenvectors

Spatial autocorrelation in a species data set can result from natural processes such as dispersal, and spatial eigenvectors generated from a distance matrix of geographic coordinates can be used to account for this type of process (Diniz-Filho et al. 2005, Dray et al. 2006, Griffith and Peres-Neto 2006). These spatial eigenvectors represent spatial patterns at different scales, and can be incorporated into a regression model as explanatory variables representing spatial processes (Dray et al. 2006). Such variables can be used to test predictions of neutral theory (Legendre et al. 2008). I generated spatial eigenvectors using the geographic coordinates of my study sites with Spatial Eigenvector Mapping in SAM software. I wanted to use the same number of neutral and niche variables in each model, and so I chose 14 spatial eigenvectors as spatial (neutral) variables to correspond with the 14 total niche variables (environmental PCs and interspecific interaction variables). Eigenvectors were chosen based on their relationship to the response variable (assemblage composition for each guild). Eigenvectors were chosen by highest r^2 value in relation to the assemblage composition value, and then by lowest p-value when r^2 values were the same.

Measuring Bird Community Composition

I used Non-metric Multidimensional Scaling (NMDS) to ordinate the bird community information and to generate a community composition variable for the multiple regression analysis. All NMDS analyses were performed using R software (R Development Core Team 2009, package Vegan). Community composition variables were calculated for each habitat, migratory, and trophic guild, as well as for each of the study years. Because NMDS will not ordinate data containing zeros for some of the sites, a dummy species was added to some analyses when no members of that guild were present at some sites. I chose the ordination with the lowest number of dimensions (to maximize the amount of information in the ordination) while making sure the stress did not exceed 20% (McCune and Grace 2002). For each guild/year, this resulted in a 2- or 3-dimensional ordination. The NMDS were rotated such that the greatest amount of variation in the assemblage composition was located on the first axis, and so the NMDS scores for the first axis were used as the assemblage composition variable.

Data Analysis

Comparison of Analysis Methods Using Preliminary Results: Distance versus Raw Data Approach

The neutral theory prediction that community similarity decreases with geographic distance (distance-decay in similarity) has often been tested using a distance approach (typically, a Mantel-based statistic that relates similarity in community composition to environmental “distances”, and geographic distances between all possible pairs of study sites). Such an approach is intuitively the best approach as it most directly answers questions about the distance decay predictions of neutral theory. And some researchers have argued that a distance approach is the only way to effectively address neutral theory hypotheses (Tuomisto and Ruokolainen 2006). However, distance approaches have been shown to underestimate the distance component in the analyses (Gilbert and Bennett 2010), and to underestimate the amount of variation attributable to the spatial and environmental variables separately and combined (Legendre et al. 2005). An alternative approach is to use a raw data method, which is an analysis run on the raw data as opposed to distances between sites. Although these methods are statistically more powerful (Legendre et al. 2008), they do not directly address questions regarding distance decay in community similarity because they are not using distances in the analysis. However, if a spatial variable can be incorporated into a raw data approach (to account for neutral processes) then raw data methods can be just as or more advantageous than a distance approach in testing neutral theory (Legendre et al. 2008). Statistical problems have also been noted with multivariate raw data approaches using spatial eigenvectors (RDA-type analyses with variation partitioning). Gilbert and Bennett (2010) found such methods overestimated the amount of variation attributable to some variables. And Smith and Lundholm (2010) found that variation partitioning inadequately identified spatial contributions from neutral processes versus spatially-structured environmental variables. Though, Peres-Neto and Legendre (2010) found that variation partitioning with spatial predictors and environmental variables is an appropriate method for discerning neutral and niche processes if a careful selection process is used to select spatial variables.

It is important to point out that spatial autocorrelation can result from multiple sources, including autocorrelated environmental variables and neutral processes such as dispersal (Griffin and Peres-Neto 2006, Peres-Neto and Legendre 2010). If unknown or unmeasured spatially structured environmental variables are not included in the model, then the spatial component attributed to neutral processes by variation partitioning may be overestimated (Diniz-Filho et al. 2012). My study area is a relatively homogeneous environment, and thus does not have a strong environmental gradient. While this does not preclude spatial autocorrelation based on the environmental variables, it does suggest that the observed autocorrelation is more likely due to neutral processes.

Before analyzing the final dataset, I compared a distance and a raw data approach with preliminary data. I used multiple regression on distance matrices as the distance approach and univariate multiple regression as the raw data approach.

Preliminary analysis. In order to determine the best method for analyzing my data, I initially used the bird data from the first field season (2008) to compare distance and raw data approaches. In this analysis, I included 20 bird species (Table 5) from the overall summer bird assemblage. Species selection was based on frequency, such that species included occurred at 19 or more of the 282 study sites. Species not considered well-sampled by my road-side point count method (such as shore birds and water birds) were excluded. I also excluded swallows in the preliminary analysis, as they occurred in large flocks at some locations which were thought might affect the statistical analysis (they were subsequently included in the final data analysis). Also, Eastern and Western Meadowlarks were combined into one group.

I then measured environmental variables using the National Landcover Database from 2001 (Homer et al. 2007). I calculated % cover, edge density, mean patch size, and fractal dimension for each of six cover types (forest, grassland, agriculture, shrub, wetland, and developed area) using FRAGSTATS software. The landscape variables were based on digital analysis of landcover patterns within a 1 km radius circle around each study site.

Distance-based, Mantel-based approach. I used Multiple Regression on Distance Matrices (MRM, Lichstein 2007), a Mantel-based statistic that regresses a response distance matrix on two or more explanatory distance matrices. It works by separating the values in the distance matrix into a single vector of distances and running a regular multiple regression on the unfolded distances. To account for the lack of independence in the pair-wise comparison of sites, the significance of the model is determined by randomizing the response variable while holding the explanatory variables constant. Bird assemblage similarity was the response variable, and geographic distance and environmental similarity were explanatory variables. Euclidian distances were used to generate the geographic distance matrix, and Bray-Curtis distances were used to generate bird assemblage and environmental distance matrices.

Table 5. Bird species (or groups) sampled in 2008 used as the summer resident bird assemblage for the preliminary data analysis.

Order	Family	Species	Common Name
Columbiformes	Columbidae	*Zenaida macroura*	Mourning Dove
Cuculiformes	Cuculidae	*Coccyzus americanus*	Yellow-billed Cuckoo
Galliformes	Odontophoridae	*Colinus virginianus*	Northern Bobwhite
Passeriformes	Cardinalidae	*Spiza americana*	Dickcissel
Passeriformes	Cardinalidae	*Cardinalis cardinalis*	Northern Cardinal
Passeriformes	Cardinalidae	*Passerina ciris*	Painted Bunting
Passeriformes	Emberizidae	*Chondestes grammacus*	Lark Sparrow
Passeriformes	Icteridae		Meadowlarks
		Sturnella magna	Eastern
		Sturnella neglecta	Western

Table 5 Continued.

Order	Family	Species	Common Name
Passeriformes	Icteridae	*Agelaius phoeniceus*	Red-winged Blackbird
Passeriformes	Mimidae	*Mimus polyglottos*	Northern Mockingbird
Passeriformes	Paridae	*Poecile carolinensis*	Carolina Chickadee
Passeriformes	Paridae	*Baeolophus bicolor*	Tufted Titmouse
Passeriformes	Passeridae	*Passer domesticus*	House Sparrow
Passeriformes	Troglodytidae	*Thryomanes bewickii*	Bewick's Wren
Passeriformes	Troglodytidae	*Thryothorus ludovicianus*	Carolina Wren
Passeriformes	Turdidae	*Sialia sialis*	Eastern Bluebird
Passeriformes	Tyrannidae	*Sayornis phoebe*	Eastern Phoebe
Passeriformes	Tyrannidae	*Tyrannus forficatus*	Scissor-tailed Flycatcher
Passeriformes	Vireonidae	*Vireo griseus*	White-eyed Vireo
Piciformes	Picidae	*Melanerpes carolinus*	Red-bellied Woodpecker

Raw-data approach (multiple regression). I used multiple regression with spatial eigenvectors as a raw data approach. Bird assemblage composition was estimated using a 3-dimensional NMDS ordination. The ordination was rotated to account for most of the variation in assemblage composition, and I used the ordination scores from the first axis as the response variable in the multiple regression. I used Principal Components Analysis (PCA) to reduce the information in the environmental variables to 5 principal components to represent niche processes. I chose 5 spatial eigenvectors, generated using Spatial Analysis in Macroecology (SAM) software, to account for neutral processes.

Alternate raw data approach: redundancy analysis (RDA). While multiple regression is a univariate approach and uses a single variable representing assemblage composition as a response variable, redundancy analysis is a multivariate, raw-data approach that incorporates all bird assemblage information as a response variable. For my analysis, RDA had the advantage of incorporating all bird assemblage information into the analysis. But when compared to the multiple regression approach for my data, RDA resulted in much lower R^2 values.

Final Analysis Method: Multiple Regression Analysis

For the final data, I used multiple regression analysis to associate niche and neutral explanatory variables with bird assemblage composition as the response variable. Despite the reduction of bird assemblage composition into a single response variable, this method was the most powerful statistical method to elucidate the relationships between assemblage composition and explanatory variables in my data. I ran a separate multiple regression analysis for each guild and year. The bird assemblage composition variable (derived from the NMDS ordination) was the designated as the response variable for the regression equations. Potential explanatory variables included 12 Principal Components and two interspecific interaction variables (niche variables) and 14 spatial eigenvectors (spatial variables). I also included three detection covariates as response variables (number of cars passing during point count, end temperature, and end wind speed). Multiple regression assumptions of linearity, homoscedasticity, normality, and independence were checked for each analysis. I used backward elimination and the sequential Bonferroni method to select variables for the final model, with a family-wide alpha value = 0.1.

I used the first four principal components for each spatial extent in the multiple regression models for each guild/year. I chose four PCs for each spatial extent and year so that I would have an equal number of niche variables and neutral variables in each model, and I did not want to exceed the sample size to variable ratio (10:1).

I used variation partitioning (partial regression) to determine the relative importance of niche and neutral variables to bird assemblage composition, as well as to determine the variance explained by each individual explanatory variable (Borcard et al. 1992). I also used standardized regression coefficients to corroborate the relative importance of the explanatory variables in each final model (Bring 1994).

CHAPTER THREE

Results

Study Sites

I sampled over 300 sites each year. The final number of sites used varied from year to year. In 2008, I sampled 319 study sites, but included 262 study sites in the final analyses. Questionable bird identification, particularly a confusion between Lark Sparrow and Bewick's Wren songs during the first part of the field season, led to the removal of 12 study sites. Another 17 sites were removed from the 2008 season because they had been accidentally placed along highways or within city limits.

An issue that resulted in the removal of sites from the analysis for certain years was if the GPS coordinates for study sites were not differentially corrected. Differential correction is a technique that improves the accuracy of the coordinates taken by the GPS unit by comparing them with measurements taken from a nearby base station. Information from the base stations was typically available online the following day after study site coordinates had been taken for up to about a week. Therefore, I typically differentially corrected the site coordinates within a few days of visiting sites. On some occasions, sites were unable to be differentially corrected. And on other occasions, I forgot to differentially correct the data before the base station information was unavailable. I consequently removed such sites (7 sites in 2008) from the analysis.

Other sites were occasionally removed each year if there was consistent noise that hindered my ability to hear bird songs lasting for >45 seconds. Noise such as lawn mowers, airplanes, or even conversations with passersby might have resulted in sites being removed due to noise distraction. Noise from passing cars did not result in sites being removed from the study as I included the number of passing cars as a covariate in the data analysis. If the noise was brief, and I could restart the count after the interruption, then I sometimes took the time to start the point count again.

Missing data for temperature, wind speed, or number of cars, or obviously incorrect data (such as temperature readings too high due to the thermometer being in direct sunlight) also resulted in the removal of sites. I also removed sites if the measured wind speed at the end of the count exceeded 19 kilometers per hour (per BBS suggestions). Factors that might affect either the behavior of the birds or my ability to correctly identify them also resulted in sites being removed. For example, I removed 6 sites from 2008 because I had another person with me during the point counts, and it's possible some bird species responded differently to the increased number of people during a point count. Also, at times I did not have the ability to record questionable bird songs/calls due to a voice recorder being either full of previous recordings or forgotten. In these cases, the sites were removed to keep things consistent.

In 2009, I sampled 343 sites during the field season, and I included 299 of those sites in the final analyses. The bulk of the sites removed from the 2009 field season were due to the lack of differentially corrected GPS locations (25 sites). I also removed 9 sites when I did not have the digital recorder on the point counts. A few other sites were removed for noise, wind, or questionable bird identity. In 2010, I sampled 334 sites during the field season, and I included 323 of those sites in the final analyses. Sites were removed due to missing or incorrect temperature data, noise, and one case where recordings were taken but distorted (low batteries in recorder perhaps). In addition to the above-mentioned reasons for site removals, I also removed a small number of sites (1-4 each year) due to outliers during the PCA analysis to reduce the information in the environmental variables down to a smaller number of principal components.

Other situations, such as rain, prevented some of the same sites from being visited on all three years. New sites were sometimes added as time permitted so that as many sites as possible could be sampled in a given field season. Also, sites were not marked in the field, and so revisiting sites involved the use of a car GPS (less accurate than the handheld GPS) to locate the site. And, after the 2008 field season, if the coordinates placed a site directly in front of a house, I pulled past the house before stopping to conduct the point count. This was done to avoid conversations with homeowners that might otherwise occur during the point count. Therefore, sites were not always in the exact same location from year to year. Since data analysis was done independently for each year and direct year-to-year comparisons were not included in this analysis, the fact that the exact same sites were not sampled each year was not a problem. In the future, I plan to conduct a temporal comparison of the results for a subset of sites that were sampled in all three years and in approximately the same locations (<100 m apart).

Bird Data

A total of 44 species or species groups were recorded over the 2008-2010 field seasons. Table 6 lists the species included in the overall formation of spatial extents (species occurring at least twice in any one field season), as well as the species included in the data analysis (species occurring at 3% or more of sites in any one field season).

Table 6. List of bird species in the study area. All species listed were included in the calculation of the medium and large spatial extents. Only species occurring at 3% or more of sites were included in the species assemblage composition calculations for the guild-level analysis. * Red-winged Blackbirds do not belong to any of the four habitat guilds used in this study, and so they were excluded from the habitat analysis. **Species groups were excluded from individual guild analyses if the member species belonged to different guilds.

Order	Family	Species	Common Name	Habitat Guild	Trophic Guild	Migratory Guild
Passeriformes	Troglodytidae	*Thryomanes bewickii*	Bewick's Wren	successional scrub	carnivore	short-distance migrant
Passeriformes	Paridae	*Poecile carolinensis*	Carolina Chickadee	woodland	omnivore	permanent resident
Passeriformes	Troglodytidae	*Thryothorus ludovicianus*	Carolina Wren	successional scrub	carnivore	permanent resident
Passeriformes	Cardinalidae	*Spiza americana*	Dickcissel	grassland	omnivore	neotropical migrant
Passeriformes	Turdidae	*Sialia sialis*	Eastern Bluebird	successional scrub	omnivore	short-distance migrant
Passeriformes	Icteridae		Meadowlarks	grassland	omnivore	short-distance migrant
		Sturnella magna	Eastern			
		Sturnella neglecta	Western			
Passeriformes	Tyrannidae	*Sayornis phoebe*	Eastern Phoebe	woodland	omnivore	short-distance migrant
Passeriformes	Passeridae	*Passer domesticus*	House Sparrow	urban	herbivore	permanent resident
Passeriformes	Emberizidae	*Chondestes grammacus*	Lark Sparrow	successional scrub	omnivore	neotropical migrant
Columbiformes	Columbidae	*Zenaida macroura*	Mourning Dove	urban	herbivore	short-distance migrant
Galliformes	Odontophoridae	*Colinus virginianus*	Northern Bobwhite	successional scrub	herbivore	permanent resident
Passeriformes	Cardinalidae	*Cardinalis cardinalis*	Northern Cardinal	successional scrub	omnivore	permanent resident
Passeriformes	Mimidae	*Mimus polyglottos*	Northern Mockingbird	urban	omnivore	permanent resident
Passeriformes	Cardinalidae	*Passerina ciris*	Painted Bunting	successional scrub	omnivore	neotropical migrant
Piciformes	Picidae	*Melanerpes carolinus*	Red-bellied Woodpecker	woodland	omnivore	permanent resident
Passeriformes	Icteridae	*Agelaius phoeniceus*	Red-winged Blackbird	*	omnivore	short-distance migrant

Table 6 Continued.

Order	Family	Species	Common Name	Habitat Guild	Trophic Guild	Migratory Guild
Passeriformes	Tyrannidae	*Tyrannus forficatus*	Scissor-tailed Flycatcher	successional scrub	carnivore	neotropical migrant
Passeriformes	Paridae	*Baeolophus bicolor*	Tufted Titmouse	woodland	omnivore	permanent resident
Passeriformes	Vireonidae	*Vireo griseus*	White-eyed Vireo	successional scrub	omnivore	neotropical migrant
Cuculiformes	Cuculidae	*Coccyzus americanus*	Yellow-billed Cuckoo	woodland	carnivore	neotropical migrant
Piciformes	Picidae	*Picoides pubescens*	Downy Woodpecker	woodland	omnivore	permanent resident
Columbiformes	Columbidae	*Streptopelia decaocto*	Eurasian Collared-Dove	urban	herbivore	permanent resident
Passeriformes	Hirundinidae	*Progne subis*	Purple Martin	urban	carnivore	neotropical migrant
			Grackles	urban	omnivore	**
Passeriformes	Icteridae	*Quiscalus quiscula*	Common			
Passeriformes	Icteridae	*Quiscalus mexicanus*	Great-tailed			
Passeriformes	Vireonidae	*Vireo bellii*	Bell's Vireo		occurred at <3% of sites	
Passeriformes	Cardinalidae	*Passerina caerulea*	Blue Grosbeak		occurred at <3% of sites	
Passeriformes	Polioptilidae	*Polioptila caerulea*	Blue-gray Gnatcatcher	woodland	carnivore	neotropical migrant
Passeriformes	Emberizidae	*Peucaea cassinii*	Cassin's Sparrow		occurred at <3% of sites	
Caprimulgiformes	Apodidae	*Chaetura pelagica*	Chimney Swift	urban	carnivore	neotropical migrant
			Swallows	**	carnivore	**
Passeriformes	Hirundinidae	*Petrochelidon pyrrhonota*	Cliff			
Passeriformes	Hirundinidae	*Hirundo rustica*	Barn			
Passeriformes	Hirundinidae	*Stelgidopteryx serripennis*	Northern Rough-winged			
Passeriformes	Hirundinidae	*Petrochelidon fulva*	Cave			
Passeriformes	Tyrannidae	*Tyrannus tyrannus*	Eastern Kingbird		occurred at <3% of sites	
Passeriformes	Tyrannidae	*Contopus virens*	Eastern Wood Pewee		occurred at <3% of sites	

Table 6 Continued.

Order	Family	Species	Common Name	Habitat Guild	Trophic Guild	Migratory Guild
Passeriformes	Sturnidae	*Sturnus vulgaris*	European Starling	urban	omnivore	short-distance migrant
Passeriformes	Emberizidae	*Spizella pusilla*	Field Sparrow	occurred at <3% of sites		
Passeriformes	Tyrannidae	*Myiarchus crinitus*	Great Crested Flycatcher	occurred at <3% of sites		
Passeriformes	Emberizidae	*Ammodramus savannarum*	Grasshopper Sparrow	occurred at <3% of sites		
			Hummingbirds	occurred at <3% of sites		
Caprimulgiformes	Trochilidae	*Archilochus colubris*	Ruby-throated			
Caprimulgiformes	Trochilidae	*Archilochus alexandri*	Black-chinned			
Passeriformes	Cardinalidae	*Passerina cyanea*	Indigo Bunting	successional scrub	omnivore	neotropical migrant
Columbiformes	Columbidae	*Columbina inca*	Inca Dove	urban	herbivore	permanent resident
Passeriformes	Icteridae	*Icterus spurius*	Orchard Oriole	occurred at <3% of sites		
Passeriformes	Vireonidae	*Vireo olivaceus*	Red-eyed Vireo	occurred at <3% of sites		
Passeriformes	Cardinalidae	*Piranga rubra*	Summer Tanager	occurred at <3% of sites		
Galliformes	Phasianidae	*Meleagris gallopavo*	Wild Turkey	occurred at <3% of sites		
Columbiformes	Columbidae	*Zenaida asiatica*	White-winged Dove	occurred at <3% of sites		

Avian predators and the Brown-headed Cowbird were not included in this list because they were used to generate the interspecific interaction variable. Some individuals were not easily identified to species, and in these cases species were combined. “Meadowlarks” included Eastern and Western Meadowlarks, as my study area was on the edge of the range for Western Meadowlarks, and Meadowlarks are difficult to distinguish by sight. “Swallows” included, primarily, Barn Swallows and Cliff Swallows but may have also included Northern Rough-winged Swallows and Cave Swallows; these species were difficult to distinguish by sight from a distance or when multiple swallows were together. “Grackles” included Common Grackles and Great-tailed Grackles, which were difficult to distinguish in flight or when only females were visible. And “Hummingbirds” included Ruby-throated Hummingbirds and Black-chinned Hummingbirds, as these species were difficult to distinguish by sight.

Guild Membership

I used only species that occurred at 3% or more of study sites in the final guild-level analyses. A core group of 25 bird species occurred this frequently in all three years (Tables 7, 8, and 9). An additional 5 species occurred this frequently in one or two of the three years. Thus, the bird assemblages (groups of species included in each guild) in the analyses varied slightly from year to year.

Audio Recordings

A digital voice recorder was used to identify unknown or unfamiliar songs/calls of species in my study area. Species that were commonly corrected based on information from the digital recorder included Northern Cardinals, Carolina Wrens, Tufted Titmice, Bewick’s Wrens, and Lark Sparrows. I typically used recordings from the Macauley Library (www.macauleylibrary.org) or the All About Birds website (www.allaboutbirds.org), both from the Cornell Lab of Ornithology, to verify bird identities.

Table 7. Bird species or species groups in four habitat guilds that occurred at 3% or more of study sites for each of the three study years. Red-winged Blackbirds do not belong to any of the four habitat guilds used in this study, and so they were excluded from the habitat analysis. Swallows were excluded from the habitat guild analyses because member species belonged to different guilds. Chimney Swifts occurred at 3% or more of sites during 2010, but their adjusted abundances were greatly inflated due to low detection probability estimates, and so they were not included in the 2010 analyses. *Indicated species occurred at 3% or more of sites for only one or two years of the study.

Habitat guilds			
Grassland	Woodland	Successional Scrub	Urban
Dickcissel	Carolina Chickadee	Bewick's Wren	House Sparrow
Meadowlarks	Eastern Phoebe	Carolina Wren	Mourning Dove
	Red-bellied Woodpecker	Eastern Bluebird	Northern Mockingbird
	Tufted Titmouse	Lark Sparrow	Purple Martin
	Yellow-billed Cuckoo	Northern Bobwhite	Grackles
	Downy Woodpecker	Northern Cardinal	European Starling*
	Blue-gray Gnatcatcher	Painted Bunting	Chimney Swift*
		Scissor-tailed Flycatcher	Inca Dove*
		White-eyed Vireo	Eurasian Collared-Dove*
		Indigo Bunting*	

Table 8. Bird species or species groups in three migratory guilds that occurred at 3% or more of study sites for each of the three study years. Grackles and Swallows were excluded from the migratory guild analyses because member species belonged to different guilds. Chimney Swifts occurred at 3% or more of sites during 2010, but their adjusted abundances were greatly inflated due to low detection probability estimates, and so they were not included in the 2010 analyses. *These species occurred at 3% or more of sites for only one or two years of the study.

	Migratory guilds	
Permanent residents	Short-distance migrants	Neotropical migrants
Carolina Chickadee	Bewick's Wren	Dickcissel
Carolina Wren	Eastern Bluebird	Lark Sparrow
House Sparrow	Meadowlarks	Painted Bunting
Northern Bobwhite	Eastern Phoebe	Scissor-tailed Flycatcher
Northern Cardinal	Mourning Dove	White-eyed Vireo
Northern Mockingbird	Red-winged Blackbird	Yellow-billed Cuckoo
Red-bellied Woodpecker	European Starling*	Purple Martin
Tufted Titmouse		Blue-gray Gnatcatcher
Downy Woodpecker		Chimney Swift*
Inca Dove*		Indigo Bunting*
Eurasian Collared-Dove*		

Adjusted Abundances

Detection probabilities ranged from about 0.3 to 0.7 for the species in my study. Adjusted abundances, therefore, were anywhere from approximately 1/3 to 3 times higher than observed abundances.

Table 9. Bird species or species groups in three trophic guilds that occurred at 3% or more of study sites for each of the three study years. Chimney Swifts occurred at 3% or more of sites during 2010, but their adjusted abundances were greatly inflated due to low detection probability estimates, and so they were not included in the 2010 analyses. *These species occurred at 3% or more of sites for only one or two years of the study.

	Trophic guilds	
Carnivores	Herbivores	Omnivores
Bewick's Wren	House Sparrow	Carolina Chickadee
Carolina Wren	Mourning Dove	Dickcissel
Scissor-tailed Flycatcher	Northern Bobwhite	Eastern Bluebird
Yellow-billed Cuckoo	Inca Dove*	Meadowlarks
Purple Martin	Eurasian Collared-Dove*	Eastern Phoebe
Blue-gray Gnatcatcher		Lark Sparrow
Swallows		Northern Cardinal
Chimney Swift*		Northern Mockingbird
		Painted Bunting
		Red-bellied Woodpecker
		Red-winged Blackbird
		Tufted Titmouse
		White-eyed Vireo
		Downy Woodpecker
		Grackles
		European Starling*
		Indigo Bunting*

Landcover Maps

10 m Resolution Landcover Map

Of the 11 landcover classes included in the 10 m resolution map, 5 were most common in my study area: agriculture, grassland, forest/shrubland, savanna grassland, and low-density urban. These 5 classes were used to measure the percent cover and patch density variables at the study sites.

30 m Resolution Landcover Map

The accuracy of the final map (with 6 cover classes) was 88.1%, with a Kappa statistic of 0.85 (Table 10). User's accuracy ranged from 0.74 (medium-density woodland/shrubland) to 0.98 (woodland). Producer's accuracy ranged from 0.72 (medium-density woodland/shrubland) to 0.97 (grassland).

Data Analysis

Comparison of Analysis Methods Using Preliminary Results

I compared distance-based and raw-data approaches using preliminary data from the 2008 study season. For both the distance-based (MRM) approach and the raw data (multiple regression) approach I used 24 environmental variables measured from the National Land Cover Database of 2001 within a 1 km radius around each of 282 study sites. The summer resident bird assemblage included 20 species that occurred at 19 or more sites.

Table 10. Accuracy assessment for 6 cover classes in the 30 meter resolution classified landcover map.

	Ground Truth Data							
Map Classes	woody	medium-density woodland/shrubland	grasses	agriculture	water	developed	total	User Accuracy
woodland	62	0	0	1	0	0	63	0.98
medium-density woodland/shrubland	11	31	0	0	0	0	42	0.74
grassland	3	11	114	3	0	2	133	0.86
agriculture	1	1	3	31	2	0	38	0.82
water	0	0	0	0	24	0	24	1.00
developed	0	0	0	0	1	27	28	0.96
total	77	43	117	35	27	29	328	
Producer Accuracy	0.81	0.72	0.97	0.89	0.89	0.93		
Map Accuracy	88.10%							
Kappa statistic	0.85, 95% CI = 0.8, 0.89, p<0.0001							

Distance-based, Mantel-based approach (MRM). Distance matrices were used as the variables of interest for the MRM analysis. Bray-Curtis distances were used to generate bird and environmental distance matrices, and Euclidean distances were used for the geographic distance matrix. The response variable was the bird assemblage composition distance matrix, and the explanatory variables were the geographic and environmental distance matrices. The MRM model yielded an R^2 value of 0.002 (p = 0.007) for the overall summer bird assemblage.

Raw-data approach (multiple regression). With the same data set, I used multiple regression with spatial eigenvectors as a raw-data approach. The response variable was bird assemblage composition, calculated using the scores from the first axis of a rotated NMDS ordination. Explanatory variables included five environmental PCs and five spatial eigenvectors. To maintain a family-wide p-value of 0.1, I retained variables that were significant with a p-value of <0.01. The final model included four significant variables (PC1, PC3, PC4, sp10) with an adjusted R^2 of 0.31.

I used two methods to determine the relative importance of the variables in the final model: standardized regression coefficients and variance partitioning. The standardized regression coefficients for the variables in the final model were, in order of magnitude: PC1 = 0.389, PC4 = 0.279, PC3 = 0.251, and sp10 = 0.131. The amount of variation attributable to each variable, using variance partitioning, was: PC1 = 0.15, PC4 =0.08, PC3 = 0.06, and sp10 = 0.01.

Alternate raw-data approach (RDA). Also using some preliminary data, I tried an alternative raw-data approach for multivariate response data that would incorporate all bird species information in the model. I used RDA using the bird assemblage data, as well as spatial eigenvectors and environmental variables. The adjusted R^2 for the overall RDA model was 0.088.

Final Analysis Method: Multiple Regression Analysis

Landscape variables. FRAGSTATS generated many of the variables I used to characterize the landscape in my study. I measured percent cover, edge length, mean patch area, nearest neighbor, contagion, evenness, and edge length between high-contrast cover types. Four cover types were most common in my study area: grassland, cropland, woodland, and medium-density woodland/shrubland (medium and large extents) or savanna (small extent). For all three years at the medium and large extents, grassland was the dominant cover type by far, covering 49-54% of the landscape depending on the year/extent (Figure 8). The second most common cover type was woodland (17-20%), followed by cropland (13-15%) and then shrubland (11-12%). For the small extent, savanna was the dominant cover type for all three years (36-39%), followed by grassland (25-26%), woodland (22-25%), and cropland (11-12%).

Edge lengths (standardized by area) were similar between medium and large extents (Figure 9). For all three years, grassland edge length was the greatest, followed by shrubland edge length, woodland edge length, and cropland edge length.

Principal components analysis: comparison with a broken stick model. I used the first four principal components for each spatial extent and year. I also compared the eigenvalues from each PCA with a broken stick model (Figure 10). The different broken-stick models indicated 2-4 components with eigenvalues greater than the broken-stick

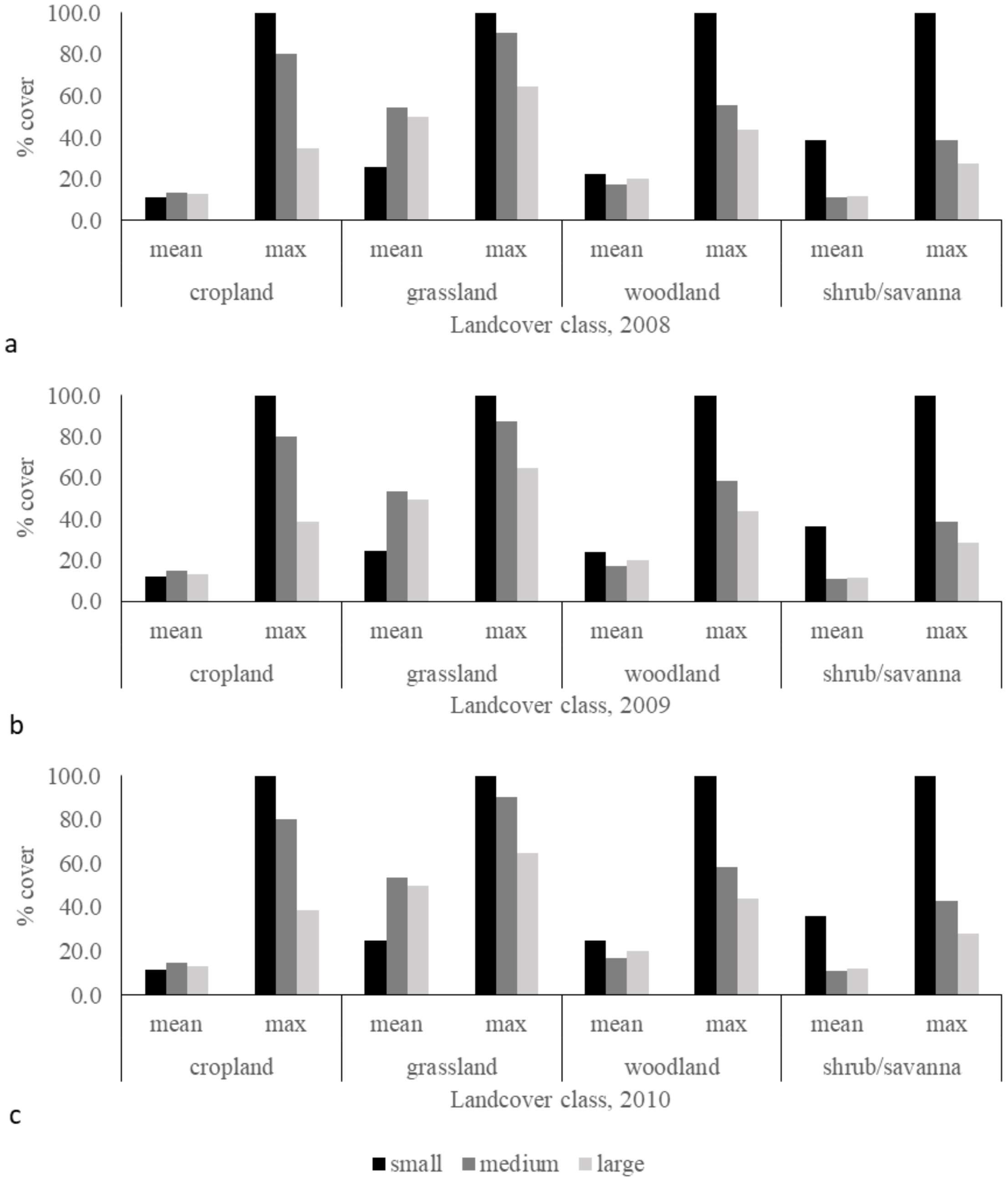


Figure 8. Mean and maximum % cover for four dominant landcover classes measured at small (black), medium (dark gray), and large (light gray) spatial extents in a) 2008, b) 2009, and c) 2010.

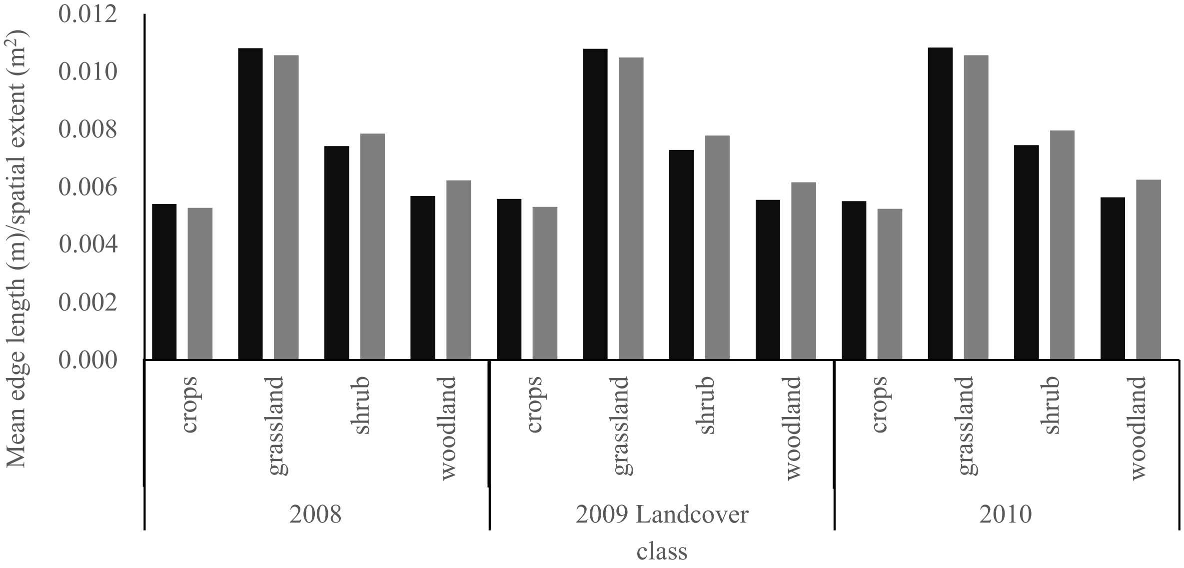


Figure 9. Mean edge length standardized by spatial extent for medium (black) and large (dark gray) extents for the four most common landcover types measured from the 30 m landcover map.

model. By using the first four PCs for each spatial extent in my models, I accounted for more than the recommended variation.

Principal components analysis: amount of variance explained. The principal components (PCs) selected accounted for 70.9 – 80.5 % of the variation in environmental variables cumulatively for each of the three years at the three spatial extents. For 2008, the first four PCs explained 70.9% of the variation at the small extent, 76.8% of the variation at the medium extent, and 78.9% of the variation at the large extent. For 2009, the first four PCs explained 73.7% of the variation at the small extent, 77.9% of the variation at the medium extent, and 80.5% of the variation at the large extent. For 2010, the first four PCs explained 71.1% of the variation at the small extent, 77.8% of the variation at the medium extent, and 80.5% of the variation at the large extent.

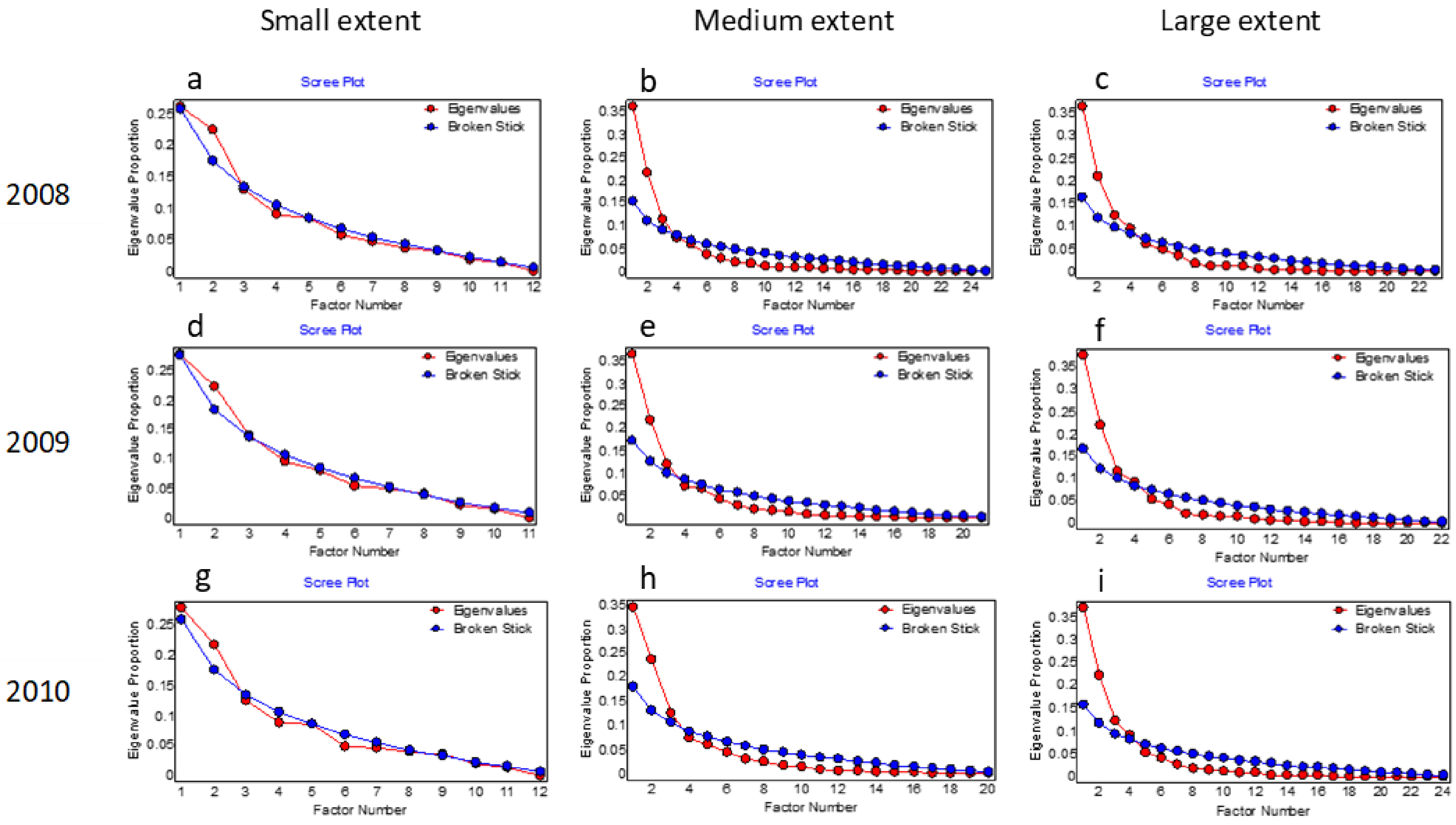


Figure 10. Scree plots relating PCA eigenvalues to a broken stick model for small, medium, and large spatial extents for three years. For scree plots a, d, and g, two eigenvalues are greater than the broken stick model, and for scree plots b, e, h, and i, three eigenvalues are greater than the broken stick model. For scree plots c and f, four eigenvalues are greater than the broken stick model.

Principal components analysis: variance explained by year and extent. In 2008, the first four PCs explained 0.364, 0.209, 0.123, and 0.094 proportion of the variance respectively for the large spatial extent (Figure 11). For the medium extent, the first four PCs explained 0.362, 0.218, 0.115, and 0.074 proportion of the variance. For the small extent, the first four PCs explained 0.263, 0.224, 0.131, and 0.092 proportion of the variance.

In 2009, the first four PCs explained 0.377, 0.22, 0.117, and 0.091 proportion of the variance respectively for the large spatial extent (Figure 11). For the medium extent, the first four PCs explained 0.344, 0.235, 0.126, and 0.073 proportion of the variance. For the small extent, the first four PCs explained 0.278, 0.224, 0.139, and 0.096 proportion of the variance.

In 2010, the first four PCs explained 0.37, 0.223, 0.123, and 0.089 proportion of the variance respectively for the large spatial extent (Figure11). For the medium extent, the first four PCs explained 0.344, 0.235, 0.126, and 0.073 proportion of the variance. For the small extent, the first four PCs explained 0.279, 0.218, 0.126, and 0.088 proportion of the variance.

In 2008, 2009, and 2010, the first PC for the large spatial extent accounted for more of the variation in the environmental variables than did the first PC for the medium spatial extent. Likewise, the first PC for the medium extent accounted for more of the variation than did the first PC for the small extent. The amount of variation explained by the 2nd, 3rd, and 4th PCs was similar for the three spatial extents for each year.

For small, medium, and large spatial extents, the first four principal components explained similar amounts of the variation in environmental variables in 2008, 2009, and 2010.

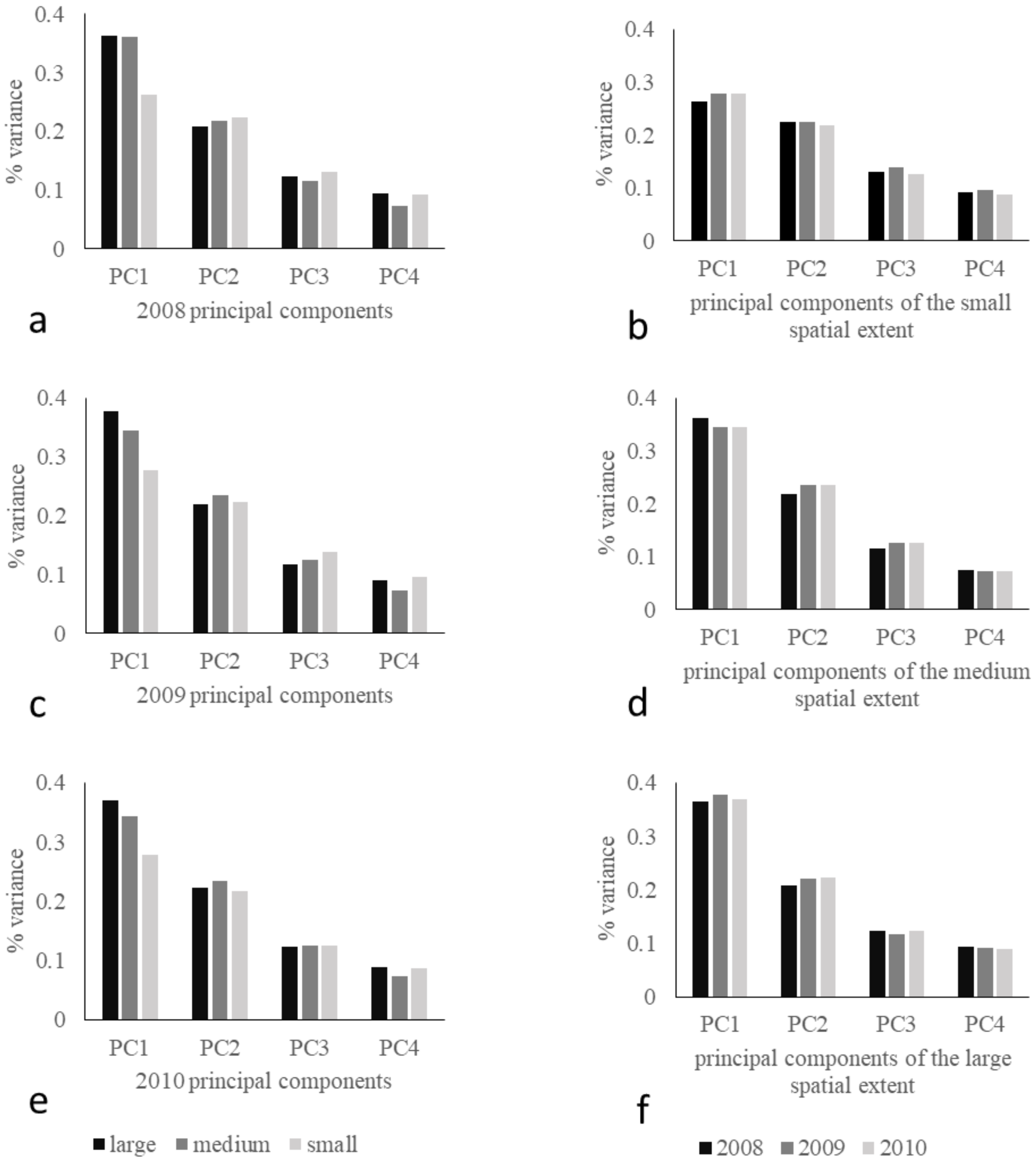


Figure 11. Percent variance in landscape variables explained by principal components by year a) 2008, c) 2009, e) 2010 and spatial extent b) small, d) medium, and f) large.

Principal components analysis: environmental variables represented. At the small spatial scale, variation in total length of edge and patch richness were most important in characterizing the landscape in 2008 (Table 4, Appendix). In 2009 and 2010, no variables at the small spatial scale were important at a loading of 0.75 or greater.

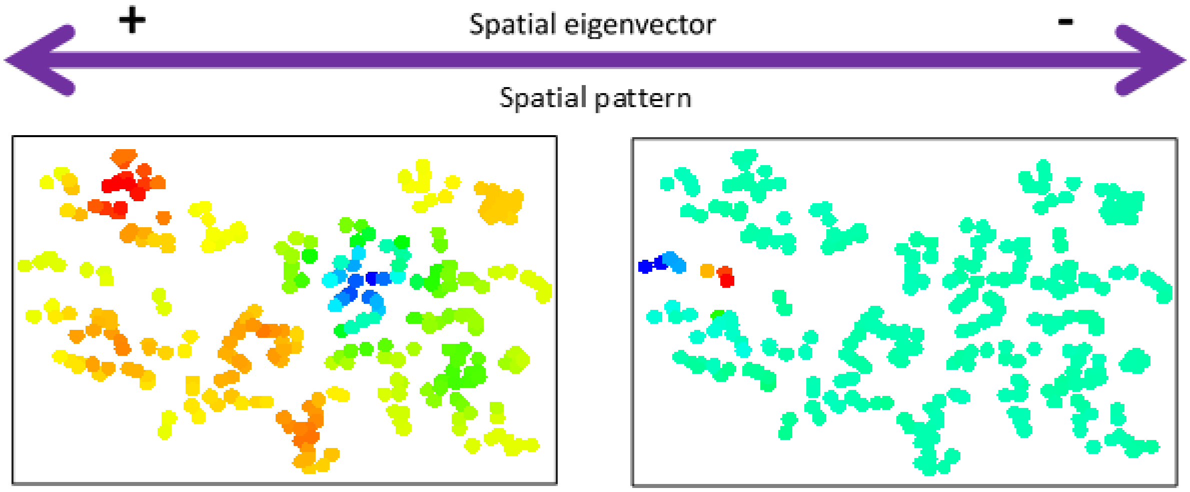
For all three years, at the medium spatial extent, differences in percent cover and total edge length of woodland and total edge length of medium-density woodland/shrubland were most important in characterizing the landscape. The percent cover of medium-density woodland/shrubland, and the distance between grassland and woodland were also important in 2008, and the Simpson's evenness index was important in 2009 and 2010. On the opposite end of the first principal component, the nearest neighbor distance for woodland and medium-density woodland/shrubland was important in 2008, and contagion was important in 2009 and 2010. For the second principal component, percent cover and total edge length of cropland were important in characterizing the landscape for all three years. On the opposite end of the second principal component, the nearest neighbor distance of cropland was important in 2008. No specific variables were important at a loading of 0.75 or greater for the third and fourth principal components at the medium scale, except for the NDVI coefficient of variation on PC4 in 2008.

For all three years, the first principal component for the landscape variables measured at the large spatial extent indicated the variation in the landscape was dominated by differences in the percent cover, total edge length, and mean patch area of cropland; as well as the nearest neighbor distance of medium-density woodland/shrubland and the edge length between cropland and medium-density woodland/shrubland (Table 4, Appendix). On the opposite end of the first principal component were the percent cover and total edge length of medium-density woodland/shrubland. In 2008 and 2010, the edge length between grassland and medium-density woodland/shrubland was also important, and in 2009 and 2010 total edge length of woodland was also important. For the second principal component, percent cover of grassland was consistently important in characterizing the landscape for all three years. In 2009 and 2010, the mean patch area of grassland was important, and in 2009, the nearest neighbor distance of woodland was important. On the opposite end of the second principal component, the nearest neighbor distance of grassland and Simpson's evenness index were important in 2008 and 2010. No specific variables were important at a loading of 0.75 or greater for the third and fourth principal components at the large scale, except for grassland total edge length in 2009.

Spatial eigenvectors. I chose 14 spatial eigenvectors to be included in the full multiple regression model for each guild/year. Eigenvectors were chosen based on their r^2 value in relation to the community composition value. Below is an example of the range of r^2 values, p-values, and Moran's I for the grassland bird guild in all three years:

In 2008, the range of r^2 values was 0.009 – 0.041, the range of p-values was <0.001 – 0.134, the range of Moran's I values was -0.117 – 1.117; in 2009, the range of r^2 values was 0.007 – 0.033, the range of p-values was 0.002 – 0.138, the range of Moran's I values was -0.116 – 1.247; in 2010 the range of r^2 values was 0.008 – 0.04, the range of p-values was 0.001 – 0.105, the range of Moran's I values was -0.119 – 1.174.

The spatial eigenvectors represented the spatial variation in the geographic data, with broad spatial patterns represented in lower numbered eigenvectors and fine spatial patterns represented in larger numbered eigenvectors (Figure 12). The spatial eigenvectors included in each model were chosen based on their relationship to the bird community composition variable (response variable).



Spatial eigenvector 2 Spatial eigenvector 40

Figure 12. Spatial eigenvectors represent spatial variation across geographic coordinates. The dots represent the study sites throughout the study area. Lower numbered eigenvectors represent broad-scale spatial patterns (environmentally induced variation), and the higher numbered eigenvectors represent fine-scale spatial patterns (local spatial variation).

Habitat guilds. Multiple regression analyses were run for bird assemblages in four habitat guilds (grassland, woodland, scrubland, and urban) for 2008, 2009, and 2010. Adjusted R^2 values ranged from 0.13 – 0.43 for habitat guild models (Figure 13). Adjusted R^2 values were highest for scrubland birds and lowest for urban birds. One model (urban 2008) had no significant variables. For grassland and woodland guilds, adjusted R^2 values decreased from 2008 to 2010. For the scrubland and urban guilds, R^2 values were highest in 2009.

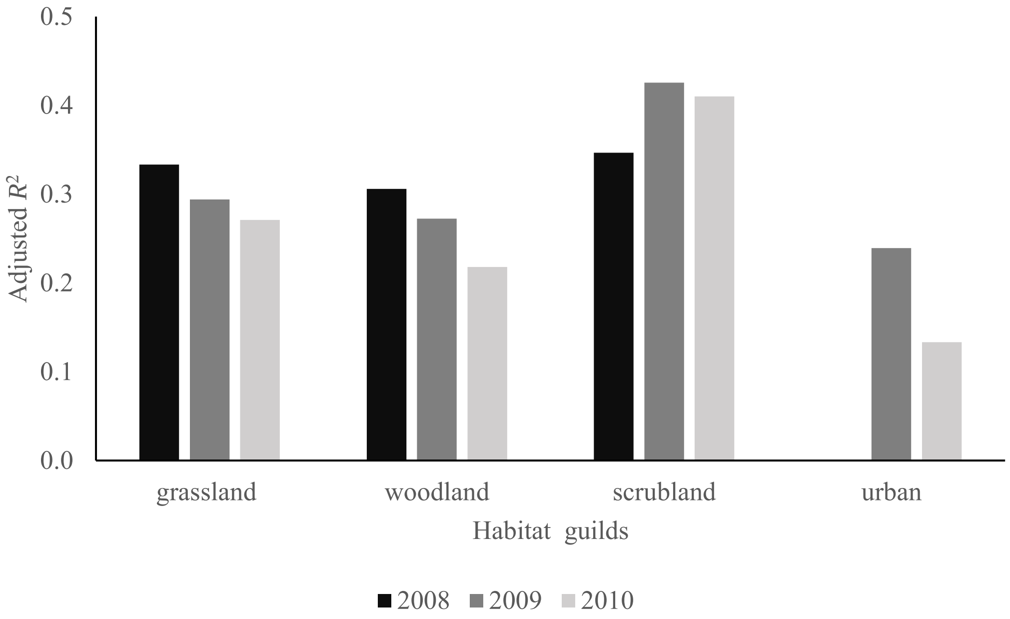


Figure 13. Total variation in bird community composition explained by all variables in multiple regression models for bird assemblages within four habitat guilds.

Habitat guilds: niche and neutral variables. For 11 of 12 habitat guild models, niche variables (environmental variables and interspecific interactions) were most important in explaining the variation in bird assemblage composition. For 1 model there were no significant variables in the final model (Figure 14). For the 11 habitat models with significant variables, a niche variable had the greatest amount of partitioned variance in 10 models, and a detection covariate (wind) had the greatest amount of partitioned variance in one model (Figure 15). For grassland and scrubland guilds, the niche variables with the greatest amount of partitioned variance were environmental variables measured at a medium scale. For woodland and urban guilds, the niche variables with the greatest amount of partitioned variance were environmental variables measured at a small scale.

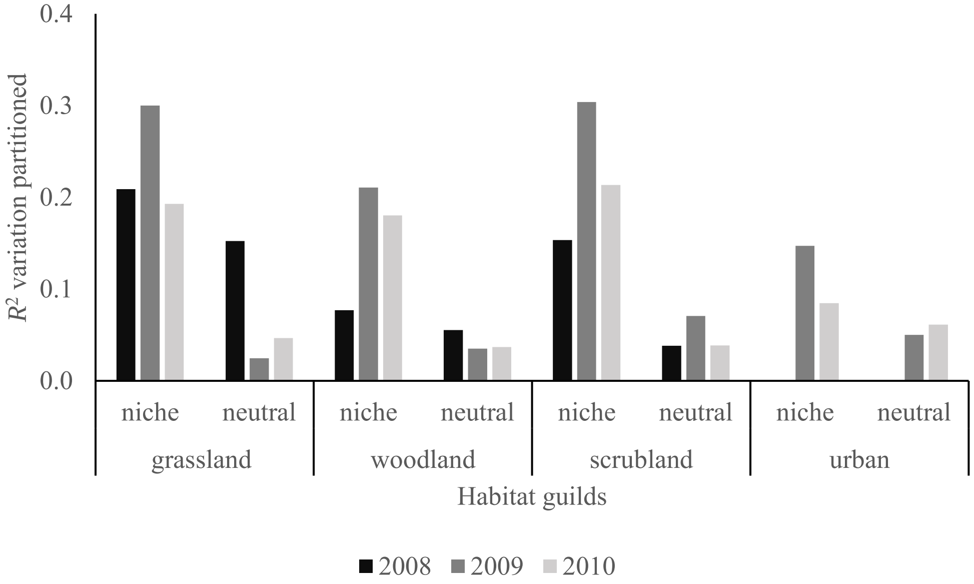


Figure 14. Niche variables accounted for the greatest amount of variance in bird composition for most of the multiple regression models representing grassland, woodland, scrubland, and urban habitat guilds over 3 years. There were no significant variables in the 2008 urban habitat model.

Habitat guilds: interspecific interactions. Nest predator abundance was significant in 4 of 12 habitat guild models (Figure 16), but it was not the variable with the greatest amount of partitioned variance for any model. Nest predator abundance was a significant variable for the woodland guild across all three years, while it was an important variable for the scrubland guild only in 2009. Nest predator abundance was not a significant variable for either the grassland or urban guilds. Brown-headed Cowbird abundance was not included in any of the final habitat guild models.

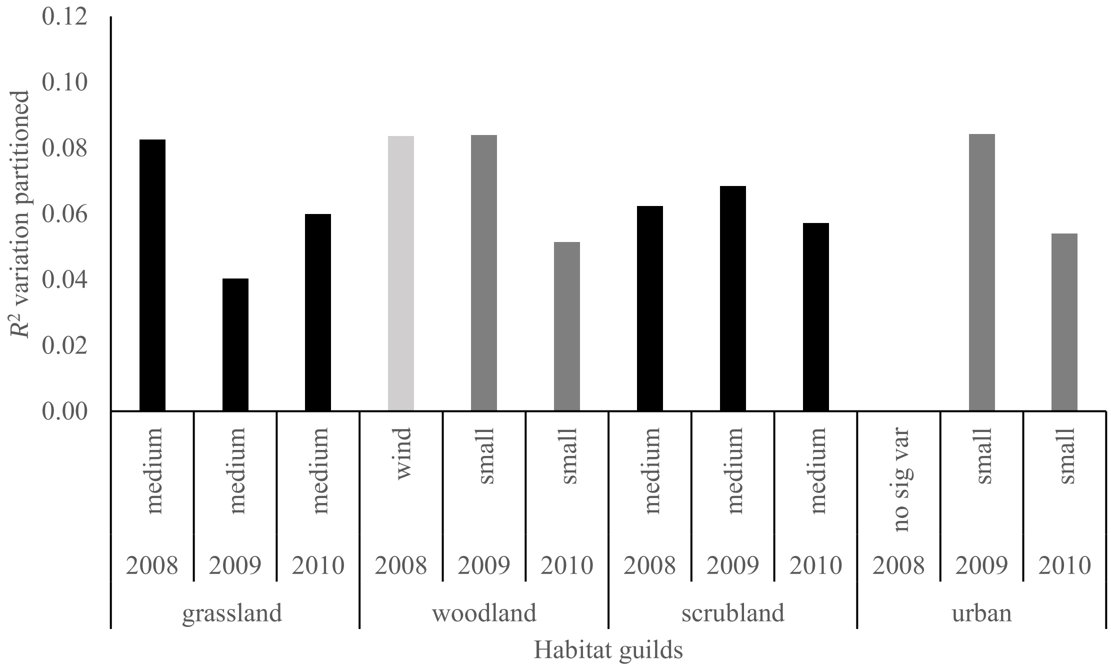


Figure 15. The single variable with the greatest amount of partitioned variance for each habitat guild model is shown. Black indicates niche (environmental) variables measured at a medium spatial extent. Dark gray indicates niche variables measured at a small spatial extent. Light gray indicates a detection covariate (wind).

Habitat guilds: environmental variables. For the habitat guild models, environmental variables measured at a small extent were important in all 11 models with significant variables. For woodland and urban guilds, small extent variables explained more of the partitioned variance than did medium- or large-extent variables (Figure 17). In fact, for the woodland guild in 2008, and both urban guild models with significant variables, small-extent variables were the only significant environmental variables. For grassland and scrubland guilds, medium-extent variables generally explained more of the partitioned environmental variance. One exception is the grassland 2009 model, in which several small-extent variables account for more of the partitioned environmental variance than the medium- or large- extent variables. Large-extent variables were significant in only 4 habitat models, and they never accounted for the largest amount of partitioned variance. Environmental variables representing the variation in woodland and low-density woodland/scrubland were among the variables most important in predicting variation in bird assemblage composition. Variables representing variation in agricultural cover and grassland were also important for some models.

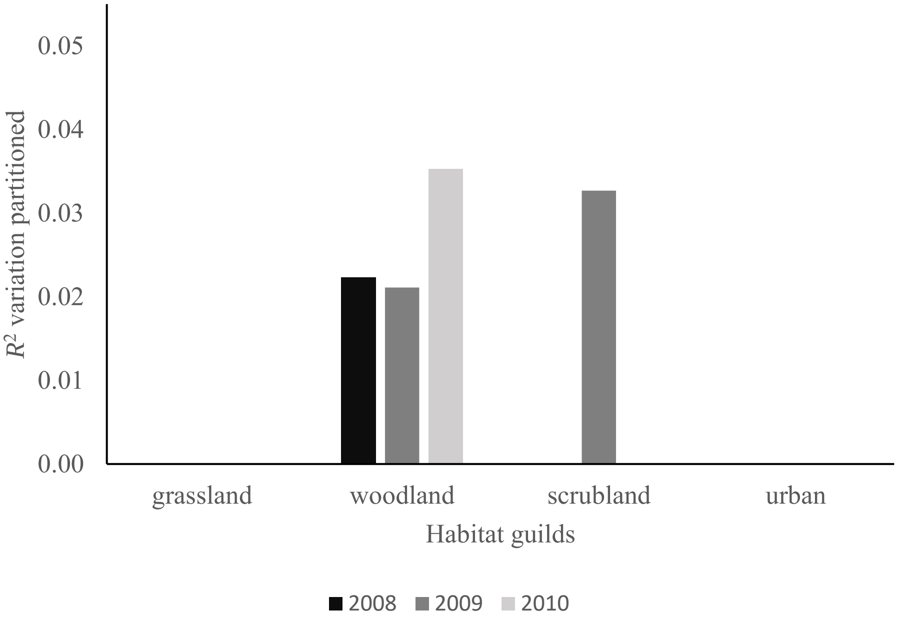


Figure 16. Amount of partitioned variation explained by nest predator abundance for habitat guilds. Nest predator abundance was significant for the woodland guild across all three years, and for the scrubland guild in 2009. It was not a significant variable for any other habitat guild model.

Habitat guilds: spatial variables. Spatial variables representing both broad and fine scale spatial variation were significant in some models. But broad-scale spatial variables were significant in a greater number of models than were fine-scale variables. Spatial variable 1 represents the broadest scale spatial variation, and it was significant in 7 of the 11 habitat models with significant variables (Figure 18). It was consistently significant all three years in the scrubland guild models, and was significant in 2 of 3 years for grassland and woodland models. It was not significant in any of the urban guild models.

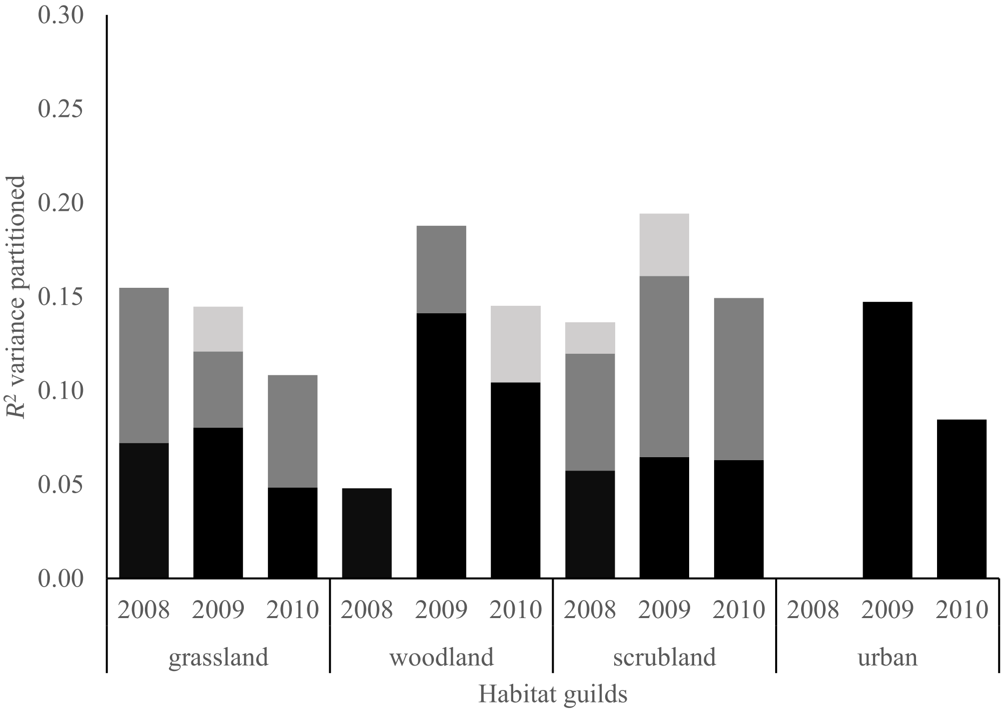


Figure 17. The amount of partitioned variance explained by environmental variables measured at three spatial extents stacked for each year by habitat guild. Black bars indicate variables measured at a small extent and scale. Dark gray bars indicate variables measured at a medium extent. Light gray bars indicate variables measured at a large extent.

Habitat guilds: detection covariates. I measured wind speed, temperature, and number of passing cars during point counts as detection covariates. Wind speed was significant for the woodland and the scrubland guilds in 2008, and for the scrubland guild in 2010 (Figure 19). Temperature was significant for the woodland and the urban guilds in 2009. Detection covariates typically accounted for low amounts of the partitioned variance in models where they were significant, but in 2008, wind speed was the variable that explained the most partitioned variance for the woodland guild.

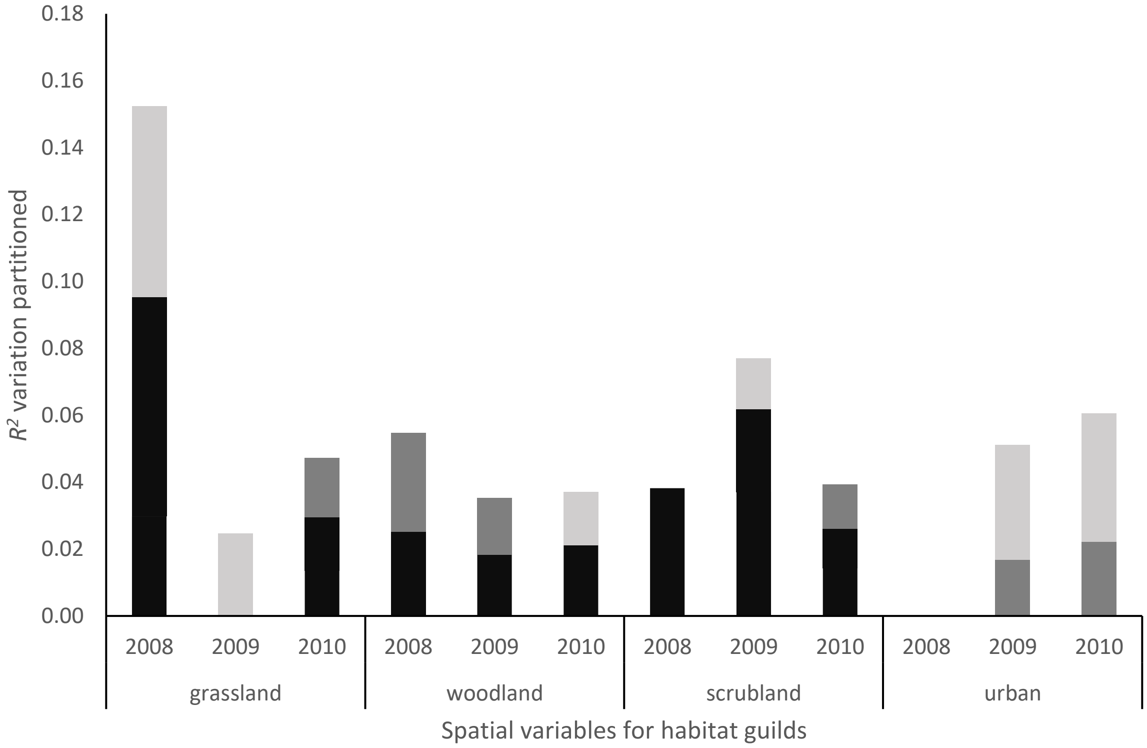


Figure 18. The amount of partitioned community composition variance explained by spatial variables stacked for each year by habitat guild. Each column represents fine-(light gray), medium-(dark gray), and/or broad-(black) scale spatial variables.

Migratory guilds. Multiple regression analyses were run for bird assemblages in three migratory guilds (permanent residents, short-distance migrants, and neotropical migrants) for 2008, 2009, and 2010. Adjusted R^2 values ranged from 0.11 – 0.41 for migratory guild models (Figure 20). Adjusted R^2 values were highest for permanent residents and lowest for short-distance migrants. Two neotropical models (for 2008 and 2010) had no significant variables.

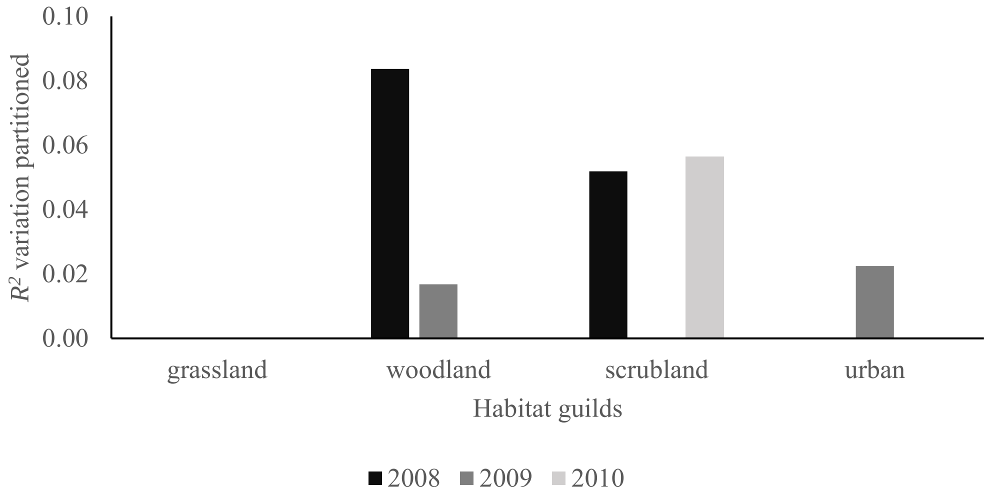


Figure 19. Detection covariates were significant in 5 of 12 habitat guild models. Wind speed was significant in 2008 and 2010, and temperature was significant in 2009 for habitat models.

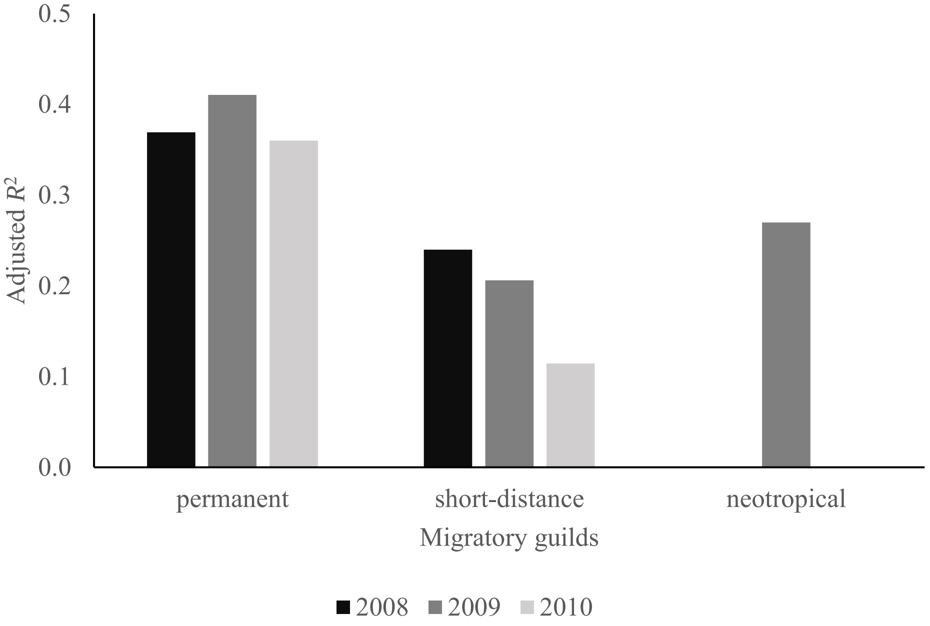


Figure 20. Total variation in bird community composition explained by all variables in multiple regression models for bird assemblages within three migratory guilds.

Migratory guilds: niche and neutral variables. For 4 of 9 models, niche variables (environmental variables and interspecific interactions) were most important in explaining the variation in bird assemblage composition. For 3 of 9 models, neutral variables (spatial variables) were most important in explaining the variation in assemblage composition. And for 2 models there were no significant variables in the final model (Figure 21).

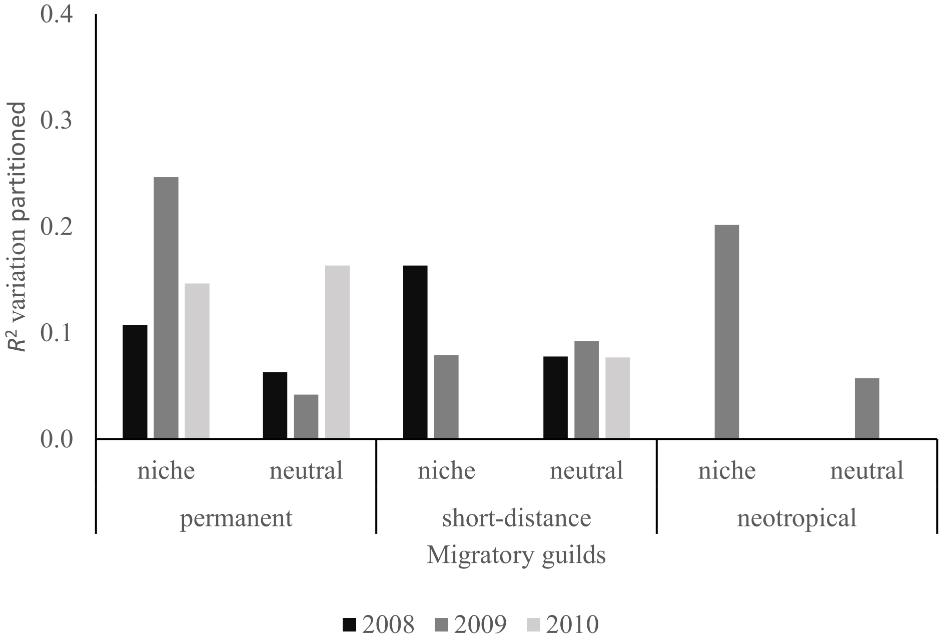


Figure 21. Niche variables accounted for the greatest amount of variance in bird assemblage composition for four of the multiple regression models representing permanent residents, short-distance migrants, and neotropical migrants over 3 years, while neutral variables accounted for the greatest amount of variance for three models. There were no significant variables in the 2008 and 2010 neotropical migrants' models.
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For the 7 migratory guild models with significant variables, a niche variable had the greatest amount of partitioned variance in 4 models, a neutral variable had the greatest amount of partitioned variance in one model, and a detection covariate had the greatest amount of partitioned variance in two models (Figure 22). The variable with the greatest amount of partitioned variance was not consistent across years for the different migratory guilds. Environmental variables measured at small and medium spatial scales had the greatest amount of partitioned variance for short-distance migrants in 2008 and 2009, and for permanent residents and neotropical migrants in 2009. A neutral (spatial) variable had the greatest amount of partitioned variance for the permanent resident model in 2010, and a detection covariate had the greatest partitioned variance in the permanent resident model in 2008 and the short distance model in 2010.

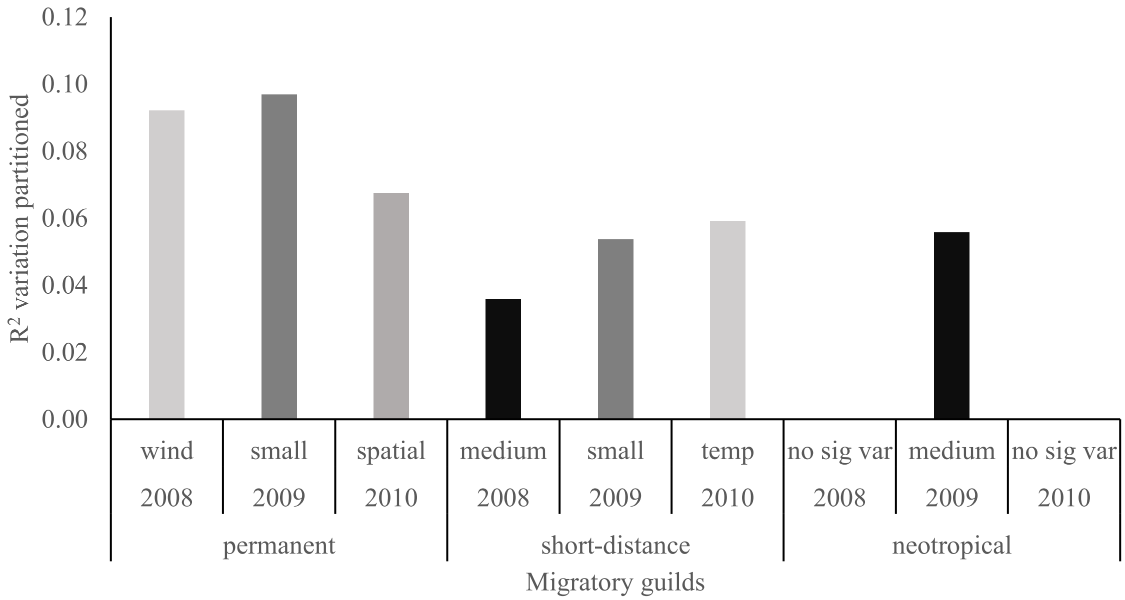

Figure 22. The single variable with the greatest amount of partitioned variance for each migratory guild model is shown. Black indicates niche (environmental) variables measured at a medium spatial extent. Dark gray indicates niche variables measured at a small spatial extent. Medium gray indicates a neutral (spatial) variable. Light gray indicates a detection covariate (wind or temperature).

Migratory guilds: interspecific interactions. Nest predator abundance was significant in 2 of 9 migratory guild models (Figure 23), but it was not the variable with the greatest amount of partitioned variance for any model. Nest predator abundance was a significant variable for the permanent resident guild in 2008 and 2009. Nest predator abundance was not a significant variable for either the short distance migrant or neotropical migrant guilds. Brown-headed Cowbird abundance was not included in any of the final migratory guild models.

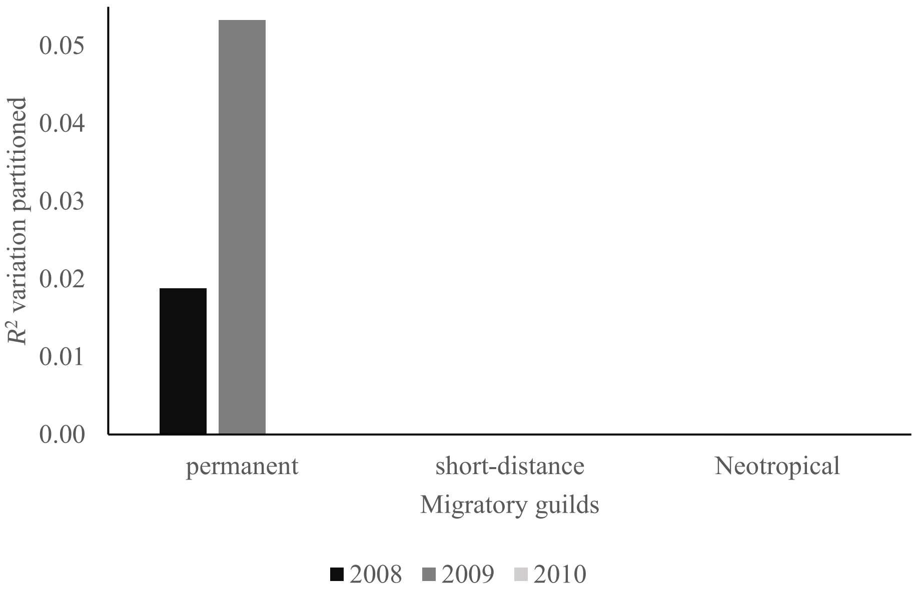

Figure 23. Amount of partitioned variation explained by nest predator abundance for migratory guilds. Nest predator abundance was significant for the permanent resident guild in 2008 and 2009. It was not a significant variable for any other migratory guild model.

Migratory guilds: environmental variables. For the migratory guild models, environmental variables measured at a small extent were important in all six models with significant niche variables (Figure 24). Environmental variables measured at a medium extent were important in four models, and variables measured at a large-extent were important in five models. For permanent residents, small extent variables had the greatest amount of partitioned variance than did medium- or large-extent variables for 2008 and 2009. For 2010, medium-extent variables had the greatest amount of the partitioned variance. For short-distance migrants, small-extent variables had the greatest amount of partitioned variance in 2008 and 2009, but in 2010, no niche variables were significant. Small-, medium- and large-extent variables were significant in 2008 for short-distance migrants, while in 2009, only small- and medium-extent variables were significant. For Neotropical migrants, only one year had any significant variables in the final model (2009), when small-, medium-, and large-extent variables were significant. In this model, environmental variables measured at a medium extent had the greatest amount of partitioned variance.

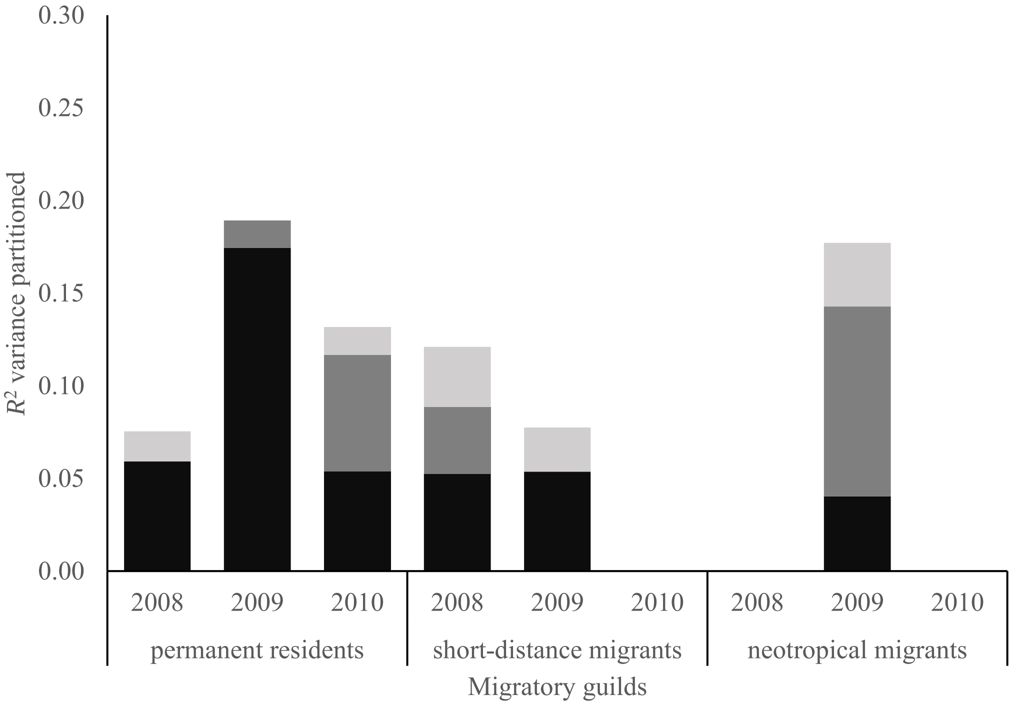

Figure 24. The amount of partitioned variance explained by environmental variables measured at three spatial extents stacked for each year by migratory guild. Black bars indicate variables measured at a small extent and scale. Dark gray bars indicate variables measured at a medium extent. Light gray bars indicate variables measured at a large extent.

Migratory guilds: spatial variables. Spatial variables representing both broad and fine scale spatial variation were significant in some models. But broad-scale spatial variables were significant in a greater number of models than were fine-scale variables.

Spatial variable 1 represents the broadest scale spatial variation, and it was significant in 6 of the 7 migratory models with significant variables (Figure 25). It was consistently significant all three years in the permanent resident model, and it was significant in 2 of 3 years for short-distance migrant models. It was also significant for neotropical migrants in 2009 (there were no significant variables in 2008 and 2010 for neotropical migrants).

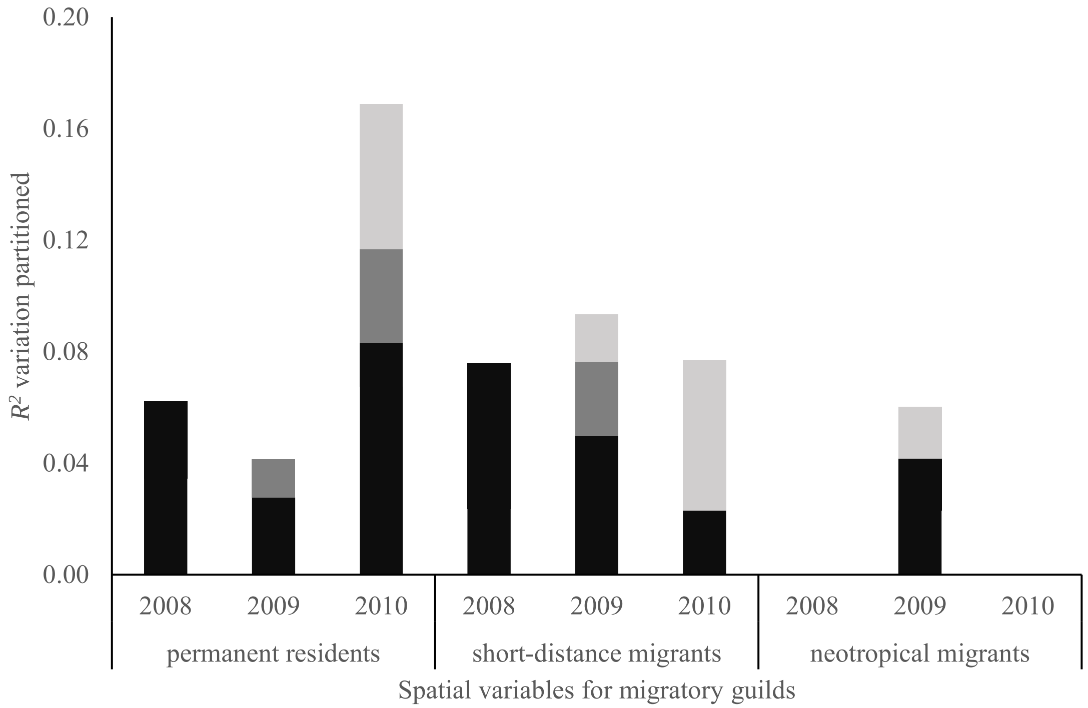

Figure 25. The amount of partitioned community composition variance explained by spatial variables stacked for each year by migratory guild. Each column represents fine-(light gray), medium-(dark gray), and/or broad-(black) scale spatial variables.

Migratory guilds: detection covariates. Wind speed was significant for permanent residents in 2008 and 2009, and temperature was significant for short-distance migrants in 2009 and 2010 (Figure 26). No detection covariates were significant in the other migratory guild models. Detection covariates typically accounted for low amounts of the partitioned variance in models where they were significant, but in 2008, wind speed was the variable that explained the most partitioned variance for the permanent resident guild, and in 2010, temperature was the variable that explained the most partitioned variance for the short-distance migrant guild.

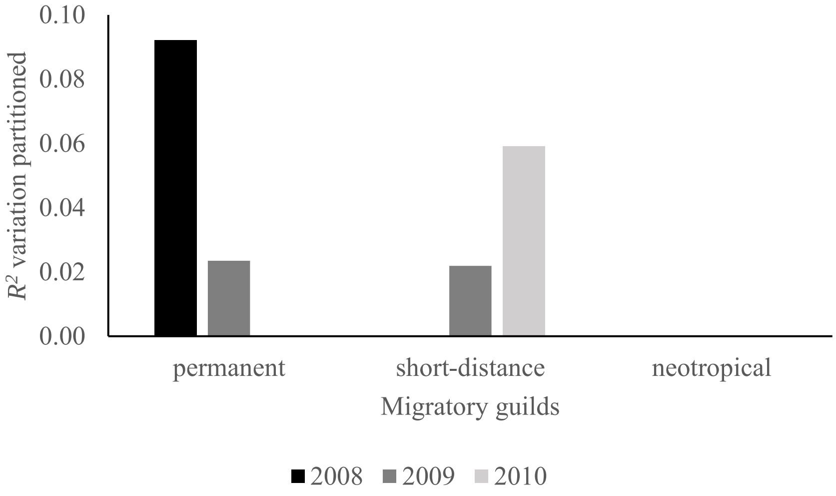

Figure 26. Detection covariates were significant in 4 of 9 migratory guild models. Wind speed was significant for permanent residents in 2008 and 2009, and temperature was significant in short-distance migrants in 2009 and 2010.

Trophic guilds. Multiple regression analyses were run for bird assemblages in three trophic guilds (carnivores, herbivores, and omnivores) for 2008, 2009, and 2010. Adjusted R^2 values ranged from 0.14 – 0.46 for trophic guild models (Figure 27). Adjusted R^2 values were highest for omnivores and lowest for herbivores. One model (herbivores 2009) had no significant variables. For carnivores and omnivores, adjusted R^2 values were highest in 2009, while adjusted R^2 values were highest in 2008 for herbivores.

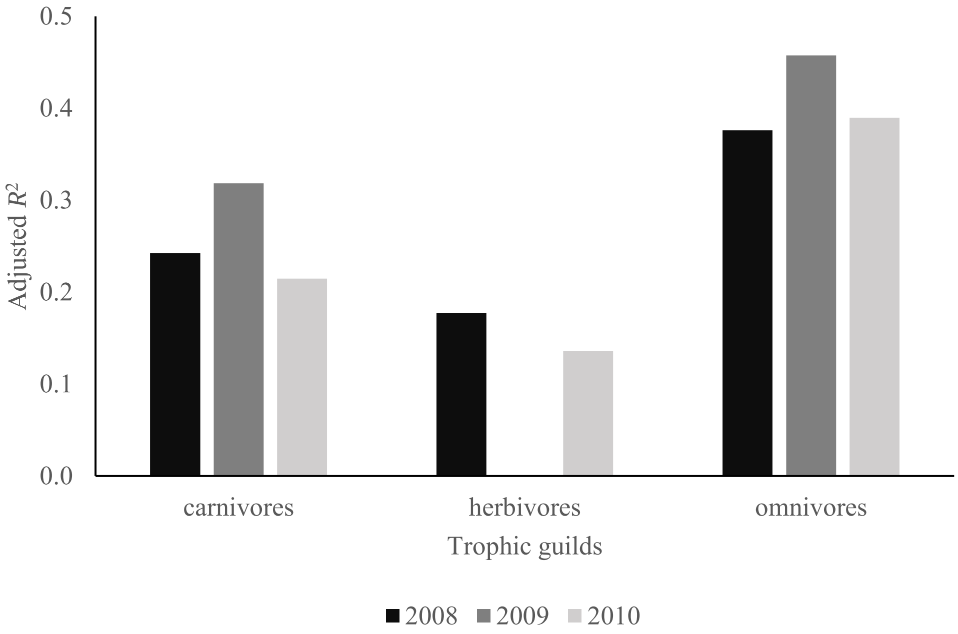

Figure 27. Total variation in bird community composition explained by all variables in multiple regression models for bird assemblages within three trophic guilds.

Trophic guilds: niche and neutral variables. For all 6 of the models representing carnivores and omnivores, niche variables (environmental variables and interspecific interactions) were most important in explaining the variation in bird assemblage composition (Figure 28). For two models representing herbivores (2008 and 2010), neutral variables (spatial variables) were most important in explaining the variation in assemblage composition. And for the herbivore 2009 model there were no significant variables in the final model.

For the 8 trophic models with significant variables, a niche variable had the greatest amount of partitioned variance in 6 models, and a neutral variable and a detection covariate (wind) each had the greatest amount of partitioned variance in one model (Figure 29). For carnivores, the niche variables with the greatest amount of partitioned variance were environmental variables measured at a small scale. For herbivores, an environmental variable measured at a small scale had the greatest amount of partitioned variance in 2010, though neutral variables accounted for more of the partitioned variance overall. A neutral (spatial) variable accounted for most of the partitioned variance for herbivores in 2008. Small scale variables accounted for the most partitioned variance for omnivores in 2009 and 2010. A detection covariate (wind) had the greatest amount of partitioned variance for omnivores in 2008.

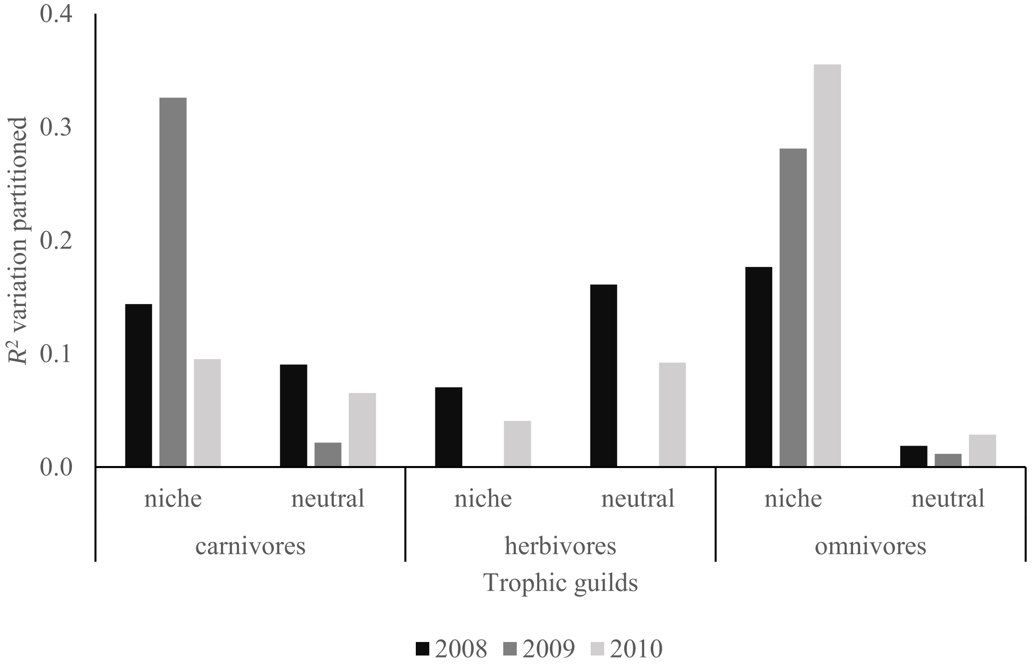

Figure 28. Niche variables accounted for the greatest amount of variance in bird assemblage composition for multiple regression models representing carnivores and omnivores over 3 years, while neutral variables accounted for the greatest amount of variance for two models representing herbivores. There were no significant variables in the 2009 herbivore model.

Trophic guilds: interspecific interactions. Nest predator abundance was significant in 3 of 9 trophic guild models (Figure 30), but it was not the variable with the greatest amount of partitioned variance for any model. Nest predator abundance was a significant variable for carnivores in 2009, and for omnivores in 2010.

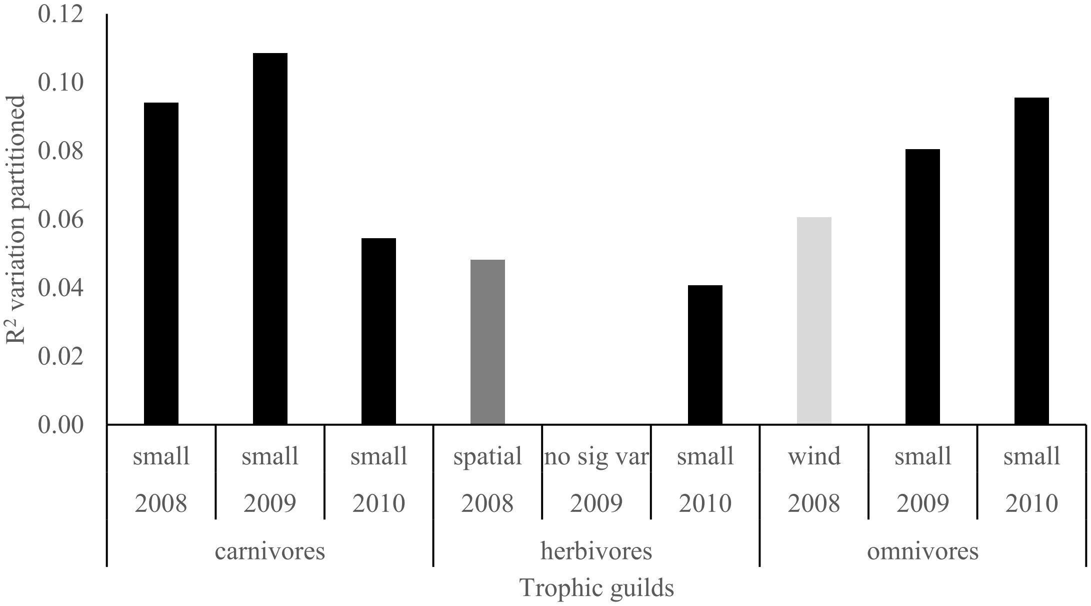

Figure 29. The single variable with the greatest amount of partitioned variance for each trophic guild model is shown. Black indicates niche (environmental) variables measured at a small spatial extent. Gray indicates a neutral (spatial) variable. Light gray indicates a detection covariate (wind).

Trophic guilds: environmental variables. For the trophic guild models, environmental variables measured at a small extent were significant in 7 of 8 models with significant variables (Figure 31). For these seven models, small extent variables explained more of the partitioned variance than did medium- or large-extent variables. For the carnivore trophic guild, small-extent variables had the greatest amount of partitioned environmental variance for all three years, with a small amount of partitioned variance attributable to medium-extent variables in 2009 and 2010. The herbivore trophic guild varied from year to year. In 2008, only medium- and large-extent variables were significant, while in 2010 only small-extent environmental variables were

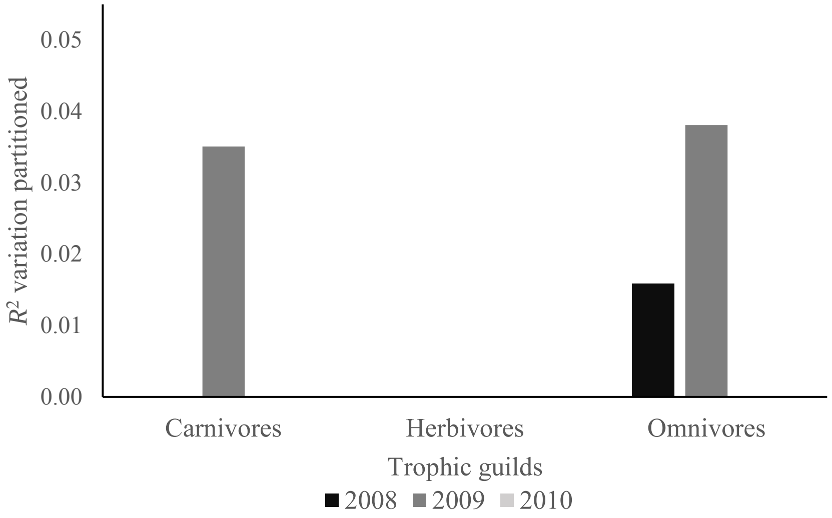

Figure 30. Amount of partitioned variation explained by nest predator abundance for trophic guilds. Nest predator abundance was significant for the carnivores 2009 and for omnivores in 2008 and 2009. It was not a significant variable for any other trophic guild model.

significant. In 2009 there were no significant variables in the herbivore final model. For omnivores, small extent variables were consistently important in all three years. Medium-extent variables were also important in all three years, though a larger portion of the partitioned variance was attributable to medium-extent variables in 2010, than in 2008 and 2009. Large extent variables were only significant in 2010 for omnivores.

Trophic guilds: spatial variables. Spatial variables representing both broad and fine scale spatial variation were significant in some models. But broad-scale spatial variables were significant in a greater number of models than were fine-scale variables. Spatial variable 1 represents the broadest scale spatial variation, and it was significant in 4 of the 8 trophic models with significant variables (Figure 32). For carnivores and herbivores, there was variation in the specific spatial variables significant in each year.

For omnivores, spatial variable 1 was the only significant spatial variable, and it was significant in all three years.

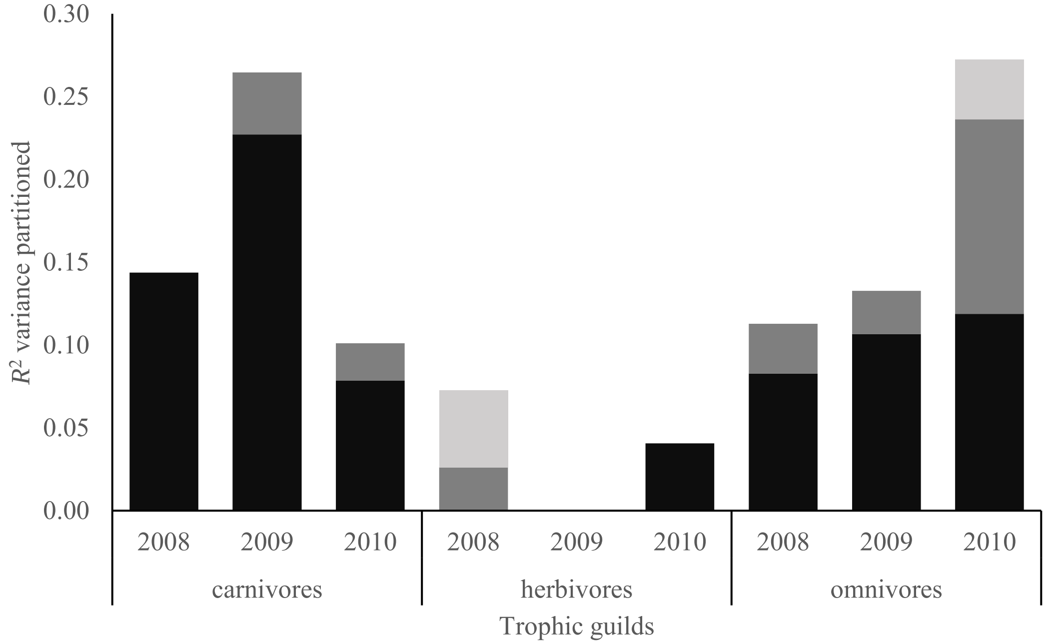

Figure 31. The amount of partitioned variance explained by environmental variables measured at three spatial extents stacked for each year by trophic guild. Black bars indicate variables measured at a small extent and scale. Dark gray bars indicate variables measured at a medium extent. Light gray bars indicate variables measured at a large extent.

Trophic guilds: detection covariates. Wind speed was significant for the carnivore guild in 2010, and for the omnivore guild in 2008 and 2009 (Figure 33). Temperature was significant for the carnivore guild in 2008 and for the herbivore guild in 2010. Detection covariates typically accounted for low amounts of the partitioned variance in models where they were significant, but in 2008, wind speed was the variable that explained the most partitioned variance for the omnivore guild.

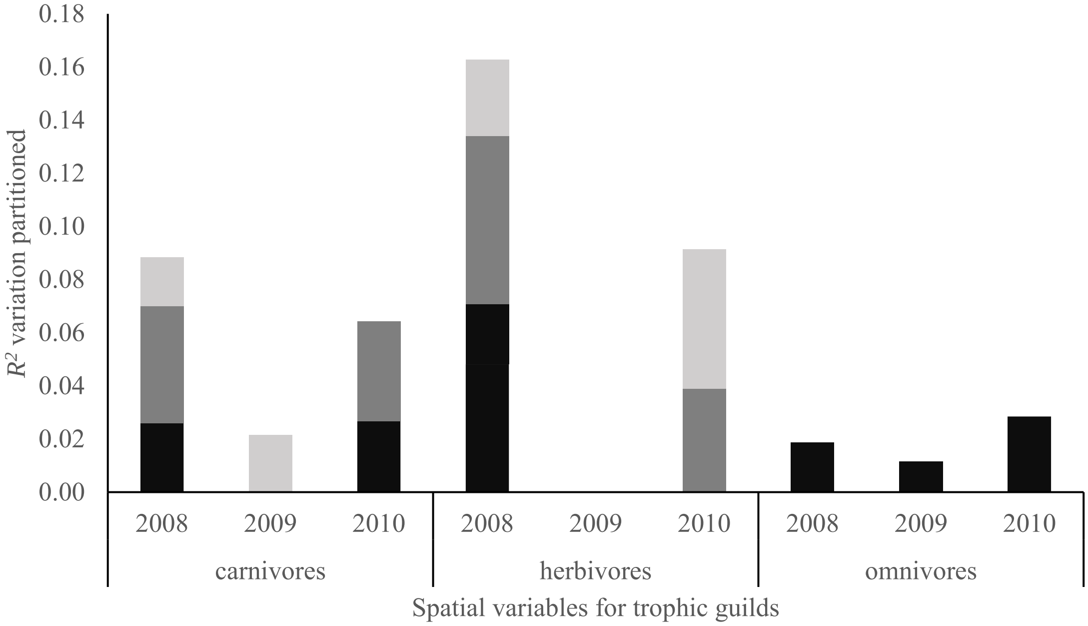

Figure 32. The amount of partitioned community composition variance explained by spatial variables stacked for each year by migratory guild. Each column represents fine-(light gray), medium-(dark gray), and/or broad-(black) scale spatial variables.

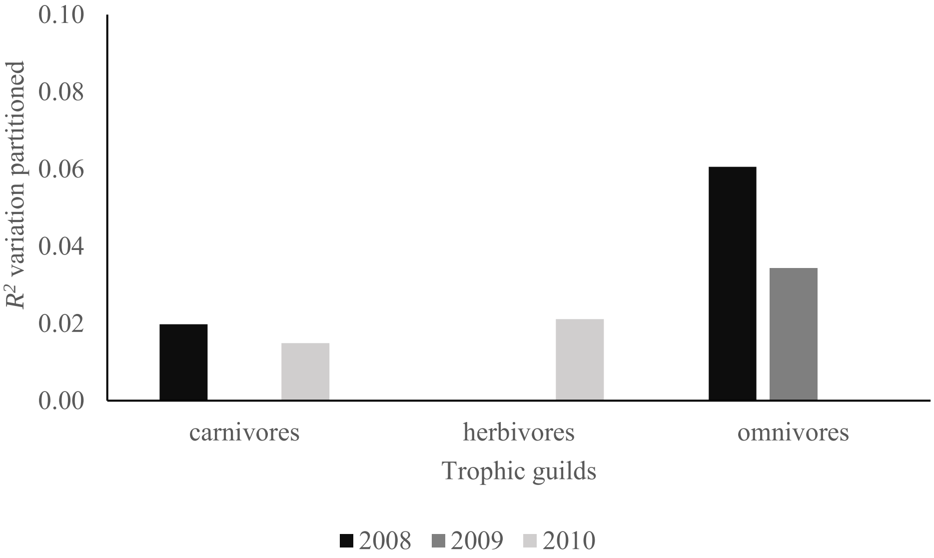

Figure 33. Detection covariates were significant in 5 of 9 migratory guild models. Wind speed was significant for omnivores in 2008 and 2009, and for carnivores in 2010. Temperature was significant for carnivores in 2008, and herbivores in 2010.

CHAPTER FOUR

Discussion

Study Sites

A variety of issues occurred with the 2008 data that led to the removal of study sites. One issue was difficulty in identifying certain bird species in the field, which arose, in part, from my inexperience as a birder in the first field season. I initially confused the song of the Bewick's Wren with the song of the Lark Sparrow, being unaware that I should expect Bewick's Wrens in the area. Though the songs are different in many ways, they both have some repetitive notes that can sound similar if you are not familiar with the Bewick's Wren song. I discovered this issue partway through the season, and once I was aware of the presence of Bewick's Wrens in the study area, I was less likely to make an incorrect identification. When possible, I used digital recordings to verify Bewick's Wren and Lark Sparrows at sites visited before I was aware of the identification problem. But there were a number of sites visited early in the field season where I indicated the presence of a Lark Sparrow, but had no recording to verify the identification. In those cases, I removed the site from the final group of sites for 2008.

The exclusion of sites due to questionable bird identity, noise, geographic location, missing or incorrect covariate data, and uncorrected GPS locations, left me with 282 sites (2008), 299 sites (2009), and 323 sites (2010) in the final analyses. As the analyses for each year were done separately, the variation in number of sites year-to-year was not a problem. The total sample size was comparable or greater than many studies utilizing avian point counts (Van Wilgenberg et al. 2017, Rodgers and Koper 2017).

Bird Data

Guild Membership

Bird species richness across the entire study area ranged from 27-28 species for each of the three study years (Tables 7, F8, 9). Guild membership was based on BBS guild membership (or species accounts for species not included in the BBS guild list). Some guilds were more species rich than others. The grassland guild (see Table 7) included only two species in each year (Dickcissel and Meadowlarks). While other species certainly utilized grassland habitats, they were not included in the grassland guild. The woodland habitat guild included 7 species in each year. The successional scrub guild was a species-rich guild with 9 or 10 species each year. It represented a wide range of habitat use by the included species. For example, Carolina Wrens are commonly found in dense woody vegetation, while Bewick's Wrens are often found in more open habitats containing woody shrubs or trees. While both are included in the successional scrub guild, they differ in their specific habitat preferences. Some species in the successional scrub guild were more commonly found in grassland habitats, while others were more commonly found in woodland habitats. The urban guild varied the most from year to year, with five species occurring at 3% or more of study sites in all three years, and an additional four species occurring at 3% or more of study sites for only one or two of the years. This variability is not surprising, as my study intentionally excluded urban areas. So many urban species were not commonly found at my study sites.

Migratory guild status was also determined based on BBS guild membership. In some cases, species that are migratory in more northern ranges may be less migratory in their southern ranges. For example, Eastern and Western Meadowlarks are included in the short-distance migratory guild, but they are most likely migratory only in the northern part of their range. In Texas, they are probably resident during the winter. And for some species, migration habits may not be fully understood, or may vary among populations. Bewick's Wrens, classified as short-distance migrants in the BBS guilds, are probably year-round residents in much of their range, with some short-distance migration occurring at times. Climate change may also be influencing migratory behaviors in birds. And so migratory groups may not accurately reflect the behavior of all species in my study, though the majority probably do migrate as indicated by their stated guild.

Trophic guild membership was based on species-specific information in the literature, and was generally an estimate of year-round diet, though most birds do eat at least some insects during the breeding season. Some species have more diet information available than others, but general information about diet and behavior provides a good estimate of trophic guild membership.

Audio Recordings

The use of recorders during avian point counts has not been a common occurrence, though the benefits of utilizing acoustic recorders and human observers for point counts is becoming more known (Van Wilgenburg et al. 2017). I initially planned to use a digital recorder during the first field season because I was still becoming familiar with the birds in my study area. However, I found the recorder to be useful even in the second and third years of the study. Though more experienced in recognizing bird songs/calls after the first year, I still heard unfamiliar songs/calls from time to time. Also, there is much variation in the songs of some species, and so familiarity with a common song may not mean a birder is likely to recognize all the song/call variants of that species. Having recordings of songs from the field allowed me to compare songs with recordings of known species to verify the species' identifications.

From the 2008 field season, I used recordings to help distinguish Lark Sparrow and Bewick's Wren songs. I continued to find the recordings useful for distinguishing the songs of these two species in 2009 and 2010 because the Lark Sparrow song is highly variable, and Bewick's Wrens have many songs in their repertoire. Other species that have similarities in some of their songs include Northern Cardinals, Carolina Wrens, and Tufted Titmice, all three of which have a 2-note song (in addition to their more commonly known songs). Identifying the 2-note song to species requires familiarity with the tone of each species, and it was much easier to identify some songs to species when I could listen to them repeatedly and compare them with recordings of known species singing similar songs. I was also able to use the recordings to correct or add bird identities when I learned a particular call or song was characteristic of a species. For example, the Carolina Wren has a distinctive trill call that I heard during all three years but did not recognize. Using the recordings, I was able utilize this information all three years and add or verify the Carolina Wren at sites when this trill call was present. Recordings were also useful to add or verify species whose songs or calls are typically softer or more monotonous than other bird songs/calls that may be present. Such songs/calls can get lost as background noise at a site with a lot of bird activity. Tufted

Titmice and House Sparrows have such songs, for which I could add or correct these bird identities for some sites based on information from recordings.

The biggest drawback to the use of a digital recorder for bird songs/calls in the field was that subsequently listening to and trying to identify or verify songs/calls was very time-intensive. Though I did not record the entire point count for sites, I still had hours of digital recordings to sort through for each year. Often, recordings had to be listened to repeatedly and compared with recordings of known species before I was sure of a bird identity for a specific site. Also, while the recordings of bird calls or songs were clear when the birds were close, distant songs or calls were more difficult to distinguish on the recordings than in person at the sites. The sounds of wind or passing cars was also more likely to obscure bird sounds on recordings than in person. Despite these drawbacks, I think the use of a digital recorder in the field improved the accuracy of my bird dataset. Audio recordings may have additional uses as well, in measuring stress levels in birds or other behavioral patterns.

Adjusted Abundances

Accounting for detection bias in bird abundance estimates is important for accurate data analysis (Royle et al. 2007). Most of the more common techniques for adjusting abundance estimates do so over an entire study area, utilizing bird count information from multiple sites to estimate an area-wide population abundance. They cannot be used to generate site-specific abundance estimates. I used the Royle repeated counts method (Royle 2004) to generate detection probabilities for each species, but I could not use the area-wide abundance estimates produced by the method. For my study, site-specific adjusted abundance estimates were calculated by taking the observed count of individuals at the site and dividing by the detection probability (Lancia et al. 2005). There were a few problems with this method. Calculated detection probabilities were usually low, and this method likely overestimated the number of individuals at each site. Since all species were likely overestimated by use of this method, there was a consistent bias in which the effect on the results was probably minimal. Also, because there is no way to adjust a zero abundance (absence of a species detection) with this method, if species were present but not observed (they did not sing or were not visible during the count) they were unaccounted for in the analysis. Despite these limitations, this adjustment is considered a standard, if not required, data-treatment method that accounts for detection bias, and generates a site-specific abundance estimate that was necessary for the data modeling I used in this study.

Landcover Maps

I used a freely-available 10 m resolution classified map (from Texas Parks and Wildlife), and a 30 m resolution classified map (that I generated from Landsat imagery) to measure landscape variables in my study area. I used the 10 meter resolution imagery to measure landscape variables at the small spatial extent of my study (153 m radius). Though finer resolution field survey data has been shown to better predict bird numbers than remotely sensed data (Rhodes et al. 2015), collecting vegetation data in the field is labor intensive, complicated by private land ownership, and not feasible for large spatial extents. Producing classified maps, though, is also labor intensive (Sheeren et al. 2014, Richards and Jia 2006) Very high resolution satellite imagery (<10 m) is available, but often at a cost (Rose et al. 2014). However, some higher resolution imagery (even <1 m resolution) has been used to create habitat maps (Onojeghuo and Blackburn 2016). To my knowledge, the Texas Ecological Mapping System has not yet been used in published habitat research.

The 30 m spatial resolution of landcover data I used here is similar to what other bird studies have used (Zuckerberg et al. 2016, Ikin et al. 2014, Buler et al. 2007). The classification of the 30 meter resolution landcover map was undertaken to provide synoptic landcover data. While, the NLCD dataset is widely available in the US, but the closest dates for which the NLCD data was produced was 2006 and 2011. Producing my own classified landcover map provided me a snapshot of the landscape in the middle year of my study (2009). It also allowed me to focus on landcover classes relevant to my study organisms, birds. For example, the medium-density woodland/shrubland landcover class (which is not a class found in NLCD data) was intended to represent a semi-open habitat type that is important to a number of bird species. I included 7 total landcover classes in the final map (including roads). The overall accuracy of these broad classes was very good (88.1%), and was slightly higher than similar NLCD maps for 2001 and 2006 (Wickham et al. 2010, Wickham et al. 2013). I did not have enough specific ground truth information to distinguish woodland vegetation into evergreen and deciduous classes. As the user's and producer's accuracies indicated, the medium-density woodland/shrubland class had the lowest specific class accuracy (74 and 72%). In general, remotely sensed data does not distinguish individual plant species well, especially when they are similar in appearance (Spanhove et al. 2012). And in my study area, mesquite trees (a common vegetation type in the medium-density woodland/shrubland class) were difficult to distinguish from grassland on the satellite imagery. Distinguishing woodland from medium-density woodland/shrubland was also challenging. For many classification problems in deriving the classified map, I was able to overcome during the refinement process. However, some problems persisted even in the final map. In addition to the afore-mentioned challenges with the medium-density woodland/shrubland class, there were areas where spectral classification of grassland and agriculture were mixed, as well as a few areas with classification errors associated with distinguishing woodland and agriculture pixels. Overall, the map accuracy was high enough to be considered a valid representation of the broad landcover classes in my study area.

Any landcover map has the downfall of being a static representation of the landscape, and this was true of my landcover map. Because of the time-intensive classification process, I could not develop a separate landcover map for each year of the study. So any changes that may have occurred in the landscape over the 3 years of my study were not accounted for in the map. However, though such changes likely occurred in some areas, they were probably not numerous over the entire area.

Data Analysis

Comparison of Analysis Methods using Preliminary Results

Initially, I used preliminary data to compare distance-based (Mantel-based) approaches and raw-data (multiple regression or RDA) approaches to investigate the relationship between bird community composition and niche and neutral variables. I found the raw data approach (multiple regression) to be a more powerful statistic for my data than the distance approach (Mantel-based MRM). In a comparison of analysis techniques using preliminary data, the overall R^2 value for the multiple regression raw data approach was 0.31, while the overall R^2 for the MRM distance approach was 0.002. Though the distance approach is a more intuitive technique with which to address questions about the distance-decay in community similarity hypothesis, the approach did not yield R^2 values high enough to discern important variables in my study. A distance approach is often more useful when a strong environmental gradient is present. I intentionally sampled in a relatively homogeneous area to more effectively address the impact of local neutral and niche processes, and so the raw data approach was much more informative for my study. Likewise, the multivariate raw data approach (RDA) did not yield high R^2 values for my study ($R^2 = 0.088$ in a preliminary analysis). Though RDA-type approaches have the advantage of including all the bird community composition information in the response variable, and they are commonly used in studies investigating the relative importance of niche and neutral processes (Legendre et al. 2009, Peres-Neto and Legendre 2010, Diniz-Filho et al. 2012), RDA lacked the statistical power to be useful for my study. Again, studies that include a strong environmental gradient may have better results with a multivariate analysis (Diniz-Filho et al. 2012). Other bird community assembly studies using multivariate raw data methods have included strong environmental gradients (Zellweger et al. 2017) or found relatively low R^2 values (Henry and Cumming 2016). One bird study (Cintra 2015) did use a univariate analysis (multiple linear models) in relating lake characteristics to waterbird assemblage composition. The univariate approach of multiple regression using spatial eigenvectors was the most useful method of elucidating the relative importance of niche and neutral variables for bird community composition in my study.

Final Analysis Method: Multiple Regression Analysis

Landscape variables. Grassland was, by far, the dominant cover type measured at the medium and large spatial extents, covering about half of the measured land area. The grassland cover type included pasture land. Woodland was the second most common type. This was as expected, as the study area occurs in an area historically dominated by prairies with woodlands throughout. Row crops and shrubland (medium-density woodland shrubland) were also common cover types.

For landscape variables measured at the small spatial extent, savanna grassland was the dominant cover type, followed by grassland, woodland, and cropland. The cover types measured at the small spatial extent and the medium/large spatial extents were slightly different, as they were measured from two different landcover maps. Savanna grassland included open grasslands with some woody species, and there may have been some overlap between the savanna grassland class of small extent and the grassland class of the medium/large extents.

Principal components analysis. The information in the landscape variables measured at each spatial extent was reduced into a smaller number of principal components. The first four PCs were retained for each of the three spatial extents in each of three years. The amount of variance explained by the first four PCs for each spatial extent/year ranged from 70.9-80.5%.

Of the four PCs retained for the analyses, the first and second explained the bulk of the variation in landscape variables represented by the PCA (about 21-38% variation explained by each of the first two PCs). But the third and fourth PCs added anywhere from 7-14% to the explained variation. The amount of variation explained by the PCA was comparable over each year of the study, but it did vary by spatial extent. Consistently, the first PC for the large spatial extent explained more variation than the first PC for the medium extent, and the first PC for the medium extent explained more variation than the first PC for the small extent. This result may reflect the amount of site to site variation among the different spatial extents. The large spatial extent (23.1 km radius) overlapped extensively from site to site, and so much of the variation in landscape features was reflected in each large extent circle. The medium extent (1.8 km radius), though still including a large area around each study site, did not overlap from site to site. This assumed that the variation in landscape features was greater between study sites than within. The small extent (153 m radius) also did not overlap between study sites, and represented such a reduced area around each site that the variation in landscape features was probably very small for each site but much greater between sites. Thus, the PCA was better able to account for the variation in landscape features at the large extent, where each of the variables occur at each site, and at the medium extent, where most of the variables occur at each site.

Principal components analysis: environmental variables represented. For the small scale, variation in only two variables (total length of edge and patch richness) had loadings of 0.75 or greater for any PC (PC1) and only for 2008 (Table 10, Appendix). No other variables had loadings of 0.75 or greater for any other year or PC. Total length of edge and patch richness reflected the diversity of the landscape at the small spatial extent. The other measured variables represented the variation in the specific landcover classes at the small scale, but there were no specific variables that dominated the overall variation in the landscape for 2009 and 2010.

At the medium spatial extent, the first PC represented variation in the woody variables, with variation in woodland (percent cover and edge length) and medium-density woodland/shrubland (edge length) for all years, and percent cover of medium-density woodland/shrubland and Simpson's evenness index for some years. On the opposite end of the first PC, woodland and medium-density woodland/shrubland nearest neighbor distance was important in 2008, and contagion was important in 2009 and 2010. In my study area, woodland and medium-density woodland/shrubland cover types were patchily distributed in the landscape, within a matrix of grassland cover. Thus, when sites have more woodland and medium-density woodland/shrubland cover, they tend to be more diverse and less aggregated (patchy in distribution). The second PC represented variation in cropland variables for all years (percent cover and edge length). Cropland nearest neighbor distance was important on the opposite end of the second PC in 2008. No specific variables were loaded strongly on PCs 3 and 4 except in 2008, when NDVI coefficient of variation (representing variation in growing vegetation) was important on PC4.

At the large spatial extent, variation in the landscape was largely dominated by differences in cropland and medium-density woodland/shrubland vegetation, with the first principal component representing cropland composition variables (percent cover, total edge length, and mean patch area) on one end and medium-density woodland/shrubland composition variables (percent cover and total edge length) on the other (Table 4, Appendix). The configuration variable of the nearest neighbor distance of medium-density woodland/shrubland and the high-contrast edge length between cropland and medium-density woodland/shrubland were also important and loaded most strongly on the same end as the cropland composition variables. In some years, woodland edge length and high contrast edge length between grassland and medium-density woodland/shrubland were also important and loaded on the same end of the first PC as the other woody variables. The second PC represented variation in percent cover of grassland in all years, with the grassland mean patch area and the woodland nearest neighbor distance important depending on the year. On the opposite end of the second PC, the grassland nearest neighbor distance (indicative of fragmented grassland habitat) and Simpson's evenness index (a measure of landscape diversity) were important in two years. Thus, sites with a large amount of grassland were less likely to be fragmented, and sites with less grassland were more likely to be diverse in cover type. Grassland was the dominant (matrix) landcover type in my study area, and so the second PC represents the variation in amount of grassland, but also the fragmentation of the landscape. Because grassland was the dominant cover type in my study area, it did not vary as much in cover as did woodland and cropland. Thus, the variation in woodland and cropland variables, followed secondarily by variation in grassland variables, accounted for most of the variation in landscape variables in my study at the large spatial extent. No specific variables were loaded strongly on PCs 3 and 4.

The variation in the landscape was represented by slightly different variables from the medium extent to the large extent. At the medium extent, landscape variation was dominated by variation in woody variables, and was influenced secondarily by variation in cropland. While at the large extent, landscape variation was dominated by a continuum of cropland and woody variables, and was influenced secondarily by variation in grassland.

Spatial eigenvectors. Spatial eigenvectors served as neutral variables, and were intended to account for spatial patterns in the geographic coordinates. 14 spatial eigenvectors were chosen based on r^2 values when related to the community composition value. Lower number eigenvectors represent broad-scale spatial patterns, while larger number eigenvectors represent fine-scale spatial patterns. The 14 specific eigenvectors chosen for each model differed depending on the guild-level community composition value. A mix of lower-numbered and higher-numbered eigenvectors was used in each guild/year model.

Habitat guilds. Overall adjusted R^2 values for the habitat guild models ranged from 0.13-0.43, with the lowest adjusted R^2 value from the urban guild 2010 model and the highest value from the successional scrubland guild in 2009. More variation in community composition was explained by the successional scrubland guild models for all three years than in any of the other guild models. The urban guild models generally explained less variation in community composition than other guilds (with the exception of the 2009 urban model, which had an adjusted R^2 value greater than the woodland guild from 2010), and in 2008, there were no significant variables in the urban guild model. For the grassland guild models, adjusted R^2 values ranged from 0.27-0.33, and for the woodland guild models, adjusted R2 values ranged from 0.22-0.31. These adjusted R^2 values (and the subsequent values presented for other guilds) are lower than some studies addressing factors relating to bird community composition, but many bird studies investigate community composition in heterogeneous land areas with strong environmental gradients (Mahon et al. 2016, Zellweger et al. 2017). Interestingly, overall adjusted R^2 values decreased from 2008 to 2010 for grassland and woodland guilds, and from 2009 to 2010 for scrubland and urban guilds. This result was surprising because the sample size increased each year from 262 sites in 2008, to 299 in 2009, and finally 323 in 2010. I expected that larger sample sizes would mean a greater ability to account for the variation in bird community composition. However, because my study area lacked a strong environmental gradient, having a greater number of study sites did not improve my ability to account for variation in community composition. Instead, other unmeasured variables, such as interspecific competition, predation threats, or fine-scale vegetation variables, were likely important in explaining the variation in community composition in my study area.

Habitat guilds: niche and neutral variables. Niche theory predicts that the variation in community composition is more related to variation in environmental variables and interspecific interactions than to variation in spatial variables. On the contrary, neutral theory predicts that the variation in community composition is more related to variation in spatial variables than to environmental variables and interspecific interactions. I predicted that both niche and neutral variables would be important in explaining the variation in bird assemblage composition, but that niche variables would explain the most variance. For all the habitat guild models with significant variables (11 models), niche variables were more important than neutral variables in explaining bird community composition (Figure 14). One model (urban guild 2008) had no significant variables. Also, for all the habitat models with significant variables, neutral variables were also significant. This result supports my prediction that niche processes would be most important in bird community assembly, but that neutral processes would also play a role. Henry and Cumming (2016) found a similar result in a study of water birds, though Sattler et al. (2010) found almost no effect from neutral variables on variation in bird community composition in an urban area.

I also investigated the relative importance of each individual variable in the final models. For the 11 habitat models with significant variables, the variable with the greatest amount of partitioned variance was an environmental variable (landscape PCs) for 10 models, and a detection covariate (wind) for one model (Figure 15). For the grassland guild and scrubland guild models in all three years, the variable explaining the most variation in community composition was the first PC measured at the medium spatial extent (representing variation in woody variables). Grassland birds and successional scrubland birds are likely sensitive to the presence and amount of woody vegetation in the landscape. For the woodland guilds, a detection covariate (wind speed) was the variable with the greatest amount of partitioned variation. Wind did seem greater to me during sampling in 2008 compared with 2009 and 2010, and the wind blowing through trees likely impacted my ability to hear woodland birds well at some sites. Therefore, this variable likely contributed to the variation in community composition as measured by my point counts in 2008. In 2009 and 2010 for both the woodland and urban guilds, a PC measured at the small spatial extent explained the greatest amount of variation in community composition. These small extent PCs represented local variation in the landscape, and both woodland habitat and developed habitat were patchily distributed in my study area. In interpret this result as birds in these guilds were likely most sensitive to local landscape features.

Habitat guilds: interspecific interactions. I predicted that variables representing interspecific interactions (nest predator abundance and Brown-headed Cowbird abundance) would be important predictors of assemblage composition, in addition to other environmental niche variables. However, nest predator abundance (including the American Crow and the Blue Jay) was only important in 4 of the 12 habitat models (Figure 16), and Brown-headed Cowbird abundance was not a significant variable for any of the habitat models. Nest predator abundance was consistently important in the woodland guild models for all three years, and was important in the successional scrubland guild model for only 2009. The American Crow is often found in open habitats with scattered trees and forest edges (Verbeek and Caffrey 2002) and the Blue Jay is often found in woodlands and woodland edge habitat (Tarvin and Woolfenden 1999). Consequently, woodland and successional scrubland birds were likely most influenced by the nest predators included in my study.

While Brown-headed Cowbirds are a ubiquitous and generalist brood parasite across North America, they have not been shown to have a significant long-term effect on songbird community composition (De Groot and Smith 2001). It is probable that, while Brown-headed Cowbirds may negatively influence some bird populations, they do not produce significant effects on the overall bird community composition.

The interspecific interactions included in my study were only those I could account for with an avian point count method. Other interspecific interactions were likely important in explaining the variation in bird community composition (Degregorio

2016), but I was logistically limited in measuring further variables. Other avian nest predators, such as raptors, were not well-sampled by my methods. And important nest predators, such as reptiles and mammals, were outside the scope of my study. Likewise, accounting for interspecific competition was not a part of this study.

Habitat guilds: environmental variables. I predicted that environmental variables measured at a large spatial extent would account for a greater amount of the partitioned variance in assemblage composition than would variables measured at medium and small extents. Likewise, I predicted that variables measured at a medium spatial extent would account for a greater amount of the partitioned variance in assemblage composition than would variables measured at a small extent. I also predicted that models containing variables measured at multiple spatial extents would explain a greater amount of variance in assemblage composition than models containing variables measured at a single spatial extent.

Contrary to my predictions, environmental variables measured at a small spatial extent were important in all the habitat models with significant variables (Figure 17). And for urban and woodland habitat guilds, small extent variables accounted for all or most of the variation in community composition explained by environmental variables. For the grassland guilds in 2008 and 2010, and for the successional scrubland guilds in all 3 years, variables measured at a medium extent accounted for most of the variation in community composition explained by environmental variables. Large-extent variables were significant in only 4 models, and they never accounted for the largest amount of partitioned variance. The successional scrubland model from 2009 did have the largest amount of variation explained by environmental variables, and it did include variables measured at all three spatial extents. But only two other models (successional scrubland 2008 and grassland 2009) included variables measured at all three spatial extents, and the variation explained by the environmental variables was comparable to other models that included variables measured by only one or two spatial extents.

This result is likely due to the homogeneity in the landscape of my study area. The site-to-site variation in the landscape at the large spatial extent is not great, as the study sites are situated in a relatively homogeneous land area. Environmental variables measured at the medium spatial extent would account for more variation in the landscape than the large extent variables, and the environmental variables measured at the small spatial extent represented the local variation that was present site to site. Thus, in my study, small-extent environmental variables were more important in explaining community composition than medium and large-extent variables. Small extent variables were particularly important for the woodland and urban guilds, as woodland and urban habitat was more patchily distributed in my study area. For the grassland and successional scrubland guilds, small extent variables were important, but medium-extent variables were also consistently important for models in all three years. Specifically, medium PC1 (representing variation in woody variables) was significant in grassland and successional scrubland guild models for all three years. Again, grassland and successional scrub birds were likely influenced by the amount or configuration of woody cover, either positively or negatively associated with woody variables. In 2009, medium PC2 (representing variation in cropland variables) and in 2010, medium PC3 (not strongly associated with specific landscape variables) were also significant in successional scrub guilds. A similar response to multi-scale variables was shown in boreal birds, where small extent (local) landscape variables were most important in explaining variation in community composition and medium (landscape) and large (regional) extent variables were significant but less important (Mahon et al. 2016).

Habitat guilds: spatial variables. All the habitat guild models with significant variables included spatial eigenvectors as spatial variables. The spatial variables included in the habitat models ranged from numbers 1 to 75, and represented broad-scale (typically induced by environmental variation) to fine-scale (related to dispersal limitation or ecological drift) spatial patterns (Borcard et al. 2011). For a highly vagile bird community, it is also likely that medium-scale spatial variables, in addition to fine-scale variables also reflected neutral processes. Broad-scale spatial variables were significant in 8 of the habitat models (Figure 18). Broad-scale spatial variables were consistently significance in the woodland and successional scrubland guilds for all three years and in grassland guilds two of three years. The broad-scale patterns represented by these spatial variables may indicate the influence of unmeasured environmental variables on community assembly (Borcard et al. 2011). Medium- and fine-scale spatial variables were significant in 10 of the habitat models. These variables likely represented the influence of neutral processes, such as dispersal distance, on community composition. Interestingly, the only spatial variables significant in the urban models and in one grassland model were medium- and fine-scale spatial variables, indicating that, of the variation in community composition explained by spatial variables, neutral processes were likely most important for these guilds. Since grassland is the matrix landcover type in my study area, it is likely that grassland bird composition was influenced, to some extent, by dispersal distance. Likewise, one of the most abundant species represented in the urban guild was the Mourning Dove, which were commonly found in open areas around agricultural areas and grassland. It is likely that the distribution of such a species was influenced to some extent by dispersal distance.

Habitat guilds: detection covariates. Detection covariates, such as wind speed, temperature, and the number of passing cars may have affected either bird behavior or my ability to detect birds. Wind has been shown to affect bird detectability (Poprach et al. 2015), and I observed that increased wind speed decreased my ability to hear bird songs/calls during point counts. I excluded some sites where wind speed exceeded a set threshold (see methods), but there was considerable variation in wind speed within the acceptable limits. Some bird species have been shown to reduce their frequency of vocalizations as temperature increased (McGrann and Furnas 2016), and there was a range of temperatures over the course of my sampling period each day. And the probability of detecting some bird species has been shown to decrease with increasing traffic noise and volume (Parris and Schneider 2009). I certainly observed that the sound of passing cars impeded my ability to hear birds singing/calling at that time.

Detection covariates were found to be significant in 5 of the 12 habitat models (Figure 19). Wind speed was important for woodland and successional scrubland guild models in 2008, and in the successional scrubland model in 2009. Temperature was important in the woodland and urban guilds in 2009. In most cases, the amount of variation explained by these covariates was small, indicating that, while important, other factors were more related to community composition. But in one case (2008 woodland guild), wind speed was the variable that explained the most variation in community composition. Wind was likely a factor in detectability for woodland (2008) and successional scrubland (2008 and 2009) birds. Though I did observe passing cars to diminish my ability to hear bird songs/calls, this effect was brief as the car passed. Because my study sites were situated along local, neighborhood, and rural roads (excluding highways), there were relatively few sites with a large volume of passing cars which explains why passing cars was not a significant variable in any habitat model. I concluded that traffic noise was likely not an important factor in either bird behavior or detectability in my study.

Migratory guilds. Overall adjusted R^2 values for migratory guild models ranged from 0.11 – 0.41 (Figure 19), with highest values in permanent resident models and lowest values in short-distant migrant models. Two neotropical models (2008 and 2010) had no significant variables. Measured variables accounted for more of the variation in permanent residents than in either of the migratory guilds, indicating that the variables included in my models were not the factors most important to migratory community composition. Overall variation explained in the permanent resident guild was similar from year to year, while the amount of variation explained in the short-distance migratory guild decreased each year from 2008 to 2010, similar to the pattern of explained variation in some of the habitat guilds (see above).

Migratory guilds: niche and neutral variables. I predicted that both niche and neutral variables would be important in explaining the variation in bird assemblage composition, but that niche variables would explain the most variance. The results from the migratory guild analyses were not always consistent with this prediction. For 4 of 9 models, niche variables were most important in explaining community composition, while for 3 of 9 models, neutral variables were most important in explaining community composition (Figure 21). For 2 models there were no significant variables in the final model. For each of the models with significant variables, both niche and neutral variables were significant in each model except for one. In the short-distance migrant guild model from 2010, only neutral variables were significant (in addition to one detection covariate). For 4 of the 7 models with significant variables, a niche variable had the greatest amount of partitioned variance, and for 1 model, a neutral variable had the greatest amount of partitioned variance (Figure 22). For 2 of the 7 models, a detection covariate had the greatest amount of partitioned variance. Interestingly, the relative importance of niche and neutral variables is inconsistent between migratory guilds and within guilds across years. For permanent residents, niche variables were most important in 2008 and 2009, though in 2009 the amount of variance explained by niche variables was considerably greater than in 2008. And in 2010, neutral variables were more important than niche variables. The single variable with the greatest amount of partitioned variance differed in all three years, with wind the most important in 2008, a small-extent environmental variable the most important in 2009, and a broad-scale neutral variable the most important in 2010. Short distance migrants exhibited similar inconsistency across years, with niche variables most important in 2008, while neutral variables were more important in 2009 and 2010. The single variable with the greatest amount of partitioned variance also different each year, with a medium-extent environmental variable (representing variation in woody variables) the most important in 2008, a small-extent environmental variable the most important in 2009, and a detection covariate (temperature) the most important in 2010. The neotropical guild had significant variables only in 2009, when niche variables were more important than neutral variables, and a medium-extent environmental variable (representing variation in woody variables) had the greatest amount of partitioned variance.

The inconsistency in results across migratory guilds and years may reflect the variation in niche and neutral processes across bird groups. When bird species are organized based on their migratory habits, which reflect their movements outside of the breeding season, neutral variables tend to become more important, compared to when birds are organized by their habitat preferences. The variation from year to year may reflect differences in the number of sample sites each year. The three models where neutral variables were more important than niche variables were 2009 and 2010 models, when sample sizes were larger. The larger sample sizes may have helped explain the variation in neutral processes in migratory guilds.

Migratory guilds: interspecific interactions. Nest predator abundance was significant in only the permanent resident migratory guild, and only in 2008 and 2009 (Figure 23). Species in the permanent resident guild may have been more sensitive to the presence of American Crows and Blue Jays. I did not find Brown-headed Cowbird abundance as a significant variable in any of the migratory guild models.

Migratory guilds: environmental variables. Similar to the habitat guild models, and contrary to my predictions, environmental variables measured at a small spatial extent were important in the 6 guild models with significant niche variables (Figure 24). For 4 of these 6 models, small extent variables were more important than medium or large extent variables, and in 2 of those models, environmental variables measured at the medium extent were more important than small and large extent variables. While not accounting for the most variation in environmental variables in any model, large extent variables were significant in 5 of the 6 models with significant niche variables.

For 3 of the 6 migratory guild models with significant niche variables, environmental variables measured at all 3 spatial extents were important. However, the models that included variables measured at all three spatial extents did not necessarily explain more of the environmental variation than models with variables measured at two spatial extents. Like the overall niche/neutral results, the results of the specific environmental variables in the migratory guilds were inconsistent within guilds and across years. For permanent residents, small extent variables were significant each year, but the specific small extent variables differed from year to year. Environmental variables measured at the medium spatial extent were important for both 2009 and 2010 (with some variation in specific variables). And large extent variables were important in 2008 and 2010, but the specific large extent variable differed between years. For short-distance migrants, environmental variables measured at the small spatial extent were important in 2008 and 2009. Variation in woody variables measured at the medium spatial extent was important in 2008 only, and environmental variables measured at the large spatial extent were important in 2008 and 2009. For neotropical migrants, only 2009 had a model with significant variables, but for that year, environmental variables measured at all 3 spatial extents were important. Neotropical migrants travel great distances before the breeding season, and consequently the importance of environmental variables measured at all three spatial extents is understandable. Large extent variables were likely important as birds traveled to the breeding grounds, and then medium and small extent variables were important for locating specific nesting sites. In general, the important environmental variables among migratory guilds varied considerably among guilds and across years. This outcome may have resulted from the difference in number and location of sites sampled between years. Also, the bird community differed by a few species from year to year (Table 8), and so changes in the bird community, though slight, may have impacted the significant variables in each model.

Migratory guilds: spatial variables. All of the migratory guild models with significant variables included spatial eigenvectors as spatial variables. The spatial variables included in the habitat models ranged from numbers 1 to 86, and represent broad scale (typically induced by environmental variation) to medium- and fine-scale (related to dispersal limitation or ecological drift) spatial patterns. Broad-scale spatial variables were the most consistent spatial variables in migratory guild models, and were significant in all 7 models with significant variables (Figure 25). The broad-scale patterns represented by these spatial variables may indicate the influence of unmeasured environmental variables on community assembly. Fine-scale and medium-scale spatial variables were present in 5 of the 7 models with significant variables. These variables likely represented the influence of neutral processes, such as dispersal distance, on community composition. Because migrants are moving into and out of the breeding habitat and assembling into communities each year, I expected that migrant guilds might reflect a greater influence of spatial variables, particularly fine-scale and medium-scale variables indicative of neutral processes. However, broad-scale spatial variables were important each year for all migratory guilds, and fine and medium-scale spatial variables were important for permanent residents, in addition to short-distance and neotropical migrants for some years. In 2008, both short-distance migrants and permanent resident models included only broad-scale spatial variables. For the one long-distance migrant model with significant variables (neotropical migrants 2009), niche variables are most important, and one fine-scale spatial variable accounts for only a small amount of the variation in community composition. This result indicates that perhaps long-distance migrants are more influenced by habitat requirements than neutral processes when returning to breeding grounds in the spring. For models where neutral variables were most important (permanent residents 2010, short-distance migrants 2009 and 2010), both broad-scale and medium to fine-scale spatial variables were important. This result may reflect the influence of neutral processes (dispersal, environmental drift) as well as environmentally induced spatial patterns in bird assemblages.

Migratory guilds: detection covariates. Wind speed was a significant detection covariate in 2008 and 2009 for permanent residents (Figure 26). In 2008, this variable was the variable with the most explained variance. This indicates that wind speed was a contributing factor to observed community composition in permanent residents in 2008 and 2009, and may have contributed to the inconsistency in results across years due to the impact of wind speed on detection probability. Temperature was an important variable in the short-distance migratory guild in 2009 and 2010, and in 2010 it was the variable with the most explained variance. This result may also have contributed to the inconsistency in short-distance migrant results across years, as variation in temperature may have affected the behavior of the species included in the short-distance migratory guild.

Trophic guilds. Overall adjusted R^2 values for the trophic guild models ranged from 0.14-0.46 (Figure 27). More variation in community composition was explained by the omnivore guild models in all three years, while the significant variables in the herbivore guild models for two years explained the least amount of variation in community composition among trophic guilds (the herbivore guild in 2009 had no significant variables). For carnivores and omnivores, overall adjusted R^2 values were highest in 2009, and for herbivores adjusted R^2 values were highest in 2008. There was no specific year-to-year trend in the amount of variation explained by trophic guild models, which may reflect the consistency in food resources across the three years. Rainfall was consistent over the three years of my study (it was sandwiched between a very wet year, 2007 and a very dry year, 2011), and so food availability linked to the local climate may have been fairly stable.

Trophic guilds: niche and neutral variables. As predicted, niche variables were more important than neutral variables for carnivore and omnivore guilds for all three years (Figure 28). However, contrary to my prediction, neutral variables were more important than niche variables for the herbivore guild in 2008 and 2010 (there were no significant variables in the herbivore 2009 model). In all trophic models with significant variables, both niche and neutral variables were significant. But the amount of variation in community composition explained by neutral variables for omnivores was very low in all three years. For carnivores, niche variables were more important than neutral variables in all three years, but in 2008 and 2010, both niche and neutral variables contributed substantially to the overall explained variation. In 2009, niche variables explained considerably more of the variation than did neutral variables. The predictions of neutral theory are that neutral processes operate within broad trophic groups (Hubbell 2001), and so a trophic guild-level analysis is particularly suited to a comparison of niche and neutral processes. Carnivores (which consume mostly insects) and omnivores (many of which consume more insects during the breeding season than at other times of the year) may have been particularly sensitive to environmental variables which may be correlated to prey populations. The herbivore guild was relatively small (see Table 9, 3-5 species, depending on the year), and the two most abundant species in that guild (Mourning Dove and Northern Bobwhite) are often found in grassland and agricultural habitats. The grassland cover type (including pastures) represented the matrix land use type in my study area, and cropland was often adjacent to grasslands. Species utilizing these cover types may have been more influenced by dispersal distance (neutral processes) than variation in environmental variables (niche processes) in forming local communities because required habitat variables were readily available throughout the landscape. In a meta-analysis of species sorting (niche assembly) across many organisms, Soininen (2014) found that the degree of species sorting was much higher for omnivores than for herbivores, suggesting that omnivores are more sensitive to environmental variation. Most bird studies investigating the relative importance of niche and neutral variables have found niche variables more important (Sattler et al. 2010, Henry and Cumming 2016). To my knowledge, no other study has found neutral processes to be this important in explaining community assembly for certain bird assemblages.

For 6 of the 8 trophic models with significant variables, a small-extent environmental variable had the greatest amount of partitioned variance (Figure 29). For one model (herbivores 2008), a broad-scale spatial variable (representing environmentally-induced spatial structure) had the greatest amount of partitioned variance, and for another (omnivores 2008), a detection covariate (wind) had the greatest amount of partitioned variance. Interestingly, even for the herbivore 2010 model, in which neutral variables were more important than niche variables, a small-extent environmental variable had the greatest amount of partitioned variance. This result indicates the importance of niche variables even in a community where composition is most influenced by neutral variables.

Trophic guilds: interspecific interactions. Nest predator abundance was significant in 3 of 9 trophic guild models (Figure 30), but it was not the variable with the greatest amount of partitioned variance for any model. Nest predator abundance was significant for carnivores and omnivores in 2009, and for omnivores in 2008. The carnivore and omnivore guilds included several species commonly found in woodland and successional scrubland habitats, and American Crows and Blue Jays are commonly found along woodland edges, as well as open areas with scattered trees and woodland habitats.

Trophic guilds: environmental variables. Similar to the results for the other guild-level analyses, environmental variables measured at the small spatial extent were generally more important in explaining community composition than environmental variables measured at medium and large spatial extents (Figure 31). Small-extent variables were significant in 7 of the 8 models with significant variables, and they were the most important environmental variables in those 7 models. Medium-extent environmental variables were significant in 6 of the 8 models with significant variables, and large-extent environmental variables were significant in only 2 models (herbivores 2008 and omnivores 2010).

For carnivores, small extent variables were the most important environmental variables in all three years, though the specific variables differed from year to year. Medium-extent variables were important for carnivores in 2009 and 2010, but the specific variables differed each year. These results indicate that carnivores were most influenced by variation in local environmental variables, such as amount of vegetation cover types, which may reflect the structure of their insect prey populations.

Interestingly, the important environmental variables for the herbivore guilds with significant variables differed completely from year to year. In 2008, one medium extent variable representing the variation in woody variables and one large extent variable were significant in explaining community composition, while in 2010, only one small extent variable was significant. This difference between years may reflect some differences in the herbivore community between the two years. In 2008, only 3 herbivore species occurred at 3% or greater of study sites (Table 9), whereas in 2010, five species occurred at 3% or greater of study sites.

For omnivores, the specific environmental variables important for community composition were somewhat consistent from year to year. Small extent variables were the most important environmental variables in all three years, though the specific variables differed some. The medium-extent variable representing variation in woody variables was significant in all three years, and the medium-extent variable representing variation in cropland variables, as well as another medium-extent variable were also significant in 2010. Large extent variables were important only in 2010. In general, omnivore community composition was influenced by variation in local environmental variables as well as variation in woody variables measured at the medium spatial extent, with additional medium-extent and large-extent variables important in 2010.

Trophic guilds: spatial variables. All of the trophic guild models with significant variables included spatial eigenvectors as spatial variables. The spatial variables included in the trophic guild models ranged from numbers 1 to 94, and represented broad scale (typically induced by environmental variation) to medium- and fine-scale (related to dispersal limitation or ecological drift) spatial patterns. Broad-scale spatial variables were the most consistent spatial variables in trophic models and were significant in 6 of the 8 models with significant variables (Figure 32). The broad-scale patterns represented by these spatial variables may indicate the influence of unmeasured environmental variables on bird community assembly. For omnivores in all three years (where spatial variables explained relatively very little variation in community composition), the only significant spatial variable was a broad-scale spatial variable. For carnivores, broad-scale spatial variables were significant in 2 of 3 years, and for herbivores, broad-scale spatial variables were significant in 1 of 2 years with significant variables. Medium- and fine-scale spatial variables were important in 5 of 8 trophic guild models. These variables likely represented the influence of neutral processes, such as dispersal distance, on community composition. In herbivore guild models, in which neutral variables were most important, several medium- and fine-scale spatial variables were significant.

Trophic guilds: detection covariates. Wind was a significant detection covariate in 3 of 9 trophic guild models (Figure 33, carnivores 2010, omnivores 2008 and 2009). For the omnivore guild in 2008, wind was the variable with the most explained variance. Wind likely impacted the detection probability of some species in the 2010 carnivore guild and the 2008 and 2009 omnivore guilds. Though the amount of variation explained was low, temperature was a significant variable in 2 of 9 trophic guild models (carnivores 2008 and omnivores 2010).

CHAPTER FIVE

Summary

Overall, I found that niche variables were more important than neutral variables in structuring bird communities in central Texas. However, neutral variables were important for all models. And neutral variables were more important than niche variables for several bird guilds (permanent residents and short-distance migrants in some years, and herbivores in both years with significant variables). To my knowledge, no other bird study has found neutral processes to be dominant in any bird assemblage. While bird community composition is likely typically structured by niche variables (environmental and interspecific interactions), neutral variables (demographic stochasticity) may play an important role in community composition for many bird assemblages. And neutral processes may be most important in structuring some bird assemblages, especially in homogeneous land areas without strong environmental gradients.

Understanding the factors that affect community assembly have important implications for conservation biology. In recent years, two main theories have dominated the conversation about community assembly processes. Niche theory is the long-held belief that habitat characteristics and interspecific interactions predict community composition, while neutral theory is a more recent idea that suggests demographic stochasticity is responsible for patterns in community composition. Since the introduction of neutral theory in 2001 (Hubbell), the debate over whether neutral or niche processes are most important has shifted to an understanding that both processes may be at work in many communities, and that niche and neutral processes express extremes of a continuum of community assembly drivers (Gravel et al. 2006). More recent still is the perspective that the community assembly argument has largely ignored the role of environmental stochasticity on community assembly (Kalyuzhny et al. 2014). Our understanding of community dynamics may well benefit from including environmental stochasticity on a temporal scale. However, practically generating meaningful environmental data may be a challenge. Also, birds may respond to landscape variables differently depending on the season (Zuckerberg et al. 2016). So factors affecting bird community composition in the breeding season may differ during migration or winter seasons. Understanding factors affecting bird community composition is a challenging problem, but one that is important as birds face a continually changing environment.

APPENDIX

APPENDIX

Additional Tables

Table A.1. Bird species diet type and body mass information used to calculate the medium and large spatial extent in which environmental variables were measured. Diet type and body mass were incorporated into allometric equations estimating median and maximum dispersal distances (Sutherland et al. 2000). The mean median and mean maximum dispersal distances were used as the radii for the medium and large spatial extents, respectively.

species	diet type	Source of diet info	body mass (g)	median disp dist (km)	maximum disp dist (km)
Bewick's Wren	carnivore	BNA account: Kennedy, E. Dale and Douglas W. White 2013	9.9	2.08	13.10
Carolina Chickadee	omnivore	BNA account: Mostrum, Alison M., Robert L. Curry and Bernard Lohr 2002	10	0.92	19.10
Carolina Wren	carnivore	BNA account: Haggerty, Thomas M. and Eugene S. Morton 2014 (revisors: Haggerty, Thomas M. and Eugene S. Morton)	18.6	3.08	19.01
Dickcissel	omnivore	BNA account: Temple, Stanley A. 2002	26.3	1.09	21.87
Eastern Bluebird	omnivore	BNA account: Gowaty, Patricia A. and Jonathan H. Plissner, 2015 (revisors: Gowaty, Patricia A.)	27.5	1.10	22.01
Meadowlarks	omnivore		96.7	1.38	26.25
Eastern		BNA account: Lanyon, Wesley E. 2012 (revisors: Jaster, Levi A. and William E. Jensen)			
Western		BNA account: Lanyon, Wesley E. 2008 (revisor: Davis, Stephen K.)			

Table A.1 Continued.

species	diet type	Source of diet info	body mass (g)	median disp dist (km)	maximum disp dist (km)
Eastern Phoebe	omnivore	BNA account: Weeks Jr., Harmon P. 2011 (revisor: Weeks Jr., Harmon P.)	19.7	1.04	21.01
House Sparrow	herbivore	BNA account: Lowther, Peter E. and Calvin L. Cink, 2006 (revisor: Lowther, Peter E.)	26	1.09	21.84
Lark Sparrow	omnivore	BNA account: Martin, John W. and Jimmie R. Parrish, 2000	29	1.11	22.17
Mourning Dove	herbivore	BNA account: Mirarchi, R. E. and T. S. Baskett 2008 (revisors: Otis, David L., John H. Schulz and David Miller)	119	1.43	27.02
Northern Cardinal	herbivore	BNA account: Brennan, Leonard A. 2014 (revisors: Brennan, Leonard A., Fidel Hernandez and Damon Williford)	172	1.53	28.45
Northern Mockingbird	omnivore	BNA account: Halkin, Sylvia L. and Susan U. Linville 1999	42.7	1.19	23.41
Painted Bunting	omnivore	BNA account: Derrickson, K. C. and R. Breitwisch 2011 (revisors: Farnsworth, George, Gustavo Adolfo Londono and Judit Ungvari Martin)	48.5	1.22	23.83
Red-bellied Woodpecker	omnivore	BNA account: Lowther, Peter E., Scott M. Lanyon and Christopher W. Thompson 2015 (revisor: Lowther, Peter E.)	15.6	0.99	20.33
Red-winged Blackbird	omnivore	BNA account: Shackelford, Clifford E., Raymond E. Brown and Richard N. Conner 2000	69.6	1.30	25.06
Scissor-tailed Flycatcher	omnivore	BNA account: Yasukawa, Ken and William A. Searcy 1995	52.4	1.24	24.09
Tufted Titmouse	carnivore	BNA account: Regosin, Jonathan V. 2013	39.3	4.89	29.56
White-eyed Vireo	omnivore	BNA account: Grubb Jr., T. C. and V. V. Pravosudov 2015 (revisor: Ritchison, Gary)	21.6	1.05	21.28

Table A.1 Continued.

species	diet type	Source of diet info	body mass (g)	median disp dist (km)	maximum disp dist (km)
	omnivore	BNA account: Hopp, Steven L., Alice Kirby	11.4	0.94	19.46
Yellow-billed Cuckoo		and Carol A. Boone 1995			
	carnivore	BNA account: Hughes, Janice M. 2015 (revisor: Hughes, Janice M.)	64	6.62	39.41
Downy Woodpecker	omnivore	BNA account: Jackson, Jerome A. and Henri R. Ouellet 2002	25.3	1.08	21.75
Eurasian Collared Dove	herbivore	BNA account: Romagosa, Christina Margarita 2012	149	1.49	27.88
Purple Martin	carnivore	BNA account: Brown, Charles R. and Scott Tarof 2013	53.8	5.95	35.57
Grackles	omnivore		137.6	1.47	27.57
Common		BNA account: Peer, Brian D. and Eric K. Bollinger 1997			
Great-tailed		Johnson, Kristine and Brian D. Peer 2001			
Bell's Vireo	carnivore	BNA account: Brown, Bryan T. 2010	8.5	1.89	11.98
		(revisors: Kus, Barbara, Steven L. Hopp and R. Roy Johnson)			
Blue Grosbeak	omnivore	Ehrlich et al. 1988	27.4	1.10	22.00
Blue-gray Gnatcather	carnivore	BNA account: Ellison, Walter G. 2012 (revisor: Kershner, Eric L.)	5.8	1.49	9.56
Cassin's Sparrow	omnivore	BNA account: Dunning Jr., John B., Richard K. Bowers Jr.,	18.9	1.03	20.88
		Sherman J. Suter and Carl E. Bock 1999			
Chimney Swift	carnivore	Ehrlich et al. 1988	23.6	3.57	21.88
Swallows	carnivore		18.7	3.09	19.07
cliff		BNA account: Brown, Charles R. and Mary B. Brown 2017			
		(revisors: Brown, Charles R., Mary B. Brown, Peter Pyle			
		and Michael A. Patten)			
barn		BNA account: Brown, Charles R. and Mary B. Brown 1999			

Table A.1 Continued.

species	diet type	Source of diet info	body mass (g)	median disp dist (km)	maximum disp dist (km)
northern rough-winged		BNA account: De Jong, Michael J. 1996			
cave		BNA account: West, Steve 2011 (revisor: Strickler, Stephanie)			
Eastern Kingbird	omnivore	Ehrlich et al. 1988	39.9	1.18	23.19
Eastern Wood Pewee	carnivore	BNA account: McCarty, John P. 1996	13.9	2.57	16.01
European Starling	omnivore	BNA account: Cabe, Paul R. 1993	74.1	1.31	25.29
Field Sparrow	omnivore	BNA account: Carey, Michael, D. E. Burhans and D. A. Nelson 2008	12.5	0.95	19.71
Great-crested Flycatcher	carnivore	BNA account: Lanyon, Wesley E. 2014 (revisor: Miller, Karl E.)	32.1	4.32	26.23
Grasshopper Sparrow	omnivore	BNA account: Vickery, Peter D. 1996	17.6	1.01	20.68
Hummingbirds	omnivore		3.3	0.75	16.36
ruby-throated		BNA account: Robinson, T. R., R. R. Sargent and M. B. Sargent 2013 (revisor: Weidensaul, Scott)			
black-chinned		BNA account: Baltosser, William H. and Stephen M. Russell 2000			
Indigo Bunting	omnivore	BNA account: Payne, Robert B. 2006 (revisor: Payne, Robert B.)	14.7	0.98	20.16
Inca Dove	herbivore	BNA account: Mueller, Allan J. 2004 (revisor: Mueller, Allan J.)	47.5	1.21	23.76
Orchard Oriole	omnivore	Ehrlich et al. 1988	19.5	1.03	20.98
Red-eyed Vireo	omnivore	BNA account: Cimprich, David A., Frank R. Moore and Michael P. Guilfoyle 2000	16.2	1.00	20.44
Summer Tanager	omnivore	Ehrlich et al. 1988	29.2	1.11	22.19

Wild Turkey	herbivore/ omnivore	BNA account: Eaton, Stephen W. 2014 (revisors: McRoberts, Jon T. and Mark C. Wallace)	6050	2.90	46.83
White-winged Dove	herbivore	BNA account:Schwertner, T. W., H. A. Mathewson, J. A. Roberson and G. L. Waggerman 2002	153	1.50	27.99
			mean	1.8 km	23.1 km

Table A.2. Bird species density information used to calculate the small spatial extent in which environmental variables were measured. Density information was used to estimate the geographic area for each breeding pair. The mean radius of the circular area was used as the radius for the small spatial extent.

Species	Birds of North America Species Account citation	Location	Density	Area/pair (m^2)	Radius (m)	Midpoint
Bewick's Wren			no usable info			
Carolina Chickadee	Mostrum, Alison M., Robert L. Curry and Bernard Lohr 2002	WV, MA	9.2 pairs/40 ha	43478.26	117.64	
		Gr Smoky Mts	1 pair/40 ha	400000.00	356.82	
			3.7 pairs/40 ha	108108.11	185.50	
			6.7 pairs/40 ha	59701.49	137.85	237.23
Carolina Wren	Haggerty, Thomas M. and Eugene S. Morton 2014 (revisors: Haggerty, Thomas M. and Eugene S. Morton)	AR	35 males/40 ha	11428.57	60.31	
			18 males/40 ha	22222.22	84.10	
		AL	32 pairs/40 ha	12500.00	63.08	72.21
Dickcissel	Temple, Stanley A. 2002	KS	70 nests/40 ha	5714.29	42.65	
		IA	110 nests/40 ha	3636.36	34.02	
		IL	67 nests/40 ha	5970.15	43.59	38.81
Eastern Bluebird			no usable info			

Table A.2 Continued.

Species	Birds of North America Species Account citation	Location	Density	Area/pair (m^2)	Radius (m)	Midpoint
Meadowlarks						
Eastern			no usable info			
Western			no usable info			
Eastern Phoebe			no usable info			
House Sparrow			no usable info			
Lark Sparrow	Martin, John W. and	MT	18 pairs/40 ha	22222.22	84.10	
	Jimmie R. Parrish, 2000		40 pairs/40 ha	10000.00	56.42	
			5 pairs/40 ha	80000.00	159.58	
		ND	(1.42 pairs/mi2, from pub)	1823943.66	761.96	409.19
Mourning Dove			no usable info			
Northern Bobwhite			no usable info			
Northern Cardinal	Halkin, Sylvia L. and	TN	0.7 males/ha	14285.71	67.43	
	Susan U. Linville 1999	Ontario	0.01 males/ha	1000000.00	564.19	315.81
Northern Mockingbird			no usable info			
Painted Bunting	Lowther, Peter E., Scott M. Lanyon and	AR	7.5 males/100 ha	133333.33	206.01	
	Christopher W. Thompson 2015	GA	51 males/100 ha	19607.84	79.00	
	(revisor: Lowther, Peter E.)	GA	9.4-21.1 males/100 ha	65573.77	144.47	
		BBS data	0 - 22.5 pairs/100 ha	88888.89	168.21	142.51
Red-bellied Woodpecker			no usable info			
Red-winged Blackbird			no usable info			

Table A.2 Continued.

Species	Birds of North America Species Account citation	Location	Density	Area/pair (m^2)	Radius (m)	Midpoint
Scissor-tailed Flycatcher	Regosin, Jonathan V. 2013	TX	1.6 - 3.3 pairs/10 ha	40816.33	113.98	
		OK	first year: 0.5, 0.7 pairs/10 ha	200000.00	252.31	
			next year: 0.5, 1.1 pairs/10 ha	111111.11	188.06	
		OK	0.5 pairs/10 ha	200000.00	252.31	183.15
Tufted Titmouse			no usable info			
White-eyed Vireo			no usable info			
Yellow-billed Cuckoo	Hughes, Janice M. 2015	IN	2 pairs/3.8 ha	19000.00	77.77	
	(revisor: Hughes, Janice M.)	NM	5-7 pairs/40 ha	66666.67	145.67	
			8-15 pairs/40 ha	34782.61	105.22	
			1-9 pairs/40 ha	80000.00	159.58	
			3.5-9.5 pairs/40 ha	61538.46	139.96	
		AZ	8.2 pairs/40 ha	48780.49	124.61	
			19.8 pairs/40 ha	20202.02	80.19	
			26.5 pairs/40 ha	15094.34	69.32	
		TX	6-10 males/40 ha	50000.00	126.16	114.45
Downy Woodpecker			no usable info			
Eurasian Collared-Dove			no usable info			
Purple Martin			no usable info			
Grackles						
Common			no usable info			

Table A.2 Continued.

Species	Birds of North America Species Account citation	Location	Density	Area/pair (m^2)	Radius (m)	Midpoint
Great-tailed	Johnson, Kristine and Brian D. Peer 2001	TX	16.3 nests/ha	613.50	13.97	13.97
Bell's Vireo			no usable info			
Blue Grosbeak	Ingold, James L. 2011	FL	30 breeding males/km2	33333.33	103.01	
	(revisor: Lowther Peter E.)	TX	31 breeding males/km2	32258.06	101.33	102.17
Blue-gray Gnatcatcher	Ellison, Walter G. 2012	SC	331 territorial males/km2	3021.15	31.01	
	(revisor: Kershner, Eric L.)	AR	289 territorial males/km2	3460.21	33.19	
		CA	71 territorial males/km2	14084.51	66.96	
		UT	45 territorial males/km2	22222.22	84.10	
		CA	0.15-0.19 territories/ha	58823.53	136.84	83.93
Cassin's Sparrow	Dunning Jr., John B.,	TX	1.7 nests/ha (mean)	5882.35	43.27	
	Richard K. Bowers Jr., Sherman J. Suter	TX	11 pairs/40.4 ha	36727.27	108.12	
	and Carl E. Bock 1999	TX	1 pair/8 ha	80000.00	159.58	101.43
Chimney Swift	Cink, Calvin L. and	KS	14 pairs (chimneys)/40 ha	28571.43	95.37	
	Charles T. Collins 2014	VA	2 pairs (territories)/40 ha	200000.00	252.31	
	(revisors: Steeves, Tanner K.,		1 pairs (territories)/40 ha	400000.00	356.82	
	Shannon B. Kearney-McGee	Southeast	1.3 pairs/40 ha	307692.31	312.96	
	and Margaret A. Rubega)		2.6 pairs/40 ha	153846.15	221.29	
			14 pairs/40 ha	28571.43	95.37	226.10

Table A.2 Continued

Species	Birds of North America Species Account citation	Location	Density	Area/pair (m^2)	Radius (m)	Midpoint
Swallows						
Cliff			no usable info			
Barn			no usable info			
Northern Rough-winged			no usable info			
Cave			no usable info			
Eastern Kingbird	Murphy, Michael T. 1996	AR	6 territorial males in 40.5 ha	67500.00	146.58	146.58
Eastern Wood-Pewee	McCarty, John P. 1996	MI	0.07 - 0.12 pairs/ha	105263.16	183.05	
			0.35 - 0.40 pairs/ha	26666.67	92.13	
		Ontario	0.1 males/ha	100000.00	178.41	
		WI	0-0.25 pairs/ha	80000.00	159.58	
		IA	0.4 pairs/ha	25000.00	89.21	
		IL	3-10 pairs/22 ha	33846.15	103.80	
		IL	0.61 pairs/ha	16393.44	72.24	
			0.42 pairs/ha	23809.52	87.06	
			0.39 pairs/ha	25641.03	90.34	
		not listed	0.06-0.53 pairs/ha	33898.31	103.88	
		OK	0.14 pairs/ha	71428.57	150.79	
		GA	0.25 pairs/ha	40000.00	112.84	
			0.02 pairs/ha	500000.00	398.94	
			0.1 pairs/ha	100000.00	178.41	
		SC	0.62 males/ha	16129.03	71.65	

Table A.2 Continued.

Species	Birds of North America Species Account citation	Location	Density	Area/pair (m^2)	Radius (m)	Midpoint
		AR	5.2-14.9 pairs/40 ha	39801.00	112.56	235.30
European Starling			no usable info			
Field Sparrow	Carey, Michael, D. E. Burhans	NC	23 males/5.95 ha	2586.96	28.70	
	and D. A. Nelson 2008		14 males/10.12 ha	7228.57	47.97	
		MD	17 males/100 ha	58823.53	136.84	
			195 males/100 ha	5128.21	40.40	
			197 males/100 ha	5076.14	40.20	
		MI	22-49 males/40.5 ha	11408.45	60.26	82.77
Great Crested Flycatcher			no usable info			
Grasshopper Sparrow	Vickery, Peter D. 1996	ND	0.24-0.25 territories/ha	40816.33	113.98	
		WI	0.75 territories/ha	13333.33	65.15	89.57
Hummingbirds						
Ruby-throated			no usable info			
Black-chinned	Baltosser, William H.	AZ	0.0 pairs/40 ha	0.00	0.00	
	and Stephen M. Russell 2000		8.2 pairs/40 ha	48780.49	124.61	
			29.7 pairs/40 ha	13468.01	65.48	
			39.7 pairs/40 ha	10075.57	56.63	
			9.9 pairs/40 ha	40404.04	113.41	
			25.4 pairs/40 ha	15748.03	70.80	
			59.4 pairs/40 ha	6734.01	46.30	
		not listed	4 pairs/40 ha	100000.00	178.41	
			40 pairs/40 ha	10000.00	56.42	

Table A.2 Continued.

Species	Birds of North America Species Account citation	Location	Density	Area/pair (m^2)	Radius (m)	Midpoint
		Grand Canyon	40-140 nests/40 ha	4444.44	37.61	
		AZ, NM	14 nests/40 ha	28571.43	95.37	
			128 nests/40 ha	3125.00	31.54	
			18 nests/40 ha	22222.22	84.10	89.21
Indigo Bunting	Payne, Robert B. 2006	North America	35 pairs/100 ha	28571.43	95.37	
	(revisor: Payne, Robert B.)	MO	18 pairs/100 ha	55555.56	132.98	
		MI	35 pairs/100 ha	28571.43	95.37	
			15 pairs/100 ha	66666.67	145.67	
		Niles (MI, IN)	6.7 pairs/km2	149253.73	217.97	
		George Res (MI)	2.89 pairs/km2	346020.76	331.88	213.63
Inca Dove			no usable info			
Orchard Oriole	Scharf, William C. and Josef Kren 2010	OK	13 nests/45.4 ha	34923.08	105.43	
	(revisor: Scharf, William C.)		1 nest/45.4 ha	454000.00	380.15	
		WV	37 males/100 ha	27027.03	92.75	
			25 males/100 ha	40000.00	112.84	236.45
Red-eyed Vireo	Cimprich, David A., Frank R. Moore	not listed	0.02 pairs/ha	500000.00	398.94	
	and Michael P. Guilfoyle 2000	IL	0.18-0.62 pairs/ha	25000.00	89.21	
			0.17-0.59 pairs/ha	26315.79	91.52	
		NH	1.6 pairs/ha	6250.00	44.60	
		se U.S.	1.5 pairs/ha	6666.67	46.07	
		Quebec	1.2 pairs/ha	8333.33	51.50	

Table A.2 Continued.

Species	Birds of North America Species Account citation	Location	Density	Area/pair (m^2)	Radius (m)	Midpoint
		IL	1.0 pairs/ha	10000.00	56.42	
		AR	0.1 territorial males/ha	100000.00	178.41	
			1.2 territorial males/ha	8333.33	51.50	221.77
Summer Tanager			no usable info			
Wild Turkey			no usable info			
White-winged Dove	Schwertner, T. W., H. A. Mathewson,	Mexico	141 nests/0.1 ha belt	7.09	1.50	
	J. A. Roberson and	TX	10-25 nests/ha	571.43	13.49	
	G. L. Waggerman 2002		75-185 nests/ha	76.92	4.95	7.50
					mean:	153 m

Table A.3. Significant variables for each final model based on guild and year. Variables for each model are listed in order from largest to smallest partitioned variance. Guilds are grouped by habitat (a.), migratory behavior (b.) and trophic category (c.).

a.

	Grassland			Woodland			Scrubland			Urban	
2008	2009	2010	2008	2009	2010	2008	2009	2010	2008	2009	2010
medPC1	medPC1	medPC1	wind	smPC3	smPC1	medPC1	medPC1	medPC1	no	smPC3	smPC1
sp2	smPC4	smPC1	smPC3	smPC1	smPC3	wind	smPC3	wind	significant	smPC4	smPC3
smPC3	smPC3	smPC3	sp12	medPC3	pred	sp1	sp1	smPC3	variables	temp	sp43
sp40	smPC1	sp22	sp6	medPC2	lgPC1	smPC3	lgPC4	medPC3		sp33	sp24
sp1	sp32	sp10	pred	pred	sp1	smPC4	pred	smPC1		sp22	sp94
smPC4	lgPC4	sp1		sp1	lgPC3	lgPC2	sp3	sp1		sp61	

Table A.3 Continued.

Grassland			Woodland			Scrubland			Urban		
2008	2009	2010	2008	2009	2010	2008	2009	2010	2008	2009	2010
sp49				sp30	sp75		medPC2	sp12			
				temp			sp48	sp8			

b.

Short-distance migrants			Permanent residents			Neotropical migrants		
2008	2009	2010	2008	2009	2010	2008	2009	2010
medPC1	smPC4	temp	wind	smPC3	sp1	no significant variables	medPC1	no significant variables
lgPC4	sp6	sp41	smPC3	pred	medPC3		smPC3	
sp4	sp30	sp1	sp1	smPC1	smPC3		medPC2	
smPC4	lgPC4	sp43	sp6	smPC4	sp32		lgPC4	
smPC3	temp		pred	sp1	medPC1		sp1	
sp1	sp32		smPC4	wind	smPC1		sp37	
sp3	sp2		lgPC3	medPC3	sp12		sp3	
				sp18	sp31			
					sp8			
					sp28			
					sp86			
					lgPC1			

Table A.3 Continued.

c.

Carnivores			Herbivores			Omnivores		
2008	2009	2010	2008	2009	2010	2008	2009	2010
smPC2	smPC3	smPC3	sp4	no	smPC1	wind	smPC3	smPC3
smPC3	smPC2	sp1	lgPC4	significant	sp43	smPC3	pred	medPC1
sp4	smPC1	smPC1	sp19	variables	temp	medPC1	wind	medPC3
sp23	pred	medPC3	sp18		sp29	smPC4	medPC1	smPC1
sp12	smPC4	sp22	sp54		sp94	smPC1	smPC4	sp1
temp	sp64	sp12	medPC1		sp13	sp1	smPC1	lgPC2
sp44	medPC4	wind	sp5			pred	sp1	lgPC4
	medPC2							medPC2

Table A.4. Principal Component loadings for the landscape variables measured in all three years (2008 – a, b, c; 2009 – d, e, f; 2010 – g, h, i). Small extent variables were measured from the 10 m resolution classified landcover map. Medium and large extent variables were measured from the 30 m resolution classified landcover map.

a.

Small Scale 2008	Principal Component Loadings			
Variable	PC1	PC2	PC3	PC4
% cover agriculture	0.092	0.62	0.431	-0.404
patch density agriculture	0.182	0.685	0.392	-0.309
% cover forest	0.213	-0.424	-0.602	-0.471
patch density forest	0.513	-0.367	-0.414	-0.172
% cover grassland	-0.062	0.696	-0.44	0.393
patch density grassland	0.371	0.563	-0.139	0.175
% cover savanna grassland	-0.286	-0.641	0.558	0.164
patch density savanna grassland	0.423	-0.523	0.361	-0.078
% cover urban	0.645	-0.117	0.123	0.457
patch density urban	0.693	-0.113	0.082	0.348
total edge length	0.866	0.06	0.014	-0.194
patch richness	0.867	0.083	0.131	-0.054

b.

Medium Scale 2008	Principal Component Loadings			
variable	PC1	PC2	PC3	PC4
% cover agriculture	0.535	0.785	0.11	0.123
% cover development	-0.102	0.045	0.241	-0.218
% cover grassland	0.439	-0.654	0.016	0.368
% cover shrubland	-0.793	-0.28	0.496	0.022
% cover water	-0.215	0.04	0.087	-0.475
% cover woodland	-0.911	0.092	-0.341	-0.01
agriculture total edge length	0.434	0.763	0.29	0.231
agriculture mean patch area	0.475	0.689	-0.065	0.032
agriculture nearest neighbor	-0.396	-0.769	-0.2	-0.111
grassland total edge length	-0.212	0.32	0.521	0.43
grassland mean patch area	0.535	-0.607	0.065	0.273
shrubland total edge length	-0.897	-0.2	0.338	0.081
shrubland mean patch area	-0.345	-0.332	0.641	-0.132
shrubland nearest neighbor	0.754	0.225	-0.453	0.007

Table A.4 Continued.

Medium Scale 2008	Principal Component Loadings			
woodland total edge length	-0.926	0.131	-0.224	0.116
woodland mean patch area	-0.735	0.152	-0.443	-0.113
woodland nearest neighbor	0.783	-0.165	0.273	-0.024
contagion	0.716	-0.555	-0.264	0.102
Simpson's evenness index	-0.663	0.6	0.137	-0.282
grassland, woodland edge length	-0.754	0.1	-0.441	0.248
agriculture, woodland edge length	-0.297	0.749	-0.231	0.304
grassland, shrubland edge length	-0.734	-0.358	0.44	0.225
agriculture, shrubland edge length	-0.05	0.672	0.499	0.206
mean NDVI	-0.702	0.119	-0.437	0.365
NDVI coefficient of variation	0.059	0.312	0.03	-0.752

c.

Large Scale 2008	Principal Component Loadings			
variable	PC1	PC2	PC3	PC4
% cover agriculture	0.924	-0.043	-0.104	-0.125
% cover development	0.054	-0.195	-0.58	-0.052
% cover grassland	-0.222	0.905	-0.023	-0.157
% cover shrubland	-0.888	-0.077	-0.37	0.161
% cover water	0.246	-0.292	-0.25	0.55
% cover woodland	-0.567	-0.685	0.386	-0.072
agriculture total edge length	0.935	-0.061	-0.16	-0.137
agriculture mean patch area	0.856	-0.091	-0.072	0.077
grassland total edge length	0.125	0.162	-0.512	-0.737
grassland nearest neighbor	-0.249	-0.788	0.339	0.206
shrubland total edge length	-0.907	-0.198	-0.262	-0.01
shrubland mean patch area	-0.689	0.232	-0.471	0.335
shrubland nearest neighbor	0.803	0.063	0.449	-0.261
woodland total edge length	-0.733	-0.549	0.046	-0.315
woodland mean patch area	-0.016	-0.642	0.571	0.223
contagion	-0.215	0.687	0.628	0.028
Simpson's evenness index	0.288	-0.846	-0.335	0.184
agriculture, woodland edge length	0.564	-0.486	-0.19	-0.334
grassland, shrubland edge length	-0.857	0.095	-0.344	-0.132
agriculture, shrubland edge length	0.765	-0.374	-0.366	-0.003

Table A.4 Continued.

Large Scale 2008	Principal Component Loadings			
grassland, woodland edge length	-0.437	-0.31	0.311	-0.676
mean NDVI	-0.365	-0.474	0.007	-0.375
NDVI coefficient of variation	0.203	0.129	0.075	0.278

d.

Small Scale 2009	Principal Component Loadings			
Variable	PC1	PC2	PC3	PC4
% cover agriculture	0.446	0.402	-0.514	-0.455
patch density agriculture	0.42	0.521	-0.47	-0.192
% cover forest	-0.492	-0.14	0.506	-0.623
patch density forest	-0.654	0.12	0.334	-0.006
% cover grassland	0.517	0.456	0.504	0.362
patch density grassland	0.193	0.651	0.207	0.273
% cover savanna grassland	-0.276	-0.653	-0.489	0.443
patch density savanna grassland	-0.653	-0.156	-0.272	-0.032
% cover urban	-0.663	0.504	-0.13	0.084
patch density urban	-0.662	0.508	-0.162	0.115
patch richness	-0.57	0.634	-0.152	0.059

e.

Medium Scale 2009	Principal Component Loadings			
variable	PC1	PC2	PC3	PC4
% cover agriculture	0.446	-0.812	0.151	-0.142
% cover development	-0.17	-0.09	0.279	0.633
% cover grassland	0.599	0.59	0.004	-0.064
% cover shrubland	-0.723	0.484	0.432	-0.046
% cover water	-0.229	-0.073	0.014	0.536
% cover woodland	-0.871	0.016	-0.405	-0.017
agriculture total edge length	0.354	-0.817	0.306	-0.168
grassland total edge length	-0.172	-0.346	0.637	-0.115
grassland mean patch area	0.646	0.556	0.037	-0.044
shrubland total edge length	-0.83	0.39	0.318	-0.078
shrubland mean patch area	-0.378	0.508	0.513	-0.008
woodland total edge length	-0.897	-0.005	-0.234	-0.1
woodland mean patch area	-0.701	-0.069	-0.572	0.012

Table A.4 Continued.

Medium Scale 2009	Principal Component Loadings			
contagion	0.795	0.433	-0.265	-0.182
Simpson's evenness index	-0.801	-0.47	0.108	0.17
agriculture, woodland edge length	-0.326	-0.737	-0.191	-0.349
grassland, shrubland edge length	-0.6	0.525	0.471	-0.15
agriculture, shrubland edge length	-0.097	-0.629	0.493	-0.326
mean NDVI	-0.713	-0.024	-0.474	-0.277
NDVI coefficient of variation	0.09	-0.561	-0.08	0.549

f.

Large Scale 2009	Principal Component Loadings			
variable	PC1	PC2	PC3	PC4
% cover agriculture	-0.937	0.179	<.001	0.087
% cover development	-0.105	0.162	-0.689	0.164
% cover grassland	0.09	-0.862	0.09	0.273
% cover shrubland	0.861	-0.137	-0.403	-0.063
% cover water	-0.14	0.172	-0.476	-0.523
% cover woodland	0.73	0.597	0.241	-0.068
agriculture total edge length	-0.937	0.186	-0.075	0.109
agriculture mean patch area	-0.851	0.2	0.018	-0.1
grassland total edge length	-0.348	-0.04	-0.352	0.768
grassland mean patch area	0.047	-0.879	0.092	0.086
shrubland total edge length	0.902	0.011	-0.292	0.06
shrubland mean patch area	0.627	-0.431	-0.493	-0.155
shrubland nearest neighbor	-0.783	0.162	0.472	0.125
woodland total edge length	0.814	0.484	-0.059	0.217
woodland mean patch area	0.215	0.628	0.436	-0.411
woodland nearest neighbor	-0.526	-0.778	-0.066	0.139
contagion	0.176	-0.636	0.717	-0.058
grassland, woodland edge length	0.516	0.44	0.274	0.567
agriculure, woodland edge length	-0.542	0.596	-0.094	0.208
agriculture, shrubland edge length	-0.773	0.378	-0.353	-0.021
mean NDVI	0.52	0.483	0.173	0.284
NDVI coefficient of variation	-0.344	-0.109	-0.068	-0.517

Table A.4 Continued.

g.

Small Scale 2010	Principal Component Loadings			
variable	PC1	PC2	PC3	PC4
% cover agriculture	0.329	0.48	-0.521	-0.345
patch density agriculture	0.306	0.62	-0.455	-0.079
% cover forest	-0.497	-0.228	0.493	-0.304
patch density forest	-0.71	0.037	0.326	0.082
% cover grassland	0.449	0.542	0.495	0.211
patch density grassland	0.129	0.695	0.212	0.414
% cover savanna grassland	-0.118	-0.683	-0.5	0.346
patch density savanna grassland	-0.616	-0.253	-0.284	0.335
% cover urban	-0.606	0.202	-0.024	-0.439
patch density urban	-0.663	0.267	-0.131	-0.293
total edge length	-0.748	0.459	-0.099	0.243
patch richness	-0.645	0.561	-0.198	0.208

h.

Medium Scale 2010	Principal Component Loadings			
variable	PC1	PC2	PC3	PC4
% cover agriculture	0.448	-0.811	0.151	-0.142
% cover development	-0.169	-0.089	0.282	0.631
% cover grassland	0.597	0.591	0.004	-0.066
% cover shrubland	-0.723	0.486	0.428	-0.048
% cover water	-0.23	-0.075	0.025	0.532
% cover woodland	-0.874	0.012	-0.4	-0.016
agriculture total edge length	0.356	-0.815	0.308	-0.172
grassland total edge length	-0.17	-0.344	0.639	-0.121
grassland mean patch area	0.645	0.557	0.038	-0.047
shrubland total edge length	-0.83	0.391	0.315	-0.079
shrubland mean patch area	-0.377	0.51	0.51	-0.01
woodland total edge length	-0.898	-0.007	-0.233	-0.1
woodland mean patch area	-0.705	-0.074	-0.566	0.013
contagion	0.794	0.433	-0.269	-0.179
Simpson's evenness index	-0.8	-0.471	0.112	0.17
agriculure, woodland edge length	-0.324	-0.738	-0.192	-0.348

Table A.4 Continued.

Medium Scale 2010	Principal Component Loadings			
grassland, shrubland edge length	-0.6	0.527	0.468	-0.153
agriculture, shrubland edge length	-0.094	-0.629	0.49	-0.33
mean NDVI	-0.714	-0.028	-0.471	-0.277
NDVI coefficient of variation	0.091	-0.562	-0.074	0.55

i.

Large Scale 2010	Principal Component Loadings			
variable	PC1	PC2	PC3	PC4
% cover agriculture	-0.946	0.014	-0.028	0.112
% cover development	-0.149	0.198	-0.654	0.175
% cover grassland	0.19	-0.905	0.031	0.197
% cover shrubland	0.896	0.03	-0.381	-0.085
% cover water	-0.212	0.209	-0.391	-0.452
% cover woodland	0.602	0.686	0.32	0.031
agriculture total edge length	-0.937	0.025	-0.111	0.163
agriculture mean patch area	-0.869	0.076	-0.005	-0.082
grassland total edge length	-0.275	-0.167	-0.425	0.73
grassland mean patch area	0.137	-0.893	0.039	0.01
grassland nearest neighbor	0.31	0.783	0.253	-0.313
shrubland total edge length	0.907	0.164	-0.291	0.026
shrubland mean patch area	0.722	-0.272	-0.466	-0.218
shrubland nearest neighbor	-0.833	0.004	0.436	0.13
woodland total edge length	0.752	0.547	-0.037	0.278
woodland mean patch area	0.026	0.647	0.531	-0.268
contagion	0.238	-0.643	0.681	-0.149
Simpson's evenness index	-0.27	0.831	-0.407	-0.12
grassland, woodland edge length	0.416	0.342	0.36	0.638
agriculure, woodland edge length	-0.609	0.422	-0.065	0.329
grassland, shrubland edge length	0.865	-0.112	-0.325	0.149
agriculture, shrubland edge length	-0.792	0.316	-0.322	0.02
mean NDVI	0.429	0.431	0.302	0.403
NDVI coefficient of variation	-0.258	-0.076	-0.159	-0.488

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