FACTORS AFFECTING HABITAT USE AND ABUNDANCE PATTERNS OF BIRDS IN A GRASSLAND-SAVANNA-WOODLAND HABITAT MOSAIC

by

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ABSTRACT

Since European settlement, land-use practices have altered the structure and composition of grassland, savanna, and woodland habitats in southwest Wisconsin. Many species of birds use these habitats, including species of conservation concern. However, it is unclear how historic and current changes in land cover affect avian biodiversity patterns. Using remotely sensed, ground-collected, and historic Public Land Survey System data, and univariate and multivariate statistical methods, I explored the utility of image texture for characterizing avian habitat, tested the relationship between avian abundance and remotely sensed metrics, examined how habitat management for an endangered butterfly affects the avian community, and shed light on two hypotheses about how shifting tree composition may affect habitat quality for neotropical migrants during spring migration stop-over. All work was conducted at Fort McCoy Military Installation and the Kickapoo Valley Reserve, which are both located in southwest Wisconsin.

Remotely sensed image texture can be used to characterize avian habitat, as described by the vegetation structure indices foliage-height diversity and horizontal vegetation structure, in a grassland-savanna-woodland mosaic. I found that image texture was not related to vegetation structure indices within habitats. However, image texture does predict density of Grasshopper Sparrow (*Ammodramus savannarum)* within grassland and Ovenbird (*Seiurus aurocapillus*) within woodland, as well as avian species richness among habitats.

Oak savanna habitat management for the federally endangered Karner blue butterfly (*Lycaeides melissa samuelis*) positively influenced avian community composition and benefited several avian species of conservation concern. I found that an important management consideration for maximizing benefits to both Karner blue butterflies and savanna birds is landscape placement of the management activities. I found Karner blue butterfly habitat management activities adjacent to remnant oak savanna patches, rather than adjacent to woodland habitats, had the highest potential for the conservation of oak savanna breeding birds.

Songbird species that use tree foraging substrates during spring migration stop-over at Kickapoo Valley Reserve woodlands use red oak (*Quercus rubra*), white oak (*Q. alba*), American elm (*Ulmus americana*) and slippery elm (*U. rubra*) more frequently than they would if using these species in proportion to their availability. The proportional use of shade-tolerant tree species such as sugar maple (*Acer saccharum*), red maple (*A. rubrum*) and basswood (*Tilia americana*) was much lower than would be the case if these species were used in proportion to their availability. I did not find support for the idea that bird foraging success among tree species varies due to food availability, but rather, that food accessibility (average leaf petiole length per tree) strongly determines bird foraging success. Forest composition has changed markedly between the 1850s and 2010, but is still dominated by maple and oak. The sapling composition was overwhelmingly sugar maple. This suggests that the future forest in the Kickapoo Valley Reserve will be dominated by shade-tolerant trees. Changes in tree species composition are likely to degrade stop-over habitat for neotropical migrants during spring migration.

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Throughout my time on the University of Wisconsin campus, a handful of professors have been far more influential then they may realize for the course of my research. Tom Givnish is one of these professors. Tom teaches the best course I've taken in my life: The Vegetation of Wisconsin. I can't describe how interesting the lectures were, how thought provoking the material was, and how much influence this course had on my understanding of my study region: the Driftless Area. Although Tom is not a member of my committee, he deserves as much praise as the preceding faculty mentioned for his impact on my work. From his class, I began developing ideas related to my fourth chapter “Changes in forest tree-species composition may affect neotropical songbirds during spring migration stop-over”. Bob Wernerehl, who is one of Tom’s doctoral students, was a teacher’s assistant for this course and was also influential in teaching me Wisconsin ecology. Other professors who provided valuable guidance include David Mladenoff, Monica Turner, Phil Townsend, Craig Lorimer, and Dan Young.

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Some of the most amazing people I’ve met have been fellow graduate students or faculty at the University of Wisconsin. I consider myself a pseudo Nelson Institute for Environmental Studies member due to instantly being adopted into the department social scene in large part because this was the group of my initial housemates upon moving to Madison, Dave Toland and Gini Knight. You both were incredibly important in helping me gain my ‘walking legs’ during my first winter. Similar to the SILVIS lab members, I can go on for pages about how important my friends in Madison are to me. Thus, I won’t list those of you whom are my ‘community’. You know who you are. Just know I love you. To summarize, I’ve been exposed to many laughs, amazing food, great parties, incredibly interesting stories, great conversation, fun bars and restaurants, warm summer nights on the terrace crowded around a table with pitchers of beer, cozy winter nights in the Rathskeller, and a top notch community of people who’ve made my experiences in Madison unforgettable. I owe a special thanks to Jesse Ellis, Tom Prestby and Jess Long, who were never shy to head out and look for birds with me. I need people like Jesse, Tom and Jess in my life. Debbie Seiler was the closest person to me throughout the majority of my PhD. You were always a great ear, a warm hug, an amazing cook, an incredible adventure partner, a dear friend, and the person who was there to help me through the rough patches and celebrate the many milestones along the way.

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As a naturalist from the west, I must admit, I felt isolated from nature when I first began exploring the environs of Madison. However, I soon discovered the Lakeshore Preserve on the University of Wisconsin campus. When the weather was appropriate, I would go for a walk, or run, always with my binoculars looking for birds, butterflies, and dragonflies and testing my plant identification skills. Although I've spent countless hours walking through the Preserve, there was always something 'new' to learn about the system's ecology and phenology. Computers can be your friend. But, just not all the time for me, please. Fresh air, sun on my face, natural sounds filling my ears, and observations of interactions among animals and their environment has and will continue to be my foundation for ecology lessons. Without the Lakeshore Preserve, and all of the folks who make it a special place, I would have collapsed early in my doctoral studies.

I spent approximately 25% of my PhD physically in the field collecting data. That does not count all the prep work, hiring technicians, wrangling with human resources about something, vehicles and data/gear sorting and cleaning, and renting field houses. This work would not have been possible without the valuable logistical support of Tim Wilder, the endangered species biologist at Fort McCoy. Sue Vos was instrumental in showing me the ropes at McCoy. Without her guidance, I may have gone down the wrong road one too many times. Marcy West was generous in her on-the-ground support, as well as letters of support for funding, for my study at the Kickapoo Valley Reserve. Gina Rae and Ben Johnston made just about everything happen regarding housing and comfort away from the field sites. Gina, the pies were amazing. Ben, your sense of humor and friendship were always welcomed in order to get my mind off of my work. Donna Bauernfiend was gracious enough to let my crew and I use her house during the 2010 field season. Without a doubt, this was the best field house I've lived in. Eric Epstein was instrumental in helping push my ideas and research to a higher level. Furthermore, thanks for the letter of support (i.e., funding). I aspire to be half the naturalist Eric is. Andy Paulios and I have had many good conservations about 'savanna' birds and their conservation over an ice cream cone or two from the Memorial Union. Without Sheila Timme's perseverance and patience, I'm not sure much of anything would have been accomplished as far as cutting checks to land lords.

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INTRODUCTION

In the area of prairie-oak transition in the American Midwest, human land-use changes have severely reduced the extent of native prairie and oak savanna (Nuzzo 1986). Loss of disturbance from the landscape (e.g., fire) has changed grasslands and savannas by allowing succession toward climax communities that differ in both their plant composition and vegetation structure (Larsen 1953, Wolf 2004, Nowacki and Abrams 2008, Rogers et al. 2008). In southern Wisconsin, in addition to the broad scale changes in habitat (e.g., loss of oak savanna), this process has led to a change in the dominant tree species. Oak (*Quercus* spp.) has declined in dominance, while shade-tolerant species like maple (*Acer* spp.) have increased in dominance (Rogers et al. 2008).

Fifty-eight species of breeding birds are known to be associated with grassland or oak savanna in Wisconsin and 26 of those are species of management concern (Sample and Mossman 1997). Many more species of nearctic-neotropical migrants utilize habitats in Wisconsin during spring migration stop-over (Ewert and Hamas 1996). Yet, it isn't clear how changes due to successional and anthropogenic land-use practices and the resulting changes in habitat affect avian biodiversity in the region.

To assess changes in habitat and their implications for breeding bird species of concern and migrant birds passing through, efficient techniques are required for measuring avian habitat. Remote sensing analysis has been used to monitor correlates of avian species and diversity patterns (Pidgeon et al. 2003, Laurent et al. 2005). Recently, image texture has been used to characterize patterns of avian diversity and distribution in heterogeneous ecosystems including eastern deciduous (Tuttle et al. 2006) and conifer forests (Hepinstall and Sader 1997), sparsely vegetated desert grasslands, shrublands, and woodlands (St-Louis et al. 2006, St-Louis et al. 2009), and South American grasslands (Bellis et al. 2008). Image texture also characterizes vegetation patterns in various ecosystems throughout the world (Hudak and Wessman 1998, Hudak and Wessman 2001, Zhang and Franklin 2002, Coburn and Roberts 2004, Estes et al., 2010). Foliage height diversity is a field based measure of vegetation structure that avian ecologists have used since the mid 20th century (MacArthur and MacArthur 1961). However, it is unclear if image texture is correlated with vegetation structure (e.g., foliage-height diversity) in a prairie-savanna-woodland habitat system. Because avian diversity is positively correlated with vegetation structure (i.e., foliage-height diversity, MacArthur and MacArthur 1961), understanding the degree of correlation between image texture and foliage height diversity is important because of the potential for deriving measures of vegetation structure across broad extents

While there is clear evidence that image texture contributes to understanding patterns of avian diversity and distribution, it is unclear if image texture is a useful predictor of avian abundance patterns (e.g., density). Density is positively related to habitat quality (Bock and Jones 2004). Thus, a better understanding of the connection between image texture and avian density could reveal information regarding a new tool for evaluation of habitat quality.

Habitat management is one approach to managing species of conservation concern In Wisconsin, the federally endangered Karner blue butterfly (Lepidoptera: Lycaenidae, *Lycaeides melissa samuelis*, hereafter Karner blue) is the subject of a recovery plan focused on restoring and managing the species' preferred habitat, oak savanna (U.S Fish and Wildlife Service 2003). While the primary goal of the Karner blue recovery plan is to restore viable metapopulations of Karner blue, a secondary goal is to create savanna habitat (U.S Fish and Wildlife Service 2003, Wisconsin Department of Natural Resources 2009). It isn't clear how management for Karner blue populations affects bird populations. This is important to understand because there is currently no comprehensive habitat conservation and management plans for oak savanna avian communities in Wisconsin (Wisconsin Bird Conservation Initiative, 2011). Thus, in addition to providing habitat for a federally endangered species, learning how habitat management for the Karner blue impacts bird populations, is an opportunity to better understand how oak savanna restoration and management impact breeding bird communities.

Effective conservation of neotropical bird species requires understanding resource and habitat use during all periods of their annual cycle. Spring migration is a taxing time in the life cycle of migratory bird species (Hutto 2000, Sillett and Holmes 2002, Newton 2004, Newton 2006). Amid the many challenges they encounter during migration, birds must make critical decisions regarding resource selection at stop-over sites (Moore et al. 2005b, Buler et al. 2007). Stop-over habitat is "…areas with the combination of resources (e.g., food, cover, water) and environmental conditions (e.g., precipitation, presence and absence of competitors and predators) that promotes site occupancy by a given species and allows individuals to survive…" (Morrison et al. 2006). In optimal stop-over habitat birds refuel (i.e. forage) efficiently, and thus are able to depart quickly for the next stop-over location or breeding area (Moore and Simons 1992, Schaub et al. 2008). Selection of habitat to use during stop-over is a critical decision with fitness and survival consequences (Berthold and Terrill 1991, Moore et al. 2005a). However, it is not clear how changes in tree-species composition of Midwestern hardwood forests will affect birds during stop-over.

The overarching goal of this dissertation is to measure factors affecting habitat use and abundance patterns of birds in grassland, savanna, and woodland habitats in southwestern Wisconsin during the breeding season and spring migration stop-over using both remotely sensed and field-measured data collected at varying spatial scales.

This dissertation is divided into four chapters. I begin in **Chapter 1** by examining the use of image texture as a tool for predicting vegetation structure as represented by foliage-height diversity and horizontal vegetation structure. Since vegetation structure is a critical component for habitat selection by birds (Cody 1981), this is an important step in the development of image texture as a tool for mapping and predicting avian biodiversity patterns. In **Chapter 2**, I examine the use of image texture in predicting two important components of avian biodiversity: focal bird density and avian species richness. The results of this analysis suggest image texture is a useful tool for predicting focal species density within habitat types, and avian species richness among habitats. This is an exciting finding highlighting the potential for using image texture to elucidate patterns of habitat quality across broad spatial extents. In **Chapter 3**, I examine how oak savanna habitat management for the Karner blue affects breeding bird communities. I learned that management for the Karner blue has a positive effect on bird communities that use oak savanna. Sparse canopy associated birds use the Karner blue butterfly-managed oak savannas in similar proportions to remnant oak savannas and in different proportions to their use of woodland. I found that an important factor influencing composition of savanna bird communities was the composition and structure of the adjacent habitat type. In **Chapter 4**, I explore how changes in tree-species composition, due to succession, influence bird species that use trees as foraging substrates during spring migration stop-over. In this analysis, conducted in the forest of the Kickapoo Valley Reserve, I first examine which tree species are used by birds. Oak, elm (*Ulmus* spp.), and to a lesser extent, big-tooth aspen (*Populus grandidentata*), and paper birch (*Betula papyrifera*) were used in higher proportion than their availability in the forest, suggesting that these species are higher quality foraging habitat. Maple and basswood (*Tilia americana*) were used in lower proportion than their availability, suggesting that they are lower quality foraging habitat. Additionally, I compare how forest composition has changed since the pre-settlement period (1850s), using Public Land Survey System data, to the current time period (2010), and, using tree sapling data, I explored potential future forest composition. My results indicate that forest composition has undergone large changes from the 1850s to 2010 and that the Kickapoo Valley reserve, perhaps together with all the forests of southwest Wisconsin, will likely be dominated by shade tolerant species such as maple and basswood in the future. Coupled with the foraging patterns I observed, this portends strongly diminished quality of southwestern forests as stop-over foraging habitat for neotropical migrant birds.

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CHAPTER 1: IMAGE TEXTURE AS A REMOTELY SENSED MEASURE OF VEGETATION STRUCTURE

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In review: Remote Sensing of Environment

Abstract

Avian ecologists commonly collect data on vegetation structure, which is an important attribute for characterizing habitat of landbird species. However, measuring vegetation structure across large areas is logistically difficult. Our goal was to evaluate the degree to which plot-level digital number values, and image texture of remotely sensed data are associated with vegetation structure in a North American grassland-savanna-woodland mosaic. In the summers of 2008-2009 we collected foliage-height diversity measurements at 193 sample points from which we calculated foliage-height diversity and horizontal vegetation structure at Fort McCoy Military Installation, Wisconsin, USA. Plot-level digital numbers, and first- and second-order image texture measures, were calculated from two remotely sensed data sources: an infrared air photo (1-m resolution) and a Landsat TM satellite image (30-m resolution). We regressed foliage-height diversity against, and correlated horizontal vegetation structure with, plot-level digital numbers and texture measures among and within habitats. Among habitats, the mean of the texture measure 'second-order contrast' from the air photo explained 79% of the variation in foliage-height diversity while 'first-order variance' from the air photo was most strongly correlated with horizontal vegetation structure (ρ = 0.73, *p-value* <0.01). Within grasslands, savanna, and woodland habitats, plot-level digital numbers and image texture measures explained 22-60% of foliage-height diversity. Similarly, within habitats, plot-level digital numbers and image texture measures were moderately to strongly correlated with horizontal vegetation structure (ρ = 0.41-0.71, *p-value* <0.01). Our results suggest that plot-level digital numbers and image texture measures calculated from remotely sensed data capture a substantial amount of the variation in foliage-height diversity and horizontal vegetation structure among and, to a lesser extent, within grassland, savanna, and woodland habitats. Vegetation structure, which is a key component of avian habitat, can thus be mapped for large areas using remotely sensed image texture.

Key words: avian habitat, Band 4, foliage-height diversity, horizontal vegetation structure, image texture, infrared air photo, Landsat, NDVI

Introduction

Vegetation structure is an important attribute of avian habitat quality (MacArthur & MacArthur, 1961; Nudds, 1977; Cody, 1981, 1985) and vegetation structure characteristics partition landbird species both within and among habitats (Rotenberry & Wiens, 1980; Wiens & Rotenberry, 1981; Hutto, 1985). Throughout their lives, landbird species make habitat selection decisions at multiple scales (Hutto, 1985; Wiens et al., 1987). At broad scales, landbirds select habitat types with strongly different structural characteristics, such as a grassland or woodland (Cody, 1985). At fine scales, differences in vertical and horizontal vegetation structure are strongly associated with nest placement (Martin, 1993), and foraging site selection during migration (Hutto, 1985) and the breeding season (Robinson & Holmes, 1984). Thus, in the half century since MacArthur and MacArthur (1961) put forth their hypothesis that vegetation structure influences avian diversity, this relationship has become a central tenet of landbird habitat selection theory.

The measure *foliage-height diversity*, (MacArthur & MacArthur, 1961), or derivations of this measure, are commonly used to characterize vegetation structure. Foliage-height diversity quantifies vertical heterogeneity in vegetation structure at a given point. Furthermore, multiple measures of foliage-height diversity can be used jointly to derive an index of horizontal vegetation structure depicting the variation in canopy heights within a habitat patch (Wiens & Rotenberry, 1981). Foliage-height diversity is a flexible measure that has been applied to describe avian habitat in ecosystems from sparse grasslands (Rotenberry & Wiens, 1980; Wiens & Rotenberry, 1981; Patterson & Best, 1996), to patchy deserts (Pidgeon et al., 2001), and dense forests (Karr & Roth, 1971; Estades, 1997). In addition to being used to describe avian habitat, foliage-height diversity has also been used to characterize habitat for tropical mammal communities (August, 1983), ant biodiversity in grazed and ungrazed habitats (Bestelmeyer & Wiens, 2001), spider communities (Greenstone, 1984), and insect diversity (Murdoch et al., 1972; Southwood et al., 1979). However, while foliage-height diversity is a key measure for describing avian habitat, it is labor intensive to collect and consequently is mainly limited to small scale studies of landbirds. Therefore, avian ecologists have been challenged with finding efficient methods for characterizing foliage-height diversity, and its derived measures, at a sufficiently fine grain yet broad extent to be useful for management and conservation applications.

Remotely sensed data are powerful for characterizing habitat at broad extents, for example to describe landscape configuration (Turner et al., 2001) and for assessing biodiversity (Roughgarden et al., 1991; Turner et al., 2003; Estes et al., 2008; Gillespie et al., 2008). Broad scale land cover classifications are useful predictors of breeding bird occurrence (Thuiller et al., 2004; Venier et al., 2004). Indices derived from remotely sensed data sources, such as the normalized difference vegetation index (NDVI), which is a proxy for vegetative cover and productivity, are associated with patterns of avian species richness (Bailey et al., 2004; Seto et al., 2004; St-Louis et al., 2009), and habitat suitability (Naugle et al., 1999). Additionally, Light Detection and Ranging (LiDAR) can characterize vegetation heights, which are positively associated with bird occurrence (Seavy et al., 2009), diversity (Goetz et al., 2007; Clawges et al., 2008; Lesak et al., 2011), and habitat quality (Hinsley et al., 2006; Goetz et al., 2010). However, among the remote sensing data that are used to characterize avian habitat, LiDAR and Synthetic Aperture Radar (SAR) are the only products from which foliage-height diversity can be mapped (Clawges et al., 2008; Bergen et al., 2009), and although SAR data is widely available, LiDAR data is not. Furthermore, there are limited image archives for LiDAR, thus it is not possible to analyze change in vegetation structure over time.

However, while optical satellite data cannot measure vegetation height directly, image texture, derived from remotely sensed imagery, may be a good proxy of vegetation structure, since image texture can successfully predict fine scale distributions of landbirds in heterogeneous habitat types including eastern North American deciduous and coniferous forests (Hepinstall & Sader, 1997; Tuttle et al., 2006; Culbert et al., 2009), desert shrublands and grasslands (St-Louis et al., 2006, 2009), and agricultural grassland ecosystems (Bellis et al., 2008). Image texture measures the heterogeneity in the tonal values of pixels (i.e., digital numbers, which represent brightness) within a defined area of an image. Image texture data is fine grained, depending on the image resolution, yet broad in extent, a combination of attributes that are desirable for landscape-scale characterization of avian habitat.

In addition to its use in characterizing avian distribution patterns, image texture has also been used for characterizing vegetation patterns (Ge et al., 2006) and as input for vegetation classifications, for example in the Canadian Rocky Mountain (Zhang & Franklin, 2002), Canadian coastal forests (Coburn & Roberts, 2004), African grasslands and savannas (Hudak & Wessman, 1998; Hudak & Wessman, 2001), and montane habitats (Estes et al., 2010). However, to our knowledge, no study has directly evaluated the use of image texture for quantifying vegetation structure as represented by foliage-height diversity, which is unfortunate, because it is presumably the ability of image texture to measure vegetation structure that underlies its strong correlation with avian diversity measures.

Our goal was to evaluate the strength of the relationship of remotely sensed digital numbers and image texture measures, calculated from air photos and satellite images, with foliage-height diversity and horizontal vegetation structure that are widely used to characterize avian habitat. We conducted this analysis in a North American grassland-savanna-woodland mosaic where a wide range of vegetation structural characteristics provided a perfect setting for testing these relationships. Our specific objectives were 1) to determine which plot-level digital number summaries and image texture measures derived from air photos and Landsat TM data are best at characterizing foliage-height diversity and horizontal vegetation structure both among and within habitats, and 2) to offer recommendations for using remotely sensed measures of texture in avian habitat models.

Methods

Study Area

Our study area was the 24, 281 ha Fort McCoy Military Installation, in the Driftless Area of southwestern Wisconsin, USA (Fig. 1). The dominant habitat types at Fort McCoy include grasslands (defined here as less than 5% tree canopy cover), composed of grasses and forbs with intermittent patches of bare ground and low shrub cover; oak savannas (5 – 50% tree canopy cover with variable shrub cover), and oak woodlands (> 50% tree canopy cover with variable shrub cover, Curtis 1959, Fig. 2). Dominant tree species include black oak (*Quercus velutina*), northern pin oak (*Q. ellipsoidalis*), bur oak (*Q. macrocarpa*), jack pine (*Pinus banksiana*), black cherry (*Prunus serotina*), red oak (*Q. rubra*), and white oak (*Q. alba*). Dominant shrubs include blueberry (*Vaccinium angustifolium*) and American hazelnut (*Corylus americana*), while dominant grasses include big bluestem (*Andropogon gerardii*) and little bluestem (*Schizachyrium scoparium*).

Fort McCoy is an operational military installation and approximately 50% of its area is off limits to non-military personnel. Of the remaining area, roughly 16% is grassland, 24% is oak savanna, and 40% is oak woodland. Small patches of cattail marshes, riparian tracts, and bogs make up the remaining 20%. Within these areas, a stratified random sampling design was used to select points for ground based foliage-height diversity quantification and image texture calculation. Three habitat types, grassland, oak savanna (hereafter savanna), and oak woodland (hereafter woodland) were classified using an infrared air photo and a digital raster graphic map depicting land cover types.

Polygons encompassing patches of the three focal habitat types were manually digitized. Within the digitized polygons, 400 random sample points were generated using Hawth's Tools extension (Beyer, 2004) in ArcGIS 9.1 (ESRI, Redlands, California, USA, 2006). Reflectance of roads or other non-vegetative areas (i.e., buildings) can influence texture calculations, so all sample points that were within 150 m of a paved road or human structures were removed from consideration. Sample points that were located within 150 m of marginal roads (i.e., non-paved, single vehicle tracts) were included in this analysis because marginal roads were similar in their effect on image texture to naturally occurring bare areas. From this set, sample points that were surrounded by at least 100 m of one habitat type, and that were separated from other sample points by at least 300 m, were retained. This resulted in a total of 193 sample points (Fig. 1).

Foliage-height Diversity Field Measurements

Foliage-height diversity was measured at each sample point once in the summers of 2008 or 2009. Mean temperatures from March 1 to August 15, which corresponded to the time frame ranging from the early spring thaw to the duration of our foliage-height diversity sampling, were not significantly different between 2008 (10.94 ° C) and 2009 (11.23 ° C, t_{167}

= -0.60, p = 0.55). Similarly, mean precipitation of 2008 (log transformed, 0.35 mm) and 2009 (log transformed, 0.51 mm) were not significantly different (t_6, = -0.04, p = 0.98).

At each sample point, measurements were collected at four sub-plots, located at the center of the sample point and with one each at azimuth angles of 0˚, 120˚, and 240˚, at a random distance between 20 and 80 m. From the center point of each sub-plot, one observer walked 5 m in each of the cardinal directions and a 12-m tall telescoping pole marked at 30-cm intervals was placed vertically on the ground. A second observer recorded the number of hits (i.e., instances where vegetation touched the pole) in each 30 cm section. If the canopy was taller than 12 m, the second observer used binoculars to estimate vegetation hits at approximate 30-cm intervals. This yielded four measurements at each of the four sub-plots totaling 16 foliage-height profiles at each sample point.

From these 16 foliage-height tallies two indices of vegetation structure were calculated. First, foliage-height diversity was computed using the Shannon diversity index (MacArthur & MacArthur, 1961; Krebs, 1989). Second, horizontal vegetation structure was derived by taking the standard deviation of canopy height at the 16 foliage-height diversity measurements per sample point (Wiens & Rotenberry, 1981).

Remote Sensing Data Sources

A leaf-on, 1-m resolution, infrared air photo taken in late August 2006, and bands 1-5 and 7 from a Landsat TM (hereafter Landsat) scene acquired July 13, 2009 (path 25, row 29) were the basis of our image texture analyses. We used the infrared air photo (hereafter air photo) because infrared film is sensitive to near-infrared light which vegetation reflects

(Gausman, 1977). Furthermore, because birds respond to vegetation productivity and greenness (Lee et al., 2004; Seto et al., 2004; Szép et al., 2006), we calculated the NDVI (Tucker, 1979).

Image Texture Analysis

Image texture was calculated as plot-level summaries of digital numbers and in a moving window analysis of first-order (occurrence) and second-order (co-occurrence) statistics (Haralick et al., 1973; Haralick, 1979). For plot-level summaries, the mean and the standard deviation of the digital numbers within 100 m of a sample point were summarized (hereafter plot-level mean or standard deviation).

To compute first-order statistics for a given scale of interest (e.g., a 3x3 or a 9x9 pixel window), the digital numbers of the pixels within a moving window were used to calculate a statistic (e.g., variance), which was assigned to the central pixel. Second-order statistics consider the spatial relationships among neighboring pixels (Haralick et al., 1973; Haralick, 1979; Hall-Beyer, 2007). To calculate second order statistics, the digital numbers for a given scale of interest, were first translated into a gray-level co-occurrence matrix (GLCM) and the texture statistics were calculated based on this matrix (Hall-Beyer, 2007). As for first order statistics, this process was repeated for every pixel across an image. Image texture was calculated using ENVI software (Research Systems Inc., Boulder, Colorado).

Since the scale (as represented by window size) of an image texture measure may affect the strength of its relationship with vegetation structure, we explored the potential of several scales to characterize vegetation structure. Image texture from the air photo was calculated in 3x3, 7x7, 15x15, 21x21, 31x31, and 51x51 moving windows. Image texture from the six Landsat spectral bands and the NDVI were calculated in 3x3, 5x5, 7x7, and 11x11 moving windows. Texture measures were selected based on their established ability to characterize vegetation structure (Kuplich et al., 2005, Lu & Batistella, 2005, Tuominen & Pekkarinen, 2005, Ge et al., 2006, Dobrowski et al., 2008). We calculated three first-order texture measures (entropy, mean, and variance), and eight second-order texture measures (angular second moment, contrast, correlation, dissimilarity, entropy, homogeneity, mean, and variance, Table 1). The tool ‘zonal statistics’ in ArcGIS 9.1 was used to summarize the mean and standard deviation of each texture measure within 100 m of each sample point.

Statistical Analysis

From the air photo, we calculated 18 first-order and 48 second-order texture measures. Summarized by the mean and standard deviation, this resulted in 132 texture measures for each sample point. Similarly, 84 first-order and 224 second-order texture measures were calculated from the six spectral bands and the NDVI of the Landsat scene. Once summarized by mean and standard deviation, this resulted in a total of 616 sample point-specific texture measures. To identify the set of most promising spectral bands and texture measures, we investigated the correlation structure among Landsat image spectral bands, among the different first- and second-order texture measures, and among the scales (i.e., window sizes) of first- and second-order entropy. We used Spearman rank correlation in this analysis because it is a non-parametric measure of statistical dependence that is robust to extreme values and monotonic relationships, which were evident from inspection of initial scatter plots (Zar, 1999). To examine the degree of collinearity among Landsat image data, we constructed Spearman rank matrices for the plot-level A) mean and B) standard deviation summary from six Landsat spectral bands and the NDVI. To investigate the degree of collinearity of texture measures with one another, we held scale constant for each data source (air photo and Landsat) as a 3x3 window and built Spearman rank matrices for the C) mean and D) standard deviation summary of three first and eight second-order texture measures derived from the air photo, and the E) mean and F) standard deviation of three first and eight second-order texture measures derived from the near-infrared band (hereafter called Band 4) of the Landsat image. Finally, to explore the effects of scale, we focused on one texture measure, entropy, which stood out for its strong relationship with other texture measures, in both our initial correlation matrices (Appendix 2 and 3) and in a previous study (St-Louis et al 2006). We calculated Spearman rank matrices for the G) mean and H) standard deviation summary of first- and second-order entropy for the six window sizes applied to the air photo, and the I) mean and J) standard deviation summary of first- and second-order entropy for the four window sizes calculated on Band 4 of the Landsat scene.

Based on the results of the correlation analyses, we limited all further analyses to the air photo, and Landsat Band 4 and NDVI. Band 4 and NDVI were chosen because we found that although the mean summaries were correlated with other Landsat spectral bands summaries, the standard deviation summaries were not strongly correlated (Appendix 1). Based on their known usefulness for vegetation monitoring (Kerr & Ostrovsky, 2003), we hypothesized that Band 4 and NDVI would be particularly useful for characterizing vegetation structure.

We also eliminated from further analysis texture measures that were strongly correlated with other texture measures $|\rho| > 0.7$, in the correlation matrices. We retained the plot-level mean and standard deviation from air photo data, Band 4, and the NDVI data. The plot-level mean values were identical to first-order mean, were mathematically less complex than second-order mean, and were not related to other texture measures (Appendix 2 and 3). We also retained first-order entropy and first-order variance because, although the mean summaries were strongly related to other texture measures, the standard deviation summaries of these measures were not strongly correlated with other measures (Appendix 2 and 3) suggesting that these measures may contribute uniquely to characterizing foliage-height diversity and horizontal vegetation structure. Furthermore, we retained second-order contrast in order to determine if using a texture measure that is calculated using the GLCM, which quantifies ‘neighborhood relationships’ is superior to first-order measures in characterizing foliage-height diversity and horizontal vegetation structure.

We retained the smallest window size for all image texture analyses. In preliminary analysis, we found the majority of window sizes for the mean, and to a lesser extent, the standard deviation summaries of first- and second-order entropy calculated on the air photo and Band 4 were highly correlated (Appendix 4 and 5). The smallest window size has the advantage of capturing heterogeneity of digital numbers over small extents. Vegetation structure varies abruptly in our study system (e.g., individual or small groups of shrubs or trees located in savanna habitat), suggesting that the smaller window sizes would best match the scale of the vegetation structure patterns.

We constructed semivariograms for both foliage-height diversity and horizontal vegetation structure among all sample points and within the three focal habitats (Legendre and Fortin, 1989). There were no apparent patterns of spatial autocorrelation for foliage-height diversity among and within habitats. There was slight spatial autocorrelation for horizontal vegetation structure within grassland habitats. However, there were no obvious patterns of spatial autocorrelation for horizontal vegetation structure within savanna and woodland sample points, and among all sample points.

To determine the amount of variance in foliage-height diversity that could be explained by image texture measures we used linear regression models. Normality of data distribution was checked using a Shapiro-Wilk test and QQ norm plots, and heteroscedasticity was checked using a Levene's test and visual inspection of residual plots (Zar, 1999). We applied logarithmic transformations for independent variables that were not normally distributed or that exhibited unequal variance. If the relationships appeared non-linear, we fit second-order polynomial models.

Horizontal vegetation structure data consistently failed to meet requirements of normality and equal variance which are necessary conditions for conducting linear regression, even when we applied logarithmic transformations. Therefore, to determine whether a relationship existed between image texture measures and horizontal vegetation structure, we used Spearman's rank correlation. All statistical analysis was completed using the R software package (R Development Core Team, 2005).

Results

As expected, grassland exhibited the lowest foliage-height diversity and horizontal vegetation structure and savanna and woodland both exhibited considerably greater mean and variation in foliage-height diversity and horizontal structure (Fig. 3A&B). The plot-level standard deviation and second-order contrast calculated from the air photo, as well as the plot-level mean from Band 4 and NDVI exhibited a similar pattern as the vegetation structure measures (Fig. 3C-F).

Correlation among Texture Measures

Three broad patterns emerged from the Spearman rank correlation analyses. First, most plot-level mean and standard deviation summaries derived from Landsat spectral bands were moderately $|\rho| > 0.4$ - 0.7, to highly correlated ($|\rho| > 0.7$, Appendix 1). Second, the mean summaries of most texture measures were highly correlated (Appendix 2 and 3), but standard deviation summaries of texture measures showed a greater range of variation in their relationships with each other (Appendix 2 and 3). Third, there were strong inter-scale correlations (i.e., among window size) with the greatest magnitude of difference occurring among the smallest and largest window sizes (Appendix 4 and 5).

Relationships between Air Photo Image Texture Measures and Vegetation Structure

Among habitats, about 80% of the variation in foliage-height diversity was associated with the mean of second-order contrast (Table 2). Horizontal vegetation structure was also strongly associated with second-order contrast, as well as the mean of first-order variance (ρ

= 0.73 for both measures, Table 3). The relationship between foliage-height diversity and second order contrast was positive and linear, and the relationship was positive and curvilinear for first-order variance and horizontal vegetation structure (Fig. 4).

Within grassland habitat, image texture weakly characterized foliage-height diversity (second-order contrast accounted for 11% of the variance, Table 2). However the standard deviation of first-order variance and second-order contrast were both moderately to strongly correlated with grassland horizontal vegetation structure (ρ = 0.71 and ρ = 0.67 respectively, Table 3). Within savanna habitat, foliage-height diversity was best characterized by the mean summaries of both first-order variance and second-order contrast, which each accounted for approximately 30% of the variance (Table 2). Savanna horizontal vegetation structure was moderately correlated with the mean summary of both first-order entropy and second-order contrast (ρ = 0.41, Table 3). Within woodland habitat, about 30% of variation in foliage-height diversity was characterized by the mean summary of second-order contrast (Table 2). In woodland habitat horizontal vegetation structure was not associated with any image texture measure.

Relationships between Landsat Image Texture and Vegetation Structure

Among habitats, 71% and 74% of the variance in foliage-height diversity was associated with the plot-level mean of both NDVI and Band 4 (Table 2). The plot-level mean of NDVI was also strongly correlated with horizontal vegetation structure (ρ = 0.70, Table 3). But in contrast to the air photo findings, first- and second-order image texture measures calculated from Landsat data did not strongly characterize foliage-height diversity and horizontal vegetation structure among habitats, explaining only 15% of the variance in foliage-height diversity (Table 2), and were weakly correlated with horizontal vegetation structure (Band 4 measures, $\rho = 0.27$, Table 3). As was the case for air photo-based regression, the relationships between the plot-level mean of the Landsat data were positive and linear for foliage-height diversity, and positive and slightly curvilinear for horizontal vegetation structure among habitats (Fig. 4).

Within grassland habitat, 26% of the variation of foliage-height diversity was associated with the plot-level standard deviation of NDVI and second-order contrast of NDVI (Table 2), and horizontal vegetation structure was moderately correlated with the plot-level mean of NDVI ($\rho = 0.48$, Table 3). Within savanna, the association was weaker, with the plot-level mean of NDVI accounting for 10% of the variance in foliage-height diversity with the strongest association capturing only 16% of the variation (Band 4, Table 2). Horizontal vegetation structure was moderately correlated with the plot-level mean of NDVI ($\rho = 0.37$, Table 3). Within woodland habitat, however, about 60% of the variation in foliage-height diversity was associated with the plot-level mean summaries of both Band 4 and NDVI (Table 2). We did not find any significant correlations between image texture measures and horizontal vegetation structure within woodlands (Table 3).

Discussion

Vegetation structure greatly influences habitat selection by landbirds. However, ornithologists lack adequate methods for measuring vegetation structure across broad extents. Our results suggest that in ecosystems that encompass strong differences in structure, such as the grassland-savanna-woodland mosaic we studied, image texture of remotely sensed data characterizes foliage-height diversity and horizontal vegetation structure very well. However, at the finer within-habitat scale, the relationships between image texture measures and foliage-height diversity and horizontal vegetation structure were less strong.

Our results were consistent with previous studies that applied image texture to discriminate among-habitat vegetation structure patterns. While investigating brush encroachment in African savannas, Hudak and Wessman (2001) found high correlations among canopy cover and image texture, and between woody stem counts and image texture (1998). These African study sites were a mosaic of shrublands and savanna, similar in vegetation structure to our grassland-savanna-woodland study site. The mean summary of first-order standard deviation, calculated from high resolution air photos, was best related to the vegetation structural measurement, woody stem counts (Hudak & Wessman, 1998). First-order standard deviation is mathematically similar to first-order variance which we found to be related to foliage-height diversity within savanna habitats (Table 2), suggesting that this is a consistent measure of vegetation structure in ecosystems that include grass, shrub, and scattered tree (i.e., savanna) elements. In a managed boreal forest in Finland, second-order image texture measures, including contrast, calculated from high resolution air photos, were moderately correlated with vegetation structural metrics (Tuominen & Pekkarinen, 2005). The strength of the correlations among image-texture measures and vegetation structure metrics used in Finland corroborate our findings about the strength of the relationship between second order contrast and vegetation structure and provide further evidence that image texture measures can discriminate among-habitat vegetation structural patterns, which may be useful for characterizing avian habitat across broad extents.

Relationships between Image Texture and Vegetation Structure

Our analysis highlighted differences among air photo- and satellite- derived data in the degree of association with vegetation structure. The fine grained air photo better characterized foliage-height diversity and horizontal vegetation structure among habitats and within savanna habitat than did the satellite data. In contrast, the plot-level mean from Band 4 and NDVI were more strongly related to foliage-height diversity within grasslands and woodlands. This finding came as a surprise to us for two reasons. First, we expected that measures calculated at the finest scale (the 3x3 pixel moving window), which most closely matched our perception of the scale of vegetation patch distribution within savanna plots, would best characterize vegetation structure. Furthermore, in Finnish boreal forests, patterns of vegetation structure exhibited stronger relationships with image texture measures than with plot-level digital numbers (Tuominen & Pekkarinen, 2005). We did not expect the plot-level mean and standard deviation of Landsat-based NDVI to emerge as a strong correlate of vegetation structure because this metric did not account for difference in scale (i.e., window sizes used to calculate image texture measures) which we hypothesized to be more strongly associated with vegetation structure. However, our results do coincide with evidence that NDVI characterizes vegetation metrics ranging from leaf-area index (Gamon et al., 1995) to plant species richness (Gould, 2000).

We suggest that image texture is a useful tool for avian ecologists interested in characterizing vegetation structure, as represented by foliage-height diversity over broad extents. Our findings suggest that image texture measures calculated using smaller window sizes with high resolution imagery and plot-level digital numbers from Band 4 and NDVI are most strongly associated with vegetation structure heterogeneity as it is measured on the ground. Other studies, in which there was a mismatch between the scale of ground data and the scale of texture processing, did not find correlations between image texture measures and vegetation metrics. For example, Lu and Batistella, (2005) used vegetation data collected in sub-plots ranging from 1 m^2 to 100 m^2 to characterize tree-height, stem-height, and diameter at breast height of early successional and mature rainforest in Brazil across a highly fragmented landscape. These data were related to Landsat imagery and image texture calculated in window sizes ranging from 150 m^2 to 750 m^2 where there were only moderate to poor correlations discovered. One explanation for why there were not stronger correlations in areas with high within-habitat heterogeneity may be that the scale of the ground-based measurements were not well matched to the scale of image texture calculation, resulting in moving windows that incorporated habitat data that was not sampled in the field plots.

Recommendations for Use of Texture Measures

We suggest that if the goals of a study are to map and characterize vegetation structure as a proxy for characterizing avian habitat in a strongly heterogeneous landscape, investigators should match the scale of analysis (i.e., type and resolution of imagery and size of moving windows) with the scale of the vegetation patches. If the goals of the study are to quantify vegetation structure at larger extents among heterogeneous habitats, in order to capture variation of adjacent habitats (i.e., landscape structural context), which may be influencing landbird habitat selection, investigators should use larger window sizes. Furthermore, we suggest using the plot level mean because this quantifies information of the 'local' area of interest (e.g., 100 m radius sample points), which we found to relate well with vegetation structure among habitats.

Finally, due to the high correlation among remotely sensed variables, we recommend using a subset of first- and second-order texture measures. We suggest using one or two first-order texture measures such as variance, or entropy. We found these texture measures to be strongly related to foliage-height diversity and horizontal vegetation structure among habitats and moderately related within savannas. Because these texture measures are strongly correlated with second-order entropy and variance (Appendix 2 and 3), we recommend the simpler first- and second-order image texture measures. We found second-order contrast to be highly related to foliage-height diversity among habitats, and others have characterized avian habitat using a closely related texture measure (i.e., second-order homogeneity, Tuttle et al., 2006). Thus, we recommend using a second-order texture measure such as contrast (Appendix 2 and 3), when characterizing foliage-height diversity. Finally, since we found the plot-level mean of Band 4 and NDVI to be strongly related to foliage-height diversity among habitats and within woodlands, and since these measures are highly collinear with first- and second-order mean, we suggest investigators use these measures when using Landsat data to characterize vegetation structure patterns across broad extents.

Conclusions

Ornithologists need effective tools for measuring avian habitat at both fine scales and broad extents. Field-based methods for fine scale habitat quantification are well established. However, efficient methods that could characterize fine grained habitat features across broad extents are lacking. The results of our study suggest that plot-level digital numbers and image texture calculated from remotely sensed data can characterize foliage-height diversity and horizontal vegetation structure among and, to a lesser extent, within grassland, savanna, and woodland habitats. These findings are important because avian diversity, richness, and distributions are linked to foliage-height diversity and horizontal vegetation structure. We provide evidence that remotely sensed data can be used to characterize foliage-height diversity and horizontal vegetation structure and thus is a useful tool for mapping avian habitat across broad spatial extents.

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Table 1-1: Eight second-order measures of image texture calculated from a gray-level co-occurrence matrix (GLCM) with description of what they measure, and the statistic formula.

Second-order statistic	**Statistic description of behavior**	**Statistic formula**†
Angular- second moment	High when the GLCM is locally homogenous. Similar to Homogeneity.	$\sum_i \sum_j \{p(i,j)\}^2$
Contrast	A measure of the amount of local variation in digital numbers among neighboring pixels. It is the opposite of homogeneity.	$\sum_{n=0}^{N-1} n^2 \left\{ \sum_{i=1}^{N} \sum_{j=1}^{N} p(i,j) \right\}$ $\lvert i-j \rvert = n$
Correlation	Linear dependency of digital numbers on those of neighboring pixels.	$\dfrac{\sum_i \sum_j (ij) p(i,j) - \mu_x \mu_y}{\sigma_x \sigma_y}$
Dissimilarity	Similar to contrast and inversely related to homogeneity.	$\sum_{n=0}^{N-1} n \left\{ \sum_{i=1}^{N} \sum_{j=1}^{N} p(i,j) \right\}$
Entropy	Shannon-diversity. High when the digital numbers of the GLCM have varying values. Opposite of angular second moment.	$-\sum_i \sum_j p(i,j) \log(p(i,j))$
Homogeneity	A measure of homogenous digital numbers across an image.	$\sum_i \sum_j \dfrac{1}{1+(i-j)^2} p(i,j)$
Mean	Gray level average in the GLCM window.	$\sum_{i,j=0}^{N-1} p(i,j)$
Variance	Gray level variance in the GLCM window.	$\sum_{i,j=0}^{N-1} p_{i,j} (i-\mu_i)^2$

[†] From Haralick et al. (1973).

Table 1-2: Univariate linear regression models of the strength of the relationship between foliage-height diversity and the mean (MEAN) and standard deviation (SD) of plot-level digital numbers and 1st and 2nd order texture measures calculated from an infrared air photo, the near-infrared spectral band from a Landsat TM scene (Band 4), and a vegetation index, NDVI from a Landsat TM scene within three habitats (grassland, savanna, and woodlands) and among all three habitats (Global). Columns that are not populated with model metrics indicate that the assumptions of linear models could not be met.

	Grasslands (*n* = 49)		Savanna (*n* = 84)		Woodland (*n* = 60)		Global (*n* = 193)	
	R^2	*p-value*	R^2	*p-value*	R^2	*p-value*	R^2	*p-value*
Air photo plot-level MEAN	-0.04	0.95	0.11	< 0.01	0.04	0.12		
Air photo plot-level SD	0.00	0.35	0.28	< 0.01				
Air photo first-order entropy MEAN	0.02	0.26	0.23†	< 0.01	0.16†	< 0.01	0.74†	< 0.01
Air photo first-order entropy SD	0.00	0.36	0.20†	< 0.01	0.14†	< 0.01	0.73†	< 0.01
Air photo first-order variance MEAN	0.05	0.12	0.32†	< 0.01	0.18†	< 0.01	0.74†	< 0.01
Air photo first-order variance SD	0.09†	0.04	0.26†	< 0.01	0.03	0.18		
Air photo second-order contrast MEAN	0.05†	0.11	0.31	< 0.01	0.31	< 0.01	0.79	< 0.01
Air photo second-order contrast SD	0.11†	0.02	0.24	< 0.01	0.06	0.04		
Band 4 plot-level MEAN	0.14	< 0.01	0.16	< 0.01	0.59	< 0.01	0.74	< 0.01
Band 4 plot-level SD	0.18	< 0.01	0.00	0.32	0.04	0.11		
Band 4 first-order entropy MEAN	0.14†	0.01	0.06†	0.03	0.02	0.20	0.15†	< 0.01
Band 4 first-order entropy SD	0.05	0.12	0.02	0.16	-0.03	0.90	0.12†	< 0.01
Band 4 first-order variance MEAN	0.19†	< 0.01	0.02	0.15	0.01	0.25	0.01	0.16
Band 4 first-order variance SD	0.15†	< 0.01	0.00	0.32	0.00	0.48	0.01	0.13
Band 4 second-order contrast MEAN	0.09	0.03	0.01	0.17	0.03	0.09	0.00	0.31
Band 4 second-order contrast SD	0.02	0.17	0.06	0.02	0.00	0.40	0.00	0.41
NDVI plot-level MEAN	0.21	< 0.01	0.10	< 0.01	0.60	< 0.01	0.71†	< 0.01
NDVI plot-level SD	0.26	< 0.01	-0.01	0.69	0.22	< 0.01		
NDVI first-order entropy MEAN	-0.01	0.45	0.00	0.32	0.06	0.07		
NDVI first-order entropy SD	-0.02	0.82	0.00	0.38	0.04	0.11	0.04	0.01
NDVI first-order variance MEAN	-0.03	0.72	0.00	0.27	0.15	< 0.01	0.00	0.84
NDVI first-order variance SD	-0.02	0.82	0.02	0.15	0.11	0.01	0.00	0.48
NDVI second-order contrast MEAN	0.26	< 0.01	0.00	0.59	0.10	< 0.01		
NDVI second-order contrast SD	0.12	< 0.01	0.00	0.68	0.00	0.40		

†Model fit using the 2nd order polynomial.

Table 1-3: Spearman rank correlations for horizontal vegetation structure against the mean (MEAN) and standard deviation (SD) of plot-level digital numbers, and 1st and 2nd order texture measures calculated from an infrared air photo, the near-infrared spectral band from a Landsat TM scene (Band 4), and a vegetation index, NDVI from a Landsat TM scene within two habitats (grassland and savanna) and among all three habitats (Global). Woodland sample points were excluded from this table because no significant correlations could be found.

	Grasslands (*n* = 49)		Savanna (*n* = 84)		Global (*n* = 193)	
	ρ	*p-value*	*ρ*	*p-value*	*ρ*	*p-value*
Air photo plot-level MEAN	-0.24	0.09	-0.15	0.16	-0.45	< 0.01
Air photo plot-level SD	0.37	0.01	0.40	< 0.01	0.72	< 0.01
Air photo first-order entropy MEAN	0.05	0.74	0.41	< 0.01	0.71	< 0.01
Air photo first-order entropy SD	-0.04	0.80	-0.39	< 0.01	-0.70	< 0.01
Air photo first-order variance MEAN	0.40	< 0.01	0.39	< 0.01	0.73	< 0.01
Air photo first-order variance SD	0.71	< 0.01	0.28	0.01	0.65	< 0.01
Air photo second-order contrast MEAN	0.37	< 0.01	0.41	< 0.01	0.73	< 0.01
Air photo second-order contrast SD	0.67	< 0.01	0.33	< 0.01	0.71	< 0.01
Band 4 plot-level MEAN	0.08	0.56	0.32	< 0.01	0.61	< 0.01
Band 4 plot-level SD	0.40	< 0.01	0.09	0.41	0.24	< 0.01
Band 4 first-order entropy MEAN	0.33	0.02	0.13	0.25	0.27	< 0.01
Band 4 first-order entropy SD	-0.15	0.32	-0.12	0.26	-0.21	< 0.01
Band 4 first-order variance MEAN	0.45	< 0.01	0.07	0.50	0.13	0.07
Band 4 first-order variance SD	0.45	< 0.01	0.09	0.43	0.10	0.18
Band 4 second-order contrast MEAN	0.37	< 0.01	0.00	0.95	0.06	0.38
Band 4 second-order contrast SD	0.31	0.03	-0.07	0.51	0.02	0.78
NDVI plot-level MEAN	0.48	< 0.01	0.37	< 0.01	0.70	< 0.01
NDVI plot-level SD	0.37	< 0.01	0.15	0.17	0.03	0.68
NDVI first-order entropy MEAN	-0.11	0.46	0.06	0.58	0.13	0.07
NDVI first-order entropy SD	0.09	0.53	-0.10	0.38	-0.13	0.08
NDVI first-order variance MEAN	0.17	0.25	-0.11	0.30	0.06	0.43
NDVI first-order variance SD	0.19	0.19	-0.10	0.36	0.05	0.47
NDVI second-order contrast MEAN	0.36	0.01	0.05	0.68	-0.13	0.07
NDVI second-order contrast SD	0.36	0.01	0.05	0.68	-0.14	0.06

Figure Captions

Figure 1-1: A) Fort McCoy Military Installation, Wisconsin, USA. B) Distribution of 193 sample points where foliage-height diversity data was collected and texture values were calculated. The sample points were distributed across an open to dense tree canopy cover gradient in three habitat types, 1) grasslands denoted by barred polygons, 2) savanna denoted by white outlined polygons, and 3) woodlands denoted by black outlined polygons.

Figure 1-2: A) Grassland, B) savanna, and C) woodland. Each habitat type depicted with a 1) ground photo, 2) a 1 m resolution infrared air photo, 3) infrared air photo-derived 2nd order contrast calculated in a 3x3 moving window, 4) NDVI calculated from a Landsat scene, and 5) NDVI-derived 2nd order contrast calculated in a 3x3 moving window. In images with cross (†) the color ramp was stretched and inverted for clearer display.

Figure 1-3: Box plot summaries of vegetation structure and image texture characteristics in grassland, savanna, and woodland vegetation types. A) foliage-height diversity, B) horizontal vegetation structure (horizontal structure), C) 2nd order contrast calculated in a 3x3 pixel moving window on an infrared air photo, then summarized by the mean of pixels found within a 100 m radius circle, D) Infrared air photo plot level values summarized by the standard deviation within a 100 m radius circle, E) Band 4 plot level values summarized by the mean within a 100 m radius circle, and F) NDVI plot level values summarized by the mean within a 100 m radius circle.

Figure 1-4: Scatter plots from least-squares regression, of best plot-level digital number summaries, or image texture measures in predicting among-habitat foliage-height diversity (Shannon diversity index, (A). Scatter plots for horizontal vegetation structure (meters) depict best Spearman's rho (ρ) correlation among habitats, (B). Plot-level digital number summaries and image texture measures were calculated from an infrared air photo (row 1) and Band 4 and NDVI from a Landsat scene (row 2). The habitat of each plot is denoted as follows: grassland -solid black circle, savanna -hollow square, woodland -gray triangle.

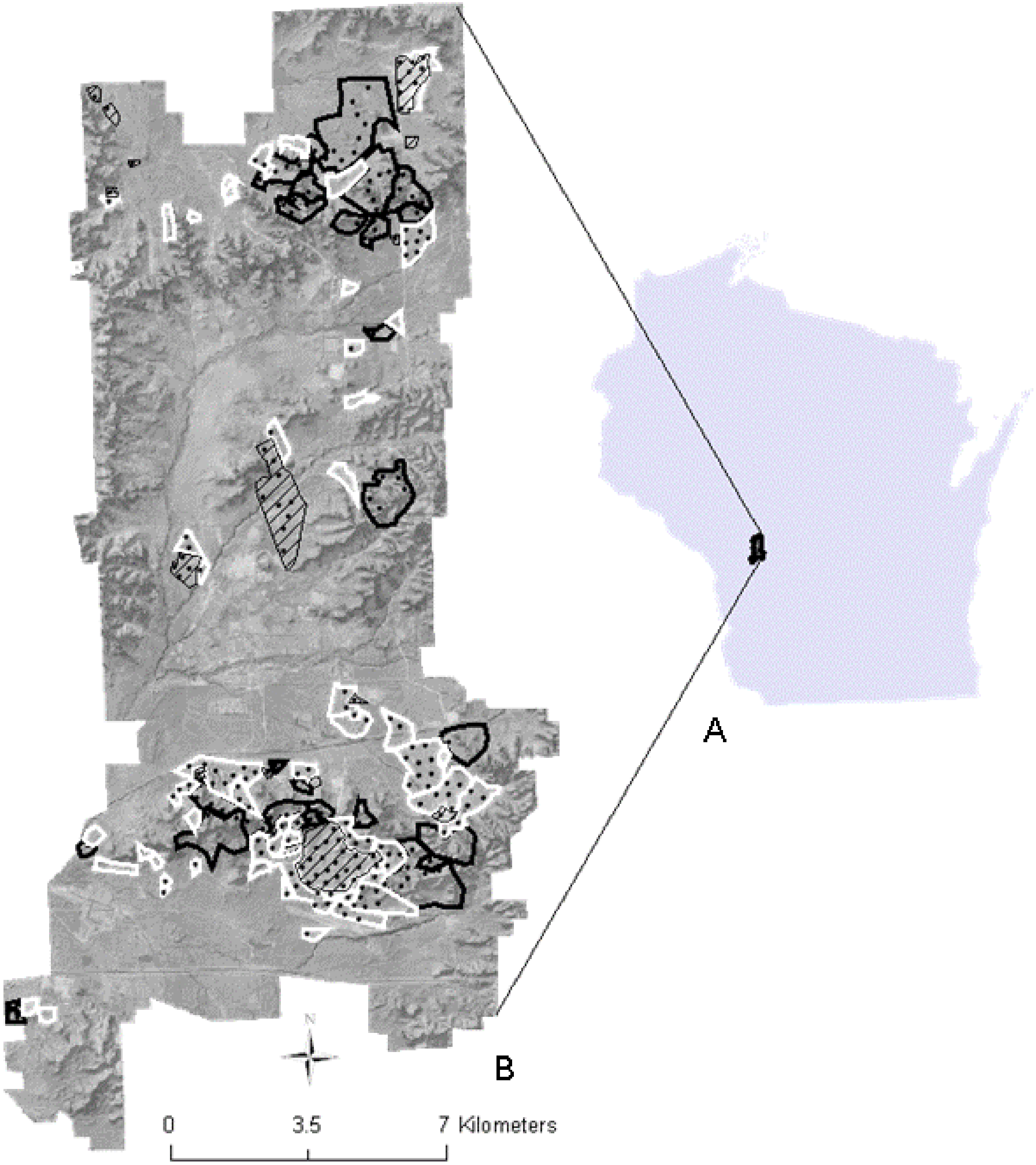
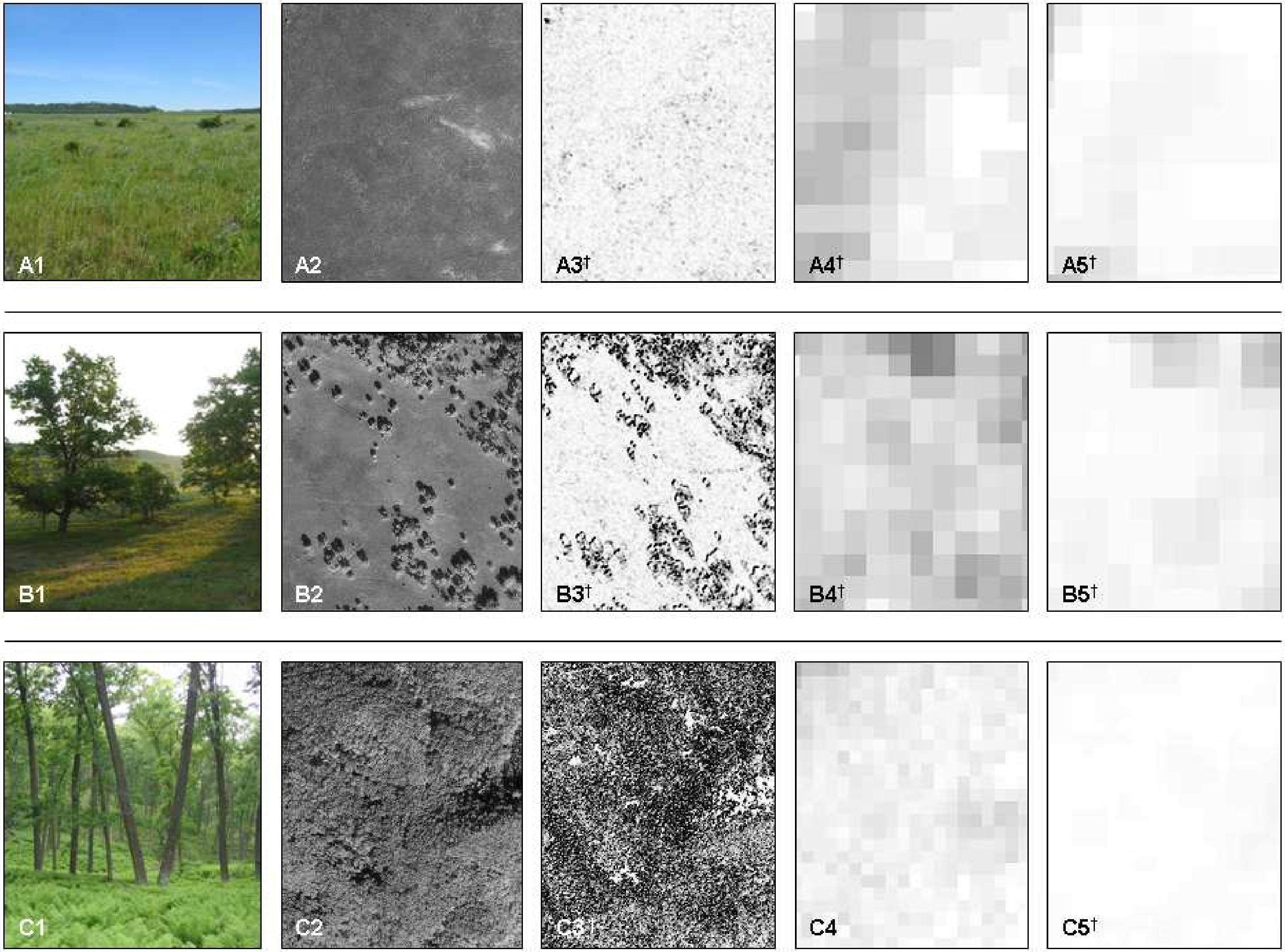


Figure 1-1

Figure 1-2



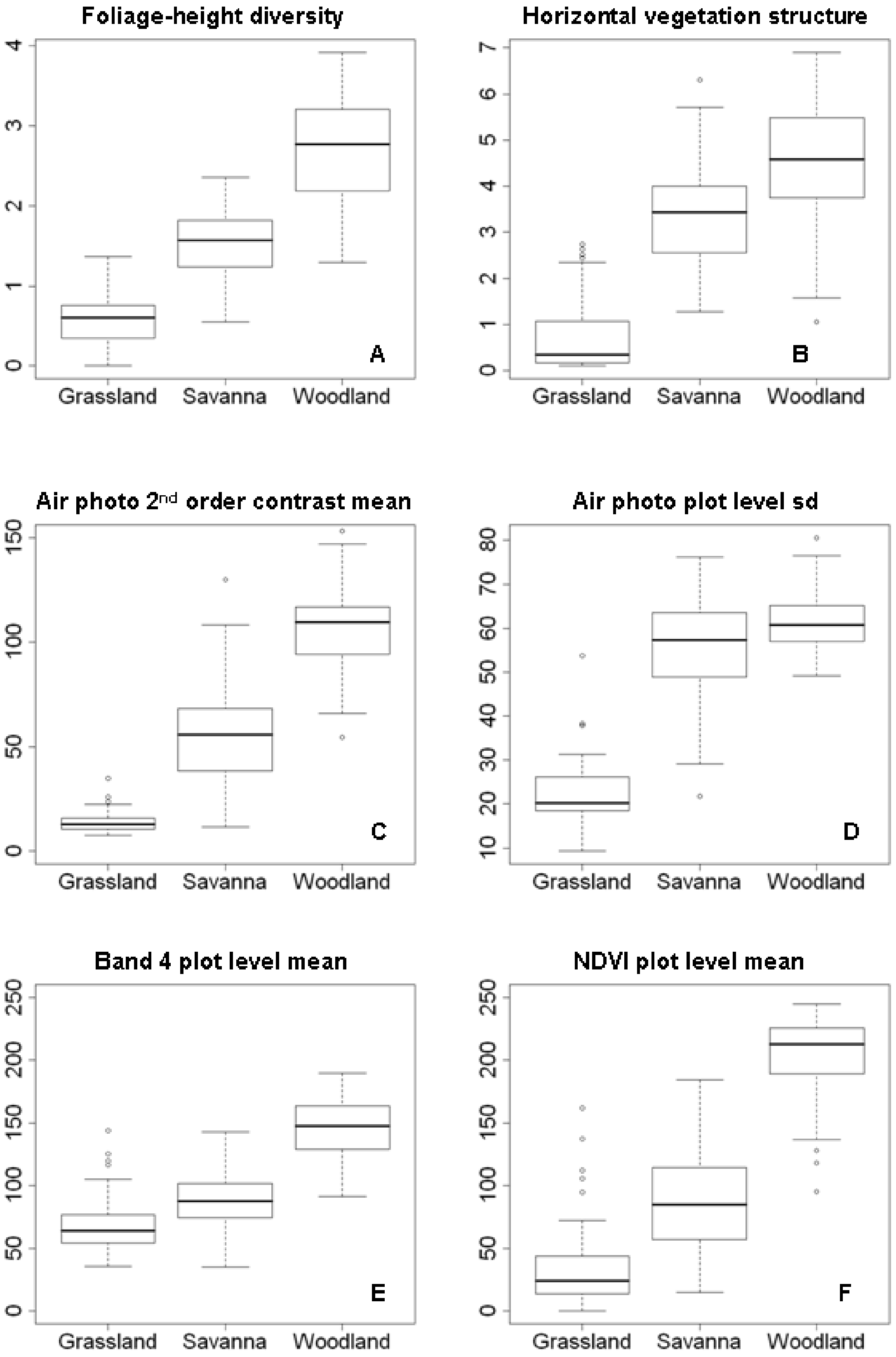

Foliage-height diversity
0
1
2
3
4
Grassland
Savanna
Woodland
A
Horizontal vegetation structure
0
1
2
3
4
5
6
7
Grassland
Savanna
Woodland
B
Air photo 2nd order contrast mean
0
50
100
150
Grassland
Savanna
Woodland
C
Air photo plot level sd
10
20
30
40
50
60
70
80
Grassland
Savanna
Woodland
D
Band 4 plot level mean
0
50
100
150
200
250
Grassland
Savanna
Woodland
E
NDVI plot level mean
0
50
100
150
200
250
Grassland
Savanna
Woodland
F

Figure 1-3

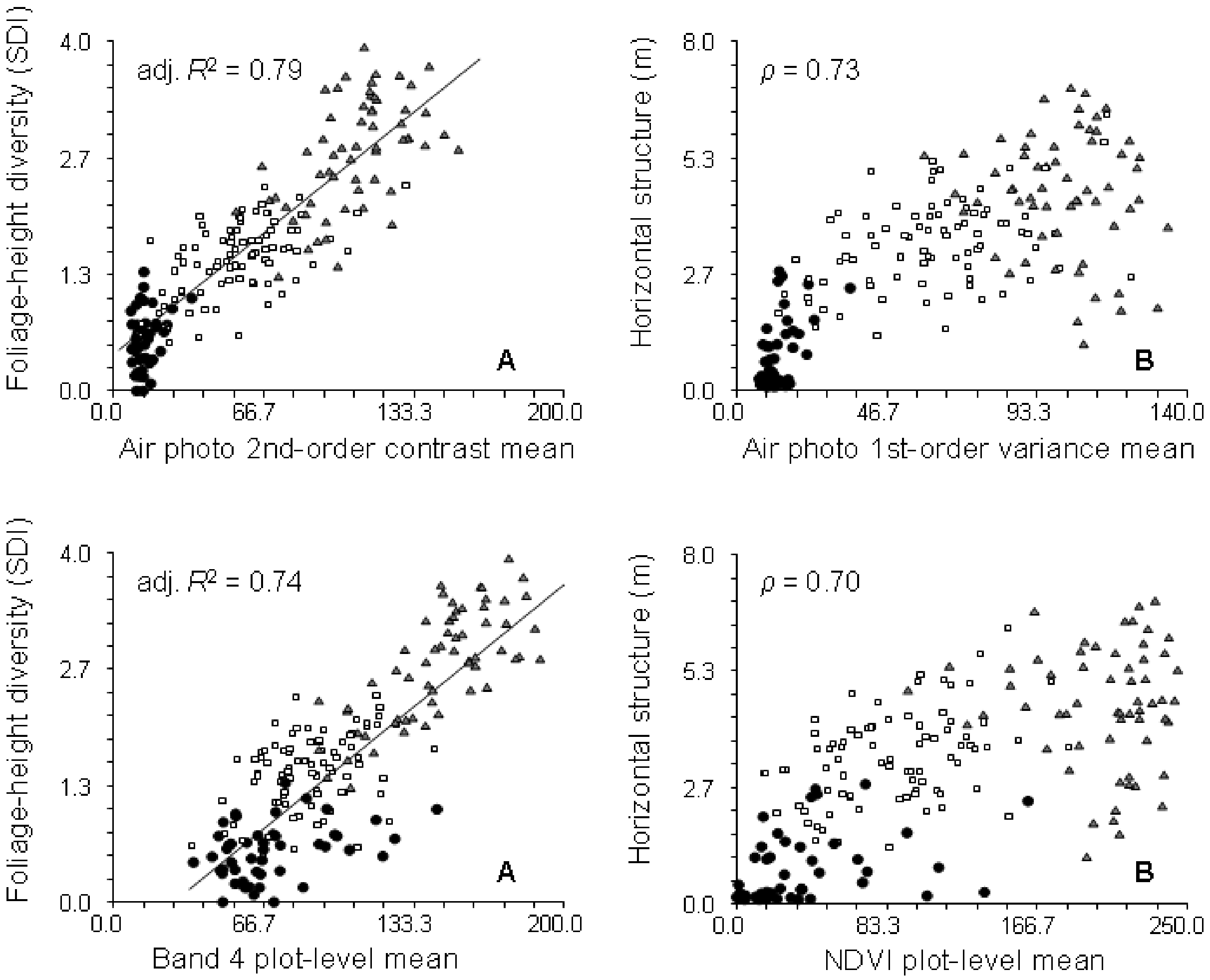

Foliage-height diversity (SDI)
4.0
2.7
1.3
0.0
adj. R^2 = 0.79
A
0.0
66.7
133.3
200.0
Air photo 2nd-order contrast mean
Horizontal structure (m)
8.0
5.3
2.7
0.0
ρ = 0.73
B
0.0
46.7
93.3
140.0
Air photo 1st-order variance mean
Foliage-height diversity (SDI)
4.0
2.7
1.3
0.0
adj. R^2 = 0.74
A
0.0
66.7
133.3
200.0
Band 4 plot-level mean
Horizontal structure (m)
8.0
5.3
2.7
0.0
ρ = 0.70
B
0.0
83.3
166.7
250.0
NDVI plot-level mean

Figure 1-4

Appendix 1-1: Spearman rank correlation coefficients of the plot-level digital numbers from a Landsat image and a vegetation index (NDVI). Above the diagonal is the standard deviation, and below the diagonal is the mean, summarized in a 100 m radius buffer around sample points. *N* sample points =193.

	Band 1	Band 2	Band 3	Band 4	Band 5	Band 7	NDVI
Band 1		0.95	0.95	0.08	0.77	0.86	0.66
Band 2	0.98		0.64	0.09	0.79	0.83	0.63
Band 3	1	0.98		0.10	0.85	0.93	0.77
Band 4	-0.82	-0.76	-0.81		0.15	0.13	0.41
Band 5	0.96	0.96	0.97	-0.73		0.90	0.76
Band 7	0.99	0.98	0.99	-0.81	0.98		0.84
NDVI	-0.98	-0.95	-0.98	0.89	-0.93	-0.98	

Appendix 1-2: Spearman rank correlation coefficients of three 1st order and eight 2nd order texture measures calculated from an infrared air photo in a 3x3 moving window in a 100 m radius buffer around 193 sample points. Above the diagonal are texture measures summarized by the standard deviation. Below the diagonal are texture measures summarized by the mean.

Measure			1st order			2nd order							
	Texture	Infrared†	ENT	MN	VAR	CON	COR	DIS	ENT	HOM	MN	ASM	VAR
	Infrared†		-0.75	0.97	0.89	0.88	-0.75	0.85	-0.72	0.06	0.97	-0.73	0.89
1st order	ENT	-0.46		-0.62	-0.70	-0.81	0.95	-0.62	0.99	0.51	-0.62	1	-0.70
	MN	1	-0.46		0.84	0.78	-0.62	0.83	-0.58	0.13	1	-0.59	0.83
	VAR	-0.51	0.95	-0.5		0.95	-0.68	0.96	-0.66	0.05	0.84	-0.68	1
2nd order	CON	-0.51	0.96	-0.51	0.99		-0.80	0.93	-0.77	-0.13	0.78	-0.79	0.95
	COR	-0.64	0.95	-0.64	0.93	0.94		-0.63	0.93	0.45	-0.62	0.94	-0.68
	DIS	-0.51	0.97	-0.5	0.99	1	0.95		-0.57	0.21	0.83	-0.59	0.96
	ENT	-0.41	0.99	-0.41	0.93	0.93	0.93	0.95		0.54	-0.58	1	-0.66
	HOM	0.48	-0.99	0.47	-0.97	-0.98	-0.96	-0.99	-0.98		0.13	0.54	0.05
	MN	1	-0.46	1	-0.50	-0.51	-0.64	-0.5	-0.41	0.47		-0.60	0.83
	ASM	0.45	-1	0.45	-0.95	-0.96	-0.95	-0.97	-0.99	0.99	0.45		-0.68
	VAR	-0.51	0.95	-0.5	1	0.99	0.93	0.99	0.92	-0.97	-0.50	-0.95	

Infrared† = Plot-level digital numbers (no moving window analysis)

First-order measures: ENT = Entropy, MN = Mean, VAR = Variance - Second-order measures: CON = Contrast, COR = Correlation, DIS = Dissimilarity, ENT = Entropy, HOM = Homogeneity, MN = Mean, ASM = Angular Second Moment, VAR = Variance.

Appendix 1-3: Spearman rank correlation coefficients of three 1st order and eight 2nd order texture measures calculated from the near-infrared band (Band 4) of a Landsat scene in a 3x3 moving window in a 100 m radius buffer around 193 sample points. Above the diagonal are texture measures summarized by the standard deviation. Below the diagonal are texture measures summarized by the mean.

Measure			1st order			2nd order							
	Texture	Band 4†	ENT	MN	VAR	CON	COR	DIS	ENT	HOM	MN	ASM	VAR
	Band 4†		-0.35	0.92	0.77	0.67	0.59	0.58	-0.39	0.42	0.94	-0.52	0.80
1st order	ENT	0.50		-0.30	-0.25	-0.22	-0.34	-0.07	0.65	0.06	-0.28	0.65	-0.24
	MN	0.99	0.51		0.78	0.61	0.47	0.56	-0.29	0.43	0.96	-0.41	0.75
	VAR	0.29	0.77	0.31		0.75	0.51	0.68	-0.23	0.50	0.75	-0.36	0.95
2nd order	CON	0.30	0.68	0.29	0.80		0.48	0.93	-0.20	0.73	0.63	-0.33	0.80
	COR	-0.30	-0.64	-0.30	-0.63	-0.62		0.41	-0.27	0.31	0.50	-0.38	0.53
	DIS	0.36	0.74	0.35	0.74	0.94	-0.62		-0.02	0.89	0.57	-0.13	0.73
	ENT	0.46	0.85	0.46	0.73	0.76	-0.68	0.86		0.19	-0.31	0.95	-0.25
	HOM	-0.39	-0.76	-0.38	-0.68	-0.88	0.62	-0.98	-0.88		0.43	0.07	0.55
	MN	1	0.50	0.99	0.30	0.31	-0.30	0.37	0.47	-0.40		-0.44	0.78
	ASM	-0.46	-0.84	-0.46	-0.70	-0.74	0.66	-0.85	-0.99	0.88	-0.46		-0.39
	VAR	0.33	0.75	0.33	0.95	0.84	-0.67	0.79	0.78	-0.74	0.34	-0.76	

Band 4† = Plot-level digital numbers of Band 4

First-order measures: ENT = Entropy, MN = Mean, VAR = Variance - Second-order measures: CON = Contrast, COR = Correlation, DIS = Dissimilarity, ENT = Entropy, HOM = Homogeneity, MN = Mean, ASM = Angular Second Moment, VAR = Variance.

Appendix 1-4: Spearman rank correlations for 1st order and 2nd order entropy calculated at different scales (window sizes) from an infrared air photo, in a 100 m radius buffer around 193 sample points. Above the diagonal are the standard deviation summaries of 1st and 2nd order entropy. Below the diagonal are the mean summaries of 1st and 2nd order entropy.

		1st order						2nd order					
	Window Size	3x3	7x7	15x15	21x21	31x31	51x51	3x3	7x7	15x15	21x21	31x31	51x51
1st order	3x3		0.55	0.56	0.60	0.65	0.72	0.99	0.82	-0.28	0.66	0.65	0.66
	7x7	0.99		0.97	0.93	0.88	0.78	0.57	0.88	0.55	0.95	0.92	0.86
	15x15	0.96	0.99		0.99	0.96	0.88	0.56	0.86	0.50	0.98	0.97	0.93
	21x21	0.94	0.98	1		0.98	0.92	0.59	0.85	0.42	0.98	0.99	0.96
	31x31	0.93	0.96	0.99	1		0.97	0.64	0.85	0.31	0.97	0.98	0.98
	51x51	0.91	0.95	0.98	0.99	1		0.70	0.83	0.15	0.91	0.94	0.97
2nd order	3x3	0.99	0.97	0.93	0.92	0.90	0.88		0.85	-0.24	0.67	0.65	0.66
	7x7	1	0.99	0.97	0.96	0.94	0.93	0.99		0.21	0.91	0.88	0.86
	15x15	0.97	0.99	0.97	0.96	0.95	0.93	0.95	0.98		0.39	0.38	0.31
	21x21	0.98	1	0.99	0.99	0.98	0.96	0.96	0.99	0.98		0.99	0.96
	31x31	0.97	0.99	1	0.99	0.98	0.97	0.95	0.98	0.98	1		0.98
	51x51	0.96	0.99	1	0.99	0.99	0.98	0.94	0.97	0.98	1	1	

Appendix 1-5: Spearman rank correlations coefficients for 1st order and 2nd order entropy calculated at different scales (window sizes) sizes from the near infrared band (Band 4) of a Landsat scene, in a 100 m radius buffer around 193 sample points. Above the diagonal are the standard deviation summaries of 1st and 2nd order entropy. Below the diagonal are the mean summaries of 1st and 2nd order entropy.

		1st order				2nd order			
	Window Size	3x3	5x5	7x7	11x11	3x3	5x5	7x7	11x11
1st order	3x3		0.67	0.36	0.23	0.65	0.58	0.37	0.24
	5x5	0.95		0.75	0.38	0.59	0.77	0.67	0.41
	7x7	0.90	0.98		0.56	0.40	0.59	0.79	0.54
	11x11	0.79	0.89	0.95		0.20	0.31	0.46	0.79
2nd order	3x3	0.85	0.86	0.84	0.76		0.77	0.42	0.22
	5x5	0.87	0.91	0.90	0.83	0.97		0.75	0.38
	7x7	0.85	0.91	0.93	0.89	0.93	0.98		0.59
	11x11	0.77	0.85	0.89	0.93	0.81	0.89	0.95	

CHAPTER 2: IMAGE TEXTURE PREDICTS DENSITY AND SPECIES RICHNESS OF BIRDS IN A GRASSLAND-SAVANNA-WOODLAND MOSAIC

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Abstract

For decades, avian ecologists have collected information in the field about habitat in order to understand and predict patterns of bird distribution and abundance. Although field-measured data provides valuable information, the scale of inference possible from such data is limited because large-scale data collection is rarely feasible. Remote sensing methods may offer an alternative, efficient approach to characterize avian habitat across broad areas. We compared the ability of field-measured foliage-height diversity and horizontal vegetation structure with remotely sensed plot-level summaries of digital values and image texture calculated from both an air photo and from a Landsat TM satellite image, to predict patterns of bird density and species richness in a grassland-oak savanna-oak woodland mosaic in the 24,281 ha Fort McCoy Military Installation, Wisconsin, USA. Within habitats, we related these predictive data to the density of three avian species: Grasshopper Sparrow (*Ammodramus savannarum*) a grassland associated bird, Field Sparrow (*Spizella pusilla*) a savanna associated bird, and Ovenbird (*Seiurus aurocapillus*) a species associated with deciduous woodlands and forests. Among habitats, we compared the ability of the field-measures and remotely sensed data to predict avian species richness. Image texture calculated from the air photo was best in predicting Grasshopper Sparrow density ($R^2 = 0.52$, *p-value* <0.01), and avian species richness (R^2 = 0.54, *p-value* <0.01). Ovenbird density was best predicted by plot-level summaries of the satellite data (mean NDVI, R^2 = 0.54, *p-value* <0.01). Field Sparrow density was not particularly well captured by either field-measured or remotely sensed variables, but was best predicted by air photo image texture (R^2 = 0.13, *p-value* <0.01). Our results highlight that image texture measures are superior to field-measured foliage-height diversity in predicting avian biodiversity patterns and thus are useful for biodiversity monitoring and mapping across broad areas.

Key words: avian density, Field Sparrow, foliage height diversity, Grasshopper Sparrow, horizontal vegetation structure, image texture, infrared air photo, NDVI, oak savanna, Ovenbird

Introduction

It is difficult to monitor and map patterns of wildlife diversity and abundance efficiently across broad areas. However, there is a strong need for effective monitoring of biodiversity, given that more than 12% of the world’s birds, 25% of the world’s mammals, 40% of the world’s amphibians, and 20% of the world’s invertebrates are threatened with extinction (Vié et al. 2009), and current trends in biodiversity loss likely to continue (McKee et al. 2004) due to human land-use (Vitousek 1994) and climate change (Botkin et al. 2007). Fine-grained information about biodiversity patterns, such as field-measured habitat measurements or avian point counts, is commonly collected at local scales using well established protocols (Ralph et al. 1995, Martin et al. 1997). However, obtaining fine grained data across broad spatial extents, which is necessary for efficient large scale management and monitoring, is logistically difficult, if not impossible.

Ecologists have long used field-measured data collection methods for measuring habitat variables that influence species diversity (MacArthur and MacArthur 1961, Cody 1981, Cody 1985, Martin et al. 1997). A common field-measured habitat metric used by ornithologists (Karr and Roth 1971, Wiens and Rotenberry 1981, Rosenzweig 1995, Pidgeon et al. 2001), and to a lesser extent mammalogists (August 1983), and entomologists (Murdoch et al. 1972, Southwood et al. 1979, Bestelmeyer and Wiens 2001) is foliage height diversity (MacArthur and MacArthur 1961). Foliage height diversity is an index of vegetation structure (MacArthur and MacArthur 1961) that characterizes heterogeneity in vertical and horizontal vegetation (MacArthur and MacArthur 1961, Wiens and Rotenberry 1981). Variation in foliage-height diversity was originally used to predict avian diversity patterns and niche partitioning among species (MacArthur and MacArthur 1961). Since MacArthur and MacArthur's (1961) seminal work, ecologists have linked foliage height diversity to biodiversity in habitats around the world (e.g., shrub-steppe, Rotenberry and Wiens 1980, Wiens and Rotenberry 1981; scrub vegetation, Greenstone 1984; grassland, Patterson and Best 1996; montane forests, Estades 1997; shrub-steppe and desert, Bestelmeyer and Wiens 2001). However, although field-measured data, such as foliage height diversity, provides valuable fine grained information about habitat heterogeneity, it is generally of limited use for large scale analyses, which is unfortunate since land management and conservation typically operates at broader scales (Burley 1988, Szaro and Johnston 1996, Sutherland 2000).

Remotely sensed data has been used to monitor biodiversity across broad areas (Roughgarden et al. 1991, Stoms and Estes 1993, Nagendra 2001, Turner et al. 2003). Typically, land-cover classes are related to animal distributions (Venier et al. 2004, Gottschalk et al. 2005, Luoto et al. 2007). However, one limitation of this method is that land-cover classes mask within-class variation in vegetation structure (Wood et al. in review). This is problematic because variation in vegetation structure influences the distribution of biodiversity (MacArthur and MacArthur 1961). Alternative approaches to characterize habitat heterogeneity include Light Detection and Ranging (LiDAR, Lesak et al. 2011), Synthetic Aperture Radar (SAR), Bergen et al., 2009, and image texture, which is a measure of the contrast in digital values of pixels. Image texture has been used to characterize vegetation patterns in heterogeneous habitats including sparsely vegetated shrubland and desert (Hudak and Wessman 1998, Hudak and Wessman 2001), grassland-savanna (Wood et al. in review), and forest habitats (Culbert et al. 2009, Estes et al. 2010). Image texture has also been used for studies of diversity (e.g., avian species richness, St-Louis et al. 2006, St-Louis et al. 2009), habitat occupancy (Hepinstall and Sader 1997), habitat selection (Tuttle et al. 2006, Estes et al. 2008), and habitat suitability (Pasher et al. 2007, Bellis et al. 2008).

While image texture offers promise as a tool for ecological studies, it is not clear how well it compares with measures of vegetation structure derived from field-measured foliage height diversity in characterizing avian distribution patterns. Furthermore, the potential of image texture for predicting avian density (i.e., abundance) is untested. Additionally, the range of habitat types in which image texture effectively predicts avian diversity measures such as species richness, is unclear.

Our goal here was to compare the variation in patterns of avian density and species richness associated with field-based vegetation structure measurement, and remotely sensed data including image texture. Our first objective was to assess the amount of variation in *density* of three bird species associated with a) field-measured foliage-height diversity and horizontal vegetation structure b) plot-level summaries of digital values, and c) image texture measures from two remotely sensed data sources. Our second objective was to assess the amount of variation in avian *species richness* associated with the same three types of data.

Methods

Study Area

We collected data on field-measured vegetation structure and avian abundance at the 24,281 ha Fort McCoy Military Installation, located in southwestern Wisconsin, USA (Fig. 1). Approximately 50% of Fort McCoy is off limits to non-military personnel. Three habitat types occur within the boundaries of the available land for study. These include: grasslands, which occur on 16% of the available land, and have less than 5% tree or shrub cover; oak savanna (hereafter referred to as savanna) which occur on 24% of the available land and are characterized by between 5 – 50% tree canopy cover and variable shrub cover; and oak woodland (hereafter referred to as woodland), which occur on 40% of the available land and are characterized by greater than 50% tree canopy cover and variable shrub cover (Fig. 1, Curtis 1959). Common tree species include, in order of dominance, black oak (*Quercus* *velutina*), northern pin oak (*Q. ellipsoidalis*), jack pine (*Pinus banksiana*), black cherry (*Prunus serotina*), red oak (*Q. rubra*), and white oak (*Q. alba*). Shrubs include blueberry (*Vaccinium angustifolium*) and American hazelnut (*Corylus americana*), and grasses include big bluestem (*Andropogon gerardii*) and little bluestem (*Schizachyrium scoparium*).

To select field sampling points, 400 random points, separated by at least 300 m, were generated within grassland, savanna, and woodland habitat, using Hawth's Tools extension in ArcGIS 9.1 (ESRI, Redlands, California, USA 2006). These habitat types were initially identified from a leaf-on infrared air photo taken in late August 2006 and a digital raster graphic map depicting land cover types. Texture calculations can be influenced by paved roads and other manmade structures (e.g., buildings and training ranges). Therefore, all sample points that were within 150 m of such features were removed from consideration. From this set, sample points that were at least 100 m away from the edge of a focal habitat type were retained. Additionally, sample points were only incorporated if there was no significant disturbance (e.g., fire or construction) between the dates when the remotely sensed data was acquired and the field data was collected. This resulted in a total of 172 sample points, with 43 in grasslands, 78 in savannas, and 51 in woodlands (Fig. 1).

Field-measured Vegetation Structure Measurements

At each sample point, foliage height profile measurements were collected in four sub-plots, one located at the center and one each at a random determined distance within 20 - 80 m in the compass directions of 0°, 120°, and 240° (MacArthur and MacArthur 1961, Wiens and Rotenberry 1981). From the center point of each sub-plot, one observer walked 5 m in each of the cardinal directions and vertically placed a 12-m tall telescoping pole, marked at 30-cm intervals, on the ground. A second observer recorded all vegetation instances where vegetation touched the pole (hits) in each 30-cm segment of pole. If the canopy was taller than 12 m, the second observer used binoculars to estimate vegetation hits at approximate 30-cm intervals. This yielded four measurements at each of the four sub-plots totaling 16 foliage height profile measurements at each sample point. From these 16 foliage height profile measurements, foliage-height diversity was computed using the Shannon diversity (MacArthur and MacArthur 1961, Zar 1999) and a horizontal vegetation structure index was calculated by taking the standard deviation of the highest intersection of vegetation with the measuring pole at the 16 sub-plots per sample point (Wiens and Rotenberry 1981).

Avian Point Counts and Focal Species

At each of the 172 sample points, four 100-m variable-radius, five-minute point counts were completed from 25 May to 4 July in both 2007 and 2008 to characterize the avian community during the breeding season (Ralph et al. 1995). In 2009 sample points were visited three times during the same time frame. Observers were trained in bird identification by EMW, who participated in data collection each year. After the training, four observers conducted one count at each sample point during 2007 and 2008. Three observers performed one count at each sample point in 2009. Avian observations were limited to those occurring within 100 m of the sample point, and distance to each detected individual was estimated using laser rangefinders. We recorded raw abundance of three bird species, Grasshopper Sparrow (*Ammodramus savannarum*), Field Sparrow (*Spizella pusilla*), and Ovenbird

(*Seiurus aurocapillus*), which were selected on the basis of their strong association, respectively, with grassland (Vicery 1996), savanna (Carey et al 2008), and woodland habitat (Van Horn and Donovan 1994). Additionally, total species richness among all three counting seasons was calculated per sample point.

Density Calculations

To reduce bias due to detectability differences, density of the three species was estimated by adjusting raw abundance data using Program Distance (Buckland et al. 2001, Buckland et al. 2004, Thomas et al. 2004, Thomas et al. 2010). We fit six distance-adjusted models (half-normal cosine, half-normal hermite polynomial, uniform cosine, uniform simple-polynomial, hazard-rate cosine, and hazard-rate simple polynomial, Buckland et al. 2001). We recorded 1119 unique observation of Grasshopper Sparrow, 1354 unique observations of Field Sparrow, and 334 unique observations for Ovenbird over the sampling period, which exceed sufficient observation levels (> 50 observations) for accurate density calculations (Thomas et al. 2010). The top model, which we used to estimate sample point-specific focal species density, was selected using Akaike's Information Criterion (AIC, Thomas et al. 2010). The resulting sample point density estimates were used as dependent variables in statistical analyses.

Image Texture Processing

Among remotely sensed data products, avian biodiversity has been linked to vegetation productivity and greenness (Lee et al. 2004, Seto et al. 2004, Szép et al. 2006).

Vegetation absorbs more red light, while reflecting about half of the near-infrared light (Gausman 1977), and variations in the ration of infrared to near-infrared reflectance are associated with variation in vegetation productivity. Thus, we calculated plot-level digital value summaries and image texture measures from two sources of remotely sensed data related to productivity and greenness. The first was an infrared air photo (hereafter air photo). Second, we used a Landsat TM image acquired July 13, 2009 (path 25, row 29) from which we calculated the Normalized Difference Vegetation Index (NDVI), which is a measure of photosynthetic capacity (greenness, Tucker 1979), for each pixel.

Plot-level mean and standard deviation summaries of the digital values were calculated using the tool ‘zonal statistics’ in ArcGIS 9.1 for all pixels within 100 m of the sample point. Image texture calculations generate many measures that are collinear (St-Louis et al. 2006, Wood et al. in review). Rather than derive an exhaustive list of image texture measures we used recent findings about the strength of association between birds or field-measured vegetation structure and specific texture measures (St-Louis et al. 2006, St-Louis et al. 2009, Wood et al. in review) to inform our selection of an initial set of image texture measures for predicting avian density and species richness patterns. We included two first-order occurrence measures, variance and entropy, and one second-order measure, contrast (Haralick et al. 1973, Haralick 1979). First-order texture measures do not consider the spatial arrangement of neighboring digital values, while second-order measures do (Haralick et al. 1973, Haralick 1979, Hall-Beyer 2007).

The first-order measures variance and entropy (i.e., Shannon diversity index, Haralick et al. 1973) were computed with a moving window (e.g., 3x3 window), and the texture measure was assigned to the central cell of each moving window. These measures were summarized both as the mean and the standard deviation for each plot. To calculate second-order contrast, the digital values within a window of pixels were translated into a gray-level co-occurrence matrix (GLCM) and the texture statistic was calculated base on this matrix (Haralick 1973, 1979). Image texture was calculated using ENVI (Research Systems Inc., Boulder, Colorado). The tool ‘zonal statistics’ in ArcGIS 9.1 was used to summarize mean and standard deviation of each texture measure within 100 m of each sample point.

Since the scale (as represented by window size) of an image texture measure may affect the strength of its relationship with avian density and species richness, we compared several window sizes. Image texture from the air photo was calculated in 3x3, 7x7, 15x15, 21x21, 31x31, and 51x51 moving windows. Image texture from the NDVI was calculated in 3x3, 5x5, 7x7, and 11x11 windows. We chose these window sizes because they matched the scale of the field-measured vegetation structure indices, they spanned the approximate territory sizes of the focal avian species, and they captured information on the landscape surrounding each plot, which may influence avian distribution patterns (Temple 1998, Mabry et al. 2010). The scales at which texture was calculated from the air photo ranged from 0.001 to 0.26 ha. The scales at which texture was calculated on the NDVI ranged from 0.81 to 10.89 ha. In Wisconsin grasslands, Grasshopper Sparrows have territory sizes from 0.32-1.34 ha (Wiens 1973). In Illinois, Field Sparrow territories range from 0.31 – 1.62 ha (Best 1977). Ovenbird territories range from 0.15 – 0.40 ha in Tennessee (Smith and Shugart 1987), and from 0.45 – 1.62 ha in Ontario (Stenger 1958).

Statistical Analysis

To check for patterns of spatial-autocorrelation, we fit semivariograms of the residuals for the models for each focal species' adjusted density patterns and the models of overall avian species richness (Legendre and Fortin 1989). Semivariograms revealed no spatial autocorrelation affecting the models of either focal species density or avian species richness.

To test our two objectives, whether the amount of variation in density of three bird species or avian species richness was best characterized by a) field-measured foliage-height diversity and horizontal vegetation structure b) plot-level summaries of digital values, or c) image texture measures from the air photo and the NDVI we derived linear regression models with the focal species' densities and avian species richness as dependent variables. For the density regressions, only data from within the focal species' habitat was used, while for regression models involving species richness, data from all 172 sample points was used. If model assumptions were met, but there was a lack of a linear relationship between independent and dependent variables, second-order polynomial (i.e., addition of a quadratic term) regression models were fit. All statistical analysis was completed using the R software package (R Development Core Team 2005).

To evaluate the predictive ability of the best fitting models (i.e., the models with the highest coefficient of determination in regression analysis) we used leave-one-out cross-validation. We used the leave-one-out approach as opposed to k-fold cross-validation because it performs better when the number of observations is low (Shao 1993) and we had only between 43-80 observations (i.e., sample points) for the focal species density regressions. Smaller prediction error values indicate stronger predictive ability. All statistical analysis was completed using the R software package (R Development Core Team 2005).

Results

Predictions of Focal Species Density

Grasshopper Sparrow density was not significantly related to foliage-height diversity or horizontal vegetation structure (Table 1). The plot-level mean summary of the air photo explained 26% of the variation in Grasshopper Sparrow density (Table 2). However, plot-level summaries of NDVI were not significantly related to Grasshopper Sparrow density (Table 3). Grasshopper Sparrow density was most strongly related to the standard deviation of second-order contrast calculated from the air photo in a 51x51 moving window (R^2 = 0.52, *p-value* <0.01, Table 2, Fig. 2). The texture measure calculated from the NDVI that best predicted Grasshopper Sparrow density was the mean of first-order entropy calculated in a 5x5 moving window (R^2 = 0.34, *p-value* <0.01, Table 3, Fig. 2). The top model based on the highest coefficient of determination (see above) had a prediction error of 3.77 (Table 2, Fig. 3).

Field Sparrow density was not significantly related to vegetation structure indices, plot-level summaries from either the air photo or NDVI, or texture measures calculated from NDVI (Table 1-3). Field Sparrow density was most strongly associated with the standard deviation of first-order entropy calculated on the air photo in a 3x3 moving window (R^2 = 0.13, *p-value* 0.02, Table 2, Fig. 2). The top model of Field Sparrow density had a prediction error of 3.82, which was slightly higher than the best prediction error of 3.66 for the second best model based on the highest coefficient of determination, standard deviation summary of first-order variance in a 7x7 moving window. However, that second-best model was associated with only 7% of the variance in Field Sparrow density (Table 2, Fig. 2 and 3).

Ovenbird density was significantly related to foliage-height diversity (R^2 = 0.10, *p-value* <0.01), but not to horizontal vegetation structure (Table 1). The top model explaining Ovenbird density was the plot-level mean summary of NDVI (R^2 = 0.54, *p-value* <0.01, Table 3, Fig. 2). The mean summary of second-order contrast in a 51x51 moving window calculated from the air photo explained 19% of the variance in Ovenbird density (Table 2, Fig. 2). The top model had a prediction error of 0.43 (Table 3, Fig. 3).

Predictions of Avian Species Richness

Foliage-height diversity was intermediate in its association with avian species richness (R^2 = 0.32, *p-value* <0.01, Table 2). Horizontal vegetation structure was the best field-collected vegetation structure index explaining avian species richness (R^2 = 0.40, *p-value* <0.01, Table 2). Plot-level summaries from the air photo were not significantly related, and NDVI-derived plot-level summaries were only weakly related with avian species richness (R^2 = 0.13, *p-value* <0.01, Table 2-3, Fig. 2). Avian species richness was best predicted by the standard deviation of first-order variance calculated from the air photo in a 15x15 moving window (R^2 = 0.54, *p-value* <0.01, Table 2, Fig. 2) and NDVI-derived texture measures were again only weakly associated with avian species richness (Table 3). The top model based on the highest coefficient of determination had a prediction error of 23.20 (Table 2, Fig. 3).

Discussion

Surprisingly, we found that image texture measures, and to a lesser extent, plot-level summaries, were more strongly related to variation in avian density and species richness than field-measured foliage height diversity and horizontal vegetation structure. This is an exciting advance, and a significant step forward in the ability to characterize variation in avian habitat over broad spatial extents. Effective methods for monitoring and mapping species distributions require broad-scale data, and remotely sensed data can provide a 'snapshot' of habitat over extensive areas. We found that image texture can predict density patterns of bird species associated with grassland and woodland habitats. However, this relationship was far weaker within savanna habitat.

For our first objective, we were interested in testing whether the amount of variation in density of three bird species is best characterized by a) field-measured foliage-height diversity and horizontal vegetation structure b) plot-level summaries of digital values, and c) image texture measures from the air photo and NDVI. In all cases, image textures measures, and for the Ovenbird, the plot-level mean of NDVI, were superior to field-measured foliage-height diversity and horizontal vegetation structure in predicting focal avian density.

Grasshopper Sparrow density was highest in areas where second-order contrast was very low in both the air photo and the NDVI data (Fig. 3). These low values correspond to the central areas of two large grassland patches, which is what we expected, because Grasshopper Sparrows use large, open grasslands with little woody cover (Vickery 1996). Furthermore, the strongest relationship with air photo-derived data occurred at the largest scale, 51x51 pixels, (0.26 ha.), and the strongest relationship with NDVI data occurred at the

5x5 window scale (2.25 ha). Thus, texture measures derived from these data sources that differ markedly in resolution, were both strongly associated with variation in Grasshopper sparrow density at scales that span the species' breeding territory size.

We found that both field-measured vegetation structure indices, and remotely sensed image texture were poor predictors of Field Sparrow density patterns. Field Sparrows use habitats with sparse canopies and moderate to high shrub cover (Carey et al. 2008). We expected image texture would capture the variability of tree cover within savanna habitats where Field Sparrow were found in high densities (Table 2) because image texture has been successfully used to characterize avian diversity in the sparsely vegetated Chihuahuan desert (St-Louis et al. 2006, St-Louis et al. 2009). While both field-measured and remotely sensed measures of vegetation structure are significantly different in savannas than in grassland or woodlands (Wood et al. in review), this component of habitat by itself was not strongly associated with patterns of Field Sparrow density. It is likely that additional habitat elements may influence Field Sparrow habitat selection, such as vegetation composition (Rotenberry 1985, MacNally 1990), or landscape scale habitat features (e.g., landscape context, Mabry et al. 2010), and these were not captured by either the field-measured vegetation structure indices or image texture measures.

We found that plot level mean summary of NDVI values was the best predictor of variation in Ovenbird density. In Michigan forests, Laurent et al. (2005) also found NDVI to be a good predictor of Ovenbird occurrence. Furthermore, in both Laurent et al.'s (2005) study and in ours, the scale at which remotely sensed data was most strongly associated with

Ovenbird patterns (in our study, 3.14 ha) corresponds well to the approximate size of the breeding territory (1.6 ha, Stenger 1958).

An unexpected finding of our study was the importance of matching the grain size of an image with the resolution of habitat heterogeneity (i.e., vegetation structure) within a habitat patch. Two habitats at Fort McCoy, grasslands and woodlands, occur in large, contiguous patches throughout the study area. Therefore, information generated using the coarser resolution NDVI was moderately successful in predicting Grasshopper Sparrow (although not as strong as image texture calculated from air photo) and Ovenbird density (Table 3, Fig. 2). Savanna habitats at Fort McCoy occur typically in smaller patches at the edge of grasslands or woodlands. We were not able to find any significant relationships between image texture calculated from NDVI and Field Sparrow density (Table 3). Therefore, we suggest that the within habitat variability of savanna habitats at Fort McCoy, which are high in avian species richness are difficult to capture using image texture measures calculated from the coarser grained NDVI because savanna's occur in small patches throughout the study area. This is an important finding suggesting plot-level summaries and image texture from NDVI may be better at capturing variation in habitat that occurs in large continuous blocks, and not as well suited to assess habitat that occurs in relatively small patches.

Estimating the density of organisms is a common practice for ecologists (Buckland et al. 2001, Thomas et al. 2002, Thomas et al. 2010), and density can provide important information about habitat quality (Bock and Jones 2004). Recent studies have focused on estimating animal densities for unique habitat types delineated by field-measured data (e.g., Grundel and Pavlovic 2007a, b), with few studies linking remotely sensed data to animal density (Clawges et al. 2008). An advantage of using remote sensing based image texture for predicting avian density patterns is that it allows making detailed maps of habitat quality across broad extents. This is often a difficult task with field-measured data. Furthermore, previous maps were generated based on broad land-cover classes which omit important within-in habitat heterogeneity (e.g., vegetation structure). Based on our findings, and those of others (e.g., St-Louis et al. 2006, St-Louis et al. 2009), image texture data can provide a significant increase in the amount of information (broader coverage than field-measured variables) and spatial detail (heterogeneity of vegetation structure), which is necessary for broad-scale conservation planning.

For our second objective, we predicted the amount of variation in avian species richness. Similar to our first objective, image texture measures, derived from the air photo, were superior to field-measured foliage-height diversity and horizontal vegetation structure, plot-level summaries, and image texture derived from the NDVI in predicting focal avian density.

It is well documented that increases in vegetation structural diversity are associated with increases in avian diversity (MacArthur and MacArthur 1961, Cody 1981, Cody 1985). We chose our study area, Fort McCoy, in part because of the wide variation in vegetation structure found there (Wood et al. in review). The top texture measure, first-order variance calculated within a 15x15 moving window from a 1-m resolution air photo, predicted 54% of the variance in avian species richness (Table 2, Fig. 2). In a similar analysis, St-Louis et al. (2006) found the standard deviation summary of first-order standard deviation calculated within a 51x51 moving window from a 1-m resolution air photo, explained approximately 56% of the variance in avian species richness in a Chihuahuan desert grassland-shrubland-pinyon-juniper study area in New Mexico. First-order standard deviation and first-order variance are very strongly correlated texture measures. Furthermore, we found that the standard deviation summary of first-order variance in a 51x51 moving window, the window size used by St-Louis et al. (2006), was also moderately related to avian species richness accounting (accounting for 42% of the variance). First-order texture measures derived from high resolution imagery exhibit strong correlation among scales (i.e., window sizes, Wood et al. in review). Together, these findings suggest avian species richness can be well characterized across broad spatial extents using image texture derived from relatively fine-grained remote sensing data. This highlights the utility of using image texture calculated from high-resolution air photos to characterize habitat and species richness patterns for large areas.

While NDVI has been useful in predicting avian biodiversity patterns in other studies (Seto et al. 2004, Szép et al. 2006, St-Louis et al. 2009) , in the grassland-savanna-woodland mosaic of our study area, it was not strongly associated with patterns of species richness. Additionally, field-measured vertical and horizontal vegetation structure performed better in explaining variation in species richness. We speculate that NDVI may not be a strong predictor of species richness due to the combination of grain size (30 m) and scales (window size) of analysis, which may not capture the strong differences in vegetation structural characteristics of the habitat types. Image texture calculated from NDVI in areas with subtle changes in vegetation may characterize within-habitat variability related to avian species richness (e.g., St-Louis et al. 2009). However, habitats that vary greatly in vegetation structure (e.g., savanna and woodland) occur in a heterogeneous mosaic throughout our study area. Depending on the landscape context of a habitat patch, for example a small savanna patch neighboring dense woodland, a moving-window analysis may quantify digital number values from the woodland habitat into the texture values assigned on the outer edge of a sample point located in the small savanna patch. This may mask the ability to quantify important vegetation structure heterogeneity (i.e., tree and shrub cover) which may be influential in determining species richness patterns.

Conclusion

The goal of our project was to compare the amount of variation in patterns of avian density and species richness that are associated with field-measured foliage height diversity and horizontal vegetation structure, remotely sensed plot-level summaries, and first- and second-order image texture measures. For Grasshopper Sparrow and Field Sparrow density, and avian species richness, field-measured vertical and horizontal vegetation structure, and plot-level summaries were inferior to image texture measures calculated from a high resolution air photo for predicting patterns within (i.e., focal species density) and among (i.e., avian species richness) habitats at Fort McCoy. The plot-level summary of NDVI was superior to field-measured vertical and horizontal vegetation structure data and image texture measures for describing Ovenbird density. Because population density is frequently related to habitat quality, and because remotely sensed data is available at the broad scales that are most relevant to management, this is an exciting development in advancing new data available to avian ecologists.

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Table 2-1. Results of field measured vegetation structure analysis relating Grasshopper Sparrow, Field Sparrow, and Ovenbird density and avian species richness to foliage-height diversity and horizontal vegetation structure. The prediction error for significant models resulting from leave-one out cross validation is also presented.

	R^2	*p*-value	Prediction error
Grasshopper Sparrow			
Foliage-height diversity	0.04	0.146	
Horizontal vegetation structure	0.06	0.060	
Field Sparrow			
Foliage-height diversity	-0.01	0.774	
Horizontal vegetation structure	0.00	0.293	
Ovenbird			
Foliage-height diversity	0.10	0.009	0.74
Horizontal vegetation structure	-0.02	0.636	
Avian species richness			
Foliage-height diversity	0.32	<0.001	47.32
Horizontal vegetation structure	0.40	<0.001	39.62

Table 2-2. Results of linear regression air photo analysis relating Grasshopper Sparrow, Field Sparrow, and Ovenbird density and avian species richness to plot level summaries of digital values, and image texture measures derived. Plot-level indicates simple summaries of digital values whereas image texture measures were calculated within moving windows of several scales (window sizes). Values within cells are R^2. The prediction error for the best model (highest R^2), resulting from leave-one out cross validation, is also presented. Non-significant models at the critical alpha value of 0.05 were not evaluated for prediction performance (i.e., leave one out cross validation).

Texture measure	Window size							Best model *p*-value	Prediction error
	Plot-level	3x3	7x7	15x15	21x21	31x31	51x51		
Grasshopper Sparrow									
Air-photo MEAN	0.26							<0.001	6.13
Air-photo SD	0.01							0.280	
Entropy MEAN		0.00		0.05	0.06			0.106	
Entropy SD		0.00					0.17	0.010	7.10
Variance MEAN		0.17	0.23					0.002	5.97
Variance SD		0.46	0.40	0.37	0.36	0.35		<0.001	4.44
Contrast MEAN									
Contrast SD		0.48	0.43	0.42	0.43	0.45	0.52	<0.001	3.77
Field Sparrow									
Air-photo MEAN	0.00							0.609	
Air-photo SD									
Entropy MEAN		0.10	0.10	0.09	0.08			0.007	3.70
Entropy SD		0.13		0.00	0.00	0.00	0.00	0.002	3.82
Variance MEAN		0.12	0.09	0.08	0.08	0.08		0.003	3.85
Variance SD		0.06	0.07	0.05	0.04	0.03	0.01	0.021	3.66
Contrast MEAN		0.09	0.09	0.09	0.00	0.09	0.09	0.010	3.95
Contrast SD		0.01	0.00	0.00	0.00	0.00	0.00	0.213	
Ovenbird									
Air-photo MEAN	0.00							0.339	
Air-photo SD	0.00							0.580	
Entropy MEAN		0.02	0.06	0.08	0.07	0.07	0.07	0.057	
Entropy SD		0.02		0.00	0.00	0.00	0.00	0.240	
Variance MEAN		0.17	0.08		0.05		0.01	0.004	0.81
Variance SD		0.07	0.00	0.00	0.00	0.00	0.00	0.072	
Contrast MEAN		0.17	0.18	0.18	0.18	0.18	0.19	0.002	0.80
Contrast SD		0.09	0.01	0.00	0.00	0.00	0.00	0.028	0.76
Avian species richness									
Air-photo MEAN									
Air-photo SD									
Entropy MEAN		0.35	0.42	0.39	0.36	0.33	0.31	<0.001	44.69
Entropy SD		0.41	0.22	0.21	0.18	0.13		<0.001	47.73
Variance MEAN		0.45						<0.001	35.76
Variance SD		0.33	0.48	0.54	0.52	0.49	0.42	<0.001	23.20
Contrast MEAN									
Contrast SD									

[†] Columns not populated with model metrics indicate assumptions of linear models could not be met.

Table 2-3. Results of linear regression NDVI analysis relating Grasshopper Sparrow, Field Sparrow, and Ovenbird density and avian species richness to, plot level summaries of digital values, and image texture measures. Plot-level summaries of digital values were not calculated in moving windows (i.e., they encompassed the entire plot) whereas image texture measures were calculated within moving windows at various scales (window sizes). Values within cells are R^2. The prediction error for the best model (highest R^2), resulting from leave-one out cross validation, is also presented. Non-significant models at the critical alpha value of 0.05 were not evaluated for prediction performance (i.e., leave one out cross validation).

Texture measure	Window size					Best model *p*-value	Prediction error
	Plot-level	3x3	5x5	7x7	11x11		
Grasshopper Sparrow							
NDVI MEAN	0.05					0.335	
NDVI SD	0.06					0.270	
Entropy MEAN			0.34	0.29		<0.001	6.01
Entropy SD							
Variance MEAN							
Variance SD							
Contrast MEAN							
Contrast SD							
Field Sparrow							
NDVI MEAN	0.02					0.195	
NDVI SD	0.00					0.731	
Entropy MEAN		0.00	0.00	0.01	0.00	0.283	
Entropy SD		0.00	0.00	0.00	0.03	0.130	
Variance MEAN		0.00	0.00	0.01	0.00	0.286	
Variance SD		0.00	0.00	0.01		0.294	
Contrast MEAN		0.00	0.00	0.00	0.00	0.574	
Contrast SD		0.00		0.00	0.00	0.367	
Ovenbird							
NDVI MEAN	0.54					<0.001	0.43
NDVI SD	0.16					0.006	0.53
Entropy MEAN			0.13	0.13	0.20	0.002	0.73
Entropy SD			0.00	0.00		0.524	
Variance MEAN		0.09	0.29	0.26	0.27	<0.001	0.65
Variance SD		0.06	0.19	0.16	0.07	0.002	0.69
Contrast MEAN		0.12	0.17	0.16	0.24	<0.001	0.48
Contrast SD			0.09	0.11	0.09	0.026	0.60
Avian species richness							
NDVI MEAN	0.13					<0.001	41.74
NDVI SD	0.00					0.598	
Entropy MEAN		0.00	0.15	0.14		<0.001	40.56
Entropy SD		0.00	0.09	0.07	0.01	<0.001	43.24
Variance MEAN							
Variance SD			0.00	0.00	0.09	<0.001	48.36
Contrast MEAN							
Contrast SD							

[†] Columns not populated with model metrics indicate assumptions of linear models could not be met.

Figure Captions

Figure 2-1: A. Location of Fort McCoy Military Installation, within Wisconsin, USA, and B, distribution of 172 sample points. White circles indicate points that are in grasslands, black circles indicate points that are in oak savanna, and white crosses indicate points that are in oak woodlands. The grey shaded area was not accessible for this study.

Figure 2-2: Scatter plots of the relationship between density of Grasshopper Sparrow at 43 grassland sample points, Field Sparrow at 78 savanna sample points, and Ovenbird at 51 woodland sample points, and avian species richness at all 172 sample points with texture measures derived from an infrared air-photo (left column), and NDVI (right column). All relationships significant at the 5% alpha level except for Field Sparrow regressed against NDVI texture measures. The black lines represent results from linear regression with least-squares fitted and 2nd order polynomial lines.

Figure 2-3: Predictive maps for A) Grasshopper Sparrow density, B) Field Sparrow density, C) Ovenbird density, and D) avian species richness. Best model obtained from linear regression analysis relating density and avian species richness versus plot-level summaries and image texture measures calculated from a black-and-white infrared air photo and a NDVI (see Tables 2, 3). Equations used: Grasshopper Sparrow: y = 9.22 + second-order contrast 51x51 sd*-0.36 + second-order contrast 51x51 sd*0.0005$^{\wedge 2}$; Field Sparrow: y = -10.85 + first-order entropy 3x3 sd*0.57 + first-order entropy 3x3 sd*-0.0052$^{\wedge 2}$; Ovenbird: y = -4.7 + NDVI plot-level mean*0.05 + NDVI plot-level mean*-0.0008$^{\wedge 2}$; avian species richness: y = 7.08 + first-order variance 15x15 sd*0.40 + first-order variance 15x15 sd*-0.0021$^{\wedge 2}$.

Figure 2-1

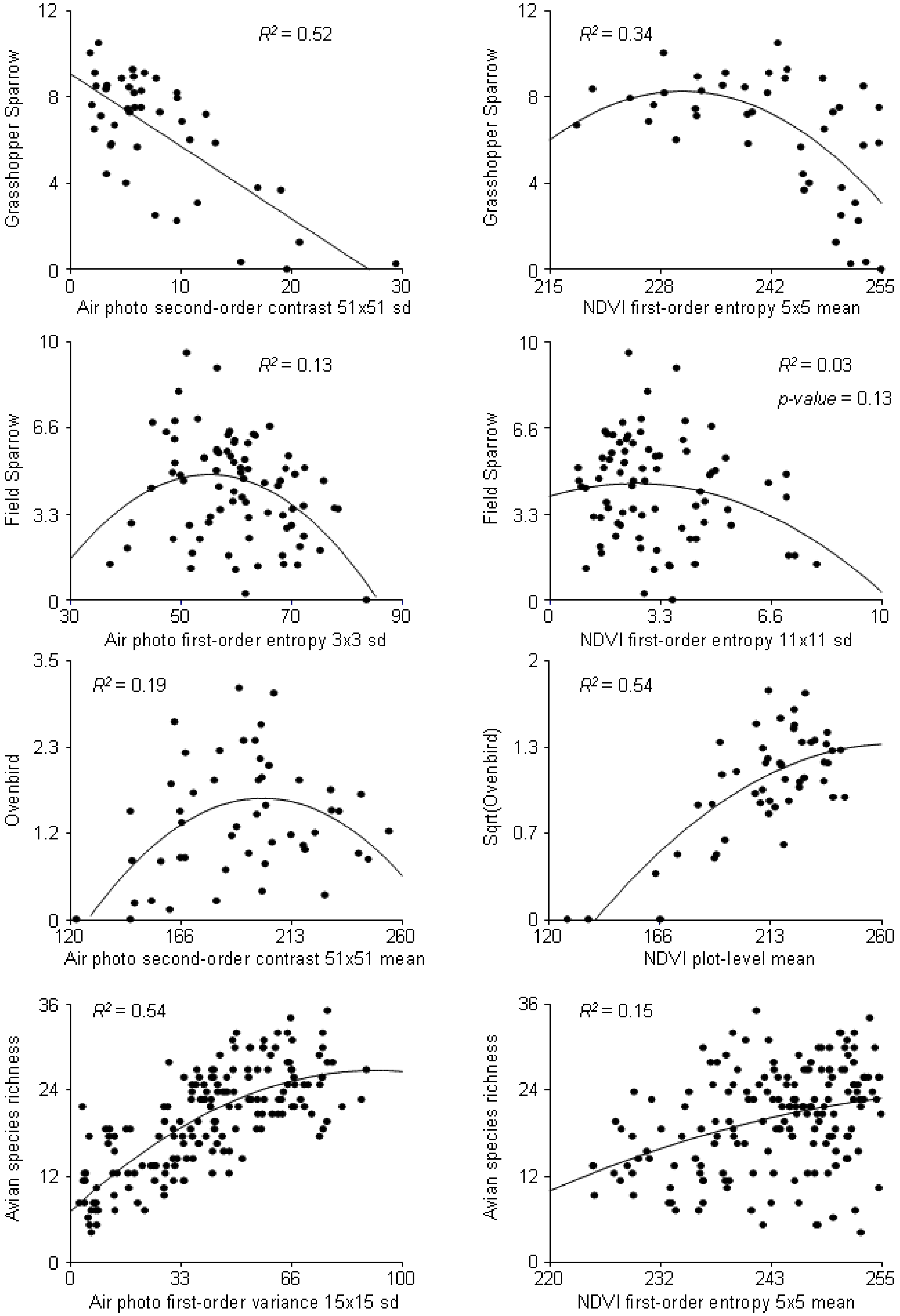
Grasshopper Sparrow
$R^2 = 0.52$
Air photo second-order contrast 51x51 sd
0
10
20
30
12
8
4
0
Grasshopper Sparrow
$R^2 = 0.34$
NDVI first-order entropy 5x5 mean
215
228
242
255
Field Sparrow
$R^2 = 0.13$
10
6.6
3.3
0
Air photo first-order entropy 3x3 sd
30
50
70
90
Field Sparrow
$R^2 = 0.03$
p-value = 0.13
NDVI first-order entropy 11x11 sd
0
3.3
6.6
10
Ovenbird
$R^2 = 0.19$
3.5
2.3
1.2
0
Air photo second-order contrast 51x51 mean
120
166
213
260
Sqrt(Ovenbird)
$R^2 = 0.54$
2
1.3
0.7
0
NDVI plot-level mean
120
166
213
260
Avian species richness
$R^2 = 0.54$
36
24
12
0
Air photo first-order variance 15x15 sd
0
33
66
100
Avian species richness
$R^2 = 0.15$
NDVI first-order entropy 5x5 mean
220
232
243
255

Figure 2-2

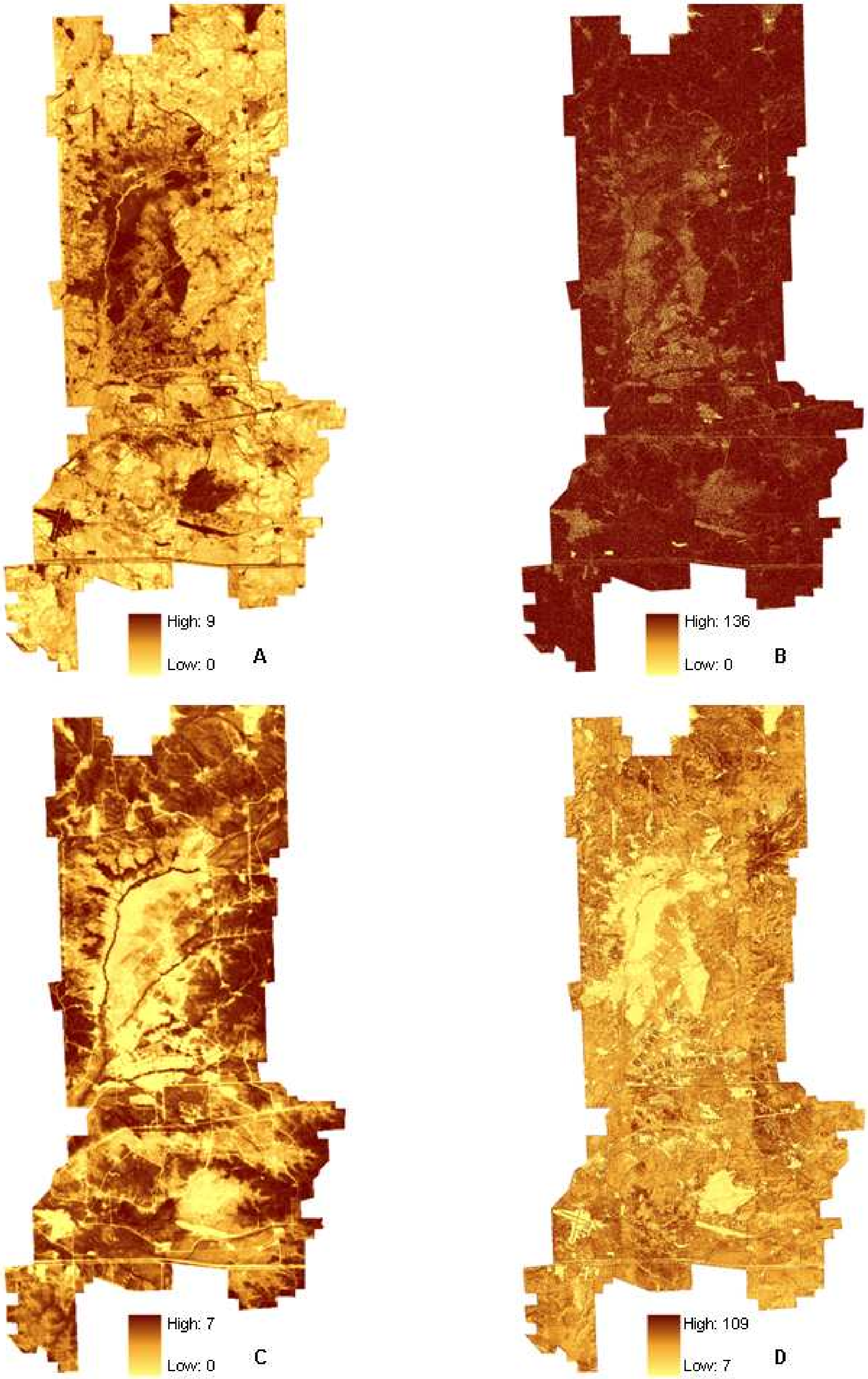

Figure 2-3

CHAPTER 3: EFFECTS OF OAK BARRENS HABITAT MANAGEMENT FOR KARNER BLUE BUTTERFLY (*LYCAEIDES MELISSA SAMUELIS*) ON THE AVIAN COMMUNITY

Coauthors: Anna M. Pidgeon, Claudio Gratton, and Timothy T. Wilder

Abstract

At Fort McCoy Military Installation in Wisconsin, USA, the federally endangered Karner blue butterfly (*Lycaeides melissa samuelis*) is the focal species for a conservation plan designed to create and maintain dry oak barrens, its' required habitat. Management of habitat affects not only target species, but also non-target species. We investigated whether habitat management for Karner blue butterflies influences avian communities using remnant oak barrens (i.e., habitat that has remained in a similar state for approximately 50 years). From 2007 through 2009 breeding bird point count and vegetation data were collected at 186 sample points in five habitats spanning a sparse to closed tree canopy gradient, including remnant oak barrens and oak barrens managed specifically for the Karner blue butterfly. Vegetation characteristics were similar in managed barrens and remnant oak barrens and significantly different from woodlands. Although the bird communities of managed barrens were not analogous to the remnant oak barrens, species of conservation concern, including the Field Sparrow and Vesper Sparrow, and sparse canopy associated bird species, such as the Baltimore Oriole and Eastern Bluebird were found to contribute similarly to the average bird community composition in managed barrens and remnant oak barrens. Adjacent habitat (i.e., vegetation composition of surrounding habitat patches) was the most influential factor in determining the community of bird species using the managed habitat. The findings of this study suggest that management for the Karner blue butterfly influences avian community composition and benefits several avian species of conservation concern. Additionally, our results suggest that Karner blue butterfly habitat management activities adjacent to remnant barrens, rather than adjacent to woodland habitats, have the highest potential for the conservation of oak barrens breeding birds.

Key words: avian community, bird, butterfly, habitat management, Karner blue butterfly, adjacent habitat, oak barren, savanna

Introduction

Without effective strategies to stem the loss of biodiversity, the current trends of species decline and ecosystem decay will likely persist (Grumbine, 1994; Bengtsson et al., 2000; Hooper et al., 2005). In response, in the United States, federal, state, and private agencies have established conservation plans aimed at species recovery. These plans often require restoring or maintaining habitat for species of concern through active management. Managing habitat to promote populations of wildlife species is a science that has evolved from focusing on altering the structure of habitat for single game species (Leopold, 1933) to complex ‘active adaptive management’ approaches aimed to optimize decision-making processes (Walters and Hilborn, 1978; Wilhere, 2002). Although habitat management planning that takes into account all species is a desired goal, practically there may be enough resources to only address the most vulnerable species. Vulnerability arises for many reasons, one of which is dependence on a very specific habitat type that has declined in extent. The degree to which the vulnerable species functions as a surrogate for other species (i.e., a species for which management benefits other species, Caro and O’Doherty, 1999) is usually unknown (Simberloff, 1998; Loyola et al., 2007).

In the north eastern and central portions of the United States, conservation and recovery plans have been implemented for the federally endangered Karner blue butterfly (Lepidoptera: Lycaenidae, *Lycaeides melissa samuelis*, hereafter Karner blue, U.S Fish and Wildlife Service, 2003). Across their range, which extends from Minnesota east to New York (Haack 1993), Karner blue populations have severely declined, due primarily to the loss of barrens habitat (Nuzzo, 1986; Heikens and Robertson, 1994). Barrens are a type of savanna habitat classified by sparse tree canopies (5 – 50% cover), with a diverse forb and grass understory, typically found on poor soils (Curtis, 1959; Bray, 1960). Barrens were historically maintained by fires (Wolf, 2004) and large native grazers (Ritchie et al., 1998). However, following European settlement, anthropogenic modifications, such as plowing and clearing for agriculture and fire suppression have reduced the extent of barrens to highly localized regions (Nuzzo, 1986; Anderson and Bowles, 1999; Leach and Givnish, 1999). The Karner blue needs barrens habitat because the host plant of Karner blue larvae, lupine (*Lupinus spp*.), along with ant species needed by larvae to reach pupation (Pierce et al., 2002) occur in these habitats (Grundel et al., 1998; Grundel et al., 2000). Additionally, the spatially heterogeneous tree canopy cover of barrens provides a diverse suite of Karner blue foraging substrates (i.e., flowering species, Grundel et al., 2000; Grundel and Pavlovic, 2007b) as well as optimal ovipositing locations for females (Grundel et al., 1998). Therefore the federal conservation and recovery plan focuses on restoring and maintaining barrens habitat with the purpose of ‘perpetuating viable metapopulations of the Karner blue’ (U.S. Fish and Wildlife Service, 1997).

Wisconsin is important for the conservation of the Karner blue (Wisconsin Department of Natural Resources, 2009) because some of the largest patches of oak and pine barren in the upper Midwest are found in the state (Anderson and Bowles, 1999). Furthermore, various federal, state, and private landowners have restored barrens habitat for the Karner blue by thinning and burning overgrown barrens or oak woodlands, in addition to mowing, and direct seeding of lupine and other associated forbs (King, 2003; Kleintjes et al., 2003; Wisconsin Department of Natural Resources, 2009). Because of the extent of remnant barrens habitats and management efforts, Wisconsin has some of the highest densities of the Karner blue (U.S Fish and Wildlife Service, 2003). Although the primary objective of federal and state habitat conservation plans is to restore populations of the Karner blue, a secondary objective is to conserve barrens habitat (U.S Fish and Wildlife Service, 2003; Wisconsin Department of Natural Resources, 2009).

Many animal species use barrens habitat in Wisconsin. These include rare species, such as the federally endangered Kirtland’s Warbler (*Dendroica kirtlandii*, Probst et al., 2003), the state endangered Western Slender Glass Lizard (*Ophisaurus attenuatus*, McConkey, 1954), and Phlox Moth (*Schinia Indiana*, Eckstein and Moss, 1995) as well as unique communities of arthropods (Siemann et al., 1997). In addition, a multitude of bird species are found in the sparse canopy habitat (Mossman et al., 1991; Grundel and Pavlovic, 2007a; Au et al., 2008; Mabry et al., 2010), including a nationally listed species of conservation concern, the Red-headed Woodpecker (Rich et al., 2004). Furthermore, many more sparse canopy associated birds that are Partner's in Flight (PIF) species of regional concern within the Prairie Hardwood Transition (Region 23) use barrens habitat such as the Brown Thrasher, Clay-colored Sparrow, Field Sparrow, and Vesper Sparrow (Rich et al., 2004). Even though barrens are an important habitat for several avian species, there are currently no state habitat conservation and management plans for oak barrens avian communities in Wisconsin (Wisconsin Bird Conservation Initiative, 2011).

It has been argued that butterflies are important umbrella taxa for invertebrate conservation (New, 1997; Kerr et al., 2000). Butterfly diversity may also be a useful surrogate for bird diversity (Blair, 1999; Swengel and Swengel, 1999; Fleishman et al., 2003; Thomson et al., 2007), but to our knowledge there are no studies assessing habitat management for a butterfly influences the avian community. We investigated how vegetation and the bird community in habitat maintained and managed for the Karner blue differs from vegetation and the bird community in unmanaged remnant habitats (i.e., habitat that has remained in a similar state for at least 50 years). Our study was conducted at Fort McCoy Military Installation, Wisconsin, USA, in five habitats spanning the continuum from sparse canopy oak barrens to closed canopy woodlands. We had four objectives. The first was to determine the degree of similarity of the vegetation characteristics among oak barrens managed for the Karner blue, remnant oak barrens and woodland habitats. We hypothesized that oak barrens managed for the Karner blue would be similar in vegetation structure characteristics to remnant barrens and different from woodlands. Our second objective was to evaluate the similarity of bird species diversity and composition in oak barrens managed for Karner blue, remnant oak barrens and woodland habitats. We hypothesized that bird species diversity and community composition of oak barrens managed for the Karner blue would be similar to remnant barrens habitats and different from woodland habitats, in large part because of differences in vegetation structure. Our third objective was to determine if individual bird species, particularly species of management and conservation concern, contribute similarly to the bird community in oak barrens managed for Karner blue as in remnant oak barrens. We hypothesized that patterns of species similarity, including sparse canopy breeding bird species of conservation concern, would be similar in the various barrens habitats and different from woodland habitats. For our fourth objective, we investigated whether management method, time since restoration, and type of adjacent habitat would be more influential in shaping the avian community in oak barrens managed for the Karner blue. See section 2.6.4 for detailed hypotheses related to our fourth objective.

Methods

Study Area

We studied bird and vegetation characteristics at the 24, 281 ha Fort McCoy Military Installation, in southwestern Wisconsin, USA (Fig. 1). Fort McCoy has been an operational military installation since 1909. The study area is characterized by varying topography with well-drained sandy soils (Curtis, 1959). The dominant habitats at Fort McCoy range from open sand prairie, to dry oak barrens, which are a sparse tree canopy cover savanna type, to open woodlands and dense forests that are representative of southern Wisconsin. Fire, which has occurred either by prescription, accidentally (e.g., military training), or naturally at Fort McCoy for the past century, has maintained some of the largest tracts of remnant oak barrens habitats in southern Wisconsin. Dominant trees, shrubs and grasses in the upland habitats where this study was focused include black oak (*Quercus velutina*), northern pin oak (*Q. ellipsoidalis*), jack pine (*Pinus banksiana*), bur oak (*Q. macrocarpa*), black cherry (*Prunus serotina*), red oak (*Q. rubra*), white oak (*Q. alba*), red maple (*Acer rubrum*), big-toothed aspen (*Populus gradidentata*), quaking aspen (*P. tremuloides*), red pine (*P. resinosa*), white pine (*P. strobus*), blueberry (*Vaccinium angustifolium*), American hazelnut (*Corylus americana*), big bluestem (*Andropogon gerardii*) and little bluestem (*Schizachyrium scoparium*).

Karner Blue Management and Conservation Areas

Fort McCoy has an approved Karner blue management plan that is used to guide survey and habitat management activities for this species (Wilder, 2006). The plan's main objective is to maintain two large viable populations of Karner blues. To achieve this objective, the installation established 17 Karner blue management areas (Fig. 1). Karner blue management areas were selected for their potential to support high Karner blue populations, were located in low use military training areas, and often contained other rare or sensitive species such as Phlox Moths and Western Slender Glass Lizards. Many different management actions have been utilized over the past three decades to maintain these open areas including: commercial timber sales (i.e., thinning), mowing, removal of small trees and brush with chainsaws, and prescribed burning (Wilder, 2006). It is estimated that to maintain high quality barrens habitat, 15 years is the maximum amount of time that can pass before a burn or thinning treatment is needed (U.S Fish and Wildlife Service, 2003). Mechanical removal of trees and brush are favored over burning in most instances because the Karner blue and many other rare insect species found at Fort McCoy are sensitive to burning (Swengel, 2001; Swengel and Swengel, 2001). On occasion, the objective is to increase the amount of wild lupine and various flowers that the adult Karner blue uses as a nectar source. This can normally be achieved through the management actions listed above, though occasionally wild lupine and other native flowers are planted.

Sample Points

One hundred and eighty six sample points were selected using a stratified random sampling design. Classifications of five upland habitats which are distributed along a sparse canopy to closed canopy gradient, including oak barrens, diverse barrens, oak barrens managed for the Karner blue (hereafter called Karner barren), open woodland, and mixed woodland were adopted and modified from Curtis (1959) and Sample and Mossman (1997) to represent habitats at Fort McCoy. Four of the habitats, oak barrens, diverse barrens, open woodland, and mixed woodland are naturally occurring habitats that are not actively managed. Forty-five sample points were located in oak barrens, which are characterized by a 5 – 50% tree canopy cover, a low percentage of shrub cover (i.e., < 20%) and a diverse herbaceous layer situated on sandy soils. Forty-three sample points were located in diverse barrens, which are similar to oak barrens but with > 20% cover consisting of shrubs (both true shrubs and oak sprouts). Twenty-eight sample points were located in Karner barrens, where active management for the Karner blue is conducted. Thirty-three sample points were located in open woodlands, which have greater canopy cover than barrens (> 50%) and low shrub cover. The previous four habitats are found on sandy soils and have relatively low tree diversity. Thirty-seven sample points were located in mixed woodlands, which are located on more nutrient rich soils than open woodlands and have greater tree diversity and shrub cover. Habitats were delineated using digitized air-photos, land-cover maps, and ground-truthing (e.g., site-surveys prior to vegetation and bird sampling). Random sample points were generated within these stratified regions using Hawth's Tools (Beyer, 2004) in ArcGIS 9.1 (ESRI, Redlands, California, USA, 2008). Sample points were separated by at least 300 m and were located at least 110 m from roads or manmade structures.

Vegetation Characteristics

Vegetation data was collected at 186 sample points following methods adapted from the Breeding Biology Research and Monitoring Database (BBIRD) protocol (Martin et al., 1997). We placed four 5-m radius sub-plots, one located at the center of the sample point, and three at a random distance within a range of 20 m to 80 m at 0°, 120°, and 240°. At each sub-plot we visually estimated percent cover for: bare ground, leaf litter, moss, fern, herbaceous materials (e.g., grass, forb, sedge, rush), and woody materials (e.g., shrub and tree saplings). From the center of each sub-plot, canopy cover was estimated using a spherical densitometer. Data from each of the four sub-plots was averaged, resulting in a single value for each vegetation variable for each sample point.

Avian Point Counts

At each of the 186 sample points, four, standardized five minute point counts were completed from 25 May to 4 July from 2007 to 2008 to characterize the avian community during the breeding season (Hutto et al., 1986; Ralph et al., 1995). In 2009 sample points were visited on three occasions during the same time frame. Observations were limited to 100 m, and distance to each bird was estimated with a laser rangefinder and flagging placed at known distances. To distribute observer variability as equally as possible, four trained observers during 2007 and 2008 and three trained observers in 2009 performed one count at each sample point. Observers were extensively trained by the lead author on bird identification and sampling protocol prior to field sampling. The lead author was one of the observers each year.

Data Analyses

To determine if there was a global difference of vegetation characteristics among habitats, we using a multiple analysis of variance (MANOVA) using six response variables, % cover of tree, shrub, bare ground, grass, forb, and leaf litter, with habitat as the treatment. Because the MANOVA revealed a global difference among the five habitat types (*p*-value <0.001), we then used a one-way analysis of variance (ANOVA) to determine the difference in the six vegetation elements among habitat types, with habitat type used as the treatment. Assumptions of normality and equal variance were checked and following all significant ANOVAs, a Tukey’s HSD test for multiple comparisons among habitats was used (Zar, 1999). Pairwise comparisons among habitats were evaluated using a Bonferroni adjustment of the critical value alpha (0.05/10 = 0.005).

To investigate the structure of the avian community among habitats, we calculated two indices of community diversity: species richness (*S*), and Shannon diversity (*H'*). Both indices were averaged among years for each sample point. We used ANOVA, with habitat as the treatment and, for all significant ANOVAs, a Tukey's HSD test for multiple comparisons. All ANOVA analyses, and species richness and Shannon diversity metrics were computed using the R statistical software program (R Development Core Team, 2005).

To identify the degree of similarity of the avian communities in the five habitat types, we performed nonmetric multidimensional scaling ordination (NMS) on the square-root transformed average abundance of bird species over the three seasons (Carr, 1997). We used a square-root transformation because it is commonly used for count data (Zar, 1999). To explore group membership of bird species among habitats, we used a hierarchical cluster analysis (Clarke and Gorley, 2006). In this analysis we used the Bray-Curtis dissimilarity measure, which is commonly used to quantify species similarity among environmental gradients (McCune et al., 2002)

In a second analysis of community similarity we conducted a one-way analysis of similarities test (ANOSIM, Carr, 1997), using the Bray-Curtis similarity of the square-root transformed average abundance of bird species. The ANOSIM test uses Monte Carlo randomization of observed data to assess whether rank similarities within habitats are more different than among habitats. We used 999 Monte Carlo permutations to generate the random test statistic, *R*, which generally ranges from 0 to 1. An *R* value near zero indicates that the avian community does not differ among habitats, while larger *R* values indicate increasing dissimilarity. Pairwise comparisons among habitats were evaluated using a Bonferroni adjusted alpha value (0.05/10 = 0.005).

To assess which bird species were primarily responsible for an observed difference in avian communities among habitats, we used a similar percentages (SIMPER) analysis, with habitat as the factor (Clarke and Warwick, 1994), on the square-root transformed bird abundance. A SIMPER analysis is a non-parametric multivariate analysis of difference in community structure in relation to factors differentiating sample points. We used Bray-Curtis as our dissimilarity measure (McCune et al., 2002). The NMS, and all ANOSIM and SIMPER analyses were completed using the PRIMER statistical software package (version 6, PRIMER-E, Ltd., Plymouth, U.K., Clarke and Gorley, 2006).

Factors Influencing the Avian Community Found in Karner Blue Managed Habitat

In order to investigate if the avian community in Karner barrens was influenced by the Karner blue management plan, randomization tests using the *R* test statistic (ANOSIM, Carr, 1997), were performed following methods described in 2.6.2. We hypothesized that three factors potentially influence community structure, diversity, and distribution, and we included these factors in randomization tests. The first factor was management method used for the management of Karner barrens, which included thinning, burning, both thinning and burning, or no treatment (i.e., existing barren habitat). We believed that bird species would respond differently to different management treatments because other studies in similar habitat to our study found management methods (e.g., burning) influenced which birds use managed oak savanna (Au et al., 2008). Of 28 sample points, 14 were thinned, 11 were burned, and three were not treated during the previous twenty years, although they were designated as Karner management areas. The second factor was time, measured in years since the last treatment used to restore habitat for the Karner blue, and ranged from 1 to 20 years. This factor was categorized into three groups; 1-10 (*n* = 17), 10-20 (*n* = 8). The third group included the three untreated sample points (> 20 years). We hypothesized that the number of years since management treatment would influence the avian community, with species that prefer structurally simpler conditions more likely to occupy sites in the years immediately after treatment, and species preferring greater structural heterogeneity to be more evident with increasing time since treatment (e.g., increase in oak sprouts and shrub growth). The third management factor we considered was habitat adjacent to Karner management patches. We hypothesized that the vegetation composition and structure of habitat patches adjacent to managed Karner barrens patches would influence the avian community within Karner barrens, because other studies in the region had found habitats adjacent to oak savanna (i.e., landscape context), to largely influence the bird community within the oak savanna habitats (Mabry et al., 2010). We classified the habitat of neighboring patches, using high-resolution air-photos, into barrens, woodlands, or other. We found that nine Karner barrens were adjacent to remnant oak barrens and 19 were adjacent to woodlands. We used a Bonferroni adjustment for pairwise comparisons for management and treatment year ($\alpha = 0.05/3 = 0.017$).

To assess which bird species were primarily responsible for an observed difference in the avian community among Karner barrens sample points, a SIMPER analysis on the square-root transformed average bird abundance was used (Clarke and Warwick, 1994).We used the Bray-Curtis as our dissimilarity measure (McCune et al., 2002). Three separate SIMPER analyses were conducted where sample points were grouped by the three factors described above for each individual analysis.

Results

Vegetation Characteristics

Unsurprisingly, vegetation characteristics varied among the five habitats (Table 1). Karner barrens were similar to the oak and diverse barrens and different from open and mixed woodlands in percent tree canopy cover and forb cover and similar to the diverse barrens and mixed woodlands in percent shrub cover. Mean percent bare ground cover was lower in Karner barrens than in either oak barrens or diverse barrens.

Patterns of Avian Community Diversity

We found that one measure of diversity, avian species richness, was highest in oak and diverse barrens and both values were significantly greater than species richness in Karner barrens. Species richness in Karner barrens and mixed woodlands was similar, and species richness in Karner barrens was greater than in open woodland (Table 1). Shannon diversity of the bird community was significantly higher in oak and diverse barrens than in the two woodland habitats. Shannon diversity in the Karner barrens was not different from diversity in any of the other four habitats (Table 1).

The hierarchical cluster analysis revealed two groupings at the 40% similarity level representing sparse canopy and dense canopy avian communities (Fig. 2). Although the community of bird species using Karner barrens was mainly grouped with the oak and diverse barrens avian communities, the Karner barrens community spans a broad range and some of the points are placed in the area of intersection between barrens and woodland groups. The ANOSIM randomization tests of species similarity matrices suggest that all five habitats harbored different avian communities (Global $R = 0.46$, $p < 0.001$; Table 2). However, on closer inspection, similarities among the three barrens habitats and between the woodland habitats indicated that the avian communities within these habitat groupings were more similar to each other. The Karner barrens avian community was most similar to the diverse barrens avian community ($R = 0.23$, $p < 0.001$), and was most different from the avian communities of mixed woodland ($R = 0.34$, $p < 0.001$), oak barren ($R = 0.36$, $p < 0.001$), and open woodland ($R = 0.53$, $p < 0.001$, Table 2). The avian communities of open woodland and mixed woodland ($R = 0.06$) and the oak barrens and diverse barrens (0.06) were most similar.

We found that birds tended to fall into one of three groups: those that used the three barrens habitats, those that used the two woodland habitats, and those that used both barrens and woodland habitat (Table 3). A species of conservation concern, the Field Sparrow, as well as American Goldfinch, Baltimore Oriole, Chipping Sparrow, Eastern Bluebird, and House Wren contributed comparable cumulative similarities in oak, diverse, and Karner barrens (Table 3). Four other species of conservation concern, the Blue-winged Warbler, Brown Thrasher, Grasshopper Sparrow, and Vesper Sparrow, together with the Eastern

Kingbird, Gray Catbird, Mourning Dove, Orchard Oriole, and Song Sparrow were most common in barrens habitats (Table 3). Bird species that contributed more to the cumulative similarity of woodland habitats included the regional stewardship species Rose-breasted Grosbeak, as well as the Blue-gray Gnatcatcher, Eastern Wood-Pewee, Great-crested Flycatcher, Ovenbird, Red-eyed Vireo, Scarlet Tanager, Veery, White-breasted Nuthatch, and Yellow-throated Vireo (Table 3). Four species, including the Blue Jay, Brown-headed Cowbird, Eastern Towhee, and Indigo Bunting contributed comparable percent similarities to all habitats (Table 3).

Factors Influencing the Avian Community Found in Karner Blue Managed Habitat

Of the three factors we tested that were directly associated with the avian community of Karner blue management areas, adjacent habitat (i.e., whether Karner barrens were adjacent to remnant barrens or woodlands) had the greatest effect on the community within the Karner managed patch ($R = 0.32$, $p < 0.001$), as we had predicted it would. Management method ($R = 0.21$, $p = 0.006$) also affected the avian communities, though to a lesser degree. In contrast to our expectation, treatment year ($R = 0.15$, $p = 0.052$) did not result in significantly different communities (Table 4).

The avian community in Karner barrens adjacent to woodlands harbored bird species more typical of dense canopy habitats such as Eastern Wood-Pewee, Red-eyed Vireo, Rose-breasted Grosbeak, and Scarlet Tanager (Table 4). Sample points in Karner barrens situated next to oak and diverse barrens harbored bird species typical of sparse to open canopy cover habitats such as Vesper Sparrow, Eastern Bluebird, Baltimore Oriole, Eastern Kingbird, Mourning Dove, Brown Thrasher, and Orchard Oriole (Table 4). In terms of the effect of management technique used to create Karner barrens, burned areas tended to harbor bird species typical of sparse canopy habitats. However, one surprising species, the Scarlet Tanager, also contributed moderately to the bird similarity within burned Karner barrens.

Discussion

Our results suggest that the management of oak barrens for the Karner blue in Wisconsin creates habitat that closely resembles remnant barrens, in both vegetation and avian community patterns. Furthermore, it appears that the adjacent habitat surrounding the management areas affects the composition of birds using the managed barrens. Thus, habitat management for the Karner blue does affect the avian communities. The Karner barrens included avian species typical of sparse canopy habitats as well as a low number of species typical of woodlands, and provided habitat for five species of conservation concern (Table 3).

One of the primary techniques used for the conservation of the Karner blue is habitat management (Kleintjes et al., 2003; King et al., 2007). For our first objective, we hypothesized Karner barrens would be similar in vegetation structure characteristics to remnant barrens and different from remnant woodlands. We found this to be true and consistent with findings of other studies in the region (King, 2003; Nielsen et al., 2003). Karner barrens also exhibited a distinctly higher percent cover of shrubs and tree sprouts than oak barrens, but not diverse barrens (Table 1). Other studies in similar systems within the region have also noted the rapid growth of shrubs and tree saplings following thinning

(Peterson and Reich, 2001; Brudvig and Asbjornsen, 2007). Not only was shrub cover in Karner barrens and diverse barrens similar, the avian communities of Karner and diverse barrens were also more similar to each other than to the avian communities of oak barrens (Fig. 2), suggesting that shrub cover is an influential driver of bird distributions in this ecosystem. Our findings echo those of (Sirami et al., 2009) who found that the amount of shrub cover in African savannas influenced bird diversity.

Species richness and diversity were highest in oak and diverse barrens, followed by Karner barrens, and lowest in woodland habitat, which was consistent with findings in other regional savannas and barrens (Temple, 1998; Au et al., 2008; Mabry et al., 2010). However our findings differed from those of (Grundel and Pavlovic, 2007a) who found woodlands and forests, in an Indiana prairie-savanna-woodland-forest mosaic to harbor more avian species and higher diversity (*H’*). It is possible that differences in the vegetation composition and structure, as well as differences in patch area and the adjacent habitat among habitats contributed to differences in avian use of the habitats between Indiana and Wisconsin.

For our second objective, we originally hypothesized that bird species diversity and community composition of oak barrens managed for Karner blue would be similar to remnant barrens habitats and different from woodland habitats. Despite the similarities among species diversity (Table 1) and the avian communities of the barrens habitat (Fig. 2), the avian species composition of the Karner barrens appear to be similar but not identical, with substantial overlap with the other two barrens types (Fig. 2). Although we found support for our hypothesis, we suggest that shrub cover accounts for the differences in the avian communities among the three barrens habitats and highlights the need to possibly manage shrub encroachment in recently treated (e.g., thinned) barrens habitats.

We found support for our hypothesis related to our third objective that sparse canopy bird species contributed similarly to the bird community in Karner barrens as in remnant barrens, and different from woodlands (Table 3). This was similar to findings in a restored Illinois oak savanna (Brawn, 2006) where sparse canopy associated bird species, such as the Baltimore Oriole, where more abundant in restored savannas than woodland habitats. Temple (1998) predicted that a given barrens (savanna) avian community will be composed of sparse canopy species such as the Baltimore Oriole and Eastern Bluebird, which occupy niches provided by the stochastic heterogeneity of barrens, along with species from neighboring open grasslands such as the Grasshopper Sparrow or closed canopy woodlands such as the Scarlet Tanager, highlighting the influence of the adjacent habitat (or landscape context) on avian communities among prairie-savanna-woodland habitats. Even though the diversity and composition of avian communities in Karner barrens did not mirror those of oak and diverse barrens (Table 2), our results suggested that management for the Karner blue provides important breeding habitat for sparse canopy associating species including some of conservation concern like the Field Sparrow, and to a lesser extent the Vesper Sparrow (Table 3).

We found greater support for the hypothesis that avian community structure within Karner barrens was more likely to be influenced by the adjacent habitat than by management technique, or time since major restoration treatment (Table 4). Our results concur with findings in Midwestern oak savannas (Temple 1998, Mabry et al., 2010) and California oak woodlands (Sisk et al., 1997) that the composition of the surrounding habitats strongly influences avian community composition. Management and treatment year were not as influential as adjacent habitat possibly because, as long as barrens habitat exists, regardless of how it was created or how long since the major treatment (i.e., time lags of vegetation succession) it meets the breeding habitat requirements of a particular set of species and influences which bird species colonized the managed breeding habitat (Dunning Jr. et al., 1992; Dunning Jr. et al., 1995).

Conservation Implications

We found that habitat management for the Karner blue at Fort McCoy not only perpetuates viable Karner blue metapopulations, but also provides habitat for oak barrens birds. Further, we found the composition and structure of habitat adjacent to sites selected for restoration and management for Karner blue habitat has a large effect on bird species composition. Although it is true that the first priority for Karner blue management is to create suitable conditions for the Karner blue butterfly, within this goal there is the opportunity to provide breeding habitat for sparse canopy associated bird species, including some species of conservation concern. This is important because there are currently no management plans for bird species using oak barrens habitats in Wisconsin. By careful consideration of patch context and selection of sites for restoration that are adjacent to existing remnant barrens, the highest habitat benefit is achieved for oak barrens breeding birds, with no compromise to Karner blue habitat and populations.

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Table 3-1. Mean summary (± SE) of percent cover of six habitat elements and of avian diversity represented by species richness and the Shannon index along a canopy cover gradient at Fort McCoy Military Installation, Wisconsin. Variables with same letter (A-C) do not differ significantly among habitats (one-way ANOVA, Tukey's HSD test, $p < 0.05$). Variables without letter were not included in multiple comparisons test because they did not meet critical assumptions of the tests.

	Oak barren	**Diverse barren**	**Karner barren**	**Open woodland**	**Mixed woodland**
Vegetation					
Tree[†]	18.29^{A} ± 1.87	24.49^{A} ± 1.93	24.21^{A} ± 2.99	86.02^{B} ± 2.49	81.13^{B} ± 2.49
Shrub[‡]	11.57^{A} ± 1.78	34.38^{B} ± 1.83	34.88^{B} ± 2.84	10.83^{A} ± 2.37	29.63^{B} ± 1.98
Bare	21.87^{A} ± 2.41	13.19^{B} ± 2.49	10.69^{B} ± 3.85	3.03 ± 3.21	1.17 ± 2.69
Grass[§]	18.76^{A} ± 1.76	17.60^{A} ± 1.82	29.02^{B} ± 2.82	4.25 ± 2.34	4.51 ± 1.96
Forb	10.76^{A} ± 0.99	12.38^{A} ± 1.02	11.50^{A} ± 1.58	3.33^{B} ± 1.31	5.42^{B} ± 1.10
Leaf Litter	14.15^{A} ± 1.99	24.39^{B} ± 2.06	18.21^{B} ± 3.18	56.20^{C} ± 2.64	44.22^{D} ± 2.22
Avian diversity					
Richness	24.71^{A} ± 0.89	24.79^{A} ± 0.78	21.10^{B} ± 0.93	16.21^{C} ± 0.90	18.72^{BC} ± 0.85
Shannon index	3.02^{A} ± 0.06	3.04^{A} ± 0.05	2.87^{AB} ± 0.06	2.64^{B} ± 0.06	2.76^{B} ± 0.05

[†] Tree – composite variable of hardwood cover and conifer cover combined.

[‡] Shrub – composite variable of percent cover of 'true' shrubs, and 'tree-shrubs' (i.e., tree saplings between 1 m > < 5 m) combined.

[§] Grass – composite variable of percent cover of grass and sedge combined.

Table 3-2. One-way analysis of similarities (ANOSIM) of avian communities in five habitats: oak barren, diverse barren, Karner managed barren (Karner barren), open woodland, and mixed woodland, from three breeding seasons, 2007-2009. Numbers below the diagonal are *R* values. Numbers above the diagonal are *p*-values. Pairwise comparisons among habitats were evaluated using a Bonferroni adjustment of the critical alpha value (0.05/10 = 0.005).

	Oak barren	Diverse barren	Karner barren	Open woodland	Mixed woodland
Oak barren†	…	0.002	<0.001	<0.001	<0.001
Diverse barren†	0.06	…	<0.001	<0.001	<0.001
Karner barren	0.36	0.22	…	<0.001	<0.001
Open woodland†	0.86	0.81	0.53	…	0.009†
Mixed woodland†	0.74	0.65	0.34	0.06	…

Global R = 0.46, *P* < 0.001

† Not significant at the Bonferonni adjusted α = 0.005

Table3-3. Contributed % of similarity calculated using a similar percentages analysis (SIMPER) for the thirty one most abundant bird species in five habitat types at Fort McCoy Military Installation, WI, USA.

	Oak barren (*n*=45)	**Diverse barren** (*n*=43)	**Karner barren** (*n*=28)	**Open woodland** (*n*=33)	**Mixed woodland** (*n*=37)
Species of conservation concern					
Blue-winged Warbler†‡	....	....	1.55	....	....
Brown Thrasher†‡	2.61	2.37	....	....	....
Field Sparrow†‡	11.57	14.30	15.07	....	2.13
Grasshopper Sparrow†‡	5.89	....	....	....	....
Rose-breasted Grosbeak§	1.53	1.91	2.00	7.52	8.11
Vesper Sparrow†‡	8.38	7.42	2.16	....	....
Species of least concern					
American Goldfinch	1.54	1.38	1.74	....	....
Baltimore Oriole	4.52	3.98	4.58	....	1.31
Black-capped Chickadee	1.39	1.67	....	....	1.81
Blue Jay	2.49	2.33	2.03	2.58	1.15
Blue-gray Gnatcatcher	....	....	2.13	2.19	1.17
Brown-headed Cowbird	9.07	9.05	9.92	12.61	10.52
Chipping Sparrow	8.24	8.09	6.84	....	2.30
Common Yellowthroat	....	....	....	....	1.06
Eastern Bluebird	6.47	6.51	4.33	....	....
Eastern Kingbird	4.10	1.61	....	....	....
Eastern Towhee	5.35	8.15	10.93	6.78	7.29
Eastern Wood-Pewee	1.72	1.75	3.00	11.87	8.26
Gray Catbird	2.09	2.04	....	....	....
Great-crested Flycatcher	....	....	2.55	1.68	1.22
House Wren	2.67	2.95	1.84	....	....
Indigo Bunting	4.90	8.22	11.90	7.66	10.09
Mourning Dove	4.38	4.08	1.53	....	....
Orchard Oriole	2.11	....	....	....	....
Ovenbird	....	....	....	14.03	12.95
Red-eyed Vireo	....	....	2.11	11.36	6.49
Scarlet Tanager	....	1.25	2.77	9.85	7.70
Song Sparrow	....	1.41	....	....	....
Veery	....	....	....	....	1.08
White-breasted Nuthatch	....	....	1.61	2.26	3.99
Yellow-throated Vireo	....	....	....	....	1.06

† Partner's in Flight priority species of continental and regional concern: Region 23 Prairie Hardwood Transition.

‡ Species of Greatest Conservation Need (SGCN) for Wisconsin's Comprehensive Wildlife Conservation Plan.

§ Partner's in Flight species of regional stewardship. Region 23 Prairie Hardwood Transition.

Table3-4. Contributed % of similarity calculated using a similar percentages analysis (SIMPER) for 23 common birds in Karner blue butterfly managed barrens. Analysis evaluated % similarity as a function of three independent factors including management method (i.e., type of management technique used to restore or maintain Karner barrens), treatment year (i.e., time since treatment method), and adjacent habitat (i.e., whether sample points located in Karner barrens were adjacent to remnant barrens or woodland habitats). *R* values represent results of randomization tests (ANOSIM) on the differences in avian communities of each of the factor groupings

	Management method			**Treatment year**			**Adjacent habitat**	
	(*R* = 0.21, p = 0.006)			(*R* = 0.15, p = 0.052)			(*R* = 0.32, p < 0.001)	
	Thinned (n=14)	Burned (n=11)	No treatment (n=3)	1 to 10 (n=17)	10 to 20 (n=8)	> 20 (n=3)	Barrens (n=9)	Woodlands (n=19)
Species of conservation concern								
Blue-winged Warbler[†‡]	....	2.04	2.51	5.62	....	....	....	1.72
Brown Thrasher[†‡]	....	2.92	....	....	4.06	....	3.22	....
Grasshopper Sparrow[†‡]	....	....	2.44	....	....	....	....	....
Field Sparrow[†‡]	13.18	11.97	12.92	11.77	10.93	12.96	11.88	12.64
Rose-breasted Grosbeak[§]	2.12	....	5.68	5.22	....	3.14	....	3.02
Vesper Sparrow[†‡]	....	4.08	....	....	4.05	....	6.09	....
Species of least concern								
Baltimore Oriole	3.71	5.09	....	....	7.77	3.02	7.33	2.64
Blue-gray Gnatcatcher	5.15	....	....	5.22	....	4.43	....	5.06
Brown-headed Cowbird	9.85	9.23	9.61	8.33	8.67	9.84	8.80	9.72
Chipping Sparrow	7.82	4.31	7.36	6.24	3.21	8.02	3.70	7.65
Eastern Bluebird	5.16	4.07	....	....	7.55	4.32	8.04	2.96
Eastern Kingbird	....	....	....	....	2.20	10.71	3.53	....
Eastern Towhee	12.06	9.67	6.80	10.22	8.79	....	8.31	11.26
Eastern Wood-Pewee	3.60	2.15	5.66	4.39	....	4.59	....	4.66
Gray Catbird	....	3.28	....	4.68	2.45	....	2.87	....
Great-crested Flycatcher	2.53	1.93	5.66	5.22	....	2.85	1.42	3.18
House Wren	2.47	2.69	....	....	3.98	1.42	3.05	1.55
Indigo Bunting	11.99	8.69	9.61	9.41	7.74	11.57	8.54	11.13
Mourning Dove	....	4.07	....	5.62	3.06	....	3.71	....
Orchard Oriole	....	....	....	....	2.82	....	2.24	....
Ovenbird	....	....	5.66	....	....	....	....	....
Red-eyed Vireo	3.35	....	2.51	....	....	3.92	....	3.48
Scarlet Tanager	1.72	2.75	7.36	5.10	1.80	2.92	1.35	3.40

[†] Partner's in Flight priority species of continental and regional concern: Region 23 Prairie Hardwood Transition.

[‡] Species of Greatest Conservation Need (SGCN), Wisconsin's Comprehensive Wildlife Conservation Plan.

[§] Partner's in Flight species of regional stewardship. Region 23 Prairie Hardwood Transition.

Figure Captions

Figure 3-1: A. Location of Fort McCoy Military Installation, Wisconsin, USA, B. Fort McCoy, C. Subset of five habitats and sample points where bird and vegetation surveys were completed during the 2007-2009 breeding season.

Figure 3-2: NMS plots of resemblance matrix (Bray-Curtis, log-transformed average bird abundance) for (A) fifty four common breeding bird species among barrens and woodland habitats, (B) and all sample points distributed among all five habitats. Stress indices were a measure of fit between the resemblance matrix and the two-dimensional representation of the similarity matrix (0.10 to 0.20 = good fit). Lines around points in (B) were groupings indicating avian community membership, independently determined by cluster analysis (group average, > 40% similarity). Dotted circle indicates barrens avian communities. Solid circle represents woodland avian communities.

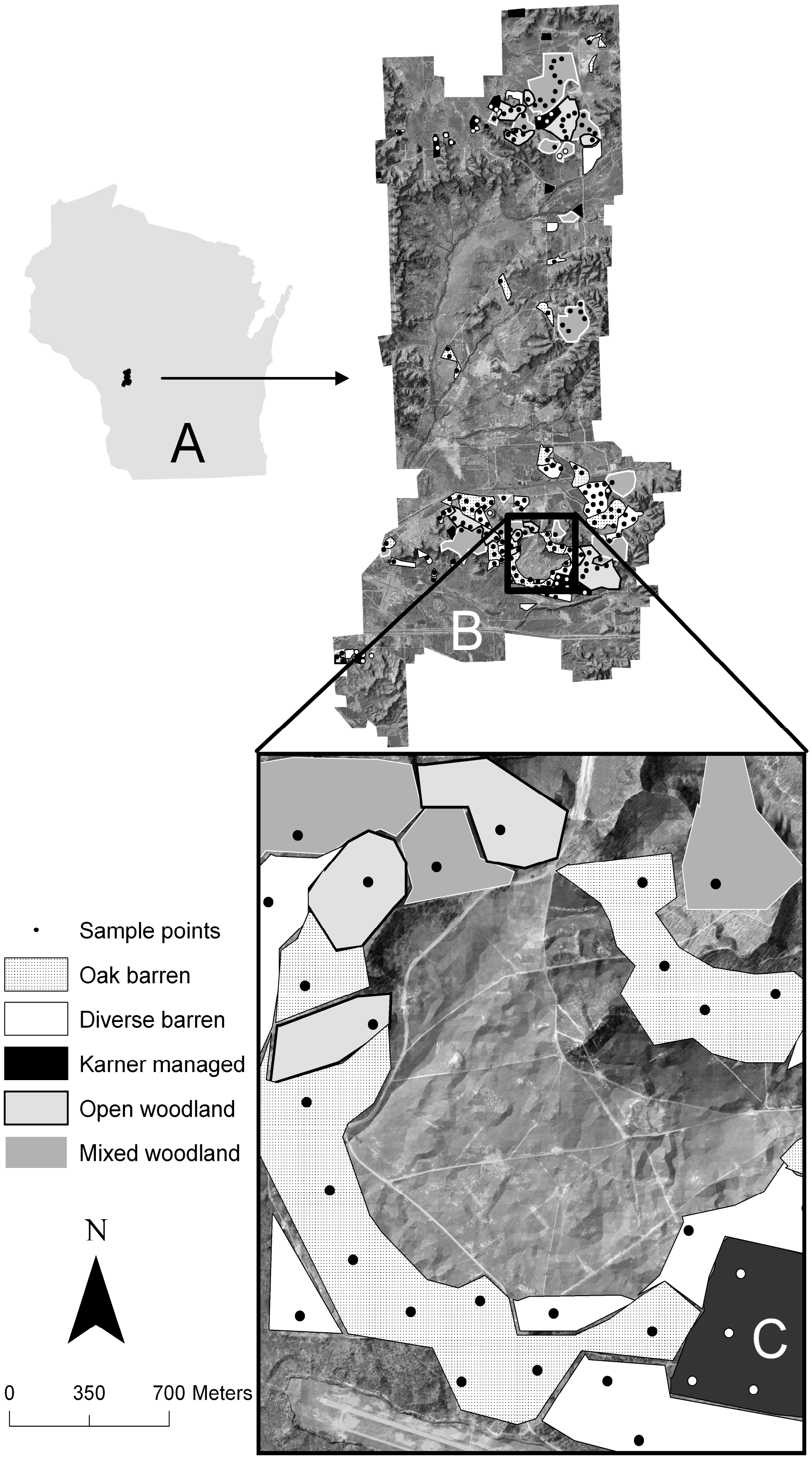
A
B
C
Sample points
Oak barren
Diverse barren
Karner managed
Open woodland
Mixed woodland
N
0
350
700 Meters

Figure 3-1

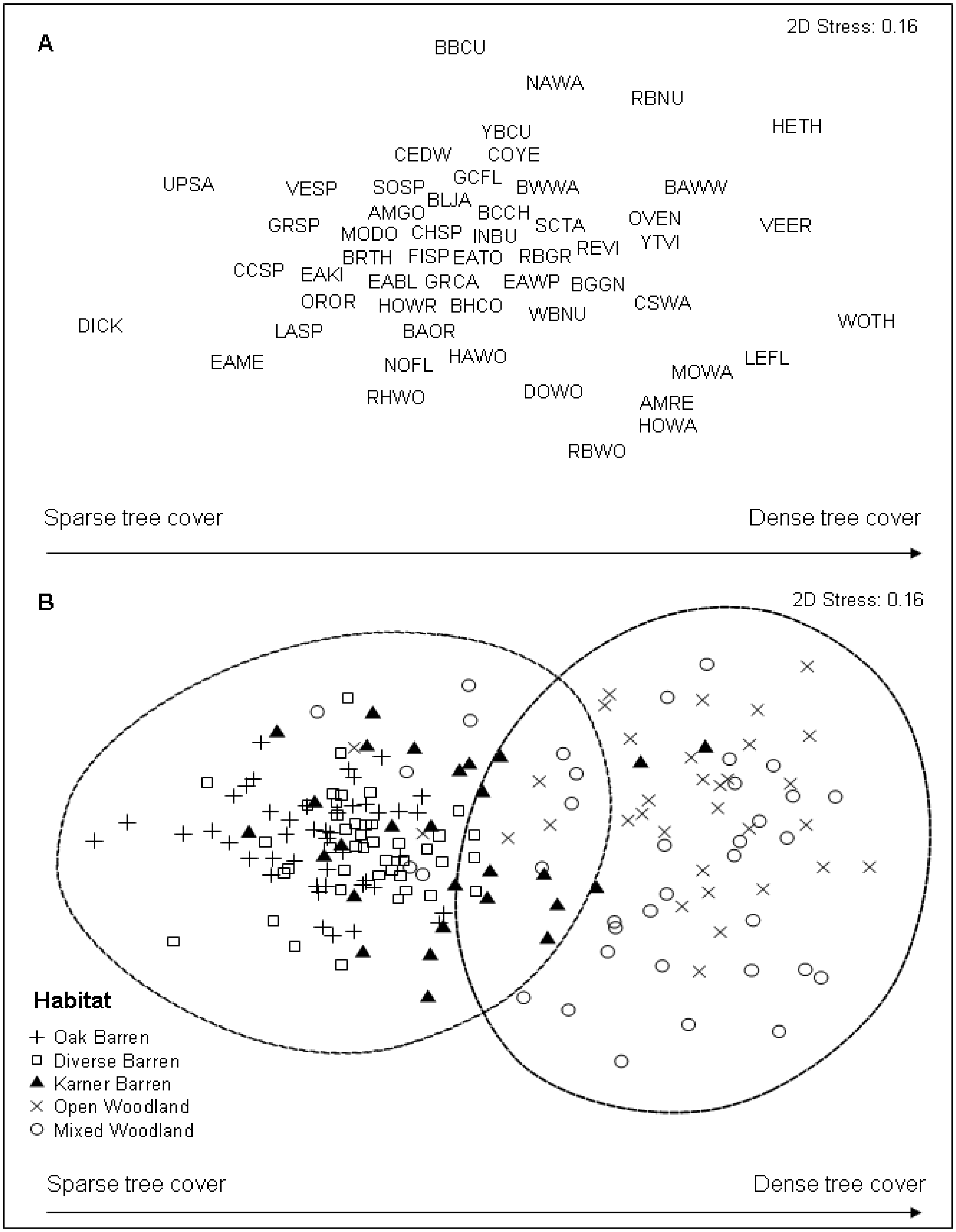
A
2D Stress: 0.16
BBCU
NAWA
RBNU
HETH
YBCU
CEDW
COYE
UPSA
VESP
SOSP
GCFL
BWWA
BAWW
BLJA
AMGO
BCCH
GRSP
MODO
CHSP
INBU
SCTA
OVEN
VEER
YTVI
REVI
BRTH
FISP
EATO
RBGR
CCSP
EAKI
EABL
GRCA
EAWP
BGGN
OROR
HOWR
BHCO
CSWA
WBNU
WOTH
DICK
LASP
BAOR
EAME
NOFL
HAWO
LEFL
MOWA
RHWO
DOWO
AMRE
HOWA
RBWO
Sparse tree cover
Dense tree cover
B
2D Stress: 0.16
Habitat
+ Oak Barren
□ Diverse Barren
▲ Karner Barren
× Open Woodland
○ Mixed Woodland
Sparse tree cover
Dense tree cover

Figure 3-2

Appendix 3-1. Common name, scientific name, and American Ornithologists' Union four-letter code (AOU) within our for fifty four common breeding bird species.

Common name	**Scientific name**	**AOU**
American Goldfinch	*Spinus tristis*	AMGO
American Redstart	*Setophaga ruticilla*	AMRE
Baltimore Oriole	*Icterus galbula*	BAOR
Black-and-white Warbler	*Mniotilta varia*	BAWW
Black-billed Cuckoo	*Coccyzus erythropthalmus*	BBCU
Black-capped Chickadee	*Poecile atricapillus*	BCCH
Blue Jay	*Cyanocitta cristata*	BLJA
Blue-gray Gnatcatcher	*Polioptila caerulea*	BGGN
Blue-winged Warbler	*Vermivora pinus*	BWWA
Brown Thrasher	*Toxostoma rufum*	BRTH
Brown-headed Cowbird	*Molothrus ater*	BHCO
Cedar Waxwing	*Bombycilla cedrorum*	CEDW
Chestnut-sided Warbler	*Dendroica pensylvanica*	CSWA
Chipping Sparrow	*Spizella passerina*	CHSP
Clay-colored Sparrow	*Spizella pallida*	CCSP
Common Yellowthroat	*Geothlypis trichas*	COYE
Dickcissel	*Spiza americana*	DICK
Downy Woodpecker	*Picoides pubescens*	DOWO
Eastern Bluebird	*Sialia sialis*	EABL
Eastern Kingbird	*Tyrannus tyrannus*	EAKI
Eastern Meadowlark	*Sturnella magna*	EAME
Eastern Towhee	*Pipilo erythrophthalmus*	EATO
Eastern Wood-Pewee	*Contopus virens*	EAWP
Field Sparrow	*Spizella pusilla*	FISP
Grasshopper Sparrow	*Ammodramus savannarum*	GRSP
Gray Catbird	*Dumetella carolinensis*	GRCA
Great-crested Flycatcher	*Myiarchus crinitus*	GCFL
Hairy Woodpecker	*Picoides villosus*	HAWO
Hermit Thrush	*Catharus guttatus*	HETH
Hooded Warbler	*Wilsonia citrina*	HOWA
House Wren	*Troglodytes aedon*	HOWR
Indigo Bunting	*Passerina cyanea*	INBU
Lark Sparrow	*Chondestes grammacus*	LASP
Least Flycatcher	*Empidonax minimus*	LEFL
Mourning Dove	*Zenaida macroura*	MODO
Mourning Warbler	*Oporornis philadelphia*	MOWA
Nashville Warbler	*Vermivora ruficapilla*	NAWA
Northern Flicker	*Colaptes auratus*	NOFL

Orchard Oriole	*Icterus spurius*	OROR
Ovenbird	*Seiurus aurocapillus*	OVEN
Red-bellied Woodpecker	*Melanerpes carolinus*	RBWO
Red-breasted Nuthatch	*Sitta canadensis*	RBNU
Red-eyed Vireo	*Vireo olivaceus*	REVI
Red-headed Woodpecker	*Melanerpes erythrocephalus*	RHWO
Rose-breasted Grosbeak	*Pheucticus ludovicianus*	RBGR
Scarlet Tanager	*Piranga olivacea*	SCTA
Song Sparrow	*Melospiza melodia*	SOSP
Upland Sandpiper	*Bartramia longicauda*	UPSA
Veery	*Catharus fuscescens*	VEER
Vesper Sparrow	*Pooecetes gramineus*	VESP
White-breasted Nuthatch	*Sitta carolinensis*	WBNU
Wood Thrush	*Hylocichla mustelina*	WOTH
Yellow-billed Cuckoo	*Coccyzus americanus*	YBCU
Yellow-throated Vireo	*Vireo flavifrons*	YTVI

CHAPTER 4: CHANGES IN FOREST TREE-SPECIES COMPOSITION MAY AFFECT NEOTROPICAL SONGBIRDS DURING SPRING MIGRATION STOPOVER

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Abstract

Since European settlement, hardwood dominated forests of eastern North America have undergone compositional changes due to fire suppression and lack of regeneration. It is not clear how these changes affect songbirds during spring migration stopover. In 2009 and 2010, from early April to early June, we quantified foraging behavior by neotropical migratory songbirds and collected data on tree and sapling diversity in the Kickapoo Valley Reserve in southwestern Wisconsin. Furthermore, we compared the 1850s distribution of tree species (from Public Land Survey System witness tree records) with current (2010) and future (sapling) tree-composition to better understand how historic and future changes in tree composition may drive patterns of tree use by neotropical migratory birds during spring migration stopover. Of 35 tree species recorded, the proportional use by the Blue-gray Gnatcatcher (*Polioptila caerulea*) and 11 wood-warbler species (*Parulinae* spp.) of several tree species, including red oak (*Quercus rubra*), white oak (*Q. alba*), American elm (*Ulmus americana*), slippery elm (*U. rubra*), big-tooth aspen (*Populus grandidentata*) and paper birch (*Betula papyrifera*) was greater than their proportional availability. On the other hand, the proportional use by these bird species of shade-tolerant tree species such as sugar maple

(*Acer saccharum*), red maple (*A. rubrum*) and American basswood (*Tilia americana*) was much lower than their proportional availability. We did not find support for the idea that bird foraging success among tree species varies due to food availability (Lepidoptera richness per tree, R^2 = 0.03, *p-value* = 0.64). However we did find evidence that food accessibility influenced bird foraging success (average leaf-petiole length of tree species, R^2 = 0.77, *p-value* = 0.001). Although tree-species composition varied considerably from the 1850s to 2010, in both time periods the forest was dominated by sugar maple and oak species. However, sugar maple saplings currently form a nearly continuous layer in the understory with very low recruitment of oak and other shade-intolerant species such as big-tooth aspen, suggesting a shift of the forest composition towards future dominance by shade-tolerant species. Our results highlight the reliance of neotropical migratory songbirds on some tree species that are legacies of a time when natural disturbances shaped forest composition. It is unclear whether the current trajectory of tree composition will provide the food resources and conditions (i.e., food accessibility) necessary for Neotropical migrants to effectively refuel during stopover

Key words: avian foraging, food availability, food accessibility, maple, oak, spring migration, stopover, tree-species composition, warbler, Public Land Survey System

Introduction

Spring migration is a taxing time in the life cycle of migratory songbird species (Hutto 2000, Sillett and Holmes 2002, Newton 2004, Newton 2006, Hedenström 2008).

Amid the many challenges birds face, such as predator avoidance (Lindström 1990, Schmaljohann and Dierschke 2005, Lind and Cresswell 2006), inhospitable weather (Rappole and Warner 1976, Richardson 1978), and inter and intra-specific competition (Moore and Yong 1991), birds must make critical decisions regarding resource selection at stopover sites (Moore et al. 2005, Chernetsov 2006, Buler et al. 2007, Smith et al. 2007). Optimal stopover locations allow birds to refuel (through foraging) efficiently and thus to depart quickly to the next stopover location or breeding area (Loria and Moore 1990, Moore and Yong 1991, Moore and Simons 1992, Moore et al. 1995, Smith and Moore 2003, Schaub et al. 2008). Since migration involves risks and energy demands, determining what foraging substrates to use to maximize energy intake during stopover is a critical decision affecting fitness and survival of individuals of all migratory species (Berthold and Terrill 1991, Moore et al. 2005).

In the eastern portion of the American Midwest, human land use has altered the structure and composition of hardwood dominated forests (Rhemtulla et al. 2007, Rhemtulla et al. 2009). During the 19th century, large portions of forest were cleared for timber extraction, agricultural development, and European settlement (Schulte et al. 2007, Rhemtulla et al. 2009). Yet, over the last approximate half century, forest cover has increased throughout the region primarily because of shifts in land use practices (Iverson et al. 1997, McShea et al. 2007, Rhemtulla et al. 2007).

In southwestern Wisconsin, the current trends in reforestation are characterized by the term ‘mesophication’ (Lorimer 1984, Lorimer 1985. Abrams 1992, Abrams 2005, Nowacki and Abrams 2008). This term embodies the process, due in large part to widespread fire suppression, of declining importance of oak (*Quercus* spp.) and other species requiring open conditions for germination or maturation, accompanied by increasing importance of shade-tolerant species like maple (*Acer* spp., Hix and Lorimer 1991, Lorimer et al. 1994, Taylor and Lorimer 2003, Rogers et al. 2008). Oak species are regarded as keystone species for their value in maintaining biodiversity throughout North American forests (Fralish 2004, McShea et al. 2007). Many, breeding birds and some mammal species are more common in oak dominated forests, due to greater resource availability (e.g., acorn mast, arthropods, cavities) than in maple dominated woodlands (Rodewald and Abrams 2002, Rodewald 2003, McShea et al. 2007). Moreover, oaks harbor higher Lepidoptera richness than other tree species (Tallamy and Shropshire 2009), thus highlighting their importance as foraging stopover substrates for neotropical migratory songbirds (Graber and Graber 1983). Yet, the effect of changes in forest tree composition on neotropical migratory songbirds at stopover habitats is unclear (Graber and Graber 1983, Strode 2004). Many neotropical canopy foraging insectivorous songbirds are in decline (Robbins et al. 1989, Rich et al. 2004) and it is important to better understand all aspects of their annual cycle that may limit their populations (Sillet and Holmes 2002). Quantifying the use of trees by neotropical migratory songbirds at their stopover habitats is important in order to understand the implications of broad scale compositional changes on their future persistence as members of the migrant community in southwestern Wisconsin forests.

The overarching goal of this project was to quantify the use of tree species by neotropical migratory songbirds during spring migration stopover in southwestern Wisconsin forests, with a specific focus on how trends in tree-species composition may affect their foraging success in future years. Within this overarching goal, we had three objectives. First, we were interested in quantifying tree-species use by neotropical migratory songbirds during spring migration stopover. Based on results of similar studies (Holmes and Robinson 1981, Graber and Graber 1983, Gabbe et al. 2002, Strode 2004, Strode 2009), we expected birds to exhibit heterogeneity in patterns of tree use. Furthermore, the importance of oak and elm species and the avoidance of shade-tolerant trees such as sugar maple and basswood by birds during spring migration in Illinois woodlots (Graber and Graber 1983 and Strode 2004) led us to expect similar patterns in Wisconsin.

Our second objective, was to determine whether food availability (Graber and Graber 1983) or food accessibility (Holmes and Robinson 1981) were most related to selection of tree species as foraging substrates by birds. Both food availability and accessibility influence foraging success by neotropical migratory songbirds. We predicted that neotropical migratory songbirds would have higher foraging success on tree species with greater diversity of prey items (e.g., Lepidoptera richness) than on tree species with lower diversity of prey items, and would therefore spend more time foraging in tree species in which prey availability was highest. Furthermore, optimal foraging theory predicts that animals will forage in a way to efficiently maximize their caloric intake within a given level of risk (Pyke 1984). Therefore, we predicted that neotropical migratory songbirds would have higher foraging success on tree species with leaf architecture more favorable to accessing prey-items (i.e., shorter leaf-petiole length) than on tree species with leaf architecture unfavorable for accessing prey-items (i.e., longer leaf-petiole length).

Our third objective was to estimate the similarity of forest tree-species composition in the historic (1850s) and the current time (2010), and to explore trends in future forest composition, in order to investigate how resource availability for neotropical migrants has and potentially will change through time.

Methods

Study Area

Our study area was the 3,468 ha Kickapoo Valley Reserve in southwestern Wisconsin, located in the Driftless Area, an area of greater topographical heterogeneity then the surrounding landscape due to its unglaciated status (Curtis 1959), which encompasses northeast Iowa, southeast Minnesota, and southwest Wisconsin (Fig. 1). The Driftless Area is an important stopover region for neotropical migratory songbirds *en route* to breeding habitat in the boreal forest (Wilson 2008). Conducting this study in the forest of the Kickapoo Valley Reserve allowed for an investigation into how neotropical migratory songbirds may be impacted by changes in tree-species composition throughout the Driftless Area. The vegetation of the Kickapoo Valley Reserve ranges from bottomland hardwood forest in the Kickapoo River floodplain, to upland dry- and southern-mesic woodland on the surrounding ridges (Curtis 1959). This study was conducted in the upland dry- and southern-mesic forests. Tree species of the upland forests, in order of importance (see Methods section Tree and Sapling Availability for formula), include white oak (*Quercus alba,* 50.57%), northern red oak (*Q. rubra,* 49.52%), sugar maple (*Acer saccharum,* 48.97%), bitternut hickory (*Carya cordiformis,* 23.93%), American basswood (*Tilia americana,* 21.40%), red maple (*A.*

rubrum, 15.44%), American elm (*Ulmus americana*, 10.75%), hophornbeam (*Ostrya virginiana*, 9.12%), white ash (*Fraxinus Americana*, 9.01%), big-tooth aspen (*Populus grandidentata*, 8.00%), eastern white pine (*Pinus strobus*, 7.53%), black cherry (*Prunus serotina*, 6.73%), bur oak (*Q. macrocarpa*, 6.72%), black oak (*Q. velutina*, 6.29%), slippery elm (*U. rubra*, 6.17%), paper birch (*Betula papyrifera*, 2.80%), quaking aspen (*P. tremuloides*, 2.72%), yellow birch (*B. alleghaniens*, 2.39%), tamarack (*Larix laricina*, 1.85%), shagbark hickory (*C. ovata*, 1.58%), box elder (*A. negundo*, 0.91%), eastern red cedar (*Juniperus virginiana*, 0.86%), black walnut (*Juglans nigra*, 0.83%), hackberry (*Celtis occidentalis*, 0.77%), black ash (*F. nigra*, 0.74%), black willow (*Salix nigra*, 0.72%), eastern hemlock (*Tsuga Canadensis*, 0.47%), butternut (*J. cinerea*, 0.43%), balsam poplar (*P. balsamifera*, 0.40%), green ash (*F. pennsylvanica*, 0.29%), musclewood (*Carpinus caroliniana*, 0.25%), and rock elm (*U. thomasii*, 0.22%).

All field work was conducted in four stands which represent some of the largest tracts of contiguous forest in the Driftless Area of Wisconsin (ranging from 80 to 107 ha, Fig. 1). In addition to being large and unfragmented, these stands were selected for their diverse tree composition (> than 20 tree species per stand) and because they are compositionally representative of smaller forest patches within the Driftless Area. Using a high-resolution air photo, we digitized each stand in ArcGIS 9.1 (ESRI, Redlands, California, USA 2006) and plotted a lattice grid of points (hereafter lattice points) separated by 100 meters, with alternate rows offset by 50 meters. Each lattice point was used as a sampling location for tree and sapling composition availability and as a reference point during avian observations.

Seventy eight, 79, 78, and 75 lattice points were plotted in the four stands for a total of 310 lattice points (Fig. 1).

Avian Foraging Observations and Calculations of Foraging Success

To determine which tree species neotropical migratory songbirds use during spring migration stopover we collected foraging data from mid-April to early June in 2009 and 2010, which encompasses the stopover period in Wisconsin for the majority of neotropical migrants *en route* to their northern breeding grounds (Temple et al. 1997). Between sunrise and 1 pm, an observer proceeded along a walking route, established to maximize coverage of a study stand, and actively searched for foraging-flocks of twelve neotropical migratory songbird species (hereafter focal species, Table 1) using standardized methods (Holmes and Robinson 1981, Remsen and Robinson 1990). Since the average length of stay of neotropical migratory songbirds during stopover is < 3 days (Moore and Kerlinger 1987), we visited the four stands on average twice a week during the sampling periods with at least three days separating visits to reduce the risk of autocorrelated foraging observations. Focal species were chosen because they are relatively common migratory songbirds that primarily use trees as foraging substrates during spring migration in our study area. Four trained observers collected data each year, including the lead author. Once a focal species was detected, an observer followed and documented the individual’s activities and movements for as long as possible up to five minutes and within the boundaries of a study stand. Although we often followed and documented foraging behavior for focal birds in multiple trees during a foraging observation, for comparisons of tree use versus availability, we only recorded ‘use’ of the first tree a focal bird was observed actively attacking a prey item (Holmes and Robinson 1981, Gabbe et al. 2002). Using a digital recorder with a built in timer, the observer documented the following data on focal species; species identity, sex (if possible), tree species, number of perch changes (e.g. hops, walks, flights), and type of attack (e.g., bud glean, flower glean, leaf glean, bark glean, hover, sally, and flush-chase, Remsen and Robinson 1990).

Once a data collection session for an individual of a focal species was concluded, the observer either moved to another individual of a focal species in the immediate area, if possible, or moved back to the walking route in search of another foraging-flock. In order to find a new foraging-flock, observers moved at least 300 m from the previous flock. Furthermore, to avoid autocorrelated foraging information, only one male or female of dichromatic species' [e.g., Blackburnian Warbler (*Dendroica fusca*)] in a flock was counted. Thus, if multiple male Blackburnian Warblers were detected in a flock, foraging data was only collected on the first male encountered. The observer then proceeded to collect foraging information on a female, if detected. For focal species that are weakly sexually dichromatic, such as a Tennessee Warbler (*Oreothlypis peregrina*), foraging data was collected on only one individual within a flock. The Blue-gray Gnatcatcher (*Polioptila caerulea*), Blue-winged Warbler (*Vermivora cyanoptera*), and Chestnut-sided Warbler (*D. pensylvanica*) are migratory birds that potentially breed in our study area (Wisconsin Breeding Bird Atlas 2011). Thus, we only collected foraging observations on individuals of these three species that were actively moving in a mixed-species foraging-flock composed mainly of focal species migrating to more northerly breeding grounds [e.g., Blackburnian Warbler and Black-throated Green Warbler (*D. virens*)].

To determine whether the focal species used tree species as foraging substrates in proportion to their availability, we used a chi-square goodness-of-fit test to compare observed use- versus expected use-frequencies for all focal species as a whole (Holmes and Robinson 1981). To obtain the expected use-frequencies, we multiplied tree importance values (see Tree and Sapling Availability section for formula) by the total number of observations of each focal species (Gabbe et al. 2002). Since most focal species in our study area only used a small proportion of the available tree species as foraging substrates, we were not able to compare observed use- with expected use-frequencies for individual focal species (i.e., many zero observations). Therefore, we pooled observed-use data from the twelve focal species and compared these with the pooled expected use-frequencies. Only sixteen tree species with an importance value percentage > 2.7% were used for all analysis since tree species with an importance percentage < 2.7% were not used in sufficient enough frequencies by our focal study birds to be useful for analysis purposes (Table 2).

Lepidoptera larvae are the main prey items of migratory songbirds during stopover (Graber and Graber 1983, Moore and Yong 1991) and we used published data on Lepidoptera richness by tree species (Tallamy and Shropshire 2009) as an index of food availability by tree species. To determine focal species foraging success, we calculated an ‘attack-index’ which is the total number of attacks per minute, divided by the total number of all searches per minute, of all focal species per tree species. A higher attack-index indicates greater foraging success per tree compared to number of search maneuvers. If a focal species used multiple trees during a foraging observation session, we partitioned the session data by tree species, and used data from each tree species to calculate the tree- species specific attack-index. Tallamy and Shropshire (2009) estimated Lepidoptera richness for tree genera rather than species. Thus, in order to match our attack-index data to their data on available Lepidopteran food per tree genus, we pooled data by tree genus to come up with attack-index composite per tree genus (e.g., *Quercus* spp.).

Tree and Sapling Availability

To gain information on the current tree composition, we used the point-center quarter method at each of the 310 lattice points (Cottam and Curtis 1956, Curtis 1959). We recorded tree species, measured dbh, and distance from lattice point of the closest tree > 10 cm dbh in each of four quadrants: 0-90°, 90-180°, 180-270°, 270-360°. We calculated the importance value, of all tree species using the formula: importance value = relative frequency + relative density + relative dominance (Curtis 1959, Cottam and Curtis 1956). Dominance of tree species was derived by first converting dbh into basal area, then using the equation:

$$\frac{\text{Total basal area per tree species}}{\text{Forest patch area (m}^2\text{)}}$$

These dominance values were then converted into relative dominance for use in importance value calculations. An importance value for each tree species was converted into importance percentage (i.e., importance of each tree relative to importance of all available trees) which represented the relative availability of each tree species as foraging substrate for neotropical migratory songbirds (Holmes and Robinson 1981).

To gain information about the potential future forest tree composition, we again used the point-center quarter method, recording species and distance to one tree sapling (< 10 cm dbh and taller than 1.3 m) in each quadrant. We calculated relative frequency of saplings, by species, for use in comparison with historic and current tree data.

Public Land Survey System Data

To determine historic tree composition of the Kickapoo Valley Region, we used Public Land Survey System data (Schulte and Mladenoff 2001). The Public Land Survey System was implemented by the United States government in 1785 to partition western lands into parcels for settlement in township (6x6 mile; 9.7 km^2) and section (1x1 mile; 2.6 km^2) increments (Schulte and Mladenoff 2001). At the midway point and corner of a section surveyors recorded the diameter at breast height (dbh), distance and species of two to four 'witness' trees. The Public Land Survey System witness tree data (hereafter PLSS) were collected in the 1850s within our study region.

The PLSS was collected at coarser resolution than our ground-collected tree and sapling composition data. Thus, in order to be able to make broad comparisons between the PLSS and our ground-collected tree and sapling data, we used a grid of corner and mid-section points that encompassed the Kickapoo reserve and surrounding upland habitats that are similar in elevation and topography to the upland forests of the Kickapoo Valley Reserve (Fig. 1). From this area, 326 corner and mid-section points and 651 witness trees were available for analysis. In order to compare compositional and importance trends in tree species since the 1850s, we calculated the IV, of each witness tree species using the above formula.

Statistical Analysis

We generated a use-index to quantify foraging selectivity by individual focal species (Holmes and Robinson 1981). The use-index for a particular focal species is calculated by taking the sum of the absolute values between the percent-use of observed focal species, among tree species, and the importance percentage of each tree species. To investigate whether focal species vary in their tree-use patterns according to when they arrive during migration, we calculated, for each species, the Spearman’s rho correlation of the mean first-arrival date in 2009 and 2010, with the use-index for the focal species.

Our first hypothesis to explain why focal species may use certain trees in higher frequencies than others during spring migration stopover was that different tree species differ in the richness (and therefore availability) of food, which influences foraging success. To explore this, we fit a linear regression model of total Lepidoptera richness per tree species (from Tallamy and Shropshire 2009) as the independent variable and bird foraging success (attack-index) as the dependent variable. It was not feasible to sample the available arthropod community by tree species with standard branch clipping methods within our study areas due to very tall tree canopies (average canopy height > 25m), steep slopes, and limited areas where a ‘cherry picker’ could be maneuvered.

Our second hypothesis about why migrants use certain trees species in higher frequencies than others was that the accessibility of food may differ among tree species. The majority of birds were observed maneuvering to the end of a branch and lunge-gleaning on emerging leaves (Table 3). Thus, we wondered if the length of the leaf petiole influenced accessibility of prey, a hypothesis first put forth by Holmes and Robinson (1981). We obtained data on leaf petiole length by measuring leaf specimens housed in the University of Wisconsin Herbarium that were obtained by branch clipping from trees (i.e., not saplings) from our study region (e.g., Vernon or Richland Country, Wisconsin). We only measured leaf specimens that had been collected in mid-May to early June (i.e., non-mature leaf samples), to match the period in which focal bird species use Driftless Area forests during stopover (Temple et al. 1997). Quaking aspen was not included in this analysis because focal species were not observed using leaves of this tree as foraging substrates. Furthermore, black oak and hophornbeam were omitted from this analysis because there were no Herbarium leaf samples available from mid-May to early June in our study region. Two tree species, white ash and bitternut hickory have compound leaves composed of individual leaflets. Focal species were observed perched on the leaf stalk of the white ash gleaning prey items from individual leaflets. Therefore, for this species we measured the length of each leaflet petiole. Focal species were not observed using the leaf stalk of the bitternut hickory. Therefore for this species we used the distance from the branch to the first leaflet-pair as a measure of food accessibility. To explore this relationship, we fit a linear regression model of the leaf attack-index, which is a similar measure to the ‘attack-index’ (see above), yet only using focal species attacks on a leaf substrate per minute divided by the total number of searches per minute, against the average leaf-petiole length (cm) of twelve tree species. As part of the regression analyses, normality was checked with normal QQ plots and constant variance was checked by visually inspecting residual plots (Zar 1999). All statistical analysis was completed using the R statistical software package (R Development Core Team 2005).

Results

Use of Foraging Substrates by Neotropical Migratory Songbirds

We recorded 330 foraging observations of focal species. We found the focal species to be highly selective in their use of trees as foraging-substrates (χ^2 = 222.13, df $_{15}$, *p-value* = < 0.001, Table 2). Trees which were used in greater proportion than their availability in the landscape during both 2009 and 2010, included slippery elm (62% more than if it were used in proportion to its availability), paper birch (55%), red oak (48%), white oak (39%), American elm (37%), and big-tooth aspen (19%, Fig. 2). Trees which were used in lower proportion than their availability in the landscape included basswood (94% less than if it were used in proportion to its availability), black cherry (87%), red maple (83%), hophornbeam (70%), quaking aspen (67%), bitternut hickory (66%), sugar maple (65%), black oak (29%), and white ash (20%, Fig. 2). There was variation in trees species use by focal birds among 2009 and 2010 (Fig. 2). There was a reduction of use of sugar maple (86%), red oak (71%), and American elm (58%), and an increase in use for white oak (72%), slippery elm (67%), hophornbeam (57%), bitternut hickory (57%), paper birch (36%), big-tooth aspen (29%), and white ash (15%) among years (Fig. 2). Black oak, basswood, and black cherry were not used in 2009 but used in 2010, with black oak being used in higher proportion than it was available. Quaking aspen and red maple were used in 2009 but not 2010.

Four patterns of tree-species use emerged (Table 2). With the exception of Golden-winged Warbler, focal species did not use sugar maple (Table 2). No species used basswood, red maple, and bitternut hickory (Fig. 3). Second, red oak, white oak, American elm, slippery elm, and big-tooth aspen were strongly used (i.e., high use-index values per tree) by many focal species (Fig. 3). The most highly selective foragers, with were the Northern Parula (*Parula americana*), Magnolia Warbler (*D. magnolia*), Black-and-white-Warbler (*Mniotilta varia*), Blackburnian Warbler, and Golden-winged Warbler.

Third, focal species vary in their tree-use patterns according to their time of arrival, as evidenced by a strong correlation between arrival times of focal species and tree selectivity (ρ = 0.78, *p-value* = 0.003, Fig. 4). Focal species that arrive earlier to the Kickapoo River Valley appear to be less selective in their use of tree foraging substrates than species that arrive later (Fig. 4).

The fourth pattern we uncovered is that foraging attacks of focal species were directed at specific parts of the tree (Table 3). For example, although focal species largely avoid sugar maple, they do direct attacks at the buds of this tree species early in the spring before the leaves are fully flushed (personal observation, Table 3). We noticed a similar pattern of use of big-tooth and quaking aspen (Table 3). The flowers (i.e., catkins) of red and white oak were highly important foraging substrates for focal species (Table 3). However the majority of attacks on most tree species were directed at the leaf surface (Table 3).

Factors Affecting Foraging Success by Neotropical Migratory Songbirds

We did not find general support for the hypothesis that total food availability influenced foraging success among tree species (R^2 = 0.03, *p-value* = 0.64, Fig. 5). However, on the oak species we observed a higher proportion of attacks relative to search time. Oak species also had the highest Lepidoptera richness (Fig. 5). In contrast, on basswood, sugar and red maple (*Acer* spp.), and bitternut hickory, which all have comparably lower Lepidoptera richness, focal species had similarly had lower ratios of attacks to search maneuvers indicating focal species search more for potentially lower food items (Fig. 5).

We found support for the hypothesis that the accessibility of food per tree influences foraging success by focal species (R^2 = 0.77, *p-value* = 0.03, Fig. 5). The leaf attack-index which we used as a measure of foraging success was higher on trees with smaller leaf-petiole lengths such as the white ash, elm species, paper birch, and oak species than on trees with larger leaf-petiole lengths such as the basswood, and maples.

Changes in Availability of Tree Foraging Substrates for Neotropical Migratory Songbirds

From the 1850s data, 18 tree species were recorded in the Kickapoo Valley Region, and 35 tree species, and 22 tree saplings were recorded during 2010 surveys in the Kickapoo Valley Reserve. The most important tree species in the Kickapoo Valley Region in the 1850s were sugar maple (33%), white oak (25%), basswood (14%), and elm spp. (8%, Fig. 6). The most important tree species in 2010 were sugar maple (18%), white oak (18%), red oak (17%), hickory spp. (9%), and basswood (7%, Fig. 6).

Tree species that were less important in 2010 then in the 1850s were red pine (100% reduction), butternut (86% reduction from 1850s importance), sugar maple (48% reduction), basswood (45% reduction), black oak (45% reduction), bur oak (33% reduction), elm spp. (30% reduction), and white oak (29% reduction, Fig. 6). Trees species that were more important in 2010 then in the 1850s included hickory spp. (mainly bitternut hickory, 93% increase from 1850s importance), red oak (88% increase), white pine (74% increase), white ash (69% increase), aspen spp. (mainly big-tooth aspen, 48% increase), cherry spp. (mainly black cherry, 33% increase), and hophornbeam (17% increase, Fig. 6). Three tree species not recorded during the 1850s but found in 2010 surveys were red maple, paper birch, and eastern red cedar.

Sapling composition, an index of the future tree-species composition in the region, was dominated by sugar maple, which made up 69% of all saplings recorded (Fig. 6). Other saplings encountered included red maple (5%), bitternut hickory (5%), basswood (4%), black cherry (4%), slippery elm (3%), white oak (3%), American elm (3%), and white ash (2%). Tree saplings which were either not encountered, or found in very low frequency (< 0.5%) included black, bur, and red oak, hophornbeam, paper birch, and big-tooth aspen (Fig. 6).

Discussion

We found that the 12 neotropical migratory songbirds we studied used the relatively important trees, red and white oak, and less important trees, slippery elm, American elm, black oak (2010), big-tooth aspen, and paper birch as foraging substrates during spring migration stopover in higher proportions then those trees were available. On the other hand, we found the same neotropical migratory songbirds to strongly avoid basswood, red maple, bitternut hickory, and sugar maple, which were relatively important tree species in our study region. We expected to find the focal species using trees in varying proportions to their availability because breeding bird studies of tree-use have indicated strong selection-patterns for certain tree species (Holmes and Robinson 1981, Gabbe et al. 2002), and we expected these patterns to hold during spring migration stopover. Our results highlighting the high use of oak and elm and avoidance of sugar maple and basswood by neotropical migratory songbirds were consistent with findings during stopover in Illinois (Strode (2004).

We tested two possible explanations for these patterns: food availability and food accessibility. Many studies have suggested the importance of food availability to foraging birds both during the breeding season (Holmes and Robinson 1981) and migration stopover (Graber and Graber 1983, Strode 2004, McGrath et al. 2008). Because of this, we hypothesized that food availability was influential in determining foraging success (attack-index) among tree species by neotropical migratory songbirds. However, we did not find evidence to support this hypothesis (Fig. 5). Some tree species, such as oaks have high Lepidoptera richness which matches the high foraging success by focal species on these trees. Maples and basswood have lower number of Lepidoptera richness and lower foraging success among focal species. However, other tree species with a high attack-index such as white ash have comparably low levels of Lepidoptera richness. We acknowledge that a big assumption in our work is that the Lepidopteran community on tree species in the mid-Atlantic region is representative of the Lepidopteran diversity on trees in the Kickapoo Valley Reserve. We have not tested that, and realize that quantifying both Lepidopteran species richness and abundance in our study region would provide more solid evidence to support or refute the hypothesis that food availability is not an influential factor.

We did find strong support for the hypothesis that food accessibility (average leaf-petiole length) was influential in determining foraging success of neotropical migratory songbirds during stopover (Fig. 5). The majority of focal species forage for prey-items by hopping toward the end of a branch, then lunge gleaning on a bud, leaf, or flower surface (Table 3). Thus, if a tree has a long leaf-petiole (e.g., maple) it may be energetically too difficult for a smaller bird (e.g., wood-warbler) foraging on this substrate to reach the available prey-item. Our finding that focal species have higher foraging success on trees with shorter leaf petioles follows predictions of optimal foraging theory, in which birds would be expected to forage in a way to efficiently maximize their caloric intake while minimizing competing risks (Pyke 1984). Trees with smaller leaf petioles, that allows access to preferred stages/parts of trees (e.g., small distance to leaf bud of sugar maple allowing access to prey-item), presumably offer optimal conditions in which focal species were able to efficiently search and acquire food while minimizing their energy expenditures. Our findings were similar to patterns of neotropical breeders, foraging in a New England forest where yellow birch (*Betula alleghaniensis*) and American beech (*Fagus grandifolia*) were used more than expected given their importance in the landscape (Holmes and Robinson 1981) and in Illinois floodplain forest where bitternut and kingnut hickory (*C. laciniosa*) as well as sycamore (*Platanus occidentalis*) were also used more than expected given their importance in the landscape (Gabbe et al 2002). What all of these tree species had in common was shorter petioles.

We found forest tree-species composition of our study region has changed substantially since the 1850s, which is consistent with studies that have described broad scale composition changes of vegetation types throughout Wisconsin over the approximate past 150 years (Rhemtulla et al. 2007, Rhemtulla et al. 2009). In general, the forest composition remains dominated by sugar maple and oak. However, there has been a shift in the importance of oak trees. While white oak is still an important tree of Driftless Area forests, it has decreased in importance, a pattern common throughout eastern deciduous forests (Abrams 2003). Bur and black oak are also losing importance on the landscape, which is indicative of loss of forest openings or oak savanna habitats (Nuzzo 1986, Curtis 1959). Therefore, with the increase in shade-tolerant species, black and bur oak will most likely be extirpated from the Driftless Area except for in managed areas, or locations where shade-tolerant trees grow poorly (e.g., sandy soils, Curtis 1959). The evidence that white oak, and to a lesser extent black oak were important foraging resources for focal species lends support that these tree species, which were once more common in the region, were potentially historically important foraging resources for neotropical migratory songbirds during stopover (Fig. 2).

Red oak was far more common in 2010 than in the 1850s, because it became established in forested stands after intense logging operations during the late 1800s and early 1900s (Nowacki et al. 1990). Red oak is a relatively fast growing tree (Lorimer 1983) and many of the specimens in our study region were super-canopy trees, whose crowns were above the surrounding canopy. This may have contributed to their high-quality as foraging substrate because the canopy of an emergent red oak is exposed to more sunlight and wind which is associated with more catkins (personal observation), which are an important foraging substrate for focal species (Table 3). Red oak was an important foraging substrate for our focal study species (Fig. 2). However, we found very few red oak saplings (*n* = 1), highlighting the fact that red oak will most likely be a single generation dominant species (Nowacki et al. 1990), and thus a critical foraging resource for neotropical migratory songbirds will eventually be gone from Driftless Area forests.

Slippery and American elm, which we found were both important resources for foraging migrants, appear to be regenerating well and, although American elm will most likely never again be a dominant canopy tree due to Dutch elm disease (Schlarbaum et al. 1997), the elm species will most likely remain at a low but constant level of importance as part of the canopy (slippery elm) and sub-canopy (both American and slippery elm) in the Driftless Area forests. Two other species that were important foraging substrates, big-tooth aspen, and paper birch, are early successional trees (Curtis 1959) and are regenerating poorly. Without disturbance (e.g., fire) or management, these species will be lost from the landscape further reducing the availability of desirable foraging substrates for neotropical migrants during spring migration stopover.

Shade-tolerant tree species, which were strongly avoided by focal birds, have also shifted in importance from the 1850s period to 2010. There was a notable decrease in sugar maple and basswood, and a substantial increase in red maple. Basswood and sugar maple typically grow in mesic conditions (e.g., north facing slopes) and can grow to large sizes in the Driftless Area (Curtis 1959). Sugar maple is a valuable timber product (Allen et al. 1999) and it is likely this species was also harvested in the Driftless Area forests following

European settlement. Furthermore, it is possible that the apparent decrease in basswood and sugar maple from the 1850s to 2010 is due, at least in part, to sampling error. Public land surveyors often sampled ‘large’ trees as witness trees, rather then the true ‘nearest’ suitable tree to a corner or mid-section point (Schulte and Mladenoff 2001). Therefore, it is possible that basswood and sugar maple were oversampled during the historic Public Land Surveys. Our finding that red maple has dramatically increased in importance throughout our study region echoes similar trends for this species throughout eastern North American forests (Lorimer 1984, Abrams 1998), and is of concern because it was strongly avoided by the focal species.

We found a large increase in bitternut hickory importance from the 1850s to 2010. Bitternut hickory is a shade-intolerant species, but is able to grown on poor sites (e.g., steep, well drained soils, Curtis 1959). We speculate that bitternut hickory is able to become established on poor sites where shade-tolerant trees do not grow well, and because it is a fast growing tree (Hix and Lorimer 1990), once established it may outcompete oak saplings. We did not find evidence that focal species use bitternut hickory as a desirable foraging substrate as was found in Illinois woodlots during spring stopover (Strode 2004) and floodplain forest during the breeding season (Gabbe et al. 2002). Sugar maple, red maple, basswood, and bitternut hickory, were used less than expected given their availability in the landscape by neotropical migrants, but are regenerating well in our study region, and therefore will likely dominate the future forest of the Driftless Area. These results are consistent with other work in the region (Hix and Lorimer 1991, Rogers et al. 2008). Furthermore, these trends in regeneration follow a common trend of forest succession in eastern mixed-hardwood forests since European settlement from white oak, to red oak to dominance by mesophytic tree species (Abrams and Copenheaver 1999). Whether neotropical migratory songbirds, adapted to conditions and plant species shaped by natural disturbance can further adapt their foraging patterns to the changing landscape of the Driftless Area, is not at all clear. The decline of oak, the decrease of canopy-dominate elm species, and the likely demise of ash to emerald ash borer beetle (*Agrilus planipennis*) in the near future, are of concern because they may bring on the severe reduction, even collapse, of a neotropical spring migrant community in this region. In the face of this plant community change, neotropical migratory songbirds must adapt to exploit different foraging substrates.

Conclusion

Our study provided evidence that shifts in tree-species composition of Midwestern oak forests toward dominance by shade-tolerant species, may have large affects on stopover foraging habitat of neotropical migratory songbirds. We found that oak and elm, and to a lesser extent, big-tooth aspen and paper birch are valuable foraging substrates for these species. Furthermore, we found that neotropical migratory songbirds have higher foraging success on tree species with shorter leaf petiole lengths, suggesting that food accessibility rather than food availability is a factor limiting neotropical migratory songbird foraging success during stopover. Although we found evidence that neotropical migratory songbirds possess considerable plasticity in foraging behaviors and ability to exploit substrates during stopover, it is not clear how successful these species can be in finding high quality foraging substrates as forest composition continues to change toward dominance by shade-tolerant species. For effective conservation of neotropical migratory songbird stopover habitat in Driftless Area forests, efforts should be made to maintain oak, elm, and other early successional tree species (e.g., big-tooth aspen) on the landscape.

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Table 4-1: Common name, American Ornithologists' Union (AOU) four-letter code, scientific classification, foraging observation sample (n), and Partner's in Flight species assessment scores (Rich et a. 2004) of twelve focal species observed during spring migration stopover in the Kickapoo Valley Reserve, Wisconsin.

Species	AOU 4-Letter	Scientific	*n*	PIF Score
Black-and-white Warbler	BAWW	*Mniotilta varia*	8	14
Blue-gray Gnatcatcher†	BGGN	*Polioptila caerulea*	20	8
Blackburnian Warbler‡	BLBW	*Dendroica fusca*	24	13
Black-throated Green Warbler	BTNW	*Dendroica virens*	30	14
Blue-winged Warbler†‡	BWWA	*Vermivora cyanoptera*	23	14
Chestnut-sided Warbler†	CSWA	*Dendroica pensylvanica*	14	14
Golden-winged Warbler‡	GWWA	*Vermivora chrysoptera*	8	19
Magnolia Warbler	MAWA	*Dendroica magnolia*	7	12
Myrtle's 'Yellow-rumped' Warbler	MYWA	*Dendroica coronata coronata*	30	11
Nashville Warbler	NAWA	*Oreothlypis ruficapilla*	32	14
Northern Parula	NOPA	*Parula americana*	8	12
Tennessee Warbler	TEWA	*Oreothlypis peregrina*	98	13

†Species breeds in study area (Wisconsin Breeding Bird Atlas).

‡Boreal Hardwood Transition Region Bird Conservation Region 12. All other PIF scores from Boreal Softwood Shield Region 8.

Table 4-2: Tree-species use and avoidance of twelve neotropical migratory songbirds and the pooled data of all twelve species (total) during stopover. Values are use and aversion values. >5 indicates high use, < -5 indicates high aversion. See Table 1 for four-letter code abbreviations.

	Focal species												
	BAWW	BGGN	BLBW	BTNW	BWWA	CSWA	GWWA	MAWA	MYWA	NAWA	NOPA	TEWA	Total
American Elm	-3.76	1.24	-3.76	9.57	4.93	24.81	21.24	24.81	-3.76	-3.76	33.74	3.38	3.84
Basswood	-7.49	-7.49	-7.49	-7.49	-7.49	-7.49	-7.49	-7.49	-4.15	-7.49	-7.49	-7.49	-7.18
Big-tooth aspen	22.20	7.20	-2.80	-2.80	-2.80	-2.80	-2.80	11.49	3.87	3.45	-2.80	1.28	1.15
Bitternut Hickory	-8.37	-3.37	-4.21	-8.37	-4.03	-1.23	-8.37	-8.37	-5.04	-2.12	-8.37	-6.33	-5.64
Black Cherry	-2.35	-2.35	-2.35	-2.35	1.99	4.79	-2.35	-2.35	-2.35	-2.35	-2.35	-2.35	-1.75
Black Oak	-2.20	7.80	-2.20	-2.20	-2.20	-2.20	-2.20	-2.20	-2.20	-2.20	-2.20	-0.16	-0.98
Bur Oak	-2.35	2.65	-2.35	0.98	-2.35	-2.35	-2.35	-2.35	-2.35	-2.35	-2.35	-2.35	-1.74
Hophornbeam	-3.19	-3.19	-3.19	0.14	1.16	-3.19	-3.19	-3.19	-3.19	-3.19	-3.19	-3.19	-2.28
Paper Birch	-0.98	4.02	-0.98	9.02	-0.98	-0.98	-0.98	-0.98	-0.98	2.14	-0.98	-0.98	0.84
Quaking Aspen	-0.95	-0.95	-0.95	-0.95	7.74	-0.95	-0.95	-0.95	-0.95	-0.95	-0.95	-0.95	-0.34
Red Maple	-5.40	-5.40	-5.40	-2.07	-1.06	-5.40	-5.40	-5.40	-5.40	-5.40	-5.40	-5.40	-4.49
Red Oak	7.67	7.67	61.84	-3.99	0.06	18.39	32.67	-3.04	12.67	7.67	20.17	29.61	19.15
Slippery Elm	-2.16	-2.16	-2.16	1.17	15.23	-2.16	-2.16	26.41	-2.16	13.47	-2.16	4.98	3.92
Sugar Maple	-17.13	-12.13	-17.13	-17.13	-4.09	-9.99	7.87	-17.13	-0.47	-4.63	-17.13	-16.11	-11.36
White Ash	-3.15	1.85	-3.15	0.18	5.54	-3.15	-3.15	-3.15	-3.15	-0.03	9.35	-1.11	-0.72
White Oak	32.27	7.27	-1.06	28.94	-9.03	-3.44	-17.73	-3.44	22.27	10.39	-5.23	9.82	10.23
Use-index [A]	121.65	76.75	121.04	97.37	70.69	93.33	120.91	122.77	74.98	71.62	123.88	95.52	75.62

[A] Use-index is a measure of the summed absolute values of all use and aversion values and represents foraging selectivity. Higher positive numbers indicate greater selectively. Lower negative numbers indicate greater aversion.

Table 4-3: Mean ± (SE) summary for total focal species search maneuver and foraging attack scaled per minute for fifteen tree species. Focal species were followed for up to five minutes often documenting behavior in multiple trees, which is represented in this table. Bur Oak was not included in this table because of limited foraging information for this tree (*n* = 1). Only most common search and tree substrate attacks (e.g., bud, flower, or leaf) displayed. Total search and attack are a composite of all search maneuvers (e.g., shuffle) and attacks (e.g., bark glean).

		Focal species search maneuver summary						Focal species foraging attack summary							
Tree species	n	Flights		Hops		Total search		Bud		Flower		Leaf		Total attacks	
American Elm	29	2.55	(0.81)	11.78	(1.34)	14.33	(1.62)	0	0	0	0	2.64	(0.50)	3.04	(0.62)
Basswood	7	3.50	(1.64)	11.84	(2.73)	15.34	(3.29)	0	0	0	0	0.38	(1.03)	0.92	(1.26)
Big-tooth aspen	27	4.75	(0.84)	10.02	(1.39)	14.77	(1.68)	0.57	(0.18)	0.35†	(0.35)	0.49	(0.52)	2.18	(0.64)
Bitternut Hickory	10	5.00	(1.37)	15.56	(2.29)	20.56	(2.75)	0.33	(0.29)	0	0	0.64	(0.86)	3.15	(1.06)
Black Cherry	7	6.06	(1.64)	3.64	(2.73)	9.69	(3.29)	0	0	0	0	0.42	(1.03)	1.34	(1.26)
Black Oak	6	2.63	(1.77)	9.08	(2.95)	11.71	(3.55)	0	0	0	0	2.00	(1.11)	2.60	(1.36)
Hophornbeam	5	2.27	(1.94)	9.88	(3.23)	12.16	(3.89)	0	0	0	0	2.11	(1.21)	2.71	(1.49)
Paper Birch	7	3.04	(1.64)	10.92	(2.73)	13.96	(3.29)	0.26	(0.35)	0	0	1.95	(1.03)	3.41	(1.26)
Quaking Aspen	3	6.23	(2.51)	5.60	(4.17)	11.83	(5.03)	0.57	(0.54)	0	0	0	0	0.57	(1.93)
Red Maple	11	4.01	(1.31)	9.25	(2.18)	13.26	(2.62)	0.09	(0.28)	0	0	0.52	(0.82)	0.75	(1.01)
Red Oak	156	3.50	(0.35)	10.73	(0.58)	14.23	(0.70)	0.12	(0.07)	1.55†	(0.15)	1.75	(0.22)	3.81	(0.27)
Slippery Elm	23	4.37	(0.90)	11.42	(1.51)	15.79	(1.81)	0	0	0	0	3.43	(0.57)	3.76	(0.70)
Sugar Maple	39	6.03	(0.69)	8.40	(1.16)	14.43	(1.39)	0.71	(0.15)	0	0	0.42	(0.43)	1.89	(0.53)
White Ash	14	3.50	(1.16)	7.92	(1.93)	11.42	(2.33)	0	0	0	0	3.24	(0.73)	3.37	(0.89)
White Oak	108	3.51	(0.42)	9.92	(0.70)	13.43	(0.84)	0.01	(0.09)	1.32†	(0.18)	1.94	(0.26)	3.62	(0.32)

†Catkin.

Figure Captions

Figure 4-1: Location of Kickapoo Valley Reserve (in green), in the Driftless Area (darker gray), Wisconsin, USA, and, distribution of forested stands within the reserve with 310 lattice points superimposed. Larger surrounding point-grid is 326 corner and mid-section Public Land Survey System locations used to estimate historic forest composition profile of the Kickapoo Valley Region.

Figure 4-2: Use of tree species by all foraging neotropical migratory songbirds at the Kickapoo Valley Reserve study sites for 2009 and 2010.

Figure 4-3: Proportion of tree use (use values > 5) and avoidance (use values < -5) by neotropical migratory songbirds during stopover. Sixteen tree species were included in this analysis (Table 2). However, focal species did not use Bur Oak during our two sampling seasons. Therefore, it is not displayed on this figure.

Figure 4-4: Scatter plot, and Spearman's rho correlation (ρ) of use-index versus mean arrival time of twelve focal species. Arrival date determined by the mean first detection of each focal species in the 2009 and 2010 foraging observation sampling period.

Figure 4-5: Results of linear regression of (A) Lepidoptera richness per tree, an indicator of food availability (from Tallamy and Shropshire 2009) versus attack-index and (B) leaf petiole length (cm) of twelve tree species, an indicator of food accessibility, versus leaf attack-index. Attack-index in (A) is the total number of attacks, whereas in (B) it refers to observed attacks of leaves only, and is the number of leaf attacks divided by total search maneuvers, scaled per minute. Higher attack-index values indicate greater success (prey items ingested) per search effort.

Figure 4-6: Public Land Survey System 1850s witness tree importance values (PLSS IVs), current tree IVs (2010), and sapling relative frequency (future) within the Kickapoo Valley Region.

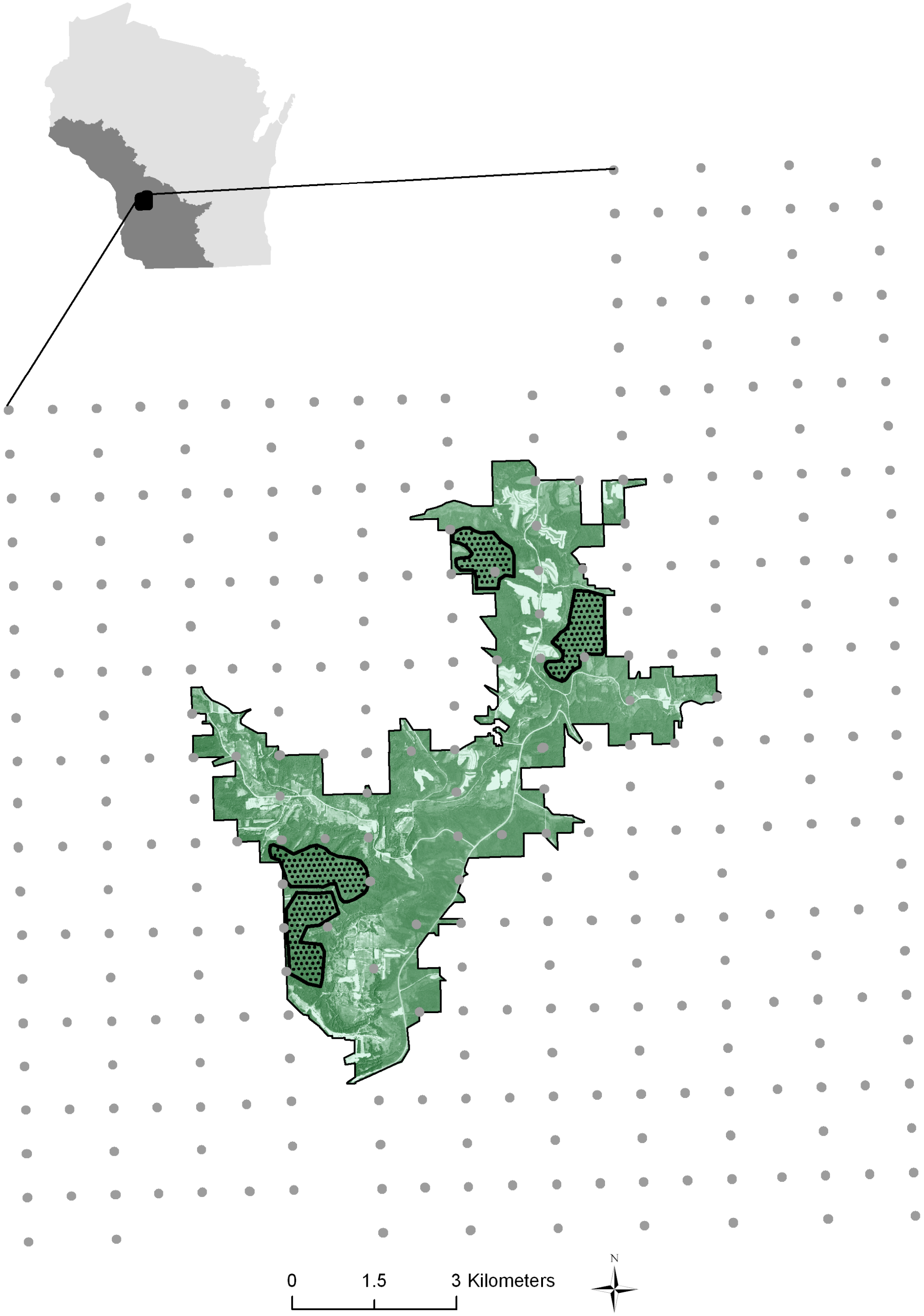
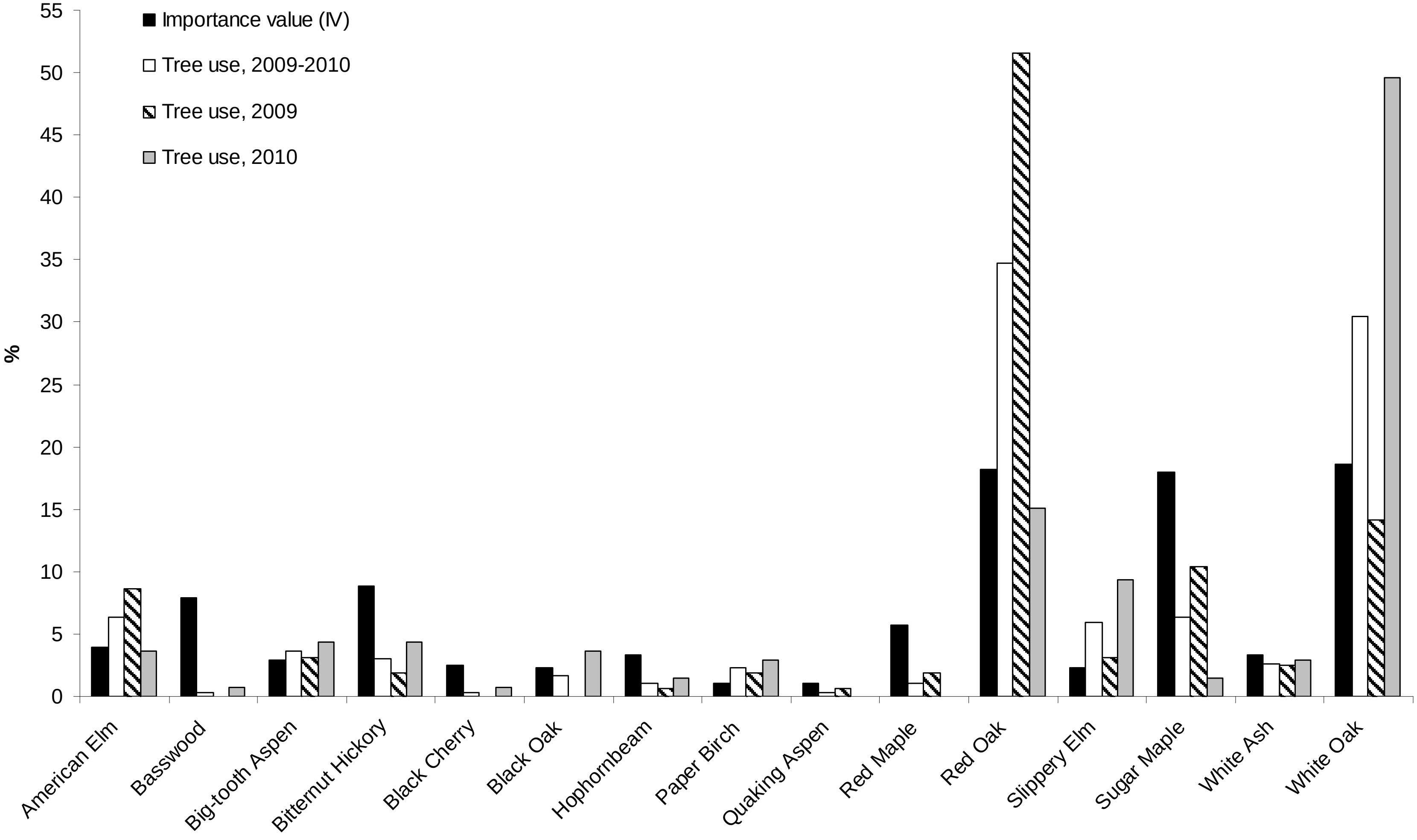


Figure 4-1

Figure 4-2



55
50
45
40
35
30
25
20
15
10
5
0
%
■ Importance value (IV)
□ Tree use, 2009-2010
▨ Tree use, 2009
▩ Tree use, 2010
American Elm
Basswood
Big-tooth Aspen
Bitternut Hickory
Black Cherry
Black Oak
Hophornbeam
Paper Birch
Quaking Aspen
Red Maple
Red Oak
Slippery Elm
Sugar Maple
White Ash
White Oak

.

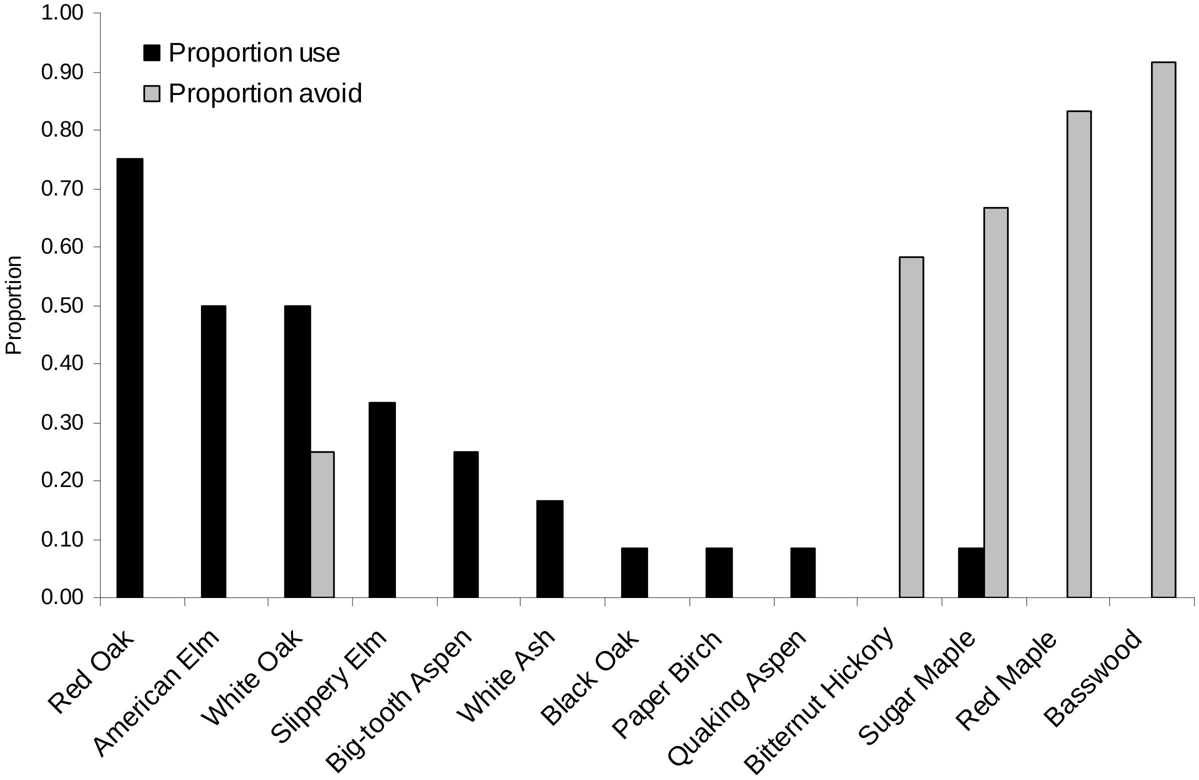

1.00
0.90
0.80
0.70
0.60
0.50
0.40
0.30
0.20
0.10
0.00
Proportion
■ Proportion use
▨ Proportion avoid
Red Oak
American Elm
White Oak
Slippery Elm
Big-tooth Aspen
White Ash
Black Oak
Paper Birch
Quaking Aspen
Bitternut Hickory
Sugar Maple
Red Maple
Basswood

Figure 4-3

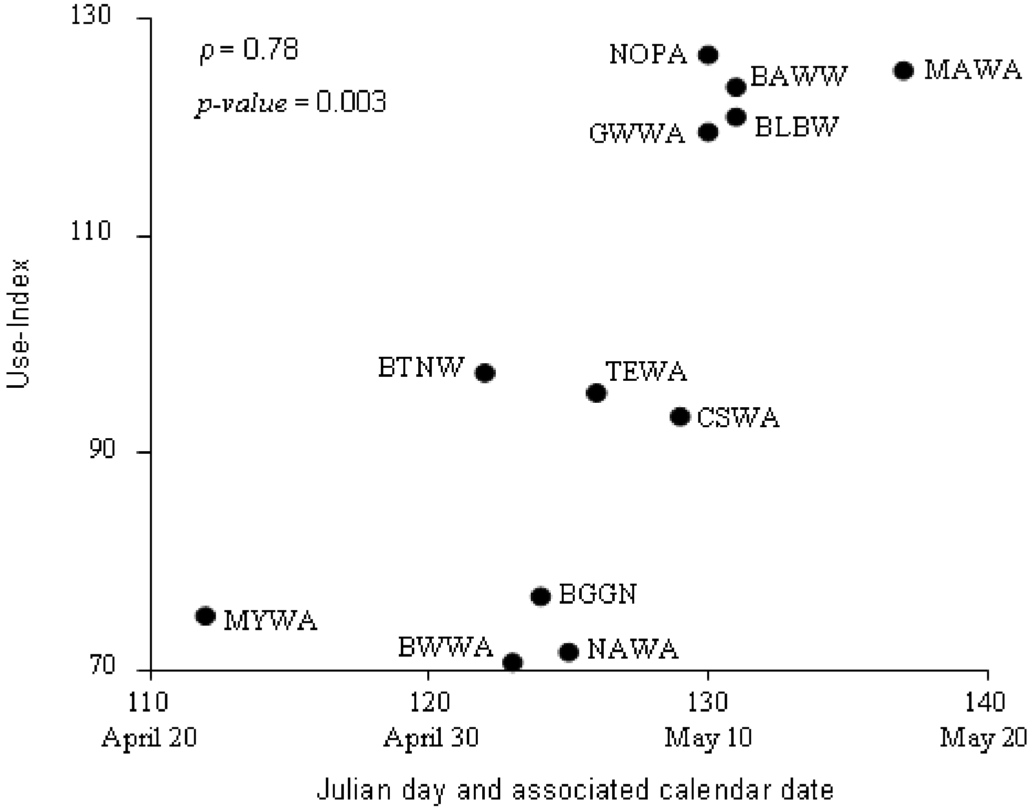

ρ = 0.78
p-value = 0.003
NOPA
BAWW
MAWA
GWWA
BLBW
BTNW
TEWA
CSWA
BGGN
MYWA
BWWA
NAWA
130
110
90
70
Use-Index
110
April 20
120
April 30
130
May 10
140
May 20
Julian day and associated calendar date

Figure 4-4

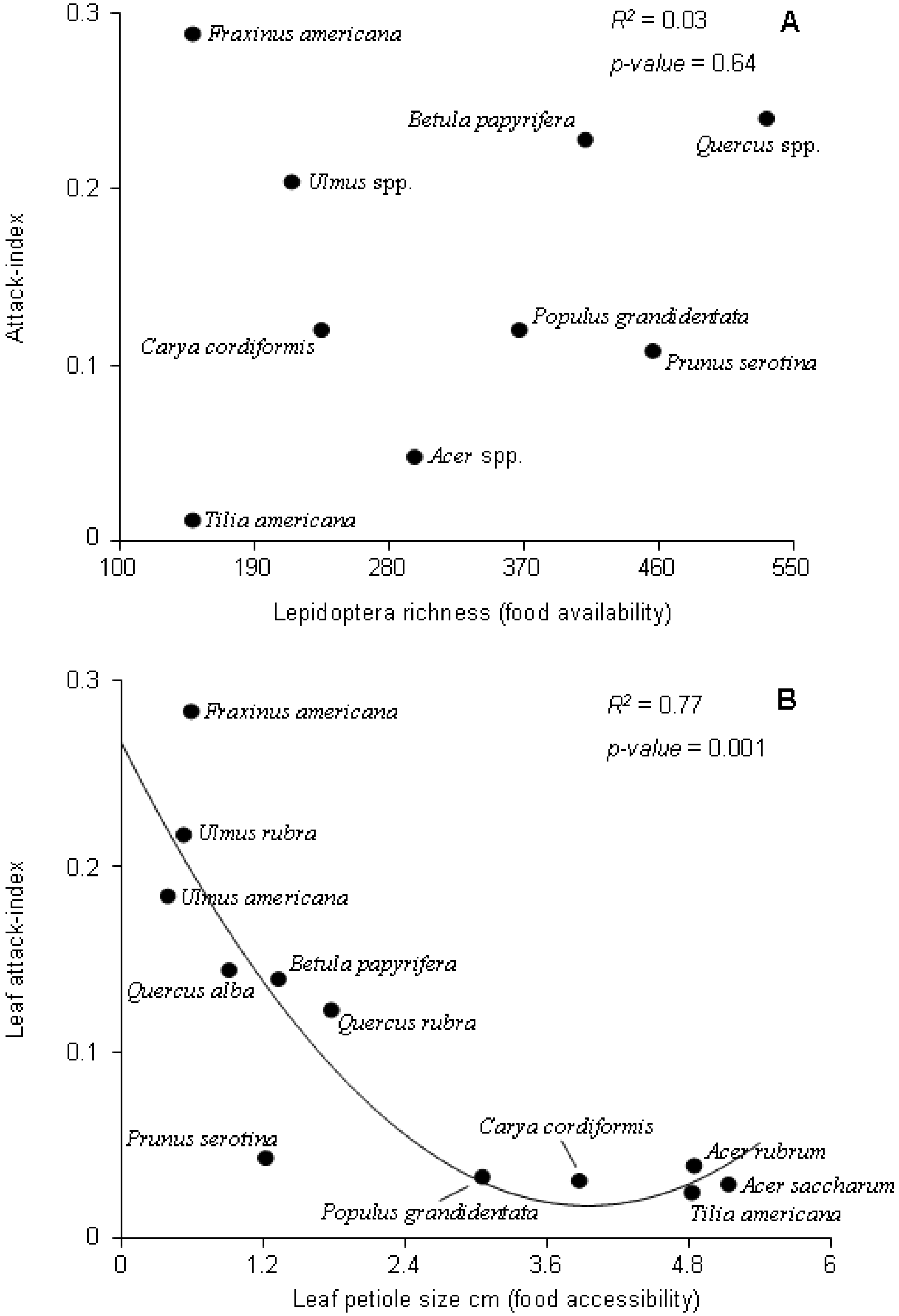
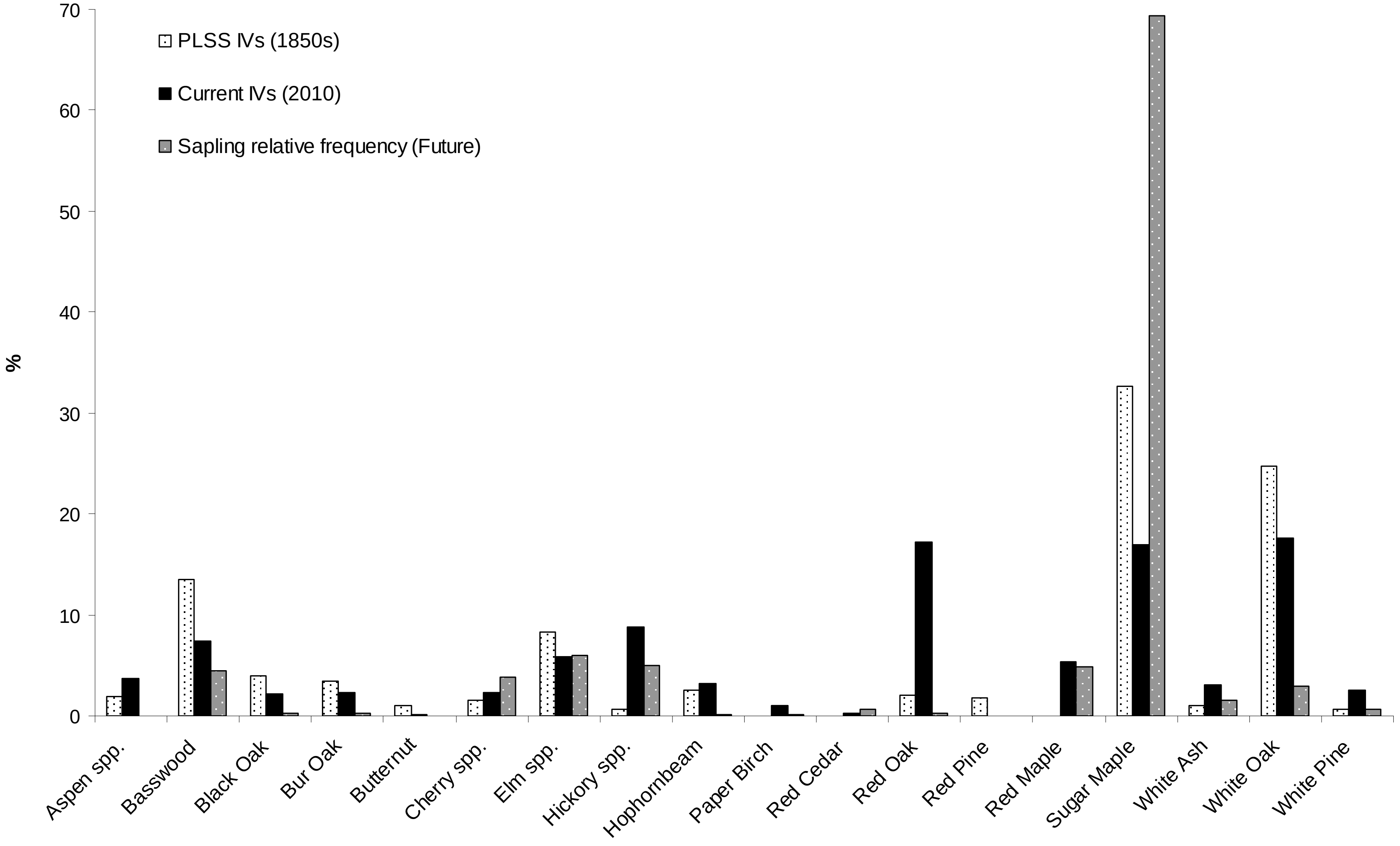

A
R^2 = 0.03
p-value = 0.64
Attack-index
0.3
0.2
0.1
0
Fraxinus americana
Betula papyrifera
Quercus spp.
Ulmus spp.
Populus grandidentata
Carya cordiformis
Prunus serotina
Acer spp.
Tilia americana
100
190
280
370
460
550
Lepidoptera richness (food availability)
B
R^2 = 0.77
p-value = 0.001
Leaf attack-index
0.3
0.2
0.1
0
Fraxinus americana
Ulmus rubra
Ulmus americana
Betula papyrifera
Quercus alba
Quercus rubra
Carya cordiformis
Prunus serotina
Acer rubrum
Acer saccharum
Populus grandidentata
Tilia americana
0
1.2
2.4
3.6
4.8
6
Leaf petiole size cm (food accessibility)

Figure 4-5

Figure 4-6



☐ PLSS IVs (1850s)
■ Current IVs (2010)
▨ Sapling relative frequency (Future)
%
70
60
50
40
30
20
10
0
Aspen spp.
Basswood
Black Oak
Bur Oak
Butternut
Cherry spp.
Elm spp.
Hickory spp.
Hophornbeam
Paper Birch
Red Cedar
Red Oak
Red Pine
Red Maple
Sugar Maple
White Ash
White Oak
White Pine

CONCLUSIONS

Since European settlement, changes in land cover have had great impacts on biodiversity in southern Wisconsin. With this dissertation, I set out to explore factors affecting habitat use and abundance patterns of breeding and migratory birds in a grassland-savanna-woodland habitat mosaic. Where others before me have indicated the broad scale changes in vegetation structure and composition in southern Wisconsin (Leach and Givnish 1999, Rogers et al. 2008), the importance of grassland and savanna habitats to breeding birds (Temple 1998, Brawn 2006, Grundel and Pavlovic 2007, Mabry et al. 2010), and the high use of oak trees as foraging substrates by bird species during spring-migration stop-over (Graber and Graber 1983), I attempted to advance our understanding of how bird species respond to structural and compositional heterogeneity of the current southwestern Wisconsin landscape, and to infer how future conditions may change habitat quality.

In Chapter 1, I examined the utility of remotely sensed image texture for characterizing vegetation structure (e.g., foliage-height diversity, MacArthur and MacArthur 1961; horizontal vegetation structure, Wiens and Rotenberry 1981), a key descriptor of avian habitat, among and within grassland, savanna, and woodland habitats. Among habitats, image texture captured the variation in foliage-height diversity and horizontal vegetation structure well. Within habitats, these relationships were not as strong. This work is important because I learned that vegetation structure, can indeed be mapped for large areas using remotely sensed image texture and is potentially promising data for broad scale avian habitat models.

In Chapter 2, I tested how well image texture predicted patterns of avian abundance and species richness. I found image texture measures were useful for predicting density of, the Grasshopper Sparrow (*Ammodramus savannarum*), and avian species richness. The mean summary of NDVI was useful for predicting density of the Ovenbird (*Seiurus aurocapillus*). Image texture measures were not strong predictors of density of the Field Sparrow (*Spizella pusilla*). An important finding of this chapter was that in some cases image texture measures and in other cases plot-level summaries were better predictors of focal bird density and avian species richness than the often-applied ground collected vegetation structure indices. These are important findings because density is positively linked with habitat quality (Bock and Jones 2004). Thus, in relating image texture and plot-level summary data to focal species density and avian species richness I advanced knowledge about the potential for use of these remotely sensed data for identifying and modeling habitat, information that is useful for a variety of habitat modeling and conservation applications. Additionally, I found that the relationship between avian species richness and image texture that has been identified in other ecosystems (St-Louis et al. 2006, 2009) also occurs in the grassland-savanna-woodland ecosystem of southern Wisconsin.

In Chapter 3, I examined how the federal and state habitat management activities for the Karner blue butterfly (Lepidoptera: Lycaenidae, *Lycaeides melissa samuelis*, hereafter Karner blue) affect bird communities. Oak savanna habitat has been nearly extirpated from the Midwest landscape (Nuzzo 1986) and is important habitat for unique assemblages of bird species, yet there are currently no state habitat conservation and management plans for oak savanna avian communities in Wisconsin (Wisconsin Bird Conservation Initiative, 2011). I learned that management for Karner blues creates habitat that structurally resembles remnant oak savanna and that the bird community of the managed savanna also resembles the bird community of remnant savanna. Additionally, two species of conservation concern, Vesper Sparrow (*Pooecetes gramineus*) and Field Sparrow (*Spizella pusilla*), that are associated with savanna habitat, use the managed habitat. I found that an important factor determining the composition of the avian community in the managed savanna was the structure and composition of the adjacent habitat. Managed savanna situated adjacent to remnant savanna are populated by a bird community that resembles a remnant savanna bird community. On the other hand, managed savanna situated adjacent to woodland habitats are populated by a bird community composed mainly of spares canopy associated species (i.e., savanna) in addition to woodland associated species, but are notably absent of some species that are associated with remnant savanna, such as Brown Thrasher (*Toxostoma rufum*), Vesper Sparrow, Eastern Kingbird (*Tyrannus tyrannus*), and Orchard Oriole (*Icterus spurius*). Although I learned that in providing habitat for the Karner blue, managers are also providing habitat for the savanna bird community These results also suggest that the Karner blue is a useful surrogate for savanna bird communities.

In Chapter 4, I explored which tree species neotropical migrant bird use as foraging substrates during spring migration and whether migrants had higher foraging success on some trees species than others. I tested two hypotheses related to this: food availability (total Lepidoptera richness per tree species, Graber and Graber 1983), and food accessibility (average leaf petiole length among trees, Holmes and Robinson 1981). Furthermore, I also examined whether forest composition has changed in the time since European settlement, and how this may have affected food availability or accessibility for birds during stop-over. The proportional use by the Blue-gray Gnatcatcher (*Polioptila caerulea*) and 11 wood-warbler species (*Parulinae* spp.), of red oak (*Quercus rubra*), white oak (*Q. alba*), American elm (*Ulmus americana*), and slippery elm (*U. rubra*) was greater than their proportional availability. The proportional use of shade-tolerant tree species such as sugar maple (*Acer saccharum*), red maple (*A. rubrum*) and American basswood (*Tilia americana*) was lower than their proportional availability. I did not find support for the hypothesis that bird foraging success among tree species varied due to food availability. Rather, I found strong support for the hypothesis that food accessibility influenced bird foraging success. I found that birds had greater foraging success on trees with smaller leaf petioles (e.g., American elm), rather than on trees with longer leaf petioles (e.g., sugar maple). Sugar maple and oak species are still the dominant tree species in the region. However, because I found that the majority of tree saplings were sugar maple, and I found almost no oak saplings, it is likely that forest composition will be dominated by shade-tolerant species in the future. This chapter is important because it documents important foraging substrates for bird species during spring-migration in the upper Midwest. It also strengthens the notion that the trend of mesophication is widespread in the upper Midwest. My study highlights past and future degradation of important stop-over foraging habitat for neotropical migrants, a guild in which many species are in decline (Robbins et al. 1989). Additionally, these findings suggest the mechanism responsible for making late-successional tree species poor foraging habitat for warblers. Food accessibility is a major factor determining bird foraging success, and the long petioles of many shade tolerant tree species that are regenerating well in southern Wisconsin forests severely limit access to food by neotropical migrants.

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