AVIAN BIODIVERSITY IN PINE FORESTS ALONG AN URBAN-RURAL/AGRICULTURE-WILDLAND GRADIENT

by

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(Under the Direction of John P. Carroll)

ABSTRACT

With rapid urbanization and extensive agriculture in the southeastern United States, natural and planted pine forests are increasingly embedded in a complex matrix of urban development and agricultural lands. For sound conservation management plans in the landscape, it is critical to understand how the matrix of urban development and/or agricultural lands influences biodiversity-habitat relationship and to identify important habitat characteristics. This requires a multiple-scale approach considering habitat characteristics at both local and landscape scale. Few studies have explored avian biodiversity-habitat relationship in pine forests, especially in urban/agricultural landscapes, at multiple-scales. Therefore, we investigated the relationship between site occupancy of avian species and spatial scales (1 local-scale and 2 landscape-scales), the effect of anthropogenic land uses on avian biodiversity (richness and RCS, Partners In Flight Regional Combined Score) along a gradient of urban-rural/agriculture-wildland, and the avian biodiversity-habitat structure-area relationship, in 3 ecoregions of Georgia. Occupancy by forest interior and forest edge species was more associated with landscape scale features, whereas occupancy of pine-grassland species more related to local scale features. Urban development and agricultural land uses positively influenced occupancy of species, avian richness and RCS. In particular, richness and RCS were higher at pine patches in a mixture of low level of urban development and agricultural land uses and in low level of agriculture matrix than other levels of human land-use including wildland. However, as human land-use increased, relative proportion of migrant and pine-grassland species in a community decreased. Richness and RCS were greater at moderate or low level of basal area (MS) which increased structural diversity within a patch. The effect of patch size varied with levels of basal area. While richness and RCS increased with size of MS patches, they did not change in patches of higher basal area (greater than MS). Our results suggest that both local and landscape scale habitat features need to be considered to improve avian biodiversity. The pine forests in the urban/agriculture matrix could play a potentially positive role in avian biodiversity conservation, and it is important to maintain moderate or level of basal area and preserve larger patches to enhance avian biodiversity.

INDEX WORDS: Agricultural land uses, avian community, basal area, detectability, forest edge, forest interior, habitat structure, habitat heterogeneity, occupancy model, pine forest, pine-grassland, RCS, richness, Sand Hills, spatial autocorrelation, spatial scale, urban-rural/agriculture-wildland gradient, urban development, patch size

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CHAPTER 1

INTRODUCTION AND LITERATURE REVIEW

INTRODUCTION

In the southeastern USA, forests are a dominant landscape component, estimated at 40% of total land area (Miller et al. 2009). In particular, loblolly-shortleaf pine forests are among the most prevalent, occupying 55 million acres (22 million ha or ~ 25 % of southern forests) (Smith et al. 2009). While southern forests have been highly fragmented and altered by timber harvest and intensive agriculture over the 2 centuries, planted pine forests for timber management has increased (20% of southern forest) and it is expected to remain stable (Miller et al. 2009). Most planted pine forests are largely managed for commercial timber; however, with a growing interest and expectation of stake holders in wildlife conservation, there are increasing efforts to improve conservation value of planted pine forests. In addition, as rural family forest owners shift from timber management to non-timber land uses, such as second homes and recreational uses (e.g. hunting, fishing, bird watching, etc.) (NCSSF 2005), these forests could play an important role in conservation if managed properly. There are also pine forest remnants in urban areas and in agricultural lands, which may function as species habitat; however, little attention has been given to these remnants and potential habitat value is rarely studied.

For birds, the majority of forest conservation management has been centered on restoring wildlife habitats of endangered, threatened, and declining species such as the Red-cockaded Woodpecker (*Picoides borealis*), Bachman's Sparrow (*Aimophila aestivalis*), and Northern

Bobwhite Quail (*Colinus virginianus*) which are all pine-grassland species. Relatively few efforts have been made to improve the habitat quality of the pine forests for other species, or to enhance avian biodiversity in general. In addition, most management plans have been applied to local (or stand) scales with little consideration of landscape context (e.g., Mitchell et al. 2006), although increasing heterogeneity at landscape scale (e.g. uneven-aged forest management) is often recommended to enhance biodiversity (e.g., Duryea and Dougherty 1990; Sallabanks and Arnett 2005). Even at local scales, the relationship between avian biodiversity and some habitat characteristics (e.g., stand size and basal area) is little known in some areas, such as the Sand Hills ecoregion. Moreover, in several areas in the Southeastern USA, including central-east Georgia, the landscape matrix surrounding planted or natural pine forests is changing drastically due to rapid urbanization. This agriculture/forest dominant landscape matrix is increasingly converted to an urban matrix resulting in pine forests being transformed to residential development. These land use changes create a landscape which includes both urban development and agricultural land use, leading to increases in the complexity of the landscape matrix surrounding the pine forest. Pine forests, whether they are natural, planted, or regenerated, are increasingly embedded in a matrix of different levels (extents or intensity) of urban development and/or agricultural land uses. In this landscape, to understand species-habitat relationships, both local and landscape scales must be examined. It is also important to have comprehensive information about the pattern of avian species distribution in a matrix of urban development and agricultural land and the relative effect of the two dominant human land-uses on avian species.

Therefore, I investigated avian species biodiversity in loblolly pine forests along an urban-rural/agriculture-wildland gradient, in 3 ecoregions of Georgia (Sand Hills, Coastal Plain Red Uplands, and Southern Outer Piedmont). As indicators of biodiversity, I focused mainly richness (number of species) and RCS (Partners in Flight Regional Combined Score for the breeding season, RCS-b; Region 27, Southeastern Coastal Plain). In Chapter 2, I first assessed scale-dependency of avian species using multiple spatial scales (1 local vs. 2 landscape scales) and an occupancy modeling. Then in Chapter 3 and 4, I examined avian biodiversity-habitat relationships separately at the landscape scale and local scale (with a different definition of local scale than in Chapter 2). At the landscape scale, I focused on the effects of urban development and agricultural land use on avian species. At the local scale, I explored relationships between avian biodiversity, patch size, and basal area (as a surrogate for habitat structure). The final goal of this study, in Chapter 5, was to provide new insights about the potential values of pine patches in urban/agricultural areas for future biodiversity conservation and to provide possible management guidelines, particularly for Fort Gordon, by examining species richness-habitat relationships based on current habitat condition at Fort Gordon.

LITERATURE REVIEW

Scale issue: exploring avian distribution in a landscape context

Spatial scale is one of the central topics that have received a great attention from ecologists over the last two decades. In the past, ecologists examined species-habitat relationship by focusing on local or patch level habitat characteristics such as vegetation structure and composition and patch size (e.g., Bond 1957; MacArthur and Wilson 1963; Wilson et al. 1974; Cody 1985; Urban and Smith 1989). However, ecologists have increasingly realized that the characteristics may not be enough or may be inappropriate to understand the relationship. They have realized the existence of habitat variation at different spatial scales and agreed the importance of choosing proper spatial scales relevant to the organisms and the ecological processes of interest (e.g., Wiens 1989; Forman 1995; Rickets 2001). Furthermore, with increasing human land-use, consideration of matrix characteristics surrounding habitat patches has been emphasized. A multiple scales approach which encompass both local scale and landscape scale or several landscape scales has been broadly adopted in avian studies to explore species-habitat relationship. A number of studies conducted in human-altered landscapes have found that variations in avian species abundance and community composition are better explained by landscape habitat features than local habitat features (e.g., Donovan et al. 1997; Sabb 1999; Atauri and de Lucio 2001; Miller et al. 2003; Devitor and Jiguet 2007).

However, few studies have examined the spatial scale dependency of avian species in pine forests. Little attention has been paid to landscape-level habitat features in these forests. Emphasis of most avian studies in pine forests has been on vegetation composition and structural characteristics within a stand, which can be considered as local scale characteristics given relatively homogeneous conditions within a stand. In particular, heterogeneous vegetation structures within a stand are known to increase avian biodiversity (e.g., Duryea and Dougherty 1990; Turner et al. 2002; Luck and Korodaj 2008). But, recently, some studies have found the importance of landscape-level characteristics to avian species occurrence or richness. Mitchell et al. (2001) reported that the presence of forest birds was predicted equally or better by landscape-level characteristics than by microhabitat characteristics. Relatively strong effects of landscape habitat characteristics were also observed in avian community studies (e.g., Loehle et al. 2005; Mitchell et al. 2006). Like structural diversity within a stand, spatial heterogeneity within a landscape has been known to positively influence avian biodiversity (richness) (e.g., Mitchell et al. 2006; Luck and Korodaj 2008). Heterogeneous age structure of pine patches within a landscape is considered an important factor affecting avian biodiversity (e.g., Turner et al. 2002;

Mitchell et al. 2006) and thus uneven-aged forest management is often recommended to promote biodiversity in planted pine forests (Sallabanks and Arnett 2005). However, those studies were performed in natural and/or planted forest dominant matrix. The relative importance of local and landscape scale habitat features to avian biodiversity in pine forests is rarely known in a matrix of urban development and agricultural land.

Although many avian studies have found strong effects of landscape scale features, explanatory power of local or landscape variables (i.e., habitat characteristics) depends on the organisms of interest, the community variables of question, or the system of study. Forest-restricted species have been found to be more responsive to local scale characteristics because they use certain types of landscape elements and move less to find resources (Graham and Blake 2001). In Portland, Oregon metropolitan areas, abundance of Brown-headed Cowbird and non-native avian species were more influenced by larger spatial scales, whereas richness and diversity of total and resident and short-distance migrant species related strongly to smaller spatial scales (Hennings and Edge 2003). In landscapes where patches of habitat are relatively large, such as the Wisconsin River floodplain, landscape measurements contributed less in explaining variation than local variables did (Miller et al. 2004). The importance of landscape-scale features can also change with characteristics of landscape elements and heterogeneity among the elements. For example, landscape features are likely to have greater explanatory power when there are strong differences among landscape elements that affect habitat quality (Wiens et al. 1987; Miller et al. 2004). Land uses may increase the contrast among the landscape elements. This may be the reason that stronger effect of landscape habitat features on avian species abundance and community composition is more often reported in the studies performed in landscapes with an urban or agricultural matrix (e.g., Saab 1999; Rottenborn 1999; Miller et al. 2003; Smith and Wachob 2006).

Avian biodiversity along an urban-rural/agriculture-wildland gradient

Human land-uses such as timber, mine, urbanization, and agriculture are considered as major causes of habitat loss and fragmentation, resulting in biodiversity loss. In particular, urbanization and agriculture are leading causes of biodiversity loss in United States (Czech 2000). Urbanization converts native vegetation to impervious surfaces and structures, resulting in permanent habitat loss. Intensive agricultural management also simplifies landscapes and reduces habitat diversity. Introduced plants and animals often replace native species and thus alter community structure and composition. Numerous studies have explored how urbanizations or agricultural land uses influence flora and fauna. Especially, as urbanized areas rapidly expand with human population, great attention has been given to the pattern of biodiversity changes along an urban (or urban-rural) gradient.

In general, urbanization decreases species abundance and overall richness; however, the pattern varies among functional guilds and it can change nonlinearly. In birds (the most-studied taxonomic group in urban studies), non-native species and synanthropic species increases with urbanization (e.g., Marzluff 2001; Hansen et al. 2005; Chase and Walsh 2006; Parris and Hepinstall-Cymerman 2012), but forest interior species and habitat specialists tend to decline (Marzluff and Rodewald 2008). Migrants are also likely to negative respond to intensive urban development (e.g., Dunford and Freemark 2004; Stratford and Robinson 2005; Marzluff and Rodewald 2008). Moreover, since urban ecosystems have similar structure and function across cities and urbanization promotes replacement of native species with non-native or urban adapted species, a bird community among the cities tends to be similar (biotic homogenization, McKinney 2006; Blair 2008). However, some species, especially edge species and early successional species can respond to urbanization positively, depending on the level or intensity of urban development in a landscape. Several studies have also documented greater avian species richness at moderate levels of urbanization (i.e., suburban area; 20-50%, or 40-50% impervious surface depending on studies) than at extremely low or high levels of urbanization (i.e., wildland and urban core, respectively). This pattern is often explained by the intermediate disturbance hypothesis (Marzluff 2005; Mckinney 2008; Marzluff and Rodewald 2008). The hypothesis predicts that species richness peaks at moderate level of disturbance because intermediate level of disturbance can allow coexistence of species by preventing dominant species from competitively excluding other species (Connell 1978; Roxburgh et al. 2004). It is also suggested that intermediate level of disturbance in urban ecosystem increases habitat heterogeneity (the disturbance heterogeneity model, Porter et al. 2001) and thus can provide diverse habitats for unique sets of birds (Marzluff 2005; Mckinney 2008). In addition, increased food availability and other resources such as water and nesting sites and reduced large predators contribute higher richness or abundance of some group of birds (called urban exploiters, Blair 2001) at urbanized areas. However, as expected in different responses of functional guilds to urbanizations, one needs to be cautious in interpreting higher richness in areas with moderate level of urban development than in wildlands. Although avian biodiversity in wildlands may not be greater than in urban areas, the natural habitats support more native species, species of conservation concern, or species sensitive to anthropogenic disturbance (e.g., Chapman and Reich 2007). The fact that more species inhabit or use habitats in urban (or other human-altered landscape) matrix suggests that those habitats can play potential roles in enhancing biodiversity and they may provide secondary habitats for some species inhabiting wildlands, in the situation where wildlands decline due to conversion to urban land uses.

The majority of the studies about avian biodiversity along urban-rural gradient emphasized urbanization itself, which is determined based on the level of human population, residential development, or impervious surface within a landscape. Although it may be due to low agricultural land uses in the landscapes, in some areas like New York, percent cover of agricultural land uses tends to increase further from urban core (Medley et al. 1995). In spite of possible variations in agricultural land uses along urban-rural gradient, agricultural land use is often less emphasized in the analysis (but, see Parris and Hepinstall-Cymerman 2012). Effects of agricultural land use is often considered negligible compared to urbanization effect because agricultural land use is less selected in preliminary valuable selection for final analysis.

A great number of avian studies have been conducted in agricultural landscapes and examined avian species responses to agricultural land uses. Some rural gradient studies have also explored avian species distribution at different extents of agricultural land uses. Those studies have reported similar avian responses observed in urban-rural gradient studies. Non-native species and edge-associated species (e.g., Brown-headed Cowbird and European Starling) and habitat generalists (e.g., Morning Dove) positively relate to agricultural landscape whereas forest specialists negatively respond to intensified agricultural land uses (e.g., Saab 1999; Rodewald and Yahner 2001; Bennett et al. 2006; Mastrangelo and Gavin 2012). But, it is little studied whether richness can peak at moderate levels of agricultural land uses or whether it varies non-linearly as observed in urbanized landscapes (but, see Mastrangelo and Gavin 2012).

In some regions in the Southeastern USA, lands in forest and agriculture are increasingly converted to residential development of varying densities, creating a complex human-altered landscape, a mixture of low or moderate level of urban development and agricultural land uses: suburban and exurban type of development adjacent to or within an agricultural landscape with several patches of forests. While a typical urban-rural gradient is most often focused on a gradient of urbanization, the landscapes with different extents of agricultural lands add another component to this gradient, resulting in two gradients of urbanization and agricultural land use. This could be called an urban-rural/agriculture-wildland gradient although wildland can be located in the middle of the gradients (e.g., from high urban area to wildland and from wildland to high agricultural land use). In this landscape, the common approach focusing on urbanization does not provide appropriate information to understand avian species distribution. It requires considering not only urban development, but also agricultural land use for analysis and inference.

Relationship between avian biodiversity, habitat structure (basal area), and patch size

Habitat heterogeneity is known to be a crucial factor influencing avian biodiversity (e.g., Pino et al. 2000; Benton et al. 2003; Devictor and Jiguet 2007; Cerezo et al. 2011). During the past several decades, conservation management in the southeastern pine forests has emphasized improving heterogeneity at local or patch (stand) scale, particularly, the structural diversity within a patch. Unlike other forests, pine forests are susceptible to encroachment of hardwoods. In the absence of disturbance or management, vegetation cover within the pine patch becomes dense. Especially, as canopy of pine is closed, structural diversity of the patch decreases and the patch can become a “biological desert” or “pine barren” (Duryea and Dougherty 1990). Thus, the amount of canopy cover within a pine patch is considered as important habitat characteristic influencing vegetation structure; however, in forest management, canopy cover is largely controlled by managing basal area because of high correlation between amount of canopy cover and basal area. High basal area results in closed canopy, reduce light penetration, increase competition among understory plants, lower herbaceous vegetation, and slow the growth of trees (e.g., Melchiors 1991; Allen et al. 1996). It can lower structural diversity and thus reduce overall habitat quality, especially for species preferring open or open-forest types of habitats such as early successional species, shrubland species, and pine-grassland species. Too low basal area of a patch (e.g., heavy thinning) can negatively affect tree nesting species and mature forest or forest interior species preferring relatively dense canopy cover. These negative or positive effects of basal area on diversity and occurrence of avian species have also observed in hardwood forests or mixed pine-hardwood forests (Canterbury et al. 2000; Wang et al. 2006; McDermott and Wood 2011). Therefore, like canopy cover, basal area is considered as one of the main factors determining structural diversity within a pine patch and maintaining appropriate basal area through practices such as thinning or spacing (at the stage of planting) has been common in forest management for wildlife (Melchiors 1991; Dickson et al. 1993).

Another stand or local characteristics important to avian biodiversity, but less explored in pine forests, is patch size. Species-area relationships have been discussed in ecological studies for long time. Especially, as habitat fragmentation and habitat loss increase, it has been a critical issue in conservation management such as reserve design. In general, patch size is known to have a positive effect on species richness or abundance in animals and plants (e.g., Arrhenius 1921; MacArthur and Wilson 1963; Rosenzweig 1995 for review; Hill and Curran 2003; Lindenmayer and Fischer 2006). In birds, the significant positive effect of patch size is often observed in habitat specialists such as forest interior, shrubland, or woodland birds compared to edge species and habitat generalists (Ambuel and Temple 1983; Blake and Karr 1987; McIntype 1995; Rodewald and Vitz 2005). One explanation about the positive effect is based on the fact that a large patch contains more interior zones than a small patch, and thus it can provide species with more areas unaffected by disturbance and negative edge effects (Pickett and Thomson 1978; Harris 1984; Baker 1992). However, it has been debated that the main factor influencing species richness in forest area is not an area *per se* but habitat diversity, which is often highly correlated with area (Shochat et al. 2001). Variations in habitat structure within a patch could also change the strength of species-area relationship. Recently, for example, Huth and Possingham (2011) modeled woodland bird species-area relationships by incorporating vegetation structural diversity. The result from the model showed that effect of patch size on richness was stronger at high habitat structural diversity (i.e., high quality habitat) whereas increasing patch size was little benefit at a patch with low structural diversity (i.e., low quality habitat). Although the finding is not new, it suggests that understanding the relationship between effect of the habitat structure and effect of patch size on biodiversity is important in making forest management decision, whether emphasis of the management should be on promoting structural diversity or expanding patch size.

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CHAPTER 2

ASSESSING SCALE DEPENDENCIES AND RESPONSES OF AVIAN SPECIES IN A PINE FOREST, AGRICULTURE, AND URBAN MATRIX[1]

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ABSTRACT

In the southeastern USA, planted pine forests are increasingly embedded in a complex matrix of urban development and/or extensive agriculture. Although the majority of the planted pine forests are primarily managed for timber harvest, there is a growing interest in management plans to conserve avian species in these habitats. However, typically most management has focused on the local or stand scale and little attention has been given to landscape scale habitat characteristics. We investigated the relationship between site occupancy of 18 avian species, spatial scales (local-scale, 50 m-circular area of a sampling point; and 2 landscape scales, 500m- and 1km-radius circular area), and anthropogenic land uses. During May-August 2010 and 2011, we conducted bird surveys and vegetation surveys at loblolly dominant pine stands in the Sand Hills region of Georgia. We performed Principal Component Analysis and used 3 principal component scores at each scale as scale-specific habitat covariates for analysis. We developed 8 single-season and 16 multi-season occupancy models in the program MARK. We also incorporated a spatial autocovariate into occupancy models to account for spatial autocorrelation. We used an information theoretic approach to identify the best supported models. Of 18 species, 6-7 species responded more to local scale habitat features and 8 species to 500m- and/or 1km-landscape scale habitat features. Occupancy by forest interior species and forest edge species was more associated with landscape scale features, whereas occupancy of pine-grassland species was more related to local scale features. Urban development and agricultural land uses positively influenced occupancy of species that responded to landscape scale features. Our results demonstrate that landscape scale habitat features can be important in conservation management plans for some species such as forest interior and forest edge species in this region. Our results

also suggest that pine forests in the urban/agriculture matrix could play a positive role in avian biodiversity conservation, depending on how we manage the forests.

INTRODUCTION

During the past two decades, ecologists have recognized the importance of landscape matrix to species distribution and of the existence of habitat variation at different spatial scales. They have emphasized examining ecological processes at multiple spatial scales (e.g., Wiens 1989; Forman 1995; Rickets 2001). A number of studies, especially those conducted in human-altered landscapes, have found that variations in avian species abundance and community composition are better accounted for by landscape habitat features than local habitat features (e.g., Donovan et al. 1997; Atauri and de Lucio 2001; Miller et al. 2003; Devitor and Jiguet 2007). These studies have also demonstrated that avian species respond to human land uses both positively and negatively, depending on the level of human land uses in a landscape. However, most studies have been conducted in predominantly urban or predominantly agricultural landscapes. The studies that examined avian species distribution along an urban-rural gradient have focused on urban development with little consideration of the effect of agricultural land uses on avian species. Although transformation of natural habitat to urban development or agricultural land results in the loss of wildlife habitat, it has been argued that a less intensive agricultural land use can be a more favorable matrix than urban development (Dunford and Freemark 2004). Few studies have examined the relative effects of the two dominant human land uses (urban development and agricultural land uses) on avian species. In particular, little is known about the responses of birds in pine forests to each of the land uses in a landscape matrix consisting of a mixture of urban development and agricultural land.

Forests in the southeastern USA have been highly fragmented and altered by timber harvest and intensive agriculture for more than 150 years. A large percentage of the original forests have been replaced by pines grown for commercial timber. In addition, several regions in the southeastern USA, including central-east Georgia, have been experiencing the rapid expansion of urban development, leading to increases in the complexity of the landscape matrix surrounding pine forest remnants as well as planted pine forests.

Although planted pine forests are primarily managed for wood production, there is growing interest in management plans to enhance avian biodiversity in the pine forests (e.g., Turner et al. 2002). In some cases, the pine forests are also managed to restore wildlife habitats or conserve endangered, threatened, and declining avian species associated with pine forests directly or indirectly, such as the Red-cockaded Woodpecker (*Picoides borealis*), Bachman's Sparrow (*Aimophila aestivalis*), and Northern Bobwhite Quail (*Colinus virginianus*). However, most management plans have been applied to local (or stand) scales with little consideration of landscape context. Relatively few studies have examined the spatial scale dependency of avian species in pine forests, even those surrounded by other types of natural habitats (Loehle et al. 2005; Mitchell et al. 2006). In spite of growing urban development in the southeastern USA, there is also little information about how avian species in pine forests respond to urban development and agricultural land uses. For a successful forest management plan to conserve avian biodiversity in pine forests embedded in a human-dominated landscape, it is important to understand the degree to which habitat characteristics at different spatial scales affect avian species and to evaluate the habitat values of pine forests in the landscape through species responses.

In this study, we investigated the relationship between spatial scale and occupancy of avian species in pine forests embedded in landscapes altered by urban development and agriculture in the Sand Hills Physiographic Region of east-central Georgia, USA. Our goals were to (1) determine which spatial scales (local vs. landscape) best explain the variation in occurrence of bird species; and (2) examine how birds respond to habitat characteristics at each scale, especially urban development and agricultural land use. To reduce bias and improve inference, we used two recently developed approaches: site occupancy models to account for imperfect detection (MacKenzie et al. 2006) and an autologistic regression model using a spatial autocovariate to account for spatial autocorrelation (Augustin et al., 1996; Klute et al., 2002; Moore and Swihart 2005).

METHODS

Study Site

The study was conducted at pine forest remnants (stands or patches) in Fort Gordon and surrounding areas of Fort Gordon in 3 ecoregions of Georgia (Sand Hills, Coastal Plain Red Uplands, and Southern Outer Piedmont), which include 7 counties: Burke, Columbia, Glascock, Jefferson, McDuffie, Richmond, and Warren (Fig. 2.1). The study areas show a gradient of urban-rural/agricultural land uses: highly urbanized areas at the northeastern part of Richmond County and little development in Fort Gordon; low agricultural land uses and low and moderate levels of urban development in Columbia and McDuffie Counties; and high and moderate levels of agricultural land uses in other counties.

Agricultural land uses are dominated by pasture and hay fields in the study areas. Pine forests are composed of mainly planted loblolly pines (*Pinus taeda*). Slash pines (*Pinus elliottii*) or shortleaf pines (*Pinus echinata*) are mixed with loblolly pines in some areas. The majority of the relatively mature longleaf pines (*Pinus palustris*) are found at Fort Gordon. The ages of pine patches vary across our study sites; however, old pine patches (> 75yrs) are relatively rare and most pine patches are young and mid-aged. Overstory and midstory of hardwood forest and mixed forest largely consist of sweetgum (*Liquidambar styraciflua*), sassafras (*Sassafras albidum*), black cherry (*Prunus serotina*), flowering dogwood (*Cornus florida*), and oak (*Quercus* spp.). Sparkleberry (*Vaccinium arboreum*) is also commonly found in the midstory. The understory is dominated by yellow jessamine (*Gelsemium sempervirens*), muscadine (*Muscadinia rotundifolia*), greenbrier (*Smilax spp.*), brambles (*Rubus* spp.), blueberry (*Vaccinium* spp.), broomsedge bluestem (*Andropogon virginicus*), low panicgrass (*Dicanthelium* spp.), wiregrass (*Aristida stricta*), and lespedeza (*Lespedeza* spp.).

Sample patches and points

Mid-aged loblolly and longleaf pine patches (20-75yrs) were randomly selected for sampling, considering the level of urban development/agricultural land uses and separation distance among patches to minimize spatial dependency. Minimum distance between sampled patches was >500m at Fort Gordon and > 1km at outside of Fort Gordon. We used the 2009 forest inventory data of Fort Gordon, 2007 digital orthophoto images (National Agriculture Imagery Program, NAIP), 1998 Digital Orthophoto Quarter Quads (DOQQs), 2006 National Land Cover Dataset (NLCD), ground-truth survey, and ArcGIS 9.2 to select sample patches. However, within Fort Gordon, the number of sample patches was limited by accessibility related to intensive military training and road condition. Since most pine patches outside of Fort Gordon were privately owned, access was limited in some cases. During 2010-2011, we contacted 140 landowners by letters and by visits. We acquired permission from 70 landowners, including several public entities, such as the cities of Augusta and Hephzibah, GA. Of 182 pine patches, 84 patches were located at private lands. Pine patches used in our study included unmanaged stands in the recent past (patches located in highly or moderately urbanized areas and some patches in agricultural lands), minimally or moderately managed stands (most patches), and relatively intensively managed stands (several patches in Fort Gordon). Patch sizes varied from 1ha to 121ha or 210ha, depending on how a patch was delineated.

Within a patch, one point was established randomly at least 50-70m from any edge (road, other types of vegetation or land cover, etc). A total of 94 points were established in 2010, but 4 of them were developed or harvested in 2011. An additional 92 points were established in 2011, but 4 points had prescribed burns after the 1st visit, and thus a total of 178 points were completely surveyed in 2011. All points within longleaf pine patches were located at Fort Gordon (Fig. 2.2).

Bird surveys and vegetation surveys (local-level data)

Bird surveys were performed three times from May through June each year during 2010-2011, using fixed-radius point counts (Ralph et al. 1993). At each point, an observer recorded species seen or heard within a 50-m radius of a sample point for a 10-min duration and also estimated the distance from the species detected to the sample point. One observer in 2010 and two observers in 2011 conducted surveys. In 2011, the observers were rotated between sites to reduce observer effects. We also alternated surveys order to minimize the effect of time-of-day. Each survey was performed between dawn and 1100 EDT. We did not conduct surveys during inclement weather such as rain or high wind.

To quantify habitat characteristics at a local scale, vegetation sampling was conducted at the same points as the bird surveys during mid-June to July, 2010-2011. A total of four 5m radius subcircular plots were established in each cardinal direction at a fixed distance of 30m from a sample point. Within each of the subcircular plots, vegetation data were collected using modified PRBO Point Count Veggie (Relevé) Protocol. Percent vegetation cover at herb (< 0.5 m in height), shrub (0.5-5m in height), and tree (>5m in height) layers were visually estimated. The tree vegetation was divided into two categories: softwood and hardwood. Dominant plant species within each layer were also recorded. DBHs (Diameter at Breast Height) of hardwood and softwood (≥ 8cm in diameter) were separately measured within four 10m radius subcircular plots. The values of each vegetation characteristic estimated or measured from four subcircular plots were averaged and used to represent the value at the sample point.

Landscape-level data

To generate landscape-level variables, we digitized 2010 NAIP and 1998 DOQQs using GIS software (ArcGIS version 9.2). Land cover was classified into 9 classes, by modifying the classification scheme of 2006 NLCD (Appendix A). We used 2 landscape scales: 500m and 1km. Landscape variables were assessed within a 500m- and 1km- circle of a sample point, using FRAGSTATS: percent cover of pine forest, other forests (hardwood and mixed forest), urban development, agricultural land, and patch density of pine forest (i.e., the number of patches in the landscape divided by area (m^2) of the landscape and multiplied by 10,000 and 100 to convert to 100 hectares).

Data analysis

Bird species and covariates

A total of 63 species were observed across the study sites during 2010-2011 (Appendix B). However, for analysis, we excluded flyovers, waterfowl, nocturnal species, raptors, and species that were detected on < 15 % of the points. A total of 23 species were analyzed: 16

species in 2010 and 22 species in 2011. However, some occupancy models of 5 species showed problems in parameter estimation, convergence, or model fit. The models generated nonsensical parameter estimates, failed to converge, or the global model did not fit the data well. To avoid biased results, we eliminated those species and used 18 species for the final analysis. We classified each species into three main ecological or functional guilds based on a review of the literature (Ehrlich et al. 1988; Harmel 1992; Wilson et al. 1995): habitat preference (forest interior, forest edge, and pine-grassland), migrant behavior (migrant and resident), and nest placement (tree, shrub, cavity, and ground). However, to make inferences, we focused primarily on the 3 habitat preference guilds.

As local scale variables of analysis, we focused on structural attributes because there were little variations in plant composition across our study sites and it is well known that the structural characteristics of vegetation within a stand are important for wildlife in pine forests (e.g., Melchiors 1991; Dickson et al. 1993). We performed a Principal Components Analysis (PCA) with varimax rotation to account for the correlation among variables and to reduce the number of variables at each of 3 scales. We retained all principal components that explained ≥15% of the variation in the explanatory variables, resulting in three principal components (PC) at each of the local, 500m-, and 1km- scales which captured 76% (2010) and 81% (2011), 84%, and 87% of the total variation, respectively. The three PC scores at each scale were used in occupancy analysis as scale-specific habitat covariates (Table 2.1).

Modeling species occupancy

One methodological problem in wildlife surveys is that the probability of detecting a species is likely to vary among species, areas, time (e.g., sampling occasion), observers, etc.

(Boulinier et al. 2001). In most field surveys, species detection probabilities are <1.0. Ignoring this imperfect detection could result in biased estimations of population attributes such as species occurrence and abundance, and it could result in misleading inferences about the relationship between habitat features and species distribution (e.g., Williams et al. 2002; MacKenzie et al, 2006; Dorazio et al. 2006). We accounted for the imperfect detection using occupancy models developed by MacKenzie et al. (2006) in all our analyses.

In the first step, we constructed a detection history for each species at each point and year using detection/nondetection data of the species. Following the approach outlined by MacKenzie et al. (2006), we developed 8 single-season occupancy models with 2 levels of detection (p) and 4 levels of occupancy (ψ) in the program MARK which uses maximum-likelihood methods to estimate occupancy and detection probabilities (Table 2.2). Detection probability can be modeled with local habitat characteristics. Initially, we included a model of detection probability that was as function of percent cover of shrub vegetation, because it may influence an observer's ability to detect species by causing visual or audible disruptions. The model was not better than other detection probability models. Thus, we eliminated the model and used 2 levels of detection probability: $p(.)$, constant detection probability; and $p(\mathrm{t})$, heterogeneous detection probability between 3 sampling occasions. Occupancy was modeled with no covariate ($\psi(.)$), local scale habitat characteristics (ψ(local)), 500m landscape scale characteristics (ψ(500m)), and 1 km landscape scale characteristics (ψ(1km)). Single season occupancy models assumed closed population over the survey periods, no false detection, and independence of detection among sampling points. We conducted our surveys during the breeding season, observers were experienced or trained, and the >500-m distance between sample points were assumed enough to avoid double counting in our study. Thus, we concluded that our models satisfied these assumptions.

Because our data included two primary sampling periods (2010 and 2011), we also performed multi-season occupancy analysis using the robust design occupancy model in the program MARK. The model assumes population closure within each of the primary sampling periods, but not between them. In the model, occupancy estimates of the first primary sampling period (2010) and estimated extinction probability and colonization probability are used to derive the occupancy estimate of the second primary sampling period (2011). Local extinction probability (ε) is the probability that a site occupied in the primary sampling period becomes unoccupied in the second primary sampling period. Local colonization probability (γ) is the probability that an unoccupied site in the primary sampling period becomes occupied in the secondary primary sampling period. Like single-season occupancy models, we fitted models with 2 levels of detection for each primary sampling period and 4 levels of occupancy, and thus we developed a total of 16 *a priori* models (Table 2.2).

Modeling spatial autocorrelation

Ecological data collected in space are often spatially autocorrelated (Fortin and Dale 2005), a condition where observations located closer together are more likely to have similar values than observations located further apart due to some unmeasured process. . Spatial autocorrelation is known to cause biased hypothesis test results, indicating false relationships between response variables and explanatory variables, and to generate biased parameter estimates (e.g., Legendre 1993; Fortin and Dale 2005; Beale et al. 2010).

However, spatial correlation can often be sufficiently explained by explanatory variables (Warren et al. 2005). We examined spatial structure in the residuals of the occupancy models to assess the degree of spatial autocorrelation in the response variable that was not accounted for by explanatory variables (Moore and Swihart 2005). We calculated residuals following Moore and Swihart (2005): the observed values (presence or absence) at a site minus the predicted probabilities of detecting the species at least once (calculated from model-averaged estimates). Then, we constructed a Moran's I correlogram of the residuals in SAM 4.0 (Spatial Analysis in Macroecology; Rangel et al. 2010. To construct the correlograms, we used a 2-km maximum lag distance for 2010 because that distance was close to the mean distance among sample points (~ 2-km) but larger than the mean distance among points in Fort Gordon (~ 1-km). A 1-km maximum lag distance was used in 2011 because it was close to the mean distance among points used in 2011 (~ 1.6-km) but greater than the mean distance among points in Fort Gordon (~ 500-m). At any given lag distance, if Moran's I was < 0.1, we considered the spatial autocorrelation to be negligible. For a species whose model residuals were positively correlated (Moran's I ≥ 0.1 and $P \leq 0.05$), typically at shorter lag distances, we calculated an autocovariate (ACOV) to account for spatial autocorrelation, following Moore and Swihart (2005):

$$autocov_i = \frac{\sum_{j=1}^{J_i} \omega_{ij} y_j}{\sum_{j=1}^{J_i} \omega_{ij}},$$

where $y_j = 1$ for all sample points where a species was detected in a set of J_i neighbors of point i; otherwise $y_j = 0$; ω_{ij}, the weight given to point j (the inverse of the Euclidean distance between points $_i$ and j). The neighborhood of J_i was determined by the distance at which the residual was autocorrelated. Moore and Swihart's approach was based on the method developed by Augustine et al. (1996) and Klute et al. (2002). The method derived ACOV as the probability of observing a species at a site conditional on the presence of the same species at a site(s) within a neighborhood of the site (Augustin et al., 1996; Klute et al., 2002). ACOV was calculated using R (R Development Core Team, 2009). We incorporated the ACOV into occupancy models as an additional covariate for the species where spatial dependency was detected.

Model selection and model averaging

To identify the best spatial scale (local vs. two landscape scales) associated with a species' occupancy, we used an information-theoretic model-selection approach based on Akaike's Information Criterion (AIC, Burnham and Anderson 2002). We used the AIC*c* (AIC adjusted for small sample size relative to the number of parameters) and AIC*c* weights generated in the program MARK. We constructed a confidence set of candidate models that whose Δ AIC*c* (the difference in AIC between the best model and the subsequent models) was <2. Each model in the confidence set can be considered a plausible explanation for the occupancy of the species, given the data. However, if Δ AIC*c* between the best model and the null models (ψ (.)p(.) and ψ (.)p(t)) was <2, we concluded that the occupancy of the species was not strongly associated with the scales used in our study.

To examine the relationship between species site occupancy and covariates, we used the model-averaging method, as described in Burnham and Anderson (2002). We calculated the model-averaged parameter estimates, unconditional standard errors, and 90% confidence intervals (CI) based on *t*-statistics for the parameters (covariates) included in the confidence set of models. Model-averaging was calculated by weighting the parameter estimates and standard errors from each model in the set using its Akaike weight and by summing the new weights across all the models that contained the parameter of interest. Since PC scores at the 500m-scale and the 1km-scale were interpreted similarly, if the confidence set of models contained the models from each of the two scales, we averaged them for each PC score. Through the model-averaging, we produced a final model with model-averaged parameter estimates, called the composite model. Inferences about the relative influence of each variable on species occupancy were made based on the composite model, considering the parameter estimates (coefficients) and their precision. Precision of model-averaged parameter estimates was determined using the 90% CI. We did not back-transform any estimates or its 90% CI. When the 90% CI included zero, the parameter estimate was considered unreliable.

To evaluate model fit to a logistic distribution, we performed the Hosmer and Lemeshow (2000) goodness-of-fit (GOF) test of all single-season occupancy models with covariates for each species in SAS v 10.0. We did not assess the fit of multi-season occupancy models, because no formal GOF test exits currently. Fit was considered poor when *p*-value was < 0.05. If models of the species showed lack-of-fit, we eliminated the species from further analysis. However, if only one of two levels of detection probability (*p*(.) or (*p*(t)) was fit poorly, we included the species. But, we used only occupancy models with the level of detection probability that fit the data well. Because our aim was primarily to determine the best spatial scale(s) at which to explain variations in species occupancy and to evaluate effects of habitat characteristics on species while taking into account imperfect detection, estimation of detection probability or occupancy probability itself was not our interest. Thus, we do not think this approach could affect our inference.

RESULTS

General distribution pattern of avian species

Of 63 species detected at least at one point across the study sites during 2 years, 50 were observed in 2010 and 60 species in 2011 (Table 2.3). All species, but 3 (Chuck-will's Widow, Hooded Warbler, and Red-cockaded Woodpecker) observed in 2010 were also detected in 2011. Pine Warbler and Summer Tanager were widely distributed throughout the study sites (detected at over 70% of sample points) in 2010 and Brown-headed Nuthatch, Carolina Chickadee, Northern Cardinal, Pine Warbler, and Summer Tanager in 2011. However, over half of the species were narrowly distributed: 26 species in 2010 and 24 species in 2011, including Red-cockaded Woodpecker, Bachman's Sparrow, and Northern Bobwhite Quail, were observed at less than 7% of total sample points. Red-cockaded Woodpecker and Bachman's Sparrow were observed only at pine patches located within Fort Gordon.

Of the 63 species that were detected, about 46 % and 30% of 63 species were forest edge species and forest interior species, respectively. Over half of the species (60%) were tree-nesters or cavity-nesters and 52% of species were migrants.

Scale

Whether local or landscape scale features better-explained species occupancy was variable among species. In 2010, of 13 species, occupancy of 7 species was better explained by local scale habitat features and occupancy of 4 species by 500m- and/or 1km- landscape scale habitat features (Table 2.4). Occupancy of 2 species was not related to either of the scales used in this study. In 2011, of 9 species, occupancy of 6 species was related to 500m- or 1km- landscape scale features, 1 species to local scale habitat features, and 2 species were not correlated to local or landscape scale habitat features (Table 2.5). Of 4 species tested in both years, 2 species (Blue-gray Gnatcatcher and Northern Cardinal) responded to a different scale in 2010 and 2011. Overall, of 18 species tested across 2 years, 6-7 species responded more to local scale habitat features and 8 species to 500m- and/or 1km- landscape scale habitat features.

Results of multi-season occupancy showed a pattern similar to that found in 2010 (Table 2.6). All species tested in single-season occupancy, but Carolina Chickadee, responded to the same spatial scale. Carolina Chickadee responded to 1km landscape scale habitat features as well as 500m landscape scale habitat features, whereas it was more associated with 500m landscape scale habitat features in 2010. Occupancy by Downy Woodpecker, which was not included in single-season occupancy, was associated with 500m- and 1km- landscape scale habitat features. Occupancy by Ovenbird was not related to any of the three scales in 2011, but it was associated with local scale habitat features when both years were considered.

At guild level, 60% of forest interior species and 50% of forest edge species were more strongly associated with 500m- and/or 1km- landscape scale habitat features. Seventy-five percent of pine-grassland species were related to local scale habitat features. If only species showing scale-dependency clearly were considered (i.e., Blue-gray Gnatcatcher, Ovenbird, Pine Warbler, and White-eyed Vireo were excluded), 70-75% of forest interior and forest edge species responded to 500m- and/or 1km- landscape scale variables and all pine-grassland species to local scale habitat features.

Responses to habitat characteristics

Among 3 habitat features at local scale, a gradient of hardwood relatively strongly influenced species occupancy (Tables 2.7 - 2.8). As hardwood vegetation cover in the tree and shrub layer sand basal area of hardwood increased within a stand, the probability of occupancy by Blue-gray Gnatcatcher, Summer Tanager, and Tufted Titmouse increased, but occupancy by Eastern Bluebird decreased. Occupancy by Blue-gray Gnatcatcher also decreased with increasing the vegetation cover and basal area of softwood. The pine-grassland species, Indigo Bunting positively responded to herbaceous vegetation cover both years. In 2011, Indigo Bunting also showed a significantly negative response to hardwood vegetation cover and softwood vegetation cover. Brown-headed Nuthatch, Eastern Wood-Pewee, and Ovenbird, which were not significantly associated with local scale habitat characteristics in single-season occupancy models, responded positively to herbaceous vegetation cover in multi-season occupancy models (Table 2.9). In the models, Brown-headed Nuthatch and Eastern Wood-Pewee were also negatively related to hardwood vegetation cover, but Ovenbird was positively associated. Overall, although species response to local scale habitat features varied, forest interior (and some forest edge) species responded positively to hardwood cover and basal area, while pine-grassland species responded negatively to the same variables, but positively to herbaceous vegetation cover.

Species associated with the landscape scale habitat features tended to respond positively to human land uses (Tables 2.7 – 2.9). The occupancy of Carolina Chickadee, Northern Cardinal, and Carolina Wren increased with urban development and fragmentation of pine forest. Carolina Wren and Northern Cardinal also tended to be more present in stands surrounded by agricultural lands. Carolina Chickadee also showed a positive response to other forest cover (i.e., hardwood forest and mixed forest cover). Downy Woodpecker and Red-bellied Woodpecker were positively related to agricultural lands and/or urban development and other forest cover.

DISCUSSION

Scale

In our study, the relationship between species occupancy and habitat characteristics at different scales was species-specific and guild-specific; that is, no single scale was appropriate across all species or guild of species. However, more species responded to landscape habitat characteristics (i.e., habitat features at 500m or 1km) than to local habitat characteristics. Although relatively few avian landscape studies have been performed in pine forests, our result is somewhat similar to the findings of several other studies. Mitchell et al. (2001) reported that the presence of forest birds was predicted equally or better by landscape-level characteristics than by microhabitat characteristics. Relatively strong effects of landscape habitat characteristics were also observed in other avian community studies (e.g., Loehle et al. 2005; Mitchell et al. 2006). However, results for individual species observed in our study were sometimes inconsistent with results from other work. For example, Hagan and Meehan (2002) found that the occurrence of Red-eyed Vireo was related to stand-level characteristics, which can be considered local habitat characteristics. Similar results were observed in the study of Michael et al. (2001) although they described the scales to which the species responded as microhabitat scale and fine landscape scale (equal to 80m circular landscape) rather than local or stand scale. In our study, occupancy of Red-eyed Vireo was related to landscape scale habitat characteristics. This different response may be associated with the matrix type in the landscape where other studies were performed. While the sampled patches in other studies were located within natural and planted forests (i.e., little urban development and agricultural land uses), our sampled patches were located along a gradient of urban-rural/agriculture-wildland. Landscape features are likely to have greater explanatory power when there are strong differences among landscape elements that affect habitat quality (Wiens et al. 1987; Miller et al. 2004). Human land-uses may increase the contrast among the landscape elements. Numerous studies conducted in forest patches in urban or agricultural matrices have found that landscape habitat features better explain the variations in avian species abundance and community composition than local habitat features (e.g., Saab 1999; Rottenborn 1999; Miller et al. 2003; Smith and Wachob 2006). Thus, it is not surprising that some species like Red-eyed Vireo showed different scale-dependent responses in our study from those in other studies.

Our results also suggest that the relative importance of different scales for explaining species occupancy varies with guild based on habitat preferences of the species: occupancy of forest interior species and forest edge species was more associated with landscape scale characteristics, and occupancy of pine-grassland species with local scale characteristics. Since the forest interior species are known to be sensitive to landscape changes, it is expected that they may respond more to landscape scale characteristics. Scale response of forest edge species could change with the matrix type surrounding the forest edge. They may not strongly respond to landscape features where the contrast between the matrix and the edge is low, but may respond more where the contrast is high, like an urban or agricultural matrix. Compared with the other 2 guilds, pine-grassland species inhabit a specific habitat, an open-pine forest with grass vegetation at understory. Pine-grassland species avoid densely vegetated pine forests (i.e., pine forests with high basal area of pine or hardwood and dense shrub vegetation). Vegetation structure within a patch, such as basal area and percent cover of different vegetation layers, is crucial to determine pine-grassland occurrence. Thus, it is expected that pine-grassland species would respond more to local scale habitat characteristics.

Some of the species analyzed in both years showed a different scale dependency between the 2 years or between single-season occupancy analysis and multi-season occupancy analysis. Northern Cardinal and Carolina Chickadee responded to 1km scale and 500m scale characteristics in 2010, respectively. But, Northern Cardinal was related to 500m scale characteristics in 2011 and Carolina Chickadee to both 500m and 1km scale characteristics in multi-season occupancy analysis. Since two spatial scales (500m and 1km) were considered for landscape scale characteristics in our study and we focused on local scale and landscape scale for inferences, this result does not affect our conclusion that landscape scale characteristics best explain occupancy of Northern Cardinal. The other two species, Blue-gray Gnatcatcher and Ovenbird, did not show sale dependency in 2011, but they responded to local scale characteristics in 2010 and in multi-season occupancy analysis. This discrepancy causes difficulty in determining the scale dependency of these species. However, in the case of Blue-gray Gnatcatcher, if a $< 2\ \Delta$ AIC*c* cutoff is extended to $< 4\ \Delta$ AIC*c*, a confidence set of candidate models include the occupancy model at local scale in 2011 and the occupancy model at 1km scale and at 500m scale in 2010 and in multi-season occupancy analysis. This seems to indicate that occupancy of Blue-gray Gnatcatcher may be related to both local and landscape scale characteristics. The relationship may be examined by modeling occupancy of Blue-gray Gnatcatcher as a function of a combination of both local and landscape (500m and 1km) scale variables. We did not include the model for our final analysis due to over-parameterization and nonsensical estimates. It is unlikely that we can make any conclusion about their scale dependency in the current study. Multi-year survey data with larger sample size in future study may help to clarify the scale dependency of Blue-gray Gnatcatcher (and probably Ovenbird). Lastly, it should also be pointed out that, although no clear distinction was made between the two landscape scales for inferences, occupancy of species tended to be more associated with characteristics at the1km scale or both 500m scale and 1km scale than with 500m scale alone. This implies that there is variation even in the landscape scale to which avian species respond. Avian species might be also related to larger landscape scales than 1km if landscape features highly vary in the larger landscape scale. In that situation, an inaccurate selection of landscape scale can lead to an erroneous management plan for avian conservation. For a sound habitat management at landscape scale, we need to identify correct landscape scale(s) crucial to avian species by including multiple-landscape scales in future studies.

Responses to habitat variables

At the local scale, we found relatively strong positive or negative effects of hardwood (vegetation cover and basal area of hardwood) on species occupancy. It tended to influence forest interior and forest edge species positively, but pine-grassland species negatively. All pine-grassland species were positively associated with the amount of herbaceous vegetation. The opposite response of pine-grassland species to the two variables is related to the habitat requirements of the guild. As described previously, the pine-grassland species inhabit open-pine forest. In our analysis, hardwood cover represented the vegetation cover of hardwood at tree and shrub layer. Basal area of hardwood was positively correlated with the cover, especially, at tree layer; if basal area of hardwood is high, vegetation cover of hardwood at tree and shrub layer is also high. In pine forests, increasing vegetation cover at the two layers to a certain level can improve the structural diversity in the forest. However, over the level, it results in dense vegetation cover at tree and shrub layer with low or no vegetation cover at herb layer. With increasing hardwood vegetation cover, basal area also increases and it leads to decreasing open space within a patch. Thus, different responses of the guilds to the variables were expected.

Among 3 landscape variables, urbanization and/or agricultural land uses positively influenced occupancy of the species that responded to the variables significantly. It is well known that urbanization alters a bird community: with urban development, bird density of non-native species and synanthropic species increases, whereas richness and evenness of native species decrease (e.g., Marzluff 2001; Hansen et al. 2005; Faeth et al. 2011). Species richness and/or abundance of riparian birds are negatively associated with percent cover of urban development (Rottenborn 1999; Miller et al. 2003; Smith and Wachob 2006, but also see Oneal and Rotenberry 2009). However, another trend observed along an urban gradient is that a low or moderate level of urban development increases overall richness or richness of habitat generalists (e.g., Fraterrigo and Wiens 2005; Marzluff 2005). In particular, in naturally sparse or fragmented habitats, richness and abundance of birds peak at a moderate level of urban development (e.g, Blair 1999; Trammell et al. 2011). Similar responses of bird species found in an urban matrix have been reported in a bird community in an agricultural matrix, although the responses seemed to vary more, depending on an ecological or functional guild of a species (e.g., Saab 1999; Bennett et al. 2006; Haslem and Bennet 2008; Mastrangelo and Gavin 2012). The positive relationship between avian species and human land uses (urban development and agriculture) is often explained by "environmental heterogeneity" promoted by mild human land uses, heterogeneous vegetation structure and composition in urban and agricultural lands, and increase in food availability and other resources such as water and nesting sites (e.g., Marzluff 2001; McKinney 2002). Heterogeneity at landscape-level as well as at stand-level is known to be a crucial factor influencing avian biodiversity in pine forests: different age of stands and habitat types within a landscape, and heterogeneous vegetation structures within a stand increase avian biodiversity (e.g., Turner et al. 2002; Mitchell et al. 2006; Luck and Korodaj 2008). The positive responses of birds in our study seem to be associated with the heterogeneity at both levels. Percent cover of urban development or agricultural land uses throughout our study sites is less than 50%, except 4 points in urban matrix and 1 point in agricultural matrix. Although levels of human land uses are somewhat arbitrarily determined, most of our sample patches located in anthropogenic landscape matrix show low level to highly moderate level of urban development and/or agricultural land uses. These levels of anthropogenic land uses may increase heterogeneity in a landscape and a stand, by creating semi-natural habitats and open-space, and by changing vegetation structure of a stand (e.g., more hardwoods at shrub and tree layer, and more forbs and grasses at the edge area of the stand located in agricultural matrix).

In particular, agricultural matrix seems to increase the heterogeneity more effectively compared to urban development. Our study found that pine patches in low level of agricultural land uses had relatively higher herbaceous vegetation cover than those in moderate and low level of urban development, although it was not statistically significant based on overlap of 90% confidence interval. In addition, pasture/hay fields, which are the dominant form of agriculture in our study sites, may provide a better foraging opportunity to birds than impervious surfaces or lawns in an urban area. Given that the parameter estimate of the agricultural gradient variable was 2-3 times higher than the urban gradient variable, agricultural land uses had stronger effects on occupancy of avian species. This is a significant finding, because it implies that agricultural lands could serve as a more amenable matrix than urban lands. Most studies have been conducted along an urban or exurban gradient or in agricultural landscape. Even the studies that were conducted along an urban-rural gradient have mainly focused on urbanization such as building structures (residential and commercial buildings) and impervious surfaces. Different levels of agricultural land uses are often excluded or less emphasized. Unlike those studies, our study was performed along a gradient of urban-rural/agriculture-wildland. By controlling the correlation between the 2 anthropogenic land uses using PCA, we investigated the relative effect of urban development and agricultural land uses on avian species. However, the relatively strong effects of agricultural land uses might be confounded with management effects. While over a half of the patches in highly or moderately urbanized areas have been unmanaged for several decades, most patches in agricultural matrix have been managed minimally or moderately. We do not have the data on the management history of each patch and we do not have enough samples to examine how the difference in the management (managed vs. unmanaged) influences our results. But, in another study (Chapter 3), we explored the local habitat characteristics along an urban-rural/agriculture-wildland gradient. No significant difference was found in most vegetation cover and basal area between patches in moderate agricultural matrix and those in moderate urban matrix although the sample patches in moderate urban matrix (unmanaged) tended to show dense hardwood vegetation (i.e., higher basal area and vegetation cover at shrub layer). Both land uses also showed similar richness of avian species. Thus, it is unlikely the difference in management significantly affects our results.

Overall, our results suggest that pine forests in a human-altered landscape can be used to promote avian conservation. However, it should be pointed out that, like other studies, the species responding significantly to at least one of the landscape variables are common species, and some of them can be considered as habitat generalists or synanthropic species (e.g., Parris and Hepinstall-Cymerman 2012). We do not know how other species, particularly species in need of conservation, respond to different levels of human land uses in our region. For better conservation management of avian biodiversity, we should investigate the relationship between urban and agricultural land uses and avian species whose populations have declined, and determine the management plans that improve the habitat quality of the pine forests for those species as well as other species.

CONCLUSIONS

Our results demonstrate that (1) landscape scale characteristics were more often important to species occupancy; (2) relative importance of local scale and landscape scale habitat features to avian species depends on the guild of the species; (3) anthropogenic land uses (urban development and agricultural land use) positively influenced species occupancy for some species in our study region; and (4) positive effects of agricultural land uses are relatively stronger than those of urban development. Given that very few studies have examined the scale dependency of avian species in pine forests embedded in different levels of urban/agricultural land uses in the southeastern USA, our study provides important insight with regard to future forest management for avian conservation. If the objective of forest management is to conserve forest interior species (and forest edge species), management needs to focus on landscape scale characteristics. If the goal is the conservation of pine-grassland species, management needs to focus on local scale characteristics. If management aims to increase avian biodiversity, it should consider habitat characteristics at both local and landscape scale rather than at only single scale, local or landscape scale. Besides the scale, avian conservation management plans should not ignore the value of the pine forests in an urban and/or agricultural matrix. Pine forests in the matrix could enhance avian biodiversity, depending on how we manage the forests. To improve the habitat value of the pine forest for avian conservation, we need a further study to identify habitat characteristics associated with positive or negative responses of birds in the matrix.

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Table 2.1. Principal component scores for environmental (or habitat) variables at each spatial scale. Scores were resulted from Principal Components Analysis (PCA) with varimax rotation.

	2010			2011		
Variable	PC1	PC2	PC3	PC1	PC2	PC3
Local [1]						
% cover of softwood	-0.10	0.86	0.05	-0.02	0.85	0.10
% cover of hardwood	0.91	-0.13	-0.05	0.89	-0.16	-0.02
% cover of shrub	0.79	-0.07	-0.12	0.72	0.15	-0.04
% cover of herb	-0.15	0.01	0.99	-0.06	-0.02	0.99
Basal area of softwood (m^2/ha)	-0.06	0.86	-0.03	0.03	0.81	-0.12
Basal area of hardwood (m^2/ha)	0.92	-0.05	-0.09	-0.02	0.85	0.10
Variance (%)	42.43	23.17	15.1	36.07	23.67	16.42
Cumulative variance (%)	42.43	65.60	80.7	36.07	59.74	76.16
500m^2						
% cover of agriculture	-0.10	0.93	-0.09	-0.05	0.97	-0.05
% cover of other forest	0.09	-0.04	0.99	0.10	-0.04	0.99
% cover of pine forest	-0.51	-0.67	-0.50	-0.54	-0.60	-0.55
% cover of urban development	0.85	0.22	0.03	0.82	0.16	0.12
Patch density of pine forest	0.70	-0.26	0.16	0.76	-0.11	0.08
Variance (%)	40.89	25.52	17.57	43.9	22.79	17.13
Cumulative variance (%)	40.89	66.42	83.98	43.9	66.68	83.81
1km^2						
% cover of agriculture	0.00	0.99	0.01	0.02	0.99	0.04
% cover of other forest	0.06	0.05	0.98	0.06	0.05	0.99
% cover of pine forest	-0.70	-0.56	-0.34	-0.69	-0.52	-0.42

Variable	2010			2011		
	PC1	PC2	PC3	PC1	PC2	PC3
% cover of urban development	0.92	-0.08	-0.21	0.92	-0.06	-0.05
Patch density of pine forest	0.69	0.07	0.31	0.76	0.09	0.10
Variance (%)	44.09	23.66	19.27	46.15	23.11	18.01
Cumulative variance (%)	44.09	67.74	87.02	46.15	69.25	87.27

Note: The principal components (PC: PC1, PC2, and PC3) in 2010 were similar to PC in 2011; that is, there was no differences in biological interpretation of each component between years. Also, PC at 500m scale was the same as PC at 1km scale in terms of interpretation.

[1] PC at local scale: PC 1 (Local 1), a gradient of increasing hardwood cover and basal area; PC 2 (Local 2), a gradient of increasing softwood cover and basal area; PC 3 (Local 3), a gradient of herbaceous vegetation cover

[2] PC at 500m- or 1km-scale: PC 1 (landscape 1), a gradient of increasing urban development and fragmentation of pine forest; PC 2 (Landscape 2), a gradient of increasing agricultural land uses; PC 3 (Landscape 3), a gradient of increasing other forest (hardwood forest and mixed forest)

Table 2.2. Occupancy models used in analysis. ψ is the probability of a site occupied; p is the detection probability; p1 is the detection probability during the first primary sampling period; p2 is the detection probability during the second primary sampling period; ε is local extinction probability; γ is local colonization probability. Detection was modeled either constant (.) or varied among sampling occasions (t). Occupancy was modeled either constant (.) or as a function of 3 PC scores of each of local scale (local), 500m scale (500m), or 1km scale (1km). ε and γ were constant (.).

Single-season occupancy		Multi-season occupancy	
Model	Number of parameters	Model	Number of parameters
ψ(.) p(.)	2	ψ(.) ε(.) γ(.) p1(.) p2(.)	5
ψ(.) p(t)	4	ψ(.) ε(.) γ(.) p1(.) p2(t)	7
ψ(local) p(.)	5	ψ(.) ε(.) γ(.) p1(t) p2(.)	7
ψ(local) p(t)	7	ψ(.) ε(.) γ(.) p1(t) p2(t)	9
ψ(500m) p(.)	5	ψ(local) ε(.) γ(.) p1(.) p2(.)	8
ψ(500m) p(t)	7	ψ(local) ε(.) γ(.) p1(.) p2(t)	10
ψ(1km) p(.)	5	ψ(local) ε(.) γ(.) p1(t) p2(.)	10
ψ(1km) p(t)	7	ψ(local) ε(.) γ(.) p1(t) p2(t)	12
ψ(local + ACOV) p(.)[1]	8	ψ(500m) ε(.) γ(.) p1(.) p2(.)	8
ψ(local + ACOV) p(t)[1]	8	ψ(500m) ε(.) γ(.) p1(.) p2(t)	10
ψ(1km + ACOV) p(.)[1]	8	ψ(500m) ε(.) γ(.) p1(t) p2(.)	10
		ψ(500m) ε(.) γ(.) p1(t) p2(t)	12
		ψ(1km) ε(.) γ(.) p1(.) p2(.)	8
		ψ(1km) ε(.) γ(.) p1(.) p2(t)	10
		ψ(1km) ε(.) γ(.) p1(t) p2(.)	10
		ψ(1km) ε(.) γ(.) p1(t) p2(t)	12

[1] The models which ACOV (spatial autocovariate) was added as an additional covariate. This was applied only to the species and scale(s) where spatial autocorrelation was found.

Table 2.3. Bird species observed in the study area, frequency (%) each species detected throughout study sites during 2010-2011. Species not used for occupancy analysis were also included. See Appendix A for scientific name and guild type of each species.

Species	Frequency (%)	
Common Name	2010	2011
Acadian Flycatcher	6.4	16.3
American Crow	4.3	18.0
American Goldfinch	5.3	7.9
American Kestrel	1.1	8.4
American Redstart	0.0	3.9
American Robin	1.1	4.5
Bachman's Sparrow	1.1	6.2
Barn Swallow	0.0	39.9
Black-and-white Warbler	5.3	7.3
Blue-gray Gnatcatcher	33.0	25.3
Brown-headed Cowbird	34.0	26.4
Brown-headed Nuthatch	44.7	71.3
Blue Grosbeak	3.2	3.9
Blue Jay	10.6	39.3
Brown Thrasher	3.2	11.8
Carolina Chickadee	67.0	82.0
Carolina Wren	52.1	59.0
Chipping Sparrow	7.4	12.9
Common Grackle	1.1	1.7
Common Nighthawk	0.0	4.5
Chuck-will's-widow	1.1	0.0
Downy Woodpecker	29.8	39.9
Eastern Bluebird	13.8	19.7
Eastern Kingbird	1.1	3.9
Eastern Phoebe	0.0	3.4
Eastern Towhee	45.7	55.6
Eastern Wood-Pewee	28.7	27.5
Fish Crow	0.0	3.9
Great Crested Flycatcher	61.7	52.2
Gray Catbird	0.0	1.7
Hairy Woodpecker	5.3	12.4
Hooded Warbler	2.1	0.0
Indigo Bunting	14.9	32.0
Kentucky Warbler	1.1	6.2

Species Common Name	Frequency (%) 2010	 2011
Mourning Dove	0.0	7.9
Northern Bobwhite	0.0	5.1
Northern Cardinal	63.8	74.7
Northern Flicker	11.7	10.1
Northern Mockingbird	4.3	12.4
Northern Parula	0.0	2.8
Orchard Oriole	1.1	2.8
Ovenbird	8.5	15.7
Pine Warbler	90.4	86.0
Pileated Woodpecker	1.1	6.7
Prairie Warbler	1.1	9.6
Purple Martin	0.0	6.2
Red-bellied Woodpecker	20.2	53.9
Red-cockaded Woodpecker	1.1	0.0
Red-eyed Vireo	20.2	12.9
Red-headed Woodpecker	12.8	9.6
Red-shouldered Hawk	0.0	1.1
Red-tailed Hawk	0.0	1.1
Ruby-throated Hummingbird	1.1	1.7
Summer Tanager	75.5	75.3
Tufted Titmouse	56.4	53.4
White-eyed Vireo	13.8	17.4
Worm-eating Warbler	8.5	3.4
Wild Turkey	0.0	1.1
Wood Thrush	5.3	6.7
Yellow-billed Cuckoo	3.2	2.8
Yellow-breasted Chat	3.2	10.7
Yellow-throated Vireo	2.1	5.6
Yellow Warbler	1.1	11.8

Table 2.4. Summary of model selection results to determine appropriate spatial scale(s) in relation to occupancy for 13 species in 2010. Models with Δ AIC*c* < 2 are shown.

Guild[1]	Species	Model	K[2]	AIC*c*[3]	Δ AIC*c*[4]	AIC*c* Weights	Scale[5]
Forest Interior	Carolina Chickadee	ψ(500m) p(t)	7	349.71	0.00	0.46	500m
		ψ(500m) p(.)	5	351.00	1.29	0.24	
		ψ(1km) p(t)	7	351.50	1.78	0.19	
	Red-bellied Woodpecker	ψ(500m) p(.)	5	159.54	0.00	0.72	500m
	Red-eyed Vireo[6]	ψ(500m) p(.)	5	166.61	0.00	0.45	500m and
		ψ(1km) p(.)	5	167.16	0.55	0.34	1km
	Summer Tanager	ψ(local) p(.)	5	376.89	0.00	0.49	Local
		ψ(local) p(t)	7	377.35	0.46	0.39	
	Tufted Titmouse	ψ(local) p(t)	7	306.79	0.00	0.89	Local
Forest Edge	Blue-gray Gnatcatcher [6]	ψ(local) p(.)	5	221.31	0.00	0.73	Local
	Eastern Bluebird	ψ(local) p(.)	5	117.11	0.00	0.57	Local
	Northern Cardinal	ψ(1km) p(.)	5	340.18	0.00	0.81	1km
	White-eyed Vireo	ψ(.) p(.)	2	125.22	0.00	0.42	None[7]
		ψ(1km) p(.)	5	126.83	1.60	0.19	
Pine-grassland	Brown-headed Nuthatch	ψ(local) p(t)	7	277.74	0.00	0.77	Local
	Eastern Wood-Pewee	ψ(local) p(t)	7	202.23	0.00	0.71	Local
	Indigo Bunting	ψ(local+Acov) p(.)	6	129.19	0.00	0.60	Local
	Pine Warbler	ψ(.) p(.)	2	380.74	0.00	0.65	None[7]

[1] Three guild types based on habitat preferences (Wilson et al. 1995); [2] The number of parameters; [3] Akaike's Information Criterion adjusted for small sample size.; [4] AIC*c* difference between model with lowest AIC*c* and each other model.

[5] Scale(s) in the occupancy models (ψ) selected; if AIC*c* weights of one of the scales were relatively low, the scale was not chosen.

[6] Species with one level of detection probability (p(.)) used.;

[7] No relationship between specie occupancy and any of the scales used in the analysis.

Table 2.5. Summary of model selection results to determine appropriate spatial scale(s) in relation to occupancy for 9 species in 2011. Models with Δ AIC*c* < 2 are shown.

Guild[1]	Species	Model	K[2]	AIC*c*[3]	Δ AIC*c*[4]	AIC*c* Weights	Scale[5]
Forest Interior	Acadian Flycatcher	ψ(500m) p(.)	5	243.53	0.00	0.30	500m
		ψ(500m) p(t)	7	243.83	0.30	0.26	
	Great Crested Flycatcher[6]	ψ(1km+Acov) p(.)	6	600.48	0.00	0.67	1km
	Ovenbird	ψ(.) p(t)	4	249.24	0.00	0.79	None[7]
	Red-bellied Woodpecker	ψ(500m) p(t)	7	589.22	0.00	0.55	500m
		ψ(500m) p(.)	5	590.43	1.20	0.30	
Forest Edge							
	Blue-gray Gnatcatcher	ψ(1km) p(.)	5	349.47	0.00	0.49	None
		ψ(.) p(.)	2	350.56	1.09	0.28	
	Brown-headed Cowbird	ψ(1km) p(t)	7	347.32	0.00	0.66	1km
	Carolina Wren	ψ(1km) p(t)	7	615.75	0.00	0.77	1km
	Northern Cardinal	ψ(500m) p(.)	5	695.63	0.00	0.88	500m
Pine-grassland	Indigo Bunting	ψ(local) p(.)	5	424.41	0.00	0.88	Local

[1] Three guild types based on habitat preferences (Wilson et al. 1995)

[2] The number of parameters

[3] Akaike's Information Criterion adjusted for small sample size.

[4] AIC*c* difference between model with lowest AIC*c* and each other model.

[5] Scale(s) in the occupancy models (ψ) selected.

[6] Species with one level of detection probability (p(.)) used.

[7] No relationship between specie occupancy and any of the scales used in the analysis.

Table 2.6. Summary of model selection results of multiple-season occupancy analysis. Models with Δ AIC*c* < 2 are shown.

Guild	Species	Model	K^1	AIC*c*^{2}	Δ AIC*c*^{3}	AIC*c* Weights	Scale^4
Forest Interior	Carolina Chickadee	ψ(500m) ε(.) γ(.) p1(t) p2(t)	12	656.80	0.00	0.29	500m and 1km
		ψ(1km) ε(.) γ(.) p1(t) p2(t)	12	656.89	0.08	0.28	
		ψ(1km) ε(.) γ(.) p1(.) p2(t)	10	657.67	0.86	0.19	
		ψ(500m) ε(.) γ(.) p1(.) p2(t)	10	657.74	0.94	0.18	
	Downy Woodpecker	ψ(1km) ε(.) γ(.) p1(.) p2(t)	10	431.71	0.00	0.36	500m and 1km
		ψ(500m) ε(.) γ(.) p1(.) p2(t)	10	432.20	0.48	0.28	
	Ovenbird	ψ(local) ε(.) γ(.) p1(t) p2(t)	12	188.67	0.00	0.59	Local
		ψ(local) ε(.) γ(.) p1(.) p2(t)	10	190.45	1.78	0.24	
	Red-eyed Vireo	ψ(500m) ε(.) γ(.) p1(.) p2(t)	10	261.61	0.00	0.19	500m and 1km
		ψ(500m) ε(.) γ(.) p1(.) p2(.)	8	262.71	1.10	0.11	
		ψ(500m) ε(.) γ(.) p1(t) p2(t)	12	262.82	1.21	0.10	
		ψ(1km) ε(.) γ(.) p1(.) p2(t)	10	262.83	1.22	0.10	
		ψ(local) ε(.) γ(.) p1(.) p2(t)	10	263.35	1.75	0.08	
Forest Edge	Blue-gray Gnatcatcher	ψ(local) ε(.) γ(.) p1(.) p2(.)	8	373.87	0.00	0.40	Local
		ψ(lkm) ε(.) γ(.) p1(.) p2(.)	8	375.69	1.82	0.16	
		ψ(local) ε(.) γ(.) p1(.) p2(t)	10	375.70	1.83	0.16	
	Eastern Bluebird	ψ(local) ε(.) γ(.) p1(.) p2(.)	8	207.60	0.00	0.69	Local

Guild	Species	Model	K[1]	AIC*c*[2]	Δ AIC*c*[3]	AIC*c* Weights	Scale[4]
Pine-grassland	Brown-headed Nuthatch	ψ(local) ε(.) γ(.) p1(t) p2(.)	10	595.84	0.00	0.72	Local
	Eastern Wood-Pewee	ψ(local) ε(.) γ(.) p1(t) p2(t)	12	357.16	0.00	0.61	Local

[1] The number of parameters

[2] Akaike's Information Criterion adjusted for small sample size.

[3] AIC*c* difference between model with lowest AIC*c* and each other model.

[4] Scale(s) in the occupancy models (ψ) selected; if AIC*c* weights of one of the scales were relatively low, the scale was not chosen.

Table 2.7. Untransformed model-averaged parameter estimates, standard errors (SE), and 90 % confidence intervals (CI) for the covariates of the occupancy models selected in 2010. Significant estimates were bolded.

Guild	Species	Scale	Parameter[1]	Estimate	SE	90% CI	
Forest Interior	Carolina Chickadee	500m and 1km	Intercept	**1.92**	0.85	0.52	3.31
			landscape1	**1.52**	0.68	0.41	2.63
			landscape2	-0.23	0.29	-0.70	0.24
			landscape3	**1.21**	0.53	0.34	2.08
	Red-bellied Woodpecker	500m	Intercept	0.27	0.81	-1.06	1.60
			landscape1	2.17	1.36	-0.07	4.40
			landscape2	0.81	0.55	-0.09	1.70
			landscape3	0.10	0.41	-0.57	0.77
	Red-eyed Vireo	500m and 1km	Intercept	**-0.66**	0.40	-1.31	-0.01
			landscape1	-0.06	0.17	-0.34	0.21
			landscape2	-0.57	0.44	-1.29	0.15
			landscape3	0.30	0.22	-0.06	0.66
	Summer Tanager	Local	Intercept	**6.87**	3.70	0.79	12.94
			local1	**6.39**	3.62	0.45	12.34
			local2	-0.30	0.38	-0.92	0.33
			local3	-0.97	0.68	-2.08	0.14
	Tufted Titmouse	Local	Intercept	**2.04**	0.92	0.53	3.55
			local1	**2.51**	1.06	0.77	4.25
			local2	-0.57	0.40	-1.23	0.09
			local3	0.09	0.37	-0.51	0.69
Forest Edge	Blue-gray Gnatcatcher	Local	Intercept	0.15	0.50	-0.84	1.14
			local1	**1.66**	0.60	0.67	2.65
			local2	**-1.31**	0.56	-2.23	-0.39

Guild	Species	Scale	Parameter[1]	Estimate	SE	90% CI	
			local3	-0.14	0.43	-0.83	0.56
	Eastern Bluebird	Local	Intercept	-1.15	0.77	-2.42	0.13
			local1	**-1.37**	0.67	-2.47	-0.28
			local2	-0.59	0.54	-1.48	0.30
			local3	-0.09	0.52	-0.95	0.77
	Northern Cardinal	1km	Intercept	**4.24**	1.86	1.18	7.30
			landscape1	**1.40**	0.65	0.33	2.46
			landscape2	**6.25**	3.07	1.22	11.27
			landscape3	-0.16	0.36	-0.75	0.43
Pine-grassland	Brown-headed Nuthatch	Local	Intercept	0.90	1.33	-1.28	3.07
			local1	-1.40	0.97	-2.99	0.19
			local2	-0.53	0.80	-1.85	0.78
			local3	0.75	0.78	-0.53	2.02
	Eastern Wood-Pewee	Local	Intercept	0.27	1.34	-1.93	2.47
			local1	-1.70	1.14	-3.56	0.17
			local2	0.40	0.60	-0.58	1.38
			local3	1.26	1.83	-1.73	4.26
	Indigo Bunting	Local	Intercept	**-2.42**	0.53	-3.30	-1.55
			local1	-0.68	0.47	-1.45	0.08
			local2	-0.60	0.45	-1.34	0.13
			local3	**0.69**	0.36	0.10	1.28

[1] Local 1, a gradient of increasing hardwood cover and basal area; Local 2, a gradient of increasing softwood cover and basal area; Local 3, a gradient of herbaceous vegetation cover; Landscape 1, a gradient of increasing urban development and fragmentation of pine forest; Landscape 2, a gradient of increasing agricultural land uses; Landscape 3, a gradient of increasing other forest (hardwood forest and mixed forest)

Table 2.8. Untransformed model-averaged parameter estimates, standard errors (SE), and 90 % confidence intervals (CI) for the covariates of the occupancy models selected in 2011. Significant estimates were bolded.

Guild	Species	Scale	Parameter[1]	Estimate	SE	90% CI	
Forest Interior	Acadian Flycatcher	500m and 1km	Intercept	-0.06	0.39	-0.70	0.58
			landscape1	0.15	0.20	-0.18	0.48
			landscape2	0.42	0.35	-0.15	0.99
			landscape3	0.40	0.27	-0.05	0.85
	Great Crested Flycatcher	1km	Intercept	0.38	0.43	-0.32	1.08
			landscape1	-0.18	0.24	-0.57	0.20
			landscape2	0.45	0.33	-0.09	0.99
			landscape3	**-0.55**	0.25	-0.96	-0.15
	Red-bellied Woodpecker	500m	Intercept	**6.94**	3.03	1.97	11.91
			landscape1	1.31	0.84	-0.07	2.68
			landscape2	**10.45**	4.68	2.77	18.13
			landscape3	0.47	0.44	-0.25	1.19
Forest Edge	Brown-headed Cowbird	1km	Intercept	0.51	0.83	-0.86	1.87
			landscape1	0.77	0.50	-0.06	1.59
			landscape2	0.59	0.42	-0.10	1.27
			landscape3	0.95	0.69	-0.19	2.09
	Carolina Wren	1km	Intercept	**1.95**	0.76	0.70	3.19
			landscape1	**1.57**	0.74	0.35	2.79
			landscape2	**1.16**	0.70	0.01	2.30
			landscape3	-0.64	0.32	-1.17	-0.11
	Northern Cardinal	500m	Intercept	**3.88**	1.38	1.63	6.14
			landscape1	**1.79**	0.76	0.54	3.04

Guild	Species	Scale	Parameter[1]	Estimate	SE	90% CI	
			landscape2	**4.43**	2.42	0.46	8.40
			landscape3	0.06	0.26	-0.36	0.49
Pine-grassland	Indigo Bunting	Local	Intercept	**-0.74**	0.22	-1.10	-0.38
			local1	**-0.77**	0.24	-1.16	-0.37
			local2	**-0.70**	0.22	-1.07	-0.33
			local3	**0.61**	0.21	0.27	0.95

[1] Local 1, a gradient of increasing hardwood cover and basal area; Local 2, a gradient of increasing softwood cover and basal area; Local 3, a gradient of herbaceous vegetation cover; Landscape 1, a gradient of increasing urban development and fragmentation of pine forest; Landscape 2, a gradient of increasing agricultural land uses; Landscape 3, a gradient of increasing other forest (hardwood forest and mixed forest)

Table 2.9. Untransformed model-averaged parameter estimates, standard errors (SE), and 90 % confidence intervals (CI) for the covariates of the multi-season occupancy models selected. Significant estimates were bolded.

Guild	Species	Scale	Parameter[1]	Estimate	SE	90% CI	
Forest Interior	Carolina Chickadee	500m and 1km	Intercept	**2.17**	0.94	3.71	0.64
			landscape1	**1.78**	0.99	3.39	0.16
			landscape2	-0.08	0.35	0.50	-0.66
			landscape3	**1.07**	0.55	1.96	0.17
	Downy Woodpecker	500m and 1km	Intercept	**1.20**	0.71	2.37	0.03
			landscape1	**0.38**	0.15	0.63	0.13
			landscape2	**1.68**	0.92	3.18	0.18
			landscape3	**0.58**	0.33	1.13	0.04
	Ovenbird	Local	Intercept	-0.61	0.53	0.25	-1.48
			local1	**1.45**	0.69	2.58	0.32
			local2	-0.07	0.31	0.45	-0.58
			local3	**0.57**	0.34	1.13	0.02
Forest Edge	Blue-gray Gnatcatcher	Local	Intercept	0.21	0.52	1.05	-0.64
			local1	**0.86**	0.38	1.48	0.25
			local2	**-0.80**	0.43	-0.10	-1.51
			local3	0.05	0.23	0.43	-0.32
	Eastern Bluebird	Local	Intercept	0.44	2.31	4.23	-3.35
			local1	-4.65	4.93	3.43	-12.74
			local2	-0.93	1.03	0.76	-2.62
			local3	4.35	5.12	12.74	-4.04
Pine-grassland	Brown-headed Nuthatch	Local	Intercept	1.09	0.84	2.46	-0.29
			local1	**-1.79**	0.86	-0.38	-3.20

Guild	Species	Scale	Parameter[1]	Estimate	SE	90% CI	
			local2	-0.08	0.44	0.65	-0.80
			local3	**1.79**	1.03	3.49	0.10
	Eastern Wood-Pewee	Local	Intercept	0.63	0.62	1.64	-0.38
			local1	**-1.42**	0.54	-0.53	-2.31
			local2	-0.04	0.33	0.50	-0.57
			local3	**1.65**	0.80	2.97	0.33

[1] Local 1, a gradient of increasing hardwood cover and basal area; Local 2, a gradient of increasing softwood cover and basal area; Local 3, a gradient of herbaceous vegetation cover; Landscape 1, a gradient of increasing urban development and fragmentation of pine forest; Landscape 2, a gradient of increasing agricultural land uses; Landscape 3, a gradient of increasing other forest (hardwood forest and mixed forest)

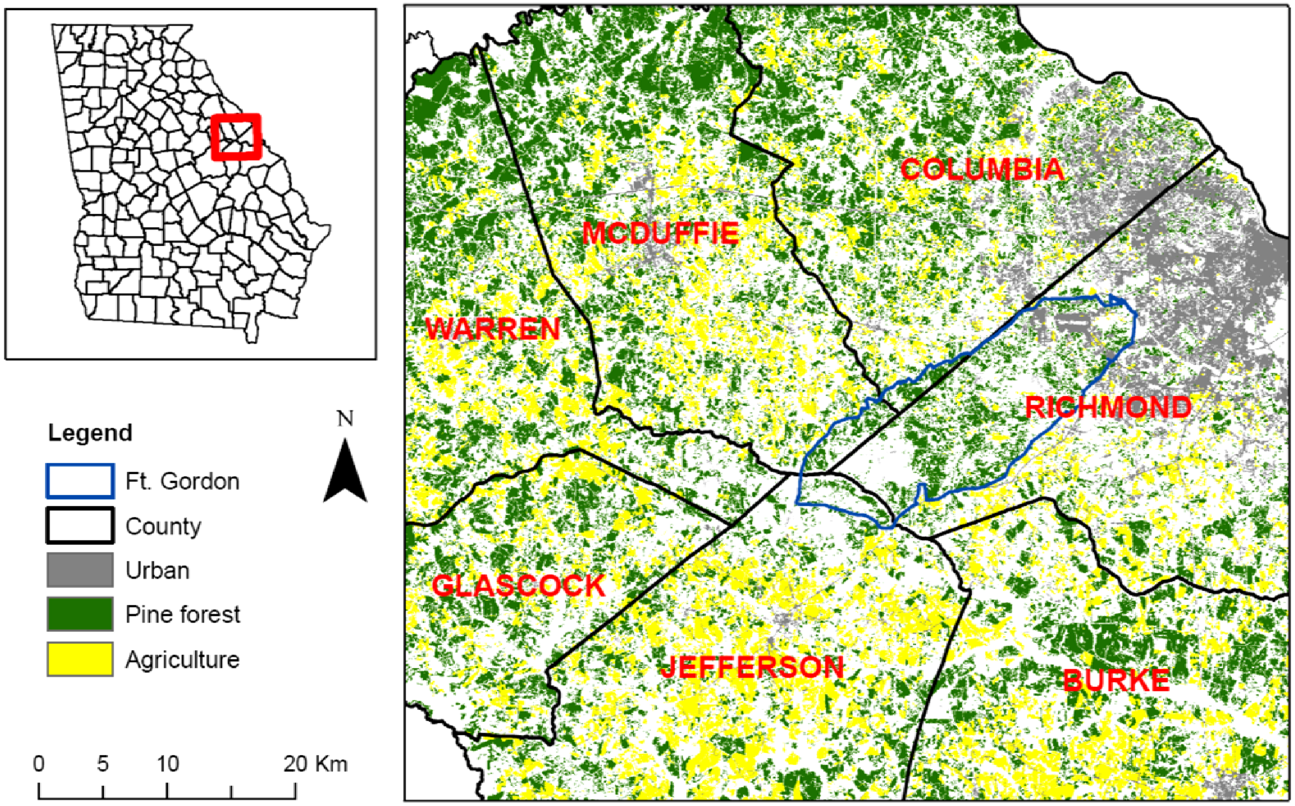

Figure 2.1. Land cover map of study areas, east-central Georgia, USA, 2010-2011. Note different levels of human land-uses (urban development and/or agricultural land uses) throughout the study sites: high or moderate level of urban development in Richmond and Columbia County; a mixture of urban development and agricultural land uses in McDuffie County and some areas in Columbia County; high or moderate agricultural land uses in other countries; relatively intact pine forests in Fort Gordon.

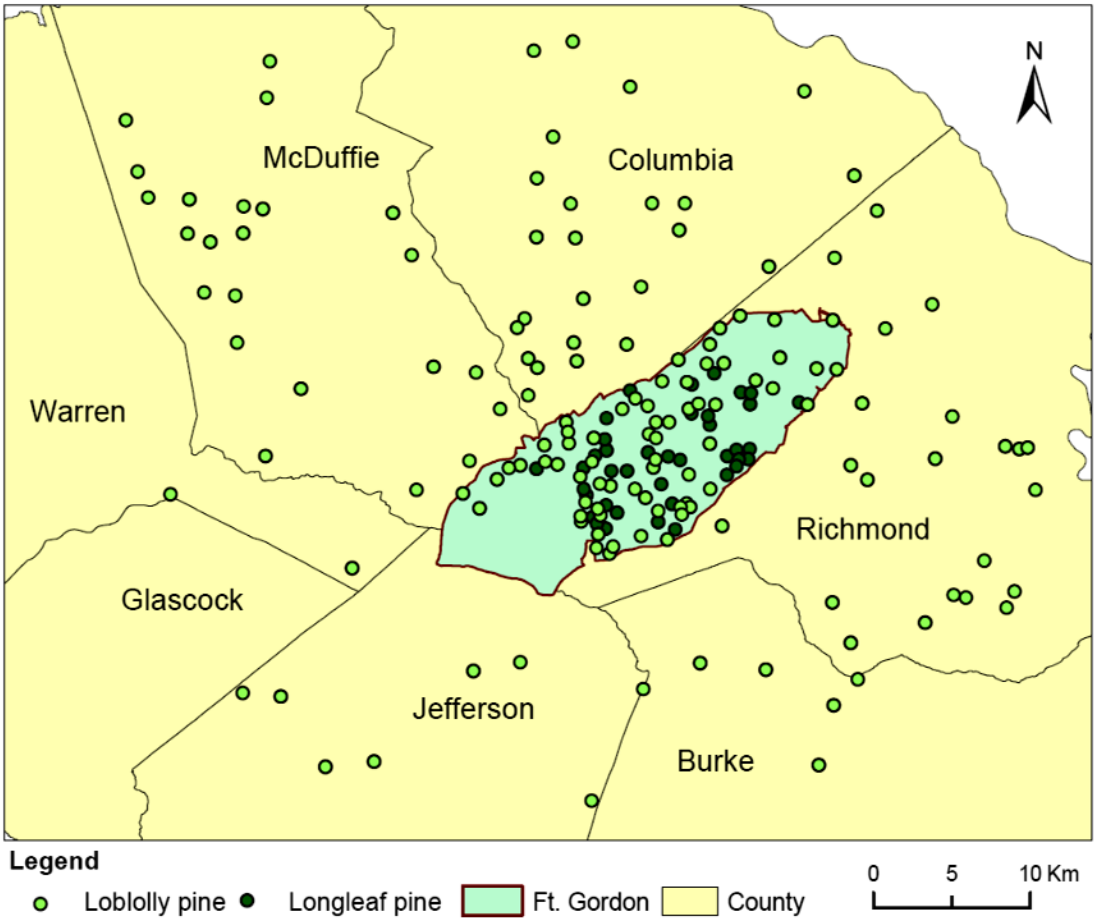

Figure 2.2. Location of sample points for avian point count and vegetation surveys, east-central Georgia, USA, 2010-2011. Note that all points established at longleaf pine stands are located within Fort Gordon.

CHAPTER 3

AVIAN COMMUNITY IN A PINE FOREST ALONG AN URBAN-RURAL/AGRICULTURE-WILDLAND GRADIENT[2]

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[2] Lee, Myung-Bok and John P. Carroll. To be submitted to *Biological Conservation*.

ABSTRACT

With rapidly growing urban development and extensive agricultural land uses in the southeastern USA, there have been increased concerns about conserving avian biodiversity in pine forests embedded in a matrix of urban development and/or agricultural lands. However, the two dominant human land-uses also bring attention to the role of pine forests in an urban/agricultural matrix—whether pine forests in the matrix can promote avian biodiversity. To better understand their role, we need comprehensive information about how avian biodiversity changes along different levels of human land-uses, not only urban development but also agricultural land uses. We investigated the relationship between avian biodiversity (richness, number of species; and RCS, Partners In Flight Regional Combined Score, RCS-b) and different levels of urban and/or agricultural land uses. We also examined the relative effects of urban development and agricultural land uses on avian biodiversity. We conducted bird surveys and vegetation surveys in pine forests in central-east Georgia, during 2010-211 breeding seasons. We classified an urban-rural/agriculture-wildland gradient into 7 human land-use classes. We performed the rank analysis of covariance to test differences in avian biodiversity among the classes. Pairwise differences in the biodiversity between the classes were examined by comparing the overlap of 90% confidence intervals. Richness and RCS showed the same patterns along an urban-rural/agriculture-wildland gradient. Significant difference in richness and RCS was found among 7 human land-use classes ($P < 0.05$). Richness and RCS were significantly lower in pine patches embedded in a wildland matrix. Although most results of pairwise differences were insignificant, richness and RCS were slightly higher at pine patches in a mixture of low level of urban development and agricultural land use and in low level of agricultural matrix. Also, richness and RCS of pine-grassland tended to be low at urban matrix, and the low biodiversity was associated

with the vegetation structure of pine patches at urban matrix. As the proportion of human-dominated land-uses increased, the relative proportion of migrant and pine-grassland in a community decreased. Our results suggest that pine forests in some human-altered landscapes may play a positive role for avian biodiversity conservation and that agricultural land uses, especially at low level, can serve as more favorable matrix than urban development.

INTRODUCTION

Human land-uses such as urban and agriculture are considered as main causes of biodiversity loss in the United States (Czech 2000). The conversion of natural habitat to urban or agricultural land uses leads to habitat loss. The land uses change natural habitats by replacing native vegetation with manmade structures (farms, housing or buildings, roads, etc) and with introduced species. Intensive urbanization or agricultural management also tends to simplify landscapes and reduce habitat diversity. Numerous empirical studies have been undertaken to investigate species distribution along an urban gradient, exurban development gradient, or urban-rural gradient. In particular, birds are widely studied among taxonomic groups of fauna. It is well documented that species richness and evenness tends to decrease with urbanization, whereas bird density, especially that of non-native species and synanthropic species, increases (e.g., Marzluff 2001; Hansen et al. 2005; Chase and Walsh 2006). Forest interior species or forest specialist species and cavity nesting species also tend to decline with urbanization. Similar avian responses have been reported in a bird community in agricultural matrix, although the responses seem to vary more among ecological or functional guilds of a species (e.g., Saab 1999; Bennett et al. 2006; Mastrangelo and Gavin 2012). However, the responses of avian species to urbanization can be positive or negative, depending on the level or intensity of urban development in a landscape.

Some studies suggest that a low or moderate level of urban development increases overall richness or richness of habitat generalists (e.g., Fraterrigo and Wiens 2005; Marzluff 2005; Marzluff and Rodewald 2008). In naturally sparse or fragmented habitats, richness and abundance of birds more often peak at a moderate level of urban development (e.g., Blair 1999; Trammell et al. 2011). Such higher biodiversity especially, at moderate urban matrix (i.e, suburban area), but lower richness at the two ends of an urban-rural gradient (i.e., urban core and relatively natural forest) has been considered to be consistent with the intermediate disturbance hypothesis (Marzluff 2005; Mckinney 2008; Marzluff and Rodewald 2008). Originally, the intermediate disturbance hypothesis was developed to explain the coexistence of species (Connell 1978). The hypothesis predicts that species richness is higher in moderately disturbed sites than in undisturbed or extremely disturbed sites because intermediate level of disturbance can allow coexistence of species that each may be dominant at undisturbed or extremely disturbed sites (Connell 1978; Roxburgh et al. 2004). In the hypothesis, urbanization (and other human land uses) can be seen as a disturbance and moderate urban development as an intermediate level of disturbance. It is also suggested that intermediate level of disturbance in urban ecosystem increases habitat heterogeneity (the disturbance heterogeneity model, Porter et al. 2001) and thus can provide diverse habitats for unique sets of birds (Marzluff 2005; Mckinney 2008).

Although greater richness at moderate urbanization is considered as one of general trends in avian urban studies, there have been few studies to explore whether richness can peak at moderate or other levels of agricultural land uses (but see Mastrangelo and Gavin 2012). The emphasis of the many studies performed along an urban-rural gradient has been on urbanization itself, which is determined based on the level of human population and/or built-up structures (houses, commercial buildings, roads, and other impervious surfaces). A gradient of agricultural land use has been less emphasized in most urban-rural gradient studies (but see Parrish and Hepinstall-Cymerman 2012) and relatively few studies have considered different levels of both urban development and agricultural land use in analysis. Agriculture is also often combined with other land covers such as open parks for analysis, causing the effects of agriculture to be confounded (e.g., Stratford and Robinson 2005). In some regions in USA (e.g., the southeastern USA), increasing residential developments creates a complex human-altered landscape, a mixture of low or moderate level of urban development and agricultural land uses: suburban and exurban type of development adjacent to or within an agricultural landscape with several patches of forests. In this landscape, the common approach focusing on urbanization alone does not provide appropriate information to understand avian species distribution and to manage the remnant forests for avian conservation. This situation requires considering not only an urban gradient but also an agricultural gradient (i.e., an urban-rural/agriculture-wildland gradient) for analysis and inference.

Forests in the southeastern USA have been highly fragmented and altered by timber harvest and intensive agriculture for more than 150 years. A large percentage of the original forests have been replaced by planted or naturally regenerated pines grown for commercial timber. In addition, several regions in the southeastern USA, including central-east Georgia, have been experiencing a rapid expansion of urban development, leading to increases in the complexity of the landscape matrix surrounding pine forest remnants as well as planted pine forests and creating an urban-rural/agriculture-wildland gradient. Although planted pine forests are primarily managed for wood production, there is a growing interest in management plans to enhance avian biodiversity in the pine forests (e.g., Turner et al. 2002). In some cases, the pine forests are also managed to restore wildlife habitats or conserve endangered, threatened, and declining pine-grassland avian species such as the Red-cockaded Woodpecker (*Picoides* *borealis*), Bachman’s Sparrow (*Aimophila aestivalis*), and Northern Bobwhite Quail (*Colinus virginianus*). However, little attention has given to the pine forests in urban and /or agricultural landscape. Few studies have explored the responses of avian communities in pine forests to different levels of urban development and/or agricultural land uses. Considering rapid changes in human land-uses, it is important to understand how avian biodiversity changes with human land-uses. The information is crucial to develop sound land use plans and pine forest management plans that enhance avian biodiversity along an urban-rural/agriculture-wildland gradient.

We investigated avian biodiversity in pine forests at different levels of urban and/agricultural land uses in the southeastern USA. Our study aimed to examine: 1) how avian richness (number of species) and composition varied along an urban-rural/agriculture-wildland gradient; and 2) what was the relative effect of urban development and agricultural land uses on the richness. We expected that richness is high at low or moderate levels of urban and/or agricultural land uses due to increased habitat heterogeneity. In addition, we expected relatively higher richness in pine patches embedded in an agricultural matrix than in urban matrix because agricultural land uses can create more favorable open-space for birds. We also expected compositional differences in the avian community along an urban-rural/agriculture-wildland gradient because of variations in habitat structure along the gradient and variations in habitat preferences and sensitivity to human disturbance (human land-uses) among species.

METHODS

Study site

The study was conducted at pine forest remnants (stands or patches) in Fort Gordon and surrounding areas of Fort Gordon in 3 ecoregions of Georgia (Sand Hills, Coastal Plain Red

Uplands, and Southern Outer Piedmont), which include 7 counties: Burke, Columbia, Glascock, Jefferson, McDuffie, Richmond, and Warren (See Fig. 2.1 in chapter 2). The study areas show a gradient of urban-rural/agriculture-wildland (See Table 3.1 for definition of wildland): highly urbanized areas at the northeastern part of Richmond County and relatively intact wildland in Fort Gordon; low agricultural land uses and low and moderate levels of urban development in Columbia and McDuffie Counties; and high and moderate levels of agricultural land uses in other counties.

Agricultural land uses are dominated by pasture and hay fields in the study areas. Pine forests are composed of mainly planted loblolly pines (*Pinus taeda*). Slash pines (*Pinus elliottii*) or shortleaf pines (*Pinus echinata*) are mixed with loblolly pines in some areas. The majority of the relatively mature longleaf pines (*Pinus palustris*) are found at Fort Gordon. The ages of pine patches vary across our study sites; however, old pine patches (> 75yrs) are relatively rare and most pine patches are young and mid-aged. Overstory and midstory of hardwood forest and mixed forest largely consist of sweetgum (Liquidambar styraciflua), sassafras (*Sassafras albidum*), black cherry (*Prunus serotina*), flowering dogwood (*Cornus florida*), and oak (*Quercus* spp.). Sparkleberry (*Vaccinium arboreum*) is also commonly found in the midstory. The understory is dominated by yellow jessamine (*Gelsemium sempervirens*), muscadine (*Muscadinia rotundifolia*), greenbrier (*Smilax* spp.), brambles (*Rubus* spp.), blueberry (*Vaccinium* spp.), broomsedge bluestem (*Andropogon virginicus*), low panicgrass (*Dicanthelium* spp.), wiregrass (*Aristida stricta*), and lespedeza (*Lespedeza* spp.).

Sample point

Mid-aged loblolly and longleaf pine patches (20-75yrs) were randomly selected for sampling, considering the level of urban development/agricultural land uses and separation distance among patches to minimize spatial dependency. We used the 2009 forest inventory data of Fort Gordon, 2007 digital orthophoto images (National Agriculture Imagery Program, NAIP), 1998 Digital Orthophoto Quarter Quads (DOQQs), 2006 National Land Cover Dataset (NLCD), ground-truth survey, and ArcGIS 9.2 to select sample patches. Since most pine patches outside of Fort Gordon were privately owned, the numbers of pine patches for sampling were constrained by the permits from landowners. During 2010-2011, we contacted 140 landowners by letters and by visits. We acquired permission from 70 landowners including several public organizations such as City of Augusta and the City of Hephzibah. Of 182 pine patches, 84 patches were located at private lands. Pine patches used in our study included unmanaged stands in the recent past (patches located in highly or moderately urbanized areas and some patches in agricultural lands), minimally or moderately managed stands (most patches), and relatively intensively managed stands (several patches in Fort Gordon).

Within a patch, one point was established randomly at least 50-70m from any edge (road, other types of vegetation or land cover, etc). A total of 94 points were established in 2010, but 4 of them were developed or harvested in 2011. An additional 92 points were established in 2011, but 4 points were prescribed burned after the 1st visit, and thus a total of 178 points were completely surveyed in 2011. All points within longleaf pine patches were established at Fort Gordon.

Bird surveys and vegetation surveys

Bird surveys were performed three times from May through June during 2010 – 2011, using fixed-radius point counts (Ralph et al. 1993). At each point, an observer recorded species seen or heard within a 50-m radius of a sample point for a 10-min duration and the distance from the species detected to the sample point. One observer in 2010 and two observers in 2011 conducted surveys. In 2011, the observers were rotated between sites to reduce observer effects. We also alternated survey order to minimize the effect of time-of-day. Each survey was performed between dawn and 1100 EDT. We did not conduct surveys during inclement situations such as high wind or rain.

To quantify habitat characteristics at a local scale, vegetation sampling was conducted at the same points as the bird surveys between mid-June and July during 2010-2011. A total of four 5m radius subcircular plots were established in each cardinal direction at a fixed distance of 30m from a sample point. Within each of the subcircular plots, vegetation data were collected using modified PRBO Point Count Veggie (Relevé) Protocol. Percent vegetation cover at herb (< 0.5 m in height), shrub (0.5-5m in height), and tree (>5m in height) layers were visually estimated. The tree vegetation was divided into two categories: softwood and hardwood. Dominant plant species within each layer were also recorded. DBHs (Diameter at Breast Height) of hardwood and softwood (≥ 8cm in diameter) were separately measured within four 10m radius subcircular plots. The values of each vegetation characteristic estimated or measured from four subcircular plots were averaged and used to represent the value at the sample point.

Urban-rural/agriculture-wildland gradient: level of human land-uses

A gradient of urban-rural/agriculture-wildland was determined based on the percent cover of urban development and/or agricultural land use within a 1 km circular area surrounding a sample point. Initially, we selected sample patches by calculating the percent cover from 2006 National Land Cover Dataset (NLCD); however, the NLCD were not precise enough for our purpose and it did not reflect recent changes in land cover. Thus, we digitized 2010 NAIP and

1998 Digital Orthophoto Quarter Quads (DOQQs) using GIS software (ArcGIS version 9.2) and re-calculated the percent cover of urban development and/or agricultural land uses. We also calculated the percent cover of other land covers such as hardwood forest, shrub, disturbed area, and open space (See *analysis*).

We classified an urban-rural/agriculture-wildland gradient into 7 levels or classes (Table 3.1). Since we focused on not only an urban gradient or an agricultural gradient but also a gradient of a combination of both land uses, we did not use the classification of Marzluff et al. (2001), which emphasized the level of urban development. However, U2 was similar to "Suburban," "Wild" to "Wildland," and the rest of the classes to "Rural/exurban" in their classification. We also acknowledge that due to very limited access to pine patches and fewer number of remnant pine forests at high urban areas (> 50% urban development) and at high agricultural lands (> 50% agricultural land uses), a gradient of urban-rural/agriculture-wildland in our study did not include the two extremes of human land-uses. We believe this is appropriate to assess these gradients in many relatively smaller urban areas throughout the southeastern USA.

Analysis

To minimize matrix effects from other types of land cover, we excluded points at which the percent cover of the sum of open space and disturbed area was > 20, the percent cover of shrub was > 10, or the percent cover of hardwood forest was > 40. A total of 89 points and 165 points were used for analysis in 2010 and 2011, respectively. Since the mean richness of total species and all guilds (but pine-grassland species) between longleaf pine stands and loblolly pine stands was not significantly different, we did not distinguish the stand types.

A total of 63 species were detected across the study sites during 2010-2011 (Appendix A). However, we excluded flyovers, waterfowl, nocturnal species, and raptors. A total of 56 species were used for analysis. We grouped the species into three main types of ecological or functional guilds based on a review of the literature (Ehrlich et al. 1988; Harmel 1992; Wilson et al. 1995): habitat preference (forest interior, forest edge, pine-grassland, and others), migrant behavior (migrant and resident), and nest placement (tree, shrub, cavity, ground and others). "Others" included species which were not classified into any of the other guilds: Barn Swallow and Northern Mockingbird. We eliminated "Others" in the analysis of two guilds, habitat preference and nest placement. Biodiversity of birds was examined using richness (the number of species) and RCS (Partners in Flight Regional Combined Score for the breeding season, RCS-b; Region 27, Southeastern Coastal Plain): total richness and total RCS and richness and RCS of each guild type. RCS is one of the species assessment scores, and it is determined by world population size and breeding distribution, regional population trend, regional threat to breeding, and relative density of breeding for the breeding season. The score of species increases with the need of conservation for the species. A bird community composed of those species would indicate a relatively high RCS. Although we were primarily interested in richness, we used RCS because it might take into account compositional differences among bird communities along an urban-rural/agriculture-wildland gradient, in terms of conservation needs.

To test differences in avian biodiversity along an urban-rural/agriculture-wildland gradient, we first performed a rank analysis of covariance (non-parametric ANCOVA) based on Mantel-Haenszel statistics. In our previous study (Chapter 2), we found that local vegetation structures are one of the crucial factors influencing species distribution in our study sites. Some local vegetation structure also varied along the gradient (see Results). To account for variations, we conducted Principal Component Analysis of local habitat variables and used 2 principal component scores (PC1 and PC2) as covariates in the rank analysis of covariance. PC1 represents a gradient of increasing vegetation cover and basal area of hardwood and PC2, a gradient of increasing vegetation cover and basal area of softwood. All analyses were performed in SAS v 10.0. We also tested pairwise differences in the biodiversity among 7 classes of urban-rural/agriculture-wildland gradient, by comparing the overlap of 90% confident intervals (CI) based on *t*-statistics. Non-overlap of 90% CI between the classes was considered as a significant difference. We also compared relative frequency (proportion) of each guild type along the gradient. The relative frequency was calculated by summing richness at each point, based on the guild type and class, and dividing the sum by the total sum of richness across points at each class.

RESULTS

Vegetation characteristics

Pine patches at wildland (Wild) showed significantly lower percent (%) vegetation cover at shrub layer and lower basal area of hardwood than pine patches in a matrix of urban (U1 and U2) or a matrix of a mixture of moderate urban development and agricultural land use (Moderate) both years (Fig. 3.1 and Fig. 3.2). Wild also tended to have lower % cover of softwood at tree layer. Patches at urban matrix (U1 and U2) and Moderate showed relatively higher % cover of hardwood at tree layer and higher basal area of hardwood than those in other classes; however, most of them but between U2 and Wild, were not significant. Lower % cover of herb and relatively higher basal area of softwood were observed at patches in moderate agricultural matrix (A2). Patches in a matrix of low level of agricultural land use (A1) or a mixture of low urban development and agricultural land use (Low) showed relatively higher % cover of herbaceous vegetation although it was not significant. A1 and Low also shwed an intermediate level of shrub vegetation cover.

Avian species

In 2010, avian biodiversity was significantly different in total species and 5 guilds at least at one class among 7 classes of an urban-rural/agriculture-wildland gradient (Table 3.2). In 2011, similar results were found, and the richness and RCS of pine-grassland species changed along the gradient (Table 3.2).

Mean total richness tended to be higher at Low in 2010 and at A1 and Low in 2011 than at the other classes although the difference was insignificant. In both years, mean total richness was significantly lower at Wild, particularly compared to the patches in moderate urban matrix (U2) and in moderate agricultural matrix (A2) (Fig. 3.3). Wild also showed significantly low mean richness of forest edge and shrub (Fig. 3.4 and Fig. 3.5). Mean richness of resident and cavity was low at Wild in 2010. Mean richness of pine-grassland, shrub, and migrant was relatively higher at patches in agricultural matrix (A1 and A2) and low level of urban/agricultural matrix (Low) than in urban matrix (U1 and U2) (Fig. 3.4 – 3.6). However, the differences were not significant. Only mean richness of pine-grassland at Low was significantly different in both years and mean richness at A1 in 2010.

Mean total RCS and mean RCS of each guild along an urban-rural/agriculture-wildland gradient showed the same pattern found in mean total richness and in mean richness of guild (Fig. 3.7 – 3.10). Mean total RCS and mean RCS of most guilds were low at Wild. Low, Al, and

A2 tended to have high mean RCS of pine-grassland, shrub, and migrant compared to U1 and U2, although most differences were not significant.

The relative frequency of each guild, especially, based on habitat preferences (3 guilds) was different along urban-rural/agriculture-wildland gradient. As human land-uses increased, the relative frequency of forest edge increased except at A1 in 2010, and the relative frequency of pine-grassland tended to decrease (Fig. 3.11). The bird community at Wild was composed of more pine-grassland and forest interior than bird communities in other classes (Fig. 3.11). While the relative frequency of shrub nesters was greater at Low compared to other classes, it was low at Wild (Fig. 3.12). The relative frequency of ground nesters tended to be low at patches in urban matrix (U1 and U2). Human land-uses also decreased the relative frequency of migrant: the relative frequency of migrant was low at urban and/or agriculture dominant matrix (U2, Moderate, and A2) (Fig. 3.13).

DISCUSSION

In our study, richness of avian species changed non-linearly along an urban-rural/agriculture-wildland gradient. Richness was significantly low at wildland, but, richness tended to be relatively higher at low level of a mixture of urban development and agricultural land use (Low) and low level of agricultural land uses (A1) than at other levels although most of the differences were insignificant. Seven classes of human land-uses in our study did not include high urban development (> 50% urban development) and high agricultural land uses (> 50% agricultural lands); however, it is unlikely that both or either of the two levels show higher richness than Low, A1, or moderate levels of urban development or agricultural land uses given the trend found in other urban-rural gradient studies and in our study. Both of the extremes of urban and agricultural land use are relatively rarer situations in southeastern USA landscapes. Low richness at undisturbed or less disturbed habitats like wildland has been reported in other studies. For example, Marzluff (2005) found low avian biodiversity at most natural landscapes, especially at relatively homogeneous coniferous forests in Seattle. Maestas et al. (2003) found that in Colorado, the number of avian species detected at nature reserves was lower than at ranches or exurban areas. However, unlike the general trend of avian biodiversity (higher richness of avian species at moderate levels of urban development, ~ 20 – 50% or 40 - 50% impervious surface depending on studies) observed in other studies (e.g., McKinney 2002; Marzluff 2005; Marzluff and Rodewald 2008), richness did not peak at moderate urban matrix. Richness was neither highest at moderate agricultural matrix. The inconsistent result between other studies and our study may be due to the characteristics of pine forests. In general, with exclusion of fire, pine forest in the Southeast is prone to encroachment of hardwoods. If hardwood continues to encroach, it creates dense shrub vegetation cover with no or low herbaceous vegetation cover and thus leads to unfavorable habitats, especially for pine-grassland species. This situation was observed at the pine patches in urban matrix (especially, moderate urban matrix) in our study. But, interestingly, richness tended to increase along urbanization gradient (low urban development, U1 to moderate urban development, U2), while richness tended to decrease along agriculture gradient (low agricultural land uses, A1 to moderate agricultural land uses, A2). It may be related to urban development type and urban age. Urban development types in our study included residential development, commercial development, roads, and any impervious surface or other built-up structures. U2 encompasses all of the types: however, a half of the pine patches in U2 are located in residential areas and some portions of the areas are vegetated with trees and shrubs. Conversely, a half of urban development types in U1 are impervious surface and newly developed buildings with little vegetation. In this case, the urban area itself does not provide much benefit to birds.

Although richness did not seem to peak at intermediate level of disturbance in our study, the results indicate that disturbance can promote biodiversity. In particular, given the relatively higher richness at Low and at A1, low disturbance appears to enhance avian biodiversity in pine forests by increasing habitat heterogeneity. At patch level, Low and A1 showed high herbaceous vegetation cover with intermediate level of hardwood cover at tree and shrub layer and basal area of hardwood, compared with other classes. The heterogeneous vegetation structure (i.e., the existence of vegetation cover at three different layers), especially with relatively high herbaceous vegetation, can provide a wide range of nesting sites and foraging opportunities for birds, which explains higher richness in several guilds such as pine-grassland, shrub, and migrant at both land uses. At landscape level, semi-natural open spaces created by the land uses and planted vegetation in yards or fields could add another type of habitat to the landscape and hence increase habitat heterogeneity. Variations in habitat heterogeneity can also explain low richness at wildland that is a relatively undisturbed habitat. Contrary to Low and A1, wildland showed lower vegetation cover at tree and shrub layer and basal area of hardwood, compared with other classes of human land-uses. This indicates that vegetation structure within a patch at wildland was less heterogeneous. At landscape level, wildland seems also homogeneous in our study sites, considering that only pine forest is a dominant form of habitat at wildland (i.e., mean percent cover of pine forests within a 1km-circular area of a sample point was 70% of the landscape); there are few heterogeneities added by human land-uses because any anthropogenic land uses at wildland are < 5 %; and ages of pine patches within most of the landscapes are relatively similar (i.e., mid-aged pine patches). This suggests that heterogeneity, particularly generated by low disturbance, may be a key factor influencing avian biodiversity in this region. The importance of habitat heterogeneity for avian diversity and conservation has been emphasized in numerous studies (e.g., Pino et al. 2000; Benton et al. 2003; Devictor and Jiguet 2007; Cerezo et al. 2011). The studies conducted in natural or planted pine forests have also found a positive relationship between avian biodiversity (richness) and spatial heterogeneity (e.g., Mitchell et al. 2006; Luck and Korodaj 2008). In particular, heterogeneous age structure of pine patches within a landscape is considered as an important factor affecting avian biodiversity (e.g., Turner et al. 2002; Mitchell et al. 2006). Uneven-aged forest management is often used to promote biodiversity in planted pine forests (Sallabanks and Arnett 2005).

Differences in richness between patches in agricultural matrix and those in urban matrix were insignificant; however, the relative effects of agricultural land uses and urban development on richness changed non-linearly with the levels of each of the land uses and the guild types. At the moderate level (U2 and A2), both land uses showed similar richness. But, higher richness of forest interior, cavity nester, tree nester, and resident was observed at U2; and higher richness of pine-grassland, shrub nester, ground nester, and migrant at A2. At low level (U1 and A1), A1 showed higher richness in most guilds and higher total richness than U1, although it varied in some guilds between 2010 and 2011, which may have been caused by too small a number of sample patches of A1 (n = 4) in 2010. A1 also showed slightly higher richness than U2. In another study, we found that an effect of agricultural land uses on occupancy of species was 2 to 3 times stronger than that of urban development. These results suggest that agricultural lands, especially low level of agricultural land, could be a more amenable matrix than urban lands in this region. However, the relative effects of agricultural land uses and urban development on avian biodiversity might be confounded with management effects. While over half of the patches in moderately urbanized areas (U2) have been unmanaged for several decades, most patches in agricultural matrix have been managed minimally or moderately. We do not have the data of the management history of each patch, and we do not have enough samples to examine how the difference in the management (managed vs. unmanaged) influences our results. However, given similar total richness between U2 (mostly unmanaged) and A2 (managed) and the relatively higher richness at A1, although most patches at both Al and U1 are managed, it is unlikely that the difference in management significantly affects our results.

We also found variations in the composition of bird community along the gradient. Relative proportion of different guild types varied along the gradient. A bird community in pine forests at wildland was composed of more forest interiors and pine-grassland species and ground nesters, but fewer forest edge species than those at urban and/or agricultural matrix except Low. The relative frequency of pine-grassland species also tended to decrease with increasing urban development and/or agricultural land uses. A bird community at urban or agriculture dominant matrix was composed of more resident species. These patterns suggest that migrants and pine-grassland species may be sensitive to human land-uses and that they avoid highly human-altered landscapes. Similar results, the negative impacts of intensive human land-uses (especially, urban development) on migrants and habitat specialist have been also found in other studies (e.g., Marzluff 2001; Dunford and Freemark 2004; Sratford and Robinson 2005). The compositional differences in an avian community between wildland or natural habitats and urban or rural areas indicate that an inference based only on richness could be misled. Some studies observed that avian biodiversity in natural habitats was not higher than in rural land or urban areas, but the natural habitats supported more native species and species of conservation concern (e.g., Chapman and Reich 2007). Moreover, a bird community or a subset of a bird community in highly urbanized areas tends to be similar across cities, which is called biotic homegenization (McKinney 2006; Blair 2008). In our study, wildland included endangered, threatened, and declining pine-grassland avian species, such as the Red-cockaded Woodpecker, Bachman's Sparrow, and Northern Bobwhite Quail. The first two species were detected only at wildland and Northern Bobwhite Quail was also mainly observed at wildland. We used RCS (Partners In Flight Regional Combined Score, RCS-b) to account for the differences in needs of conservation among avian species. However, the result of RCS was almost the same as that of richness. Given that RCS is a broad and coarse scale of estimates and some species that were scored relatively highly are common species in our study region, RCS may not be precise enough to detect compositional differences of avian species along the gradient in our study. Furthermore, we did not consider heterogeneous detectability among species in our analysis. Incomplete detection is a well-recognized issue in wildlife survey (e.g., Williams et al. 2002; MacKenzie et al, 2006). At community level, some species are easily detected due to conspicuous song or color; however, some species are cryptic and so they are hardly detected. Most conservation-related species are the latter. It is possible that we could not detect those species, even if they were present at wildland patches. We need further study to develop an index accounting for the variations in conservational status among avian species and an analysis method incorporating the heterogeneous detectability into an urban-rural/agricultural gradient study.

CONCLUSIONS

Our study demonstrates that 1) diversity of avian species tended to be relatively high at low disturbance (i.e., low level of a mixture of urban development and agricultural land uses, Low and low level of agricultural land uses, A1) rather than at moderate disturbance, 2) agricultural matrix, especially at low level could be more favorable than urban matrix, 3) habitat specialists such as pine-grassland species were more dominant at wildland and agricultural matrix, and 4) habitat heterogeneity could be an important factor to determine the pattern of avian diversity along urban-rural/agriculture-wildland gradient in this region. The results provide important insights for future forest managements for avian biodiversity conservation. The first, our results indicate that currently, pine patches at wildland cannot fully preserve avian biodiversity although they are a crucial refuge for conservation-related species. We need to develop a management plan to improve avian biodiversity at wildland and at the same time, to maintain the values of the pine patches for conservation-related species. The plan should consider increasing habitat heterogeneity more than current level both at patch and landscape scale, for example, by increasing vegetation structural diversity within a patch, by creating low disturbance (e.g, small open space), and by diversifying age structure of pine patches. Also, given that most human land-uses adjacent to wildland show low level (A1 and Low), it may be possible to establish a habitat network among pine patches by increasing connectivity. Then, pine patches at wildland continue to function as core habitats for conservation-related species and those at A1 and Low function as satellite habitats for other species as well as the species. The second, traditionally remnant habitats in urban matrix and agricultural matrix are considered unsuitable because of negative impacts of urban development and agricultural land uses on biodiversity. Recently, some studies have paid attention to the positive effects of the human land-uses and suggest that the habitats in human-altered landscapes can play an important role in biodiversity conservation (e.g., Marzluff and Rodewald 2008; Faeth et al. 2011). Our study supports the view. In particular, with fast-growing urbanization, more agricultural lands and natural or planted pine forests will be converted and more wild habitats will interface with urban areas. The management focusing only on wild habitats cannot protect biodiversity. We need to recognize the potential value of habitats in urban matrix (and agricultural matrix) and we should develop a strategy to manage the habitats and the matrix for biodiversity conservation. It should be also pointed out that improvement of the habitat and matrix quality can enhance sustainability of development by providing diverse ecosystem services. For example, increased vegetation can contribute to ameliorate air quality and decrease ambient temperature (thus reduce energy-usage). Well-managed habitats can be used for educations as well as recreational activities such as bird watching. But, managing the habitats in an urbanizing landscape will be challenging because it requires cooperation with many stakeholders such as land owners or homeowners, land managers, developers, planners, and policy makers. However, if we can convince the stakeholders that enhancement of biodiversity in the landscape also increases sustainability of development and if we can provide information about how it can be achieved, it is likely that they will participate in. Lastly, we stress a need of future studies to examine avian demographics along an urban-rural/agriculture-wildland gradient and to explore the effect of spatial configuration of the human land-uses and pine patches on avian biodiversity along the gradient. Although we support using the habitats (pine patches) in urban and agricultural matrix for biodiversity conservation, it is also essential to know annual productivity and survival of avian species in the matrix before we make any final management plan. In spite of relatively higher richness, it is possible that the habitats in the matrix, especially in moderate level of urban development (U2) may function as ecological traps, which will jeopardize long term persistence of the species (e.g., Purcell and Verner 1998; Boal and Mannan 1999; Robertson and Hutto 2006) and eventually reduce biodiversity. A study estimating demographic parameters such as annual productivity rate and survival rate of avian species can clarify the possibility, help re-evaluating the value of the habitats, and developing more proper management plans. A future study should also explore how spatial configuration of landscape elements (e.g., urban and agricultural lands, pine patches, open-space, etc) influences the pattern of avian biodiversity along the gradient. Increasing human land-uses causes reduction in amount of habitats available in a landscape. As available habitats declines, configuration of landscape elements becomes a major landscape feature affecting species distribution and persistence (e.g., Fahrig 1998; Flather and Bevers 20002). In our study, we did not account for possible variations in spatial configurations among urban development, agricultural land uses, and pine patches due to limited sample patches, although we tried to minimize matrix effects from other types of dominant land covers along the gradient. Some of our results (e.g., insignificant differences in richness between some of human land-use classes) might be influenced by these variations. A study incorporating configuration features into analysis can provide better information in understanding avian species response along the gradient, improving habitat connectivity, and determining an optimum land mosaic that enhance biodiversity and sustainability of development.

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Table 3.1. Classification (level) of human land-uses that represents an urban-rural/agricultural wildland gradient.

Class (Level)	% Urban development	% Agriculture	Number of Points	
			2010	2011
Moderate urban (U2) [1]	≥20	<5-10	19	27
Low urban (U1)	5< <20	<5-10	8	14
Moderate[2]	10 - 25	10-25	6	10
Moderate agriculture (A2) [1]	<5-10	≥20	11	14
Low agriculture (A1)	<5-10	5< <20	4	12
Low[2]	5 - 10	5 – 10	6	13
Wildland (Wild) [3]	<5	<5	35	75

[1] Points included in U2 and A2 were < 50 % urban development and < 50% agriculture, respectively. However, 2 points in U2 were ≥ 50% urban development.

[2] The difference between % urban development and % agriculture is ≤ 5-7.

[3] Sum of % urban development and % agriculture is < 5.

Table 3.2. Summary (x^2 values and statistical significance, *P*) of rank analysis of covariance for bird community. Two principal component scores that represent a gradient of increasing vegetation cover and basal area of hardwood and a gradient of increasing vegetation cover and basal area of softwood were used as covariates in the rank analysis of covariance. Statistical significance: * $P < 0.01$; **, $P < 0.001$. See Figures (Fig. 3-10) for actual richness (number of bird species) and RCS (Partners In Flight Regional Combined Score, RCS-b).

	2010		2011	
Guild	Richness	RCS	Richness	RCS
Total	19.88 *	18.46*	23.20**	25.11**
Habitat preference				
Forest interior	5.09	5.30	4.61	4.94
Forest edge	24.62*	24.29*	31.91**	33.39**
Pine-grassland	4.95	3.50	14.78*	14.51*
Nest placement				
Cavity	22.86*	20.06*	13.42**	14.18**
Tree	1.04	1.81	9.11	11.20
Shrub	25.55*	21.94*	35.35**	34.77**
Ground	4.88	4.05	2.35	1.54
Migratory status				
Resident	20.21*	22.80*	26.81**	30.56**
Migrant	6.74	6.47	9.66	10.33

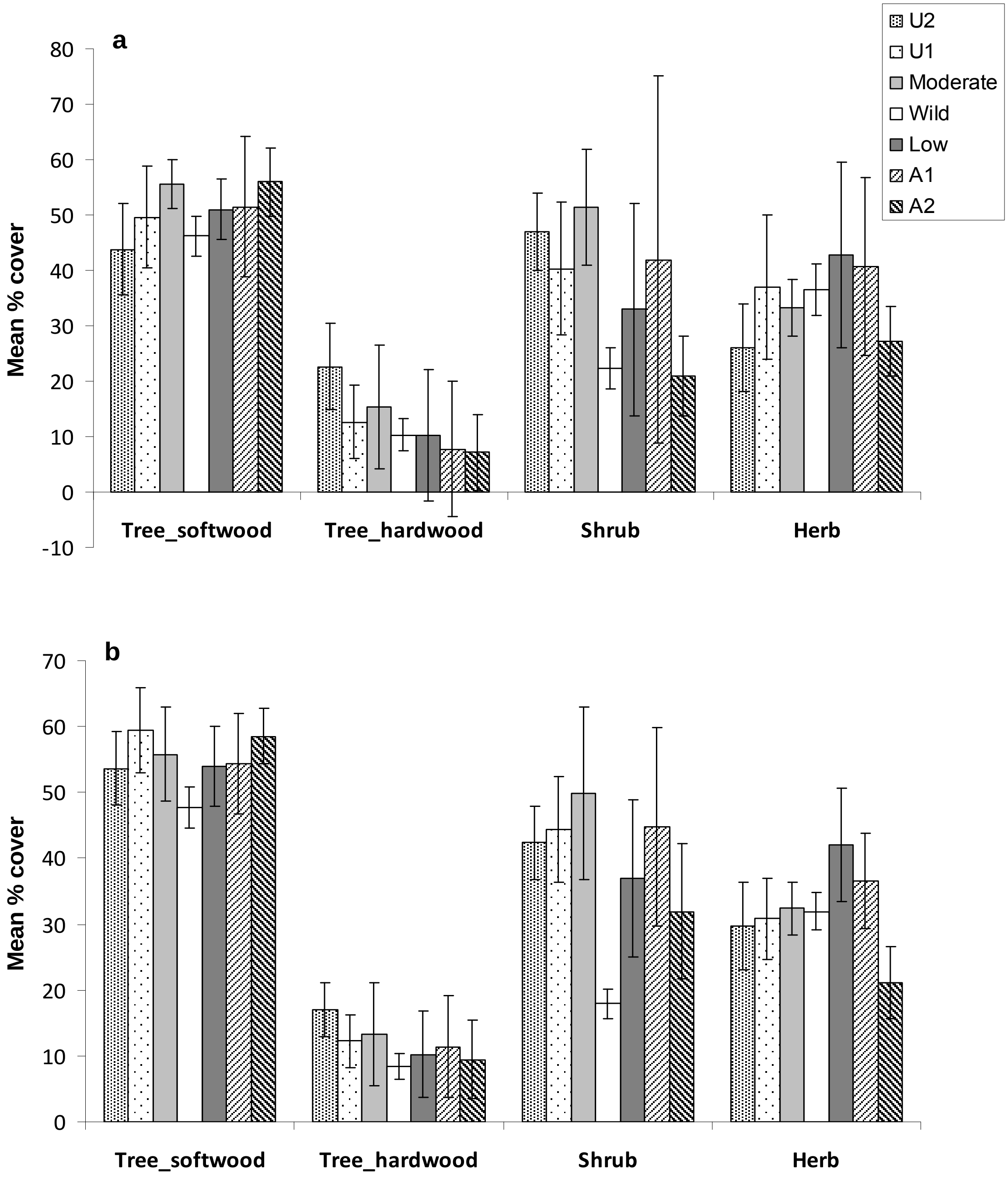

Figure 3.1. Mean percent vegetation cover at tree (softwood and hardwood), shrub, and herb layer along urban-rural/agricultural wildland gradient in 2010 (a) and in 2011 (b). Bars represent 90% CI. See Table 3.1 for abbreviations of 7 classes of human land-uses which represent a gradient of urban-rural/agricultural wildland.

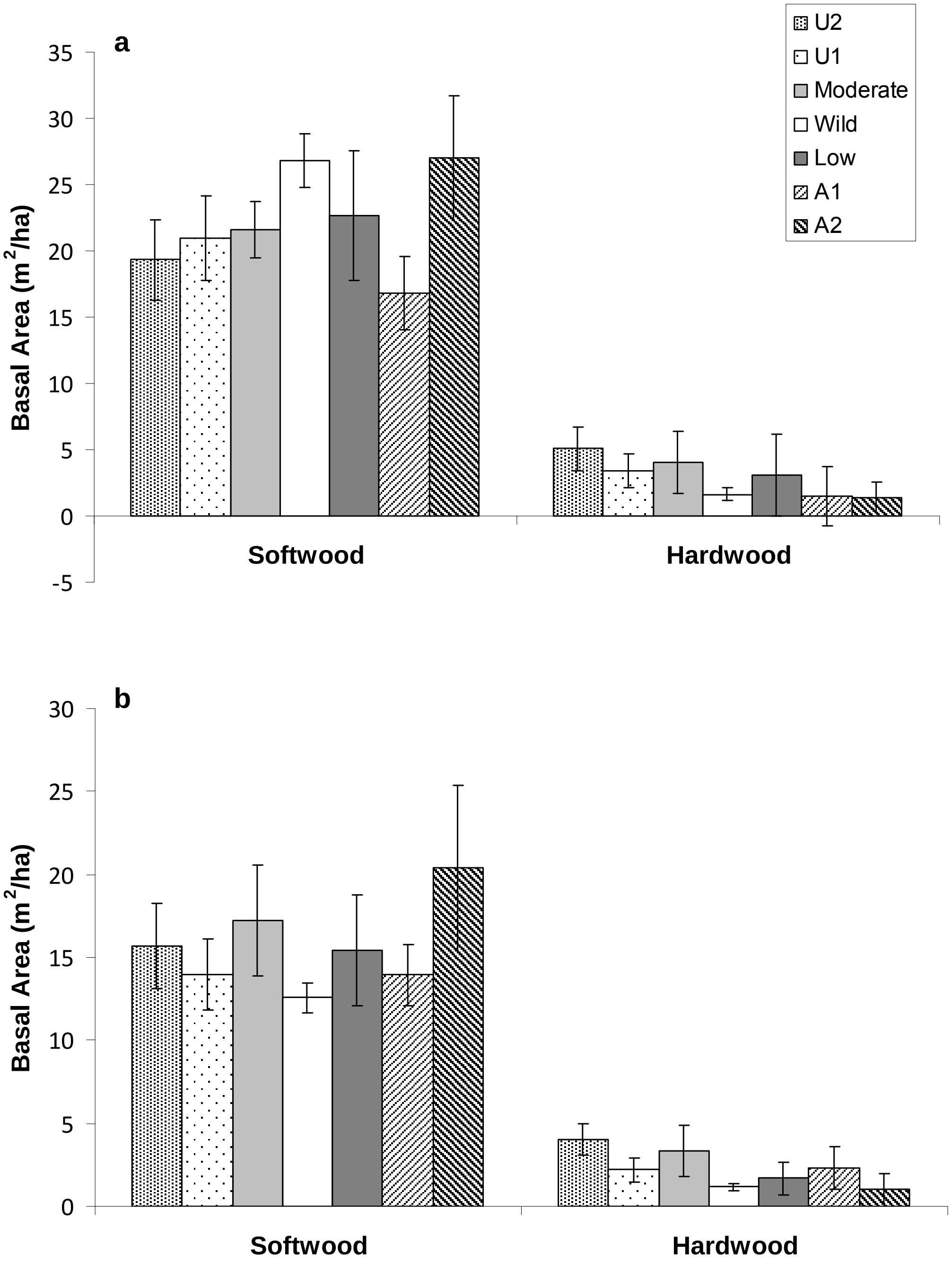

Figure 3.2. Mean basal area of softwood and hardwood urban-rural/agricultural wildland gradient in 2010 (a) and in 2011 (b). Bars represent 90% CI. See Table 3.1 for abbreviations of 7 classes of human land-uses which represent a gradient of urban-rural/agricultural wildland.

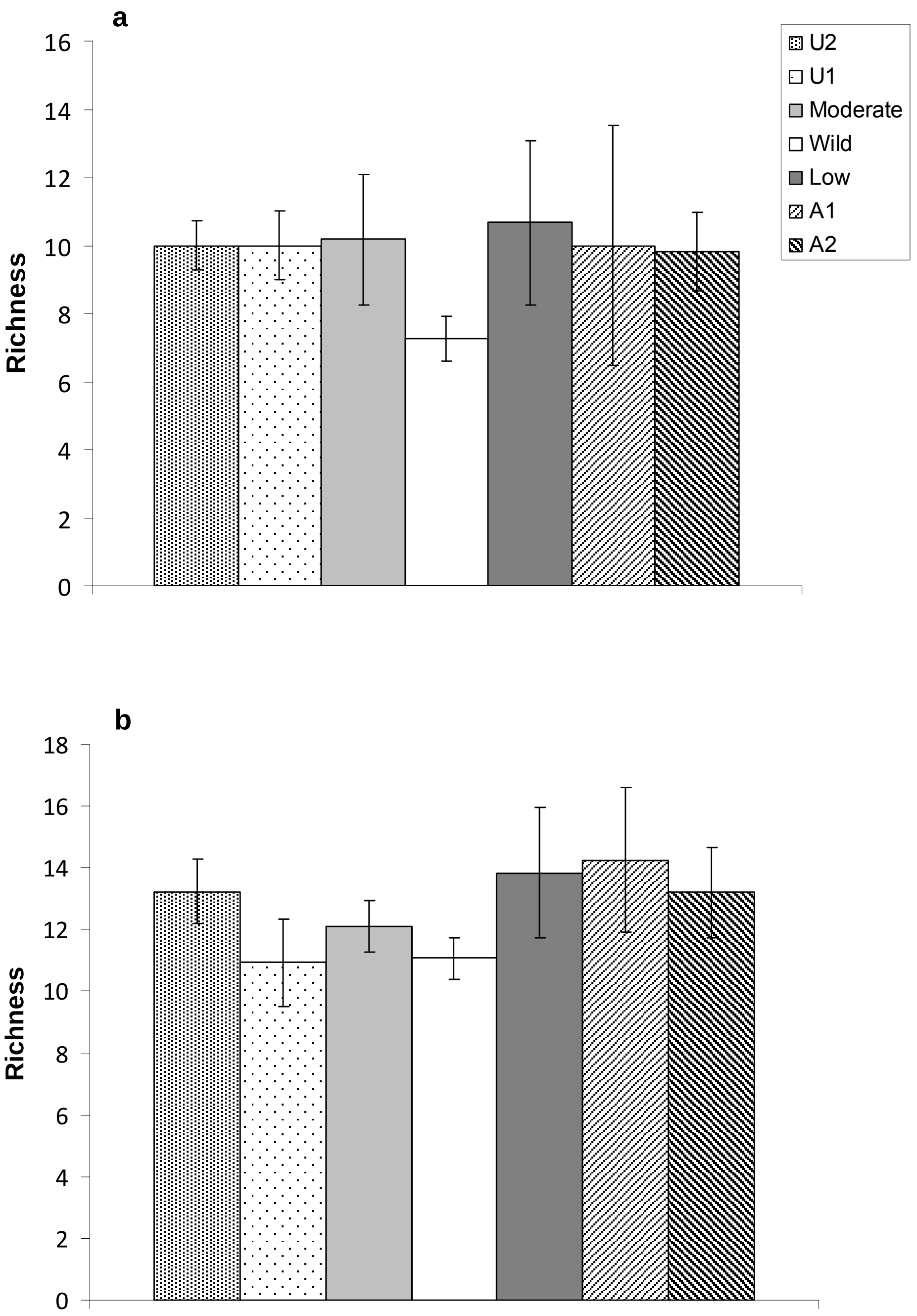

Figure 3.3. Mean total richness (number of bird species ± 90% CI) along urban-rural/agricultural wildland gradient in 2010 (a) and in 2011 (b). See Table 3.1 for abbreviations of 7 classes of human land-uses which represent a gradient of urban-rural/agricultural wildland.

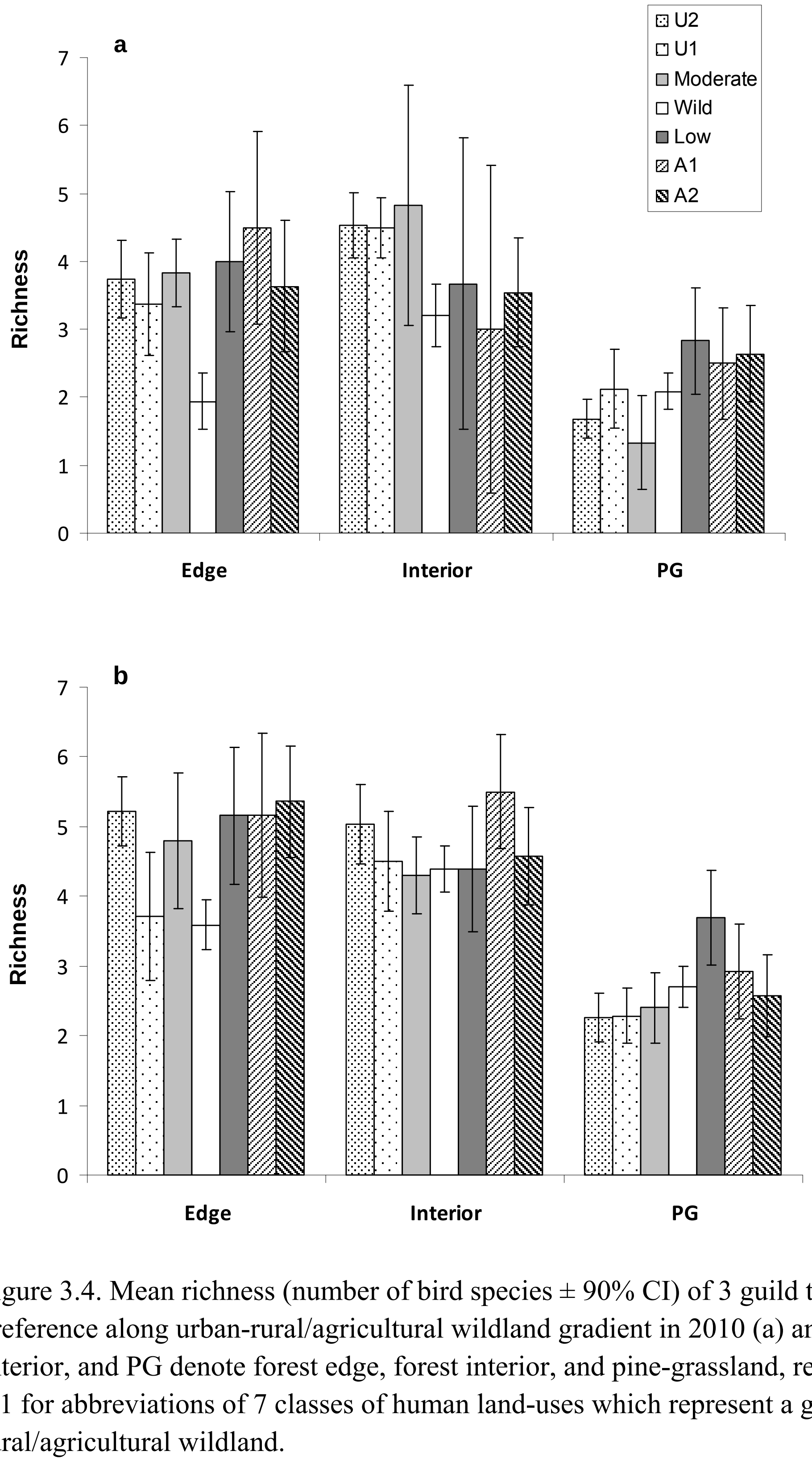

Figure 3.4. Mean richness (number of bird species ± 90% CI) of 3 guild types based on habitat preference along urban-rural/agricultural wildland gradient in 2010 (a) and in 2011 (b). Edge, Interior, and PG denote forest edge, forest interior, and pine-grassland, respectively. See Table 3.1 for abbreviations of 7 classes of human land-uses which represent a gradient of urban-rural/agricultural wildland.

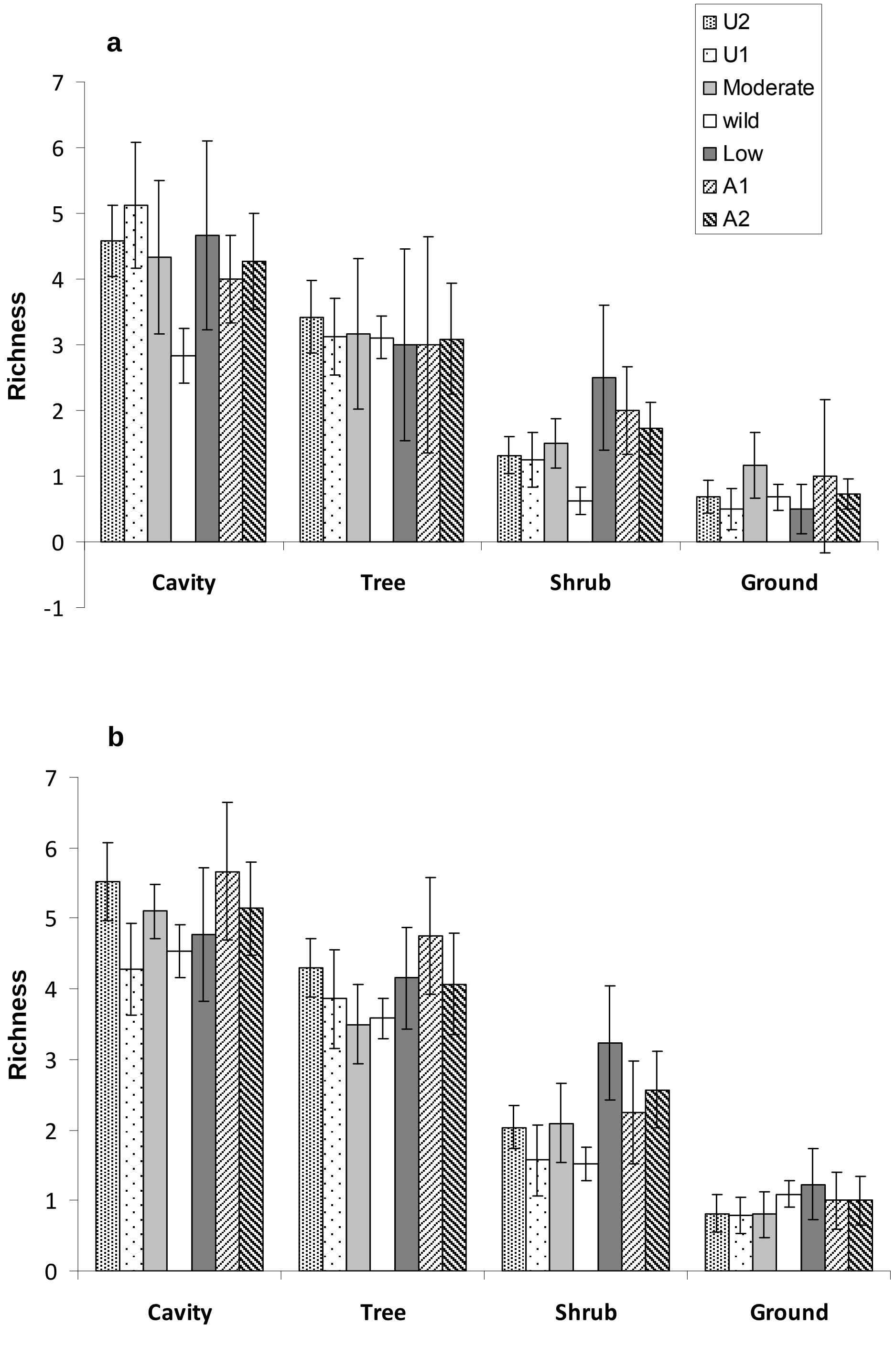

Figure 3.5. Mean richness (number of bird species ± 90% CI) of 4 guild types based on nest placement along urban-rural/agricultural wildland gradient in 2010 (a) and in 2011 (b). See Table 3.1 for abbreviations of 7 classes of human land-uses which represent a gradient of urban-rural/agricultural wildland.

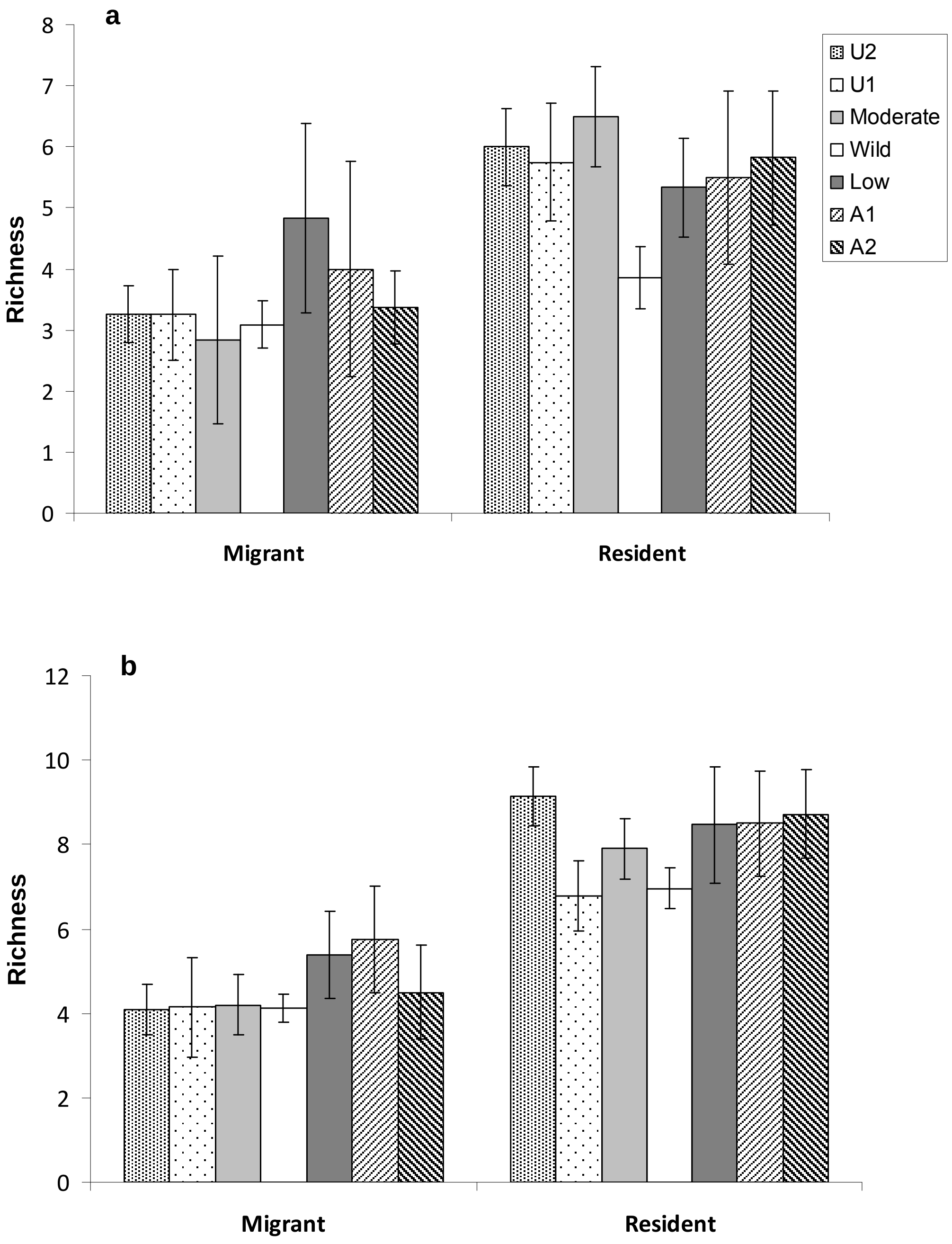

Figure 3.6. Mean richness (number of bird species ± 90% CI) of 2 guild types based on migratory status along urban-rural/agricultural wildland gradient in 2010 (a) and in 2011 (b). See Table 3.1 for abbreviations of 7 classes of human land-uses which represent a gradient of urban-rural/agricultural wildland. See table 1 for abbreviations.

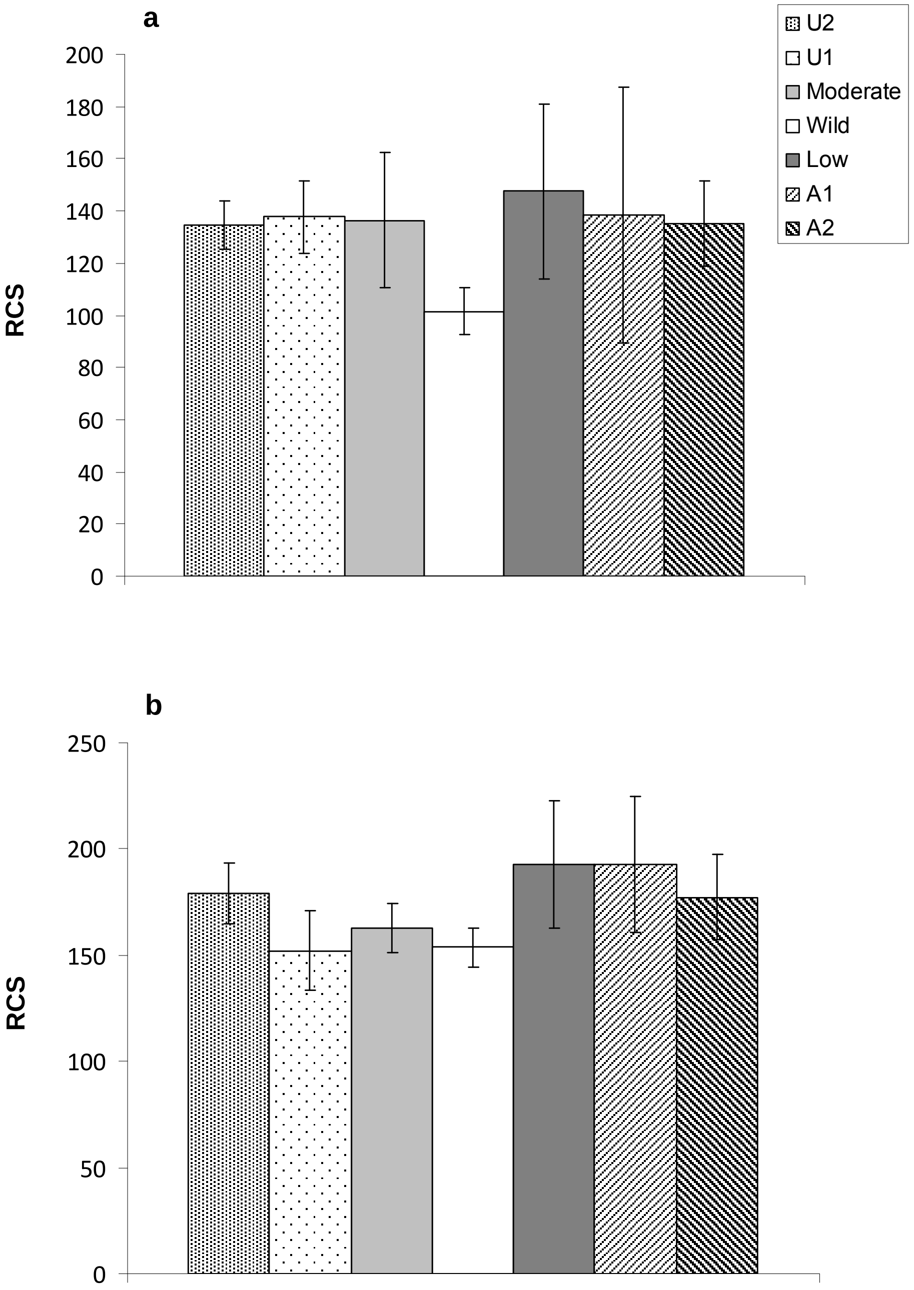

Figure 3.7. Mean total RCS (Partners In Flight Regional Combined Score, RCS-b) along urban-rural/agricultural wildland gradient in 2010 (a) and in 2011 (b). Bars represent 90% CI. See Table 3.1 for abbreviations of 7 classes of human land-uses which represent a gradient of urban-rural/agricultural wildland.

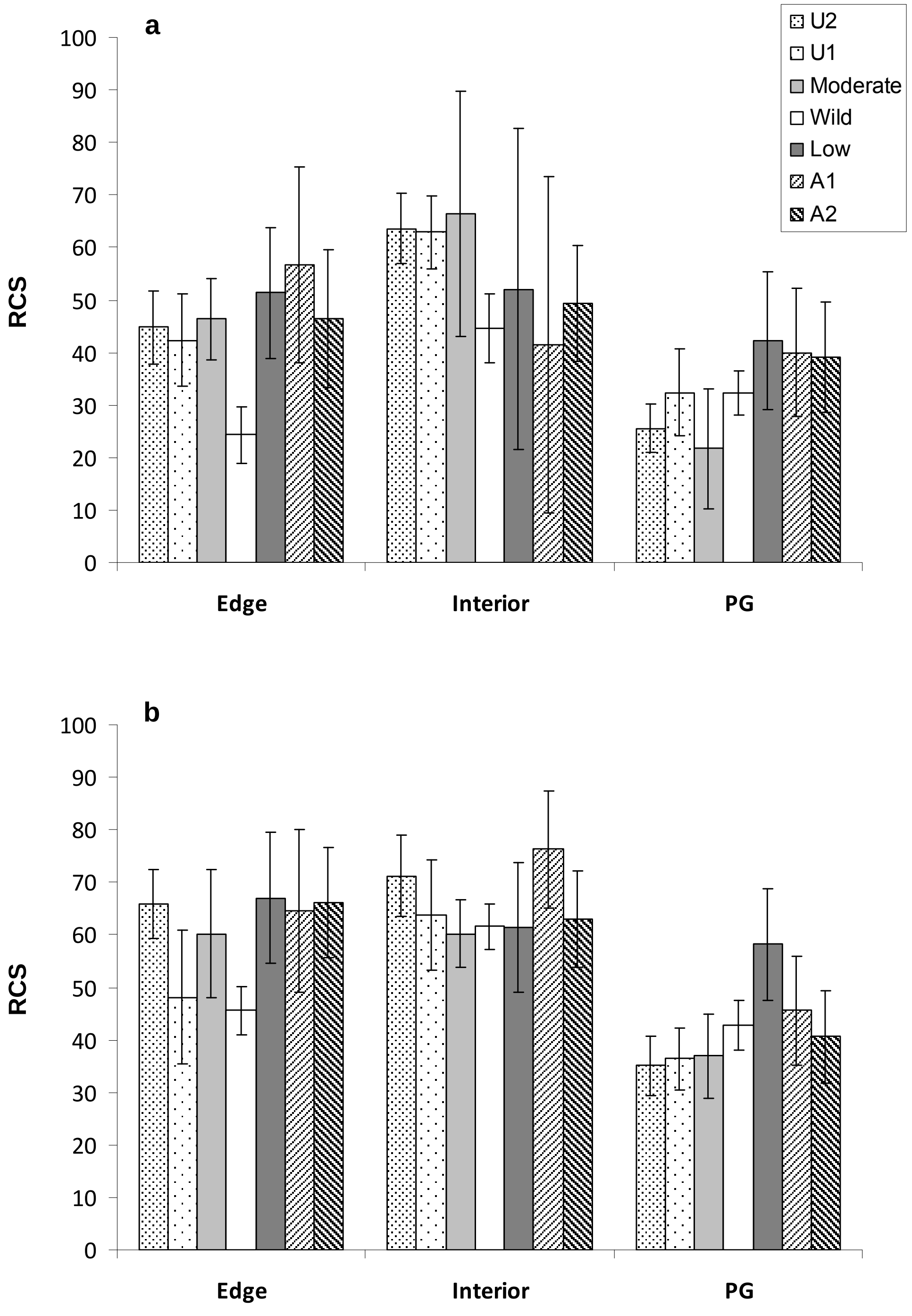

Figure 3.8. Mean RCS (Partners In Flight Regional Combined Score, RCS-b) of 3 guild types based on habitat preference along urban-rural/agricultural wildland gradient in 2010 (a) and in 2011 (b). Edge, Interior, and PG denote forest edge, forest interior, and pine-grassland, respectively. Bars represent 90% CI. See Table 3.1 for abbreviations of 7 classes of human land-uses which represent a gradient of urban-rural/agricultural wildland.

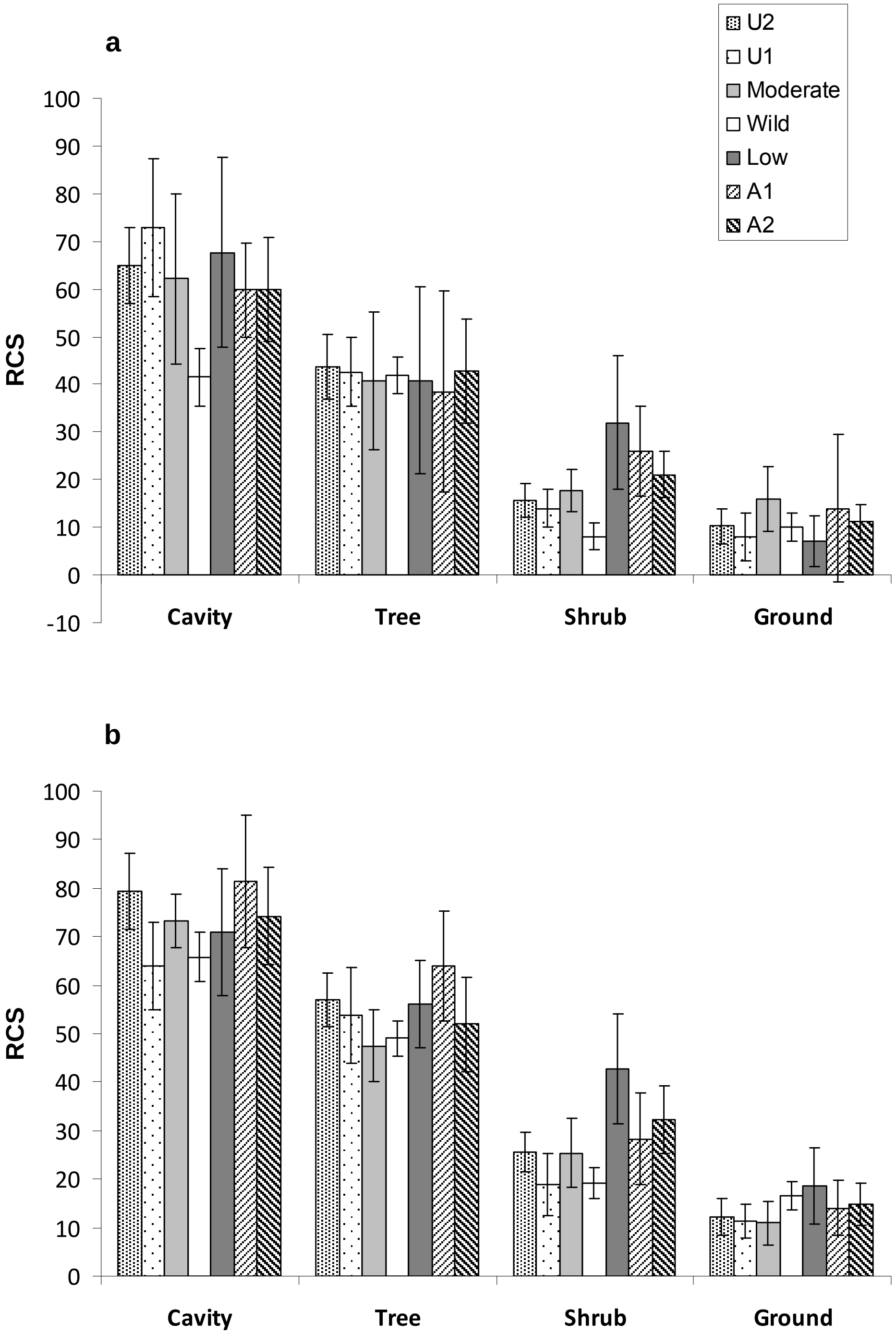

Figure 3.9. Mean RCS (Partners In Flight Regional Combined Score, RCS-b) of 4 guild types based on nest placement along urban-rural/agricultural wildland gradient in 2010 (a) and in 2011 (b). Bars represent 90% CI. See Table 3.1 for abbreviations of 7 classes of human land-uses which represent a gradient of urban-rural/agricultural wildland.

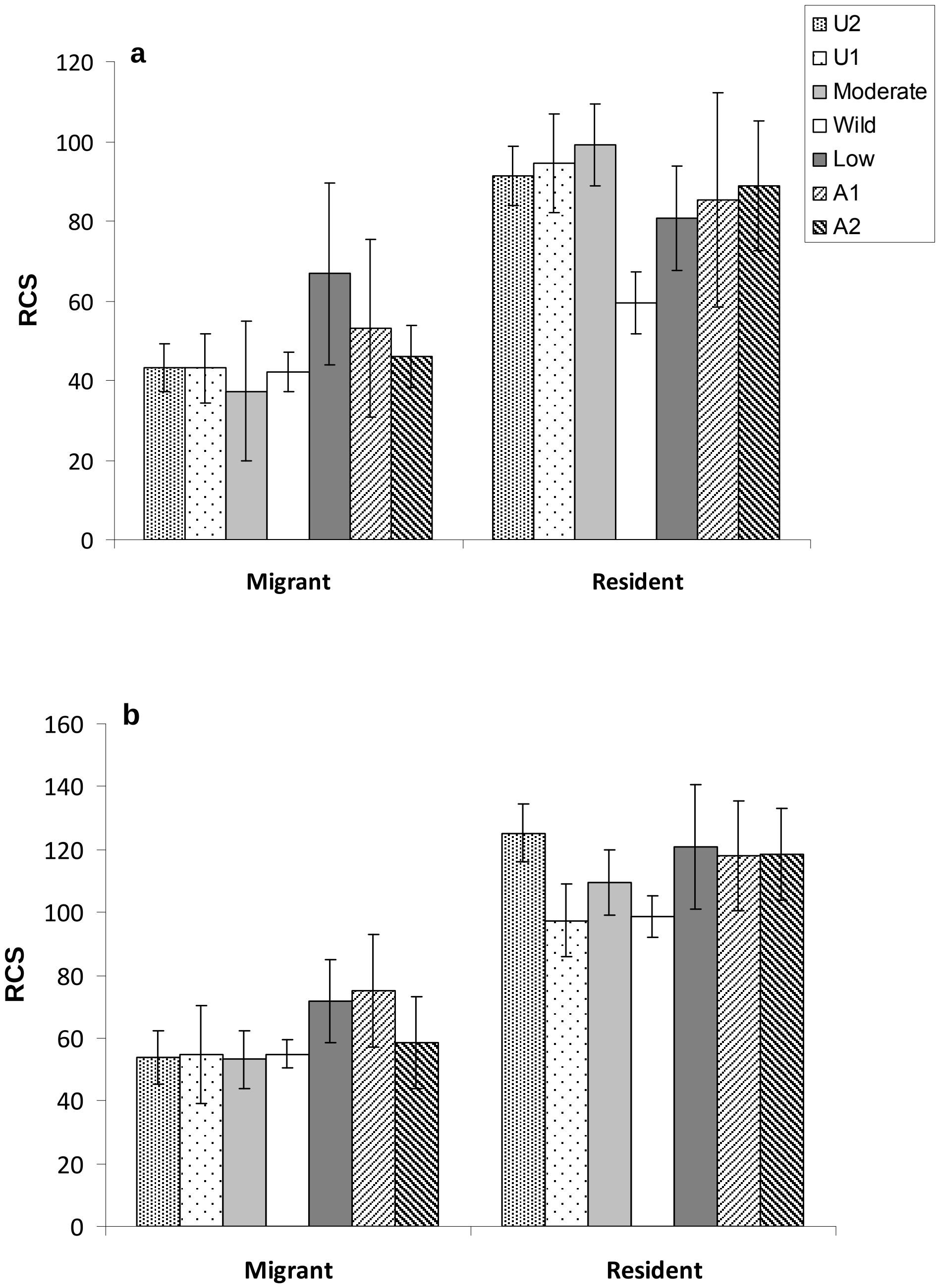

Figure 3.10. Mean RCS (Partners In Flight Regional Combined Score, RCS-b) of 2 guild types based on migratory status along urban-rural/agricultural wildland gradient in 2010 (a) and in 2011 (b). Bars represent 90% CI. See Table 3.1 for abbreviations of 7 classes of human land-uses which represent a gradient of urban-rural/agricultural wildland.

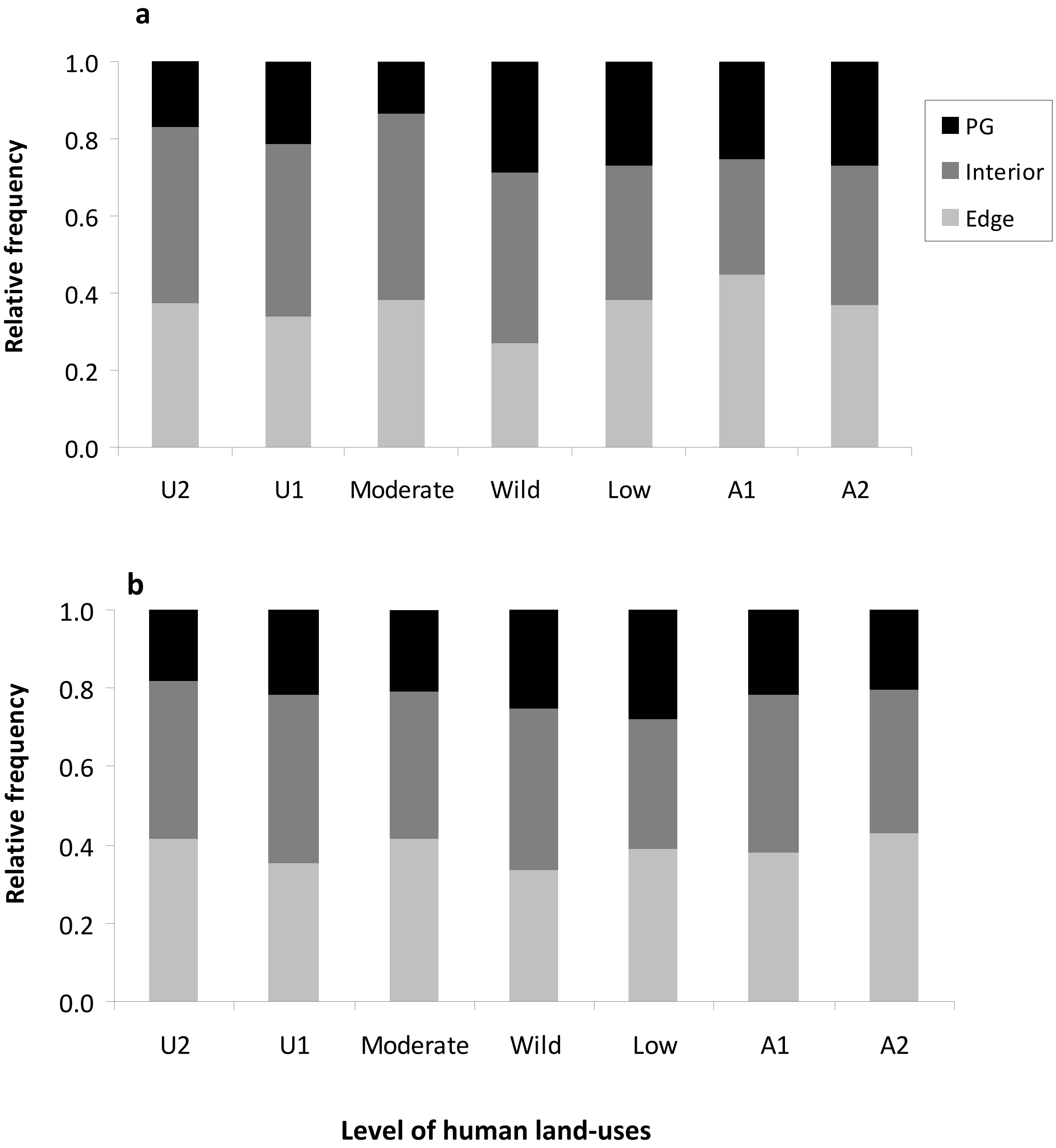

Figure 3.11. Relative frequency (proportion) of 3 guild types based on habitat preference at each of 7 different levels of human land-uses in 2010 (a) and in 2011 (b). Edge, Interior, and PG denote forest edge, forest interior, and pine-grassland, respectively. See Table 3.1 for abbreviations of 7 classes of human land-uses which represent a gradient of urban-rural/agricultural wildland.

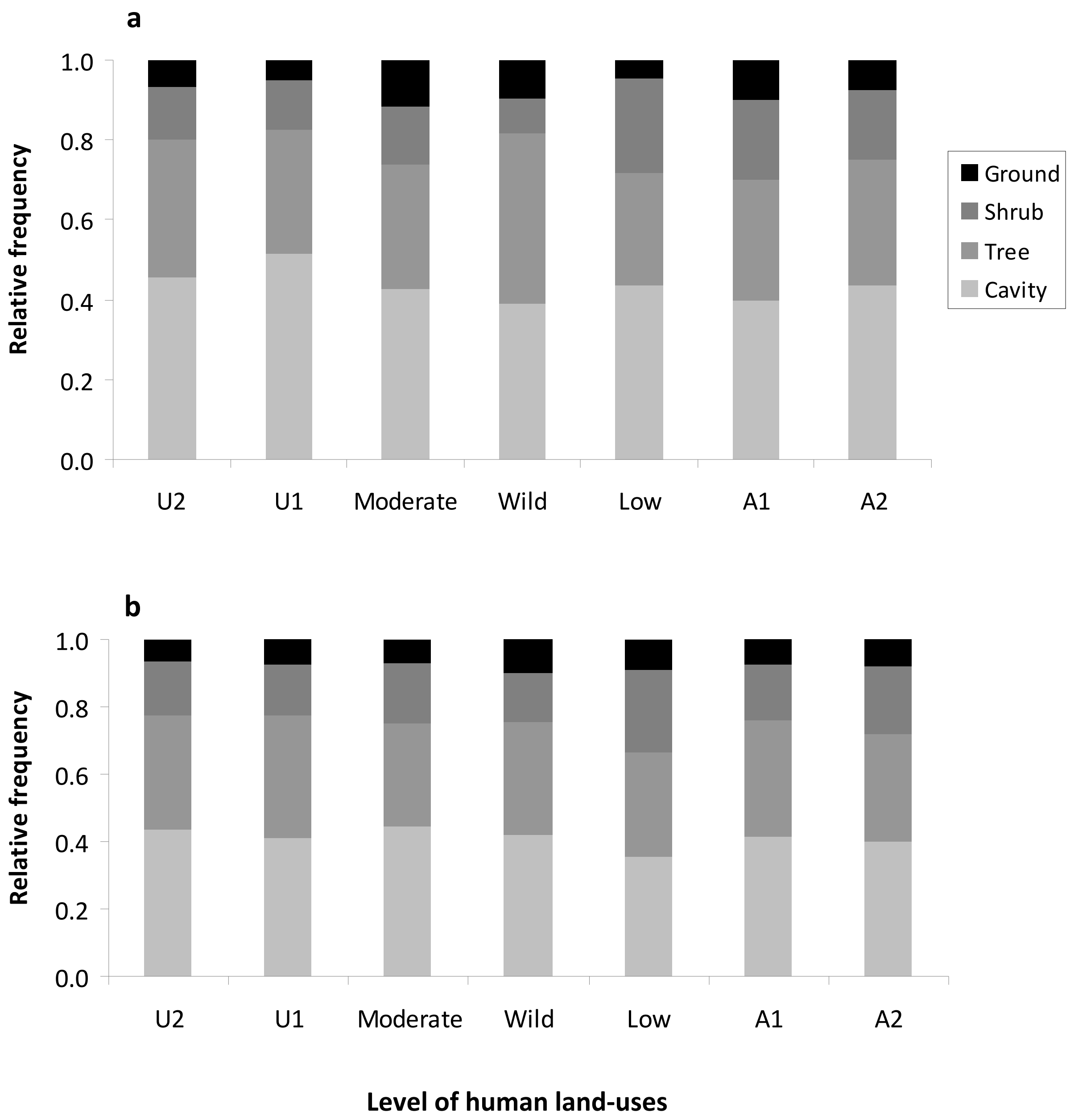

Figure 3.12. Relative frequency (proportion) of 4 guild types based on nest placement at each of 7 different levels of human land-uses in 2010 (a) and in 2011 (b). See Table 3.1 for abbreviations of 7 classes of human land-uses which represent a gradient of urban-rural/agricultural wildland.

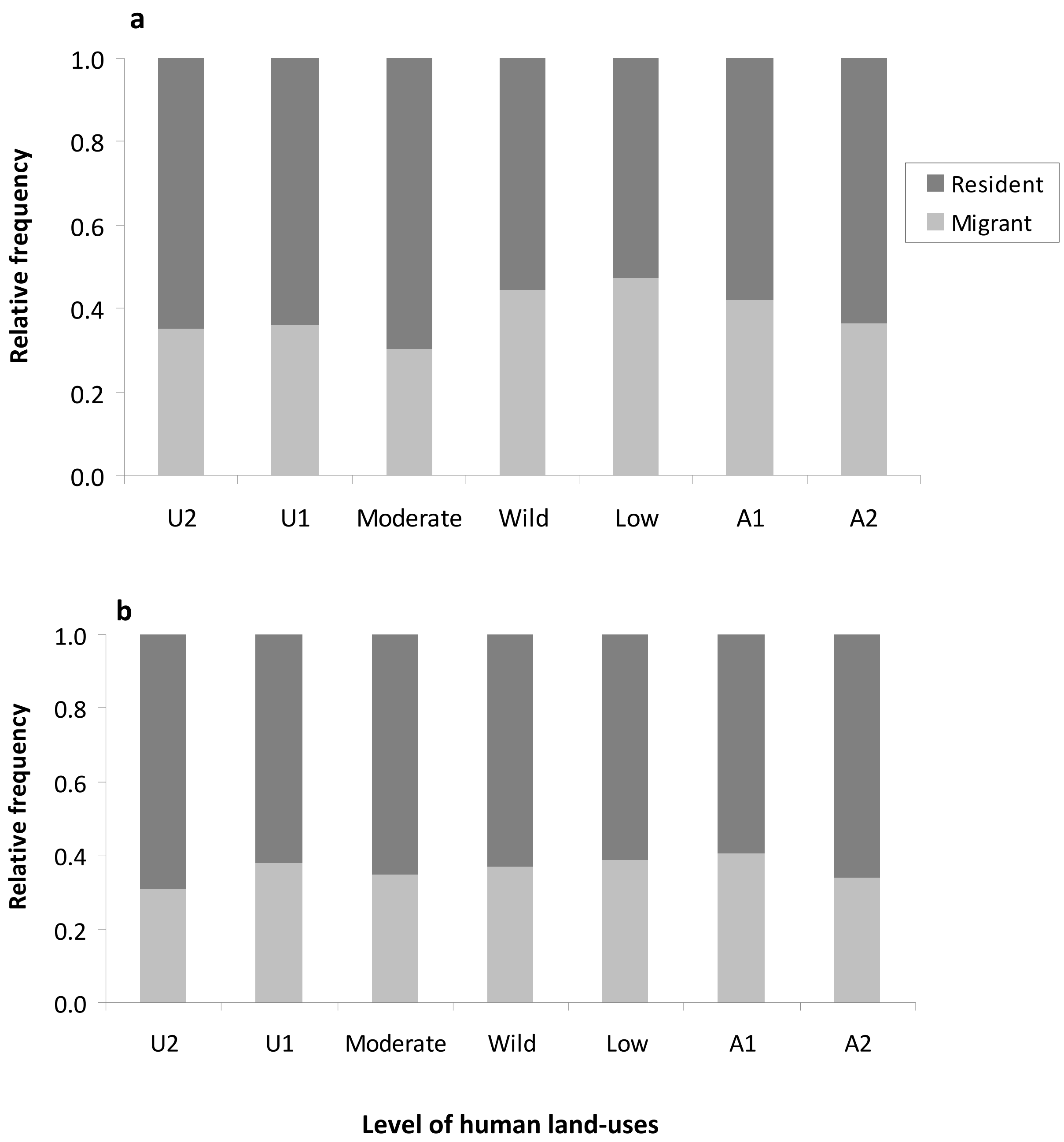

Figure 3.13. Relative frequency (proportion) of 2 guild types based on migratory status at each of 7 different levels of human land-uses in 2010 (a) and in 2011 (b). See Table 3.1 for abbreviations of 7 classes of human land-uses which represent a gradient of urban-rural/agricultural wildland.

CHAPTER 4

RELATIONSHIP BETWEEN PATCH SIZE, VEGETATION STRUCTURE, AND AVIAN COMMUNITY IN THE SOUTHERN USA: IMPLICATIONS FOR PINE FOREST MANAGEMENT[3]

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[3] Lee, Myung-Bok and John P. Carroll. To be submitted to *Forest Ecology and Management*.

ABSTRACT

We investigated the relationship between avian biodiversity, habitat structure, and patch size in a pine forest. We conducted avian point count and vegetation sampling on mid-aged pine (*Pinus* spp.) stands, mainly in Fort Gordon and some surrounding areas in the Sand Hills region of Georgia, during breeding season of 2011. We divided stand basal area (BA; m^2/ha) into 3 classes by modifying 5-classification BA data of Fort Gordon: OS, overstocked (> 23m^2/ha, n=21); FS, fully/densely stocked (13.8 - 23m^2/ha, n=52); MS, moderately stocked (2.3 -13.8 m^2/ha, n=27). We classified 56 bird species we detected into 8 guilds based on habitat preference, nest placement, and migratory status. We used richness and RSC (Partners in Flight Regional Combined Score for the breeding season, RCS-b) as index for biodiversity. Since percent cover of tree varied significantly among the 3 BA classes and was positively correlated with BA, we considered BA as an appropriate surrogate for vegetation structure within a patch at our study sites. We performed Kruskal-Wallis tests to determine whether there was a difference in biodiversity among BA classes, and regression analysis to examine the relationship between patch size and richness. Total richness and RCS and mean richness and RCS of most guilds were greater at MS and a difference was found among 3 classes ($P < 0.05$). Based on 95% confidence intervals, mean richness and RCS were different between MS and OS; however, no difference was found between OS and FS. The relationship between patch size and richness and RCS varied with BA classes and guilds; however, as the patch size increased, there were more species at MS patch. Our results suggest that it is important to maintain moderate or low level of basal area and preserve larger patches to enhance avian biodiversity in this region.

INTRODUCTION

Planted pine forests are one of dominant forests in the southeastern USA. Although the majority of the planted pine forests are managed for commercial wood production, there have been growing efforts to manage the forests for avian conservation, especially in public lands (e.g., military bases) retaining some remnants of relatively natural pine forests. A great number of studies have explored how pine patch (stand) characteristics such as age and vegetation or habitat structure within a patch influence avian species richness and abundance and how different management practices affect the characteristics (e.g., Dickson et al .1993; Wilson and Watts 2000; Sallabanks and Arnett 2005). Among the characteristics, habitat structure within a pine patch has been known to strongly affect avian species. Basal area is considered as one of main factors determining the habitat structure, by influencing the amount of canopy cover. Maintaining appropriate basal area through practices such as thinning has been common in forest management for wildlife (Melchiors 1991; Dickson et al. 1993). Although numerous studies have been conducted to determine the effects of basal area in other ecoregions, few studies have been performed in the Sand Hills ecoregion and little is known about the effect of basal area on avian species richness.

High basal area is known to result in closed canopy, reduce light penetration, increase competition among understory plants, lower herbaceous vegetation, and slow the growth of trees (e.g., Melchiors 1991; Allen et al. 1996). It can simplify habitat structure (i.e., lower structural diversity) and thus reduce overall habitat quality, especially for species preferring open or open-forest types of habitats such as early successional species, shrubland species, and pine-grassland species. Like high basal area, too low basal area of a patch (e.g., heavy thinning) can have a negative impact on tree nesting species and mature forest or forest interior species, which prefer relatively dense canopy cover. Determining the proper level of basal area depends on the target species or specific ecological guild (e.g., early successional species or forest interior species) of the forest management. But, if the objective of the management is to maximize overall richness, the richness may be maximized at some level between the two extremes, namely, intermediate or relatively low level of basal area.

Species-area relationship is one of the major issues that has been widely studied and discussed in ecology for decades. However, few studies have investigated the relationship in planted or natural pine forests. While the positive relationship between patch size or area and richness or abundance has been well documented in both plants and animals (e.g., Arrhenius 1921; MacArthur and Wilson 1963; Rosenzweig 1995 for review; Hill and Curran 2003; Lindenmayer and Fischer 2006), the relationship can vary with matrix types, habitat structure/ diversity, degree of fragmentation and connectivity, and so on (e.g., Boecklen 1986; Hinsley et al. 1996; Scheffer et al. 2006). Moreover, it has been debated that the main factor influencing species richness is not an area *per se* but habitat diversity, which is often highly correlated with area (Shochat et al. 2001). It is also unclear how the habitat structure affects the species-area relationship (Blake and Karr 1987). Unlike natural forests, most planted mature pine forests maintain relatively homogeneous habitat structure within a patch because they are managed at the patch (stand) level. Thus, the managed pine forests provide a good opportunity to explore the relationship between patch size and species richness by reducing the confounding effects of habitat structure within the patch or by easily incorporating the effects of the habitat structure into the analysis.

We investigated the relationship between patch size, basal area (as a surrogate for habitat structure), and avian species biodiversity in planted mature pine forests, which are located in the

Sand Hills ecoregion in central-east Georgia. Our goal was to determine what levels of basal area and patch size are necessary for successful pine forest management for improving avian biodiversity in the region. We first examined the effect of basal area (high to intermediate or relatively low levels of basal area) on species diversity and then compared the effect of patch size on species diversity at different levels of basal area. We expected decreasing species diversity with increasing basal area because high basal area would reduce structural diversity of vegetation within a stand by creating too dense canopy cover. We also expected positive effect of patch size on diversity; however, we anticipated that the degree of the effect would vary with guild type and the level of basal area (i.e., quality of habitat).

METHODS

Study areas and sample patches

The study was conducted at pine patches (or stands) mainly in Fort Gordon and in surrounding areas of Fort Gordon in the Sand Hills ecoregion of Georgia, including Burke, Columbia, McDuffie, and Richmond county (Fig. 4.1). Pine forests are dominated by planted loblolly pine (*Pinus taeda*) throughout the study areas. Slash pines (*Pinus elliottii*) or shortleaf pines (*Pinus echinata*) are mixed with loblolly pines in some areas. The majority of the relatively mature longleaf pines (*Pinus palustris*) are found at Fort Gordon. The ages of pine patches vary across our study sites; however, old pine patches (> 75yrs) are relatively rare and most pine patches are young and mid-aged. Overstory and midstory of hardwood forest and mixed forest largely consist of sweetgum (*Liquidambar styraciflua*), sassafras (*Sassafras albidum*), black cherry (*Prunus serotina*), flowering dogwood (*Cornus florida*), and oak (*Quercus* spp.). Sparkleberry (*Vaccinium arboreum*) is also commonly found in the midstory. The understory is dominated by yellow jessamine (*Gelsemium* *sempervirens*), muscadine grapes (*Muscadinia rotundifolia*), greenbrier (*Smilax spp.*), brambles (*Rubus* spp.), blueberry (*Vaccinium* spp.), broomsedge bluestem (*Andropogon virginicus*), low panicgrass (*Dicanthelium* spp.), wiregrass (*Aristida stricta*), and lespedeza (*Lespedeza* spp.).

Mid-aged (20-75yrs) loblolly and longleaf pine patches were selected by using modified 2011 forest inventory data and 2009 land cover map of Fort Gordon. For pine patches outside of Fort Gordon, we developed a land cover map by digitizing 2010 digital orthophoto images (NAIP), 1998 Digital Orthophoto Quarter Quads, and ArcGIS. Within a patch, one point was established randomly at 50-70m far from any edge (road, other types of vegetation or land cover, etc.). All patches were located at relatively undisturbed landscape: less than 5-7 percent of human land-uses within a 500m circle surrounding a sample point.

Patch size and basal area

We defined a pine patch as a stand that had a relatively homogeneous vegetation composition and structure. We also considered a pine patch divided by any road (paved and unpaved roads or firebreaks) as an independent patch. If basal area varied within a patch (especially, in Ft. Gordon), we divided the patch to keep homogeneous characteristics. Patch boundaries were delineated from aerial photos and ground truthing and patch size was calculated using ArcGIS and ranged from 1.34 ha to 54.17 ha.

We grouped basal area (BA; m^2/ha) into 3 classes by modifying 5 classes of BA data of Fort Gordon: OS, overstocked (>23 m^2/ha); FS, dense/fully stocked (13.8 m^2/ha - 23 m^2/ha); MS, moderately/sparsely stocked (2.3 m^2/ha - <13.8 m^2/ha). BA class of sample patches was determined using inventory data of Fort Gordon for the patches located at Fort Gordon and our vegetation data for other patches. BA data of Fort Gordon were collected using the 10 BAF variable plot method at > 3plots/stand (~ 1plot/1.6ha). The data included both softwoods and hardwoods, but hardwoods were minor in most sample patches, therefore we assumed that BA data of Fort Gordon could represent the BA of softwoods. BA data were also verified with our vegetation data collected in 2011.

Bird surveys and vegetation surveys

Bird surveys were performed three times from May – June, 2011, using fixed-radius point counts (Ralph et al. 1993). At each point, an observer recorded species seen or heard within a 50m radius of a sampling point for a 10-min duration. Distance to the species detected from a sampling point was also recorded. Two observers conducted the survey, and they were rotated between sites to reduce observer effects. We also alternated survey order to minimize the effect of time-of-day. Each survey was performed between dawn to 1100 EDT. We did not conduct surveys during inclement situations such as high wind or rain.

To explore variations in local vegetation structure (percent cover of tree, shrub, and herb vegetation) among BA classes and the relationship between BA and the vegetation structure, we performed vegetation sampling at the same points as the bird survey between late June and early August in 2011. A total of four 5m- radius subcircular plots were established in each cardinal direction at a fixed distance of 30m from a sample point. Within each of the subcircular plots, vegetation data were collected using modified PRBO Point Count Veggie (Relevé) Protocol. Percent cover of tree (>5m in height), shrub (0.5-5m in height), and herb (< 0.5 m in height) vegetation layer was visually estimated. DBHs of tree (≥ 8cm in diameter) were measured within four 10m-radius subcircular plots. The values of each vegetation characteristic estimated or measured from 4 subcircular plots were averaged. The averaged values were used to represent the value at the sample point.

Analysis

We compared percent vegetation cover at tree, shrub, and herb layer among 3 BA classes. Only percent vegetation cover at tree layer varied significantly and it was moderately correlated with BA ($r = 0.52$, $P < 0.01$). Given the relationship, we considered BA as an appropriate surrogate for vegetation or habitat structure within a patch at our study sites.

Although all sample patches were located at relatively undisturbed sites, to minimize potential matrix effect from other types of land cover, we excluded points based on the following criteria: percent cover of pine forest < 50%, and percent cover of any open space and/or disturbed lands >20% within 500 m radius circle of the sample point using FRAGSTATS 3.3. A total of 99 points were chosen for final analysis: OS, n=20; FS, n=52; MS, n=27.

To verify BA class of each patch, we calculated basal area using DBH data collected in our vegetation survey. Of 99 patches, 9 patches showed a discrepancy between BA class determined with Fort Gordon data and BA class classified with our vegetation survey data. We determined BA class of those patches by examining 2011 aerial photographs of Fort Gordon.

We included all bird species, except nocturnal species and raptors, detected at least once during the survey. We classified 56 bird species detected into three types of ecological or functional guilds based on the literature review (Ehrlich et al. 1988; Harmel 1992; Wilson et al. 1995): habitat preference (forest interior, forest edge, pine-grassland, and others), migratory status (migrant and resident), and nest placement (tree, shrub, cavity, ground and others). “Others” included species that did not group into any of other guilds: Barn Swallow and

Northern Mockingbird. We eliminated “Others” in the analysis of two guilds, habitat preference and nest placement. Biodiversity of bird was examined using richness (the number of species) and RCS (Partners in Flight Regional Combined Score for the breeding season, RCS-b; Region 27, Southeastern Coastal Plain): total richness and total RCS and richness and RCS at each guild type. RCS is one of the species assessment scores. RCS is determined by global population size and breeding distribution, regional population trend, regional threat to breeding, and relative density of breeding for the breeding season. The score of species increases with degree of conservation needs for the species. A bird community composed of the species would show relatively high RCS. Although we were primarily interested in richness, we used RCS because it might take into account compositional differences between bird communities, in terms of conservation criteria. We combined longleaf and loblolly stand types, because we found no significant difference in mean total richness, mean total RCS, and mean richness and mean RCS at each guild type (but pine-grassland species).

To determine whether there was a difference in mean richness or RCS among BA classes, we performed the Kruskal-Wallis test due to the relatively small sample sizes and skewness in the data. Pairwise differences among the 3 classes were decided by comparing the overlap of 95% confident intervals (CI). If 95% CI of the classes did not overlapped, they were considered significantly different. The relationship between patch size and avian biodiversity was examined at each BA class using regression analysis. Before the analysis, we performed the analysis of covariance (PROC GLM) with BA class as a covariate to determine an interaction effect of patch size and BA class. All analyses were conducted in SAS v 10.0.

RESULTS

Effect of basal area

Mean total richness of the bird community significantly varied with the 3 BA (Table 4.1 and Fig. 4.2, a). Total richness was greater in MS patch than either OS or FS patch. The same pattern was observed in the mean richness of 5 guilds: shrub, migrant, resident, forest edge, and pine-grassland (Table 4.1 and Fig. 4.2, b-d). Based on 95% CI, mean richness was significantly different between MS and OS in most guilds; however, no difference was found between FS and MS in migrant and between OS and FS in all 5 guilds. Mean richness of the other 3 guilds, cavity, tree, and forest interior, did not show significant differences among any of the 3 classes.

Mean RCS among the 3 classes also showed the same pattern found in the mean richness (Table 4.1 and Fig. 4.3). Mean total RCS were significantly different and mean RCS of 5 guilds varied with BA classes: shrub, migrant, resident, forest edge, and pine-grassland (Table 4.1). Mean RCS was significantly different between MS and OS in those guilds (Fig. 4.3). No difference was found between FS and MS in migrant, and between OS and FS in all the guilds but shrub. Mean RCS of the other 3 guilds, cavity, tree, and forest interior was not different.

Effect of patch size

Significant interaction effect of BA class and patch size was found in total richness and total RCS and richness and RCS of two guilds, tree and pine-grassland (Table 4.2). Basal area significantly influenced richness or RCS of more guilds than patch size did. As patch size increased, there tended to be more species at MS patch ($P < 0.05$, Fig. 4.4).

Results of the regression analysis showed that the effect of patch size changed with the level of basal area and guild types. Significant positive effect of patch size on richness of ground and especially strong effect on richness of pine-grassland were observed at MS patch, and a weak positive effect of patch size (marginally significant, $P < 0.1$) on tree, shrub, and resident was also found at MS patch (Fig. 4.5 – 4.7). Richness of shrub, ground, and migrant at FS patch showed a weak positive response to increasing patch size. Richness of most guilds at OS patch was not significant; however, richness of tree tended to significantly decrease with patch size.

RCS showed the similar patterns found in richness: the significant positive relationship between patch size and RCS at MS patch was found in total species (Fig. 4.8) and ground (Fig. 4.9), and the weak positive relationship in migrant and resident (Fig. 4.10). In particular, like richness, pine-grassland showed the strong positive responses to patch size (Fig. 4.11). The negative relationship was observed in tree at OS patch and the significant positive relationship at FS patch in shrub and migrant (Fig. 4.9 – 4.11).

Although the patch size effect varied with BA classes, when a patch is small, richness or RCS was not different among BA classes. However, when a patch size reached 5-10ha, the regression lines of 3 BA classes started to cross in some guilds and richness or RCS began to show the pattern described above.

DISCUSSION

Effect of basal area

Our results demonstrated a negative relationship between basal area and species richness: species richness tended to increase with decreasing basal area, although most significant differences in species richness were observed between MS (moderately/sparsely stocked) and OS (overstocked) among the 3 classes of basal area. A similar pattern has been documented in some guilds in other studies (e.g., Canterbury et al. 2000; Wang et al. 2006). In particular, Canterbury et al. (2000) found that richness of shrubland species was strongly negatively correlated with tree basal area; however, they found strong positive effects of basal area on richness of mature forest species. While Wang et al. (2006) described greater occurrences of some forest interior species at plots with higher basal area (i.e., *closed canopy,* to use their term), richness of forest interior species in our study did not vary with the classes of basal area. This different response of forest species in the study and ours may be associated with the tree types measured for basal area. Basal area in Wang et al.'s study represented completely basal area of hardwoods, whereas basal area in our study rarely contained hardwoods. At the same level of basal area, the relative effect of hardwood and softwood on habitat structure may differ, and some avian species may respond differently to the canopy cover of hardwood and softwood. Moreover, the study did not clearly describe the levels of basal area. The range of basal area in the study may be different from ours. Then, the inconsistent result is not surprising.

Although high basal area can be detrimental to species inhabiting open-forest, too low basal area could also negatively affect mature forest or forest interior species preferring relatively dense canopy cover. Thus, overall richness may be high at the level between the two extremes (i.e., intermediate or relatively low level of basal area). Wang et al. (2006) reported that in oak-hickory forest, Red-eyed Vireo (forest interior) was most abundant at closed canopy (i.e., control and 25% basal area removal plots), and Indigo Bunting (early successional species or pine-grassland species in our study) was most abundant at open canopy (≥ 50% basal area removal plots). Some forest interior species such as Wood Thrush, Ovenbird, and Hooded Warbler occurred only at closed canopy of control plots, and some early successional or forest edge species such as Blue Grosbeak, Prairie Warbler, and Eastern Bluebird were observed only at open canopy. Similar responses of some of the species were also described in other studies that compared species abundance or richness at thinned plots and unthinned plots (Garrison 1986; Kerpez and Stauffer 1989). In addition, Wang et al. (2006) found the highest territory density and species richness at intermediate open canopy (50% and 75% basal area removal plots, respectively). In our study, we observed the highest richness at MS. Although Wang et al. (2006) did not indicate the level of basal area, the intermediate open canopy seems similar to MS. In our study, richness of forest edge and pine-grassland species was also high at MS; however, richness of forest interior species did not vary with basal area, which may indicate that MS is not so low as to affect forest interior species negatively. The patch retaining very low basal area like a clearcut stand or a heavily thinned stand would reduce richness of forest interior species. McDermott and Wood (2011) reported that during the post-breeding period, richness and abundance of late successional (mature forest) species were low at clearcut stands compared to hardwood stands of two classes of basal area (2.0-3.7 m^2/ha and 5.3-7.0 m^2/ha), although the difference was not statistically significant. The basal area classified as MS in our study was broader than the basal area in their study; however, the two classes of basal area could be classified as MS. If we included a class of very low basal area, it is likely that species richness at the class would be lower than at MS.

Effect of patch size

Our study demonstrates that the effect of patch size on species richness varied with habitat structure (different levels of basal area), and the degree of the effect changed based on guilds. Patch size positively affected overall richness and richness of several guilds when basal area was moderate or low (MS). Conversely, patch size did not show significant effects on species richness when basal area was high (OS) and it tended to negatively influence richness of tree nesters at OS. However, the negative response needs to be interpreted carefully because it may be caused by a small number of large OS patches in our study given that only one OS patch was > 30 ha in size. Pine-grassland species showed a strong positive relationship with patch size at MS. The positive relationship between patch size and avian species richness has been found in many studies (e.g., Blake and Karr 1987; McIntype 1995; Bellamy et al. 1996; Turner et al. 2002; Yamaura et al. 2008). In particular, the significant effect of patch size is often observed in habitat specialists. For example, Blake and Karr (1987) and McIntype (1995) compared species richness and composition among different sizes of woodlots in agricultural matrix. Both studies found that habitat generalists (Blake and Karr (1987) and edge species (McIntype 1995) were dominant at smaller woodlots, but forest interior species were more observed at larger woodlots. Several other studies also found the positive effect of patch size on the richness of other habitat specialists such as shrubland or woodland birds (Ambuel and Temple 1983; Rodewald and Vitz 2005; Lehnen and Rodewald 2009; Huth and Possingha 2011). In our study, the strong response of pine-grassland species to patch size is consistent with the findings of some of the studies. Among the 3 guilds based on habitat preference, pine-grassland species require a unique habitat structure, open-forest habitat. Pine-grassland species include some of the species classified as early successional and shrubland birds in the above studies. They also encompass conservation concern species which are sensitive to disturbance or avoid edge zones. A large patch is likely to contain more interior zones that reduce negative edge effects than a small patch, and thus it can provide the species with more areas unaffected by disturbance (Pickett and Thomson 1978; Harris 1984; Baker 1992).

While the species-area relationship is well documented, relatively few studies have explored the combined effects of area and habitat structural diversity on avian species richness.

Recently, Huth and Possingham (2011) modeled woodland bird species-area relationships by incorporating vegetation structural diversity. The results from their model showed that the impact of patch size was stronger at high habitat structural diversity (i.e., high quality habitat) than at low habitat structural diversity (i.e., low quality habitat). They recommended that the conservation management for small patches of low quality should focus on improving habitat quality rather than increasing area, whereas the management for small patches of high quality needs to increase the patch area. Our result was somewhat similar to their findings. In our study, OS patches and MS patches can represent low quality habitats and high quality habitats, respectively. FS (fully/densely stocked) may be considered as moderate quality habitat or more likely between low and moderate quality habitat. When a patch size was small (5-10 ha where regression lines of OS and FS crossed), species richness did not differ among the 3 classes. This seems to indicate that species richness at small patch may be more influenced by the quality of matrix surrounding the patch or influxes of avian species from the matrix or other adjacent habitats. However, as patch size increased, the pattern changed. Richness at MS increased relatively fast in pine-grassland species and ground nesting species, but richness at OS did not show a significant response in most guilds. Richness at FS did not significantly vary with patch size although richness of some guilds showed a weak positive (i.e., marginally significant positive) response. These patterns imply that management plans for avian biodiversity conservation in pine forests need to be decided by considering both level of basal area (i.e., habitat quality) and patch size: if basal area of a patch is high (i.e., low quality habitat like OS and maybe FS), attention should be given to reduction of basal area; if basal area of a patch is appropriate (i.e., high quality habitat like MS), an expansion of the patch would be a better management promoting avian biodiversity.

CONCLUSIONS

Overall, our results suggest that 1) moderate or low level of basal area needs to be maintained to improve avian biodiversity in pine forests, and 2) avian diversity, especially diversity of pines-grassland species, which contain major conservation concern species in the southeastern USA, can be promoted by increasing the size of a patch with moderate or low level of basal area. These findings provide some important information for future forest management at Fort Gordon. We first recommend reducing basal area to moderate or low level, given that levels of basal area of most stands at Fort Gordon are relatively high (overstocked or fully/densely stocked). We also recommend preserving large patches of moderate or low level of basal area and increasing the size of patches with that level of basal area. But, how big should the patch size be? Greater species richness tended to be observed at ≥ 10 ha of MS patch, and if the trends of OS (overstocked) and FS (fully/densely stocked) were compared, richness of some guilds at OS started to be lower than at FS when patch size was approximately ≥ 5-10ha. Therefore, 10 ha may be the minimum patch size that needs to be maintained for the conservation of avian diversity. We need further investigation to verify the threshold of patch size. Also, it should be pointed out that patch size can be affected by some landscape features. Although we reduced matrix effects by selecting sample patches whose landscape characteristics were similar based on the percent of land covers within a 500m radius surrounding a sample point, we did not account for the spatial arrangement of the patches, particularly the connectivity among the patches, and possible variations in landscape characteristics at larger landscape scale. If the connectivity is high, smaller-sized patches can still play an important role in the conservation of avian species. If land covers or other habitat types which were minor matrix in our study become dominant at larger landscape scale, they may influence the avian community in the patch: if the matrix is inhospitable, minimum patch size should be larger than the size in favorable matrix because adverse edge effects will penetrate further into the patch in inhospitable matrix. Moreover, the patch shape affects the amount of the edge of the patch. As complexity of patch shape increases, the amount of edge increases. More complex shapes are often observed at larger patches (e.g., Krummel et al. 1987; Ewers and Didham 2007). Therefore, there is a trade-off between shape complexity and patch size. Since the patch shape is relatively uniform in planted pine forests, we assumed the patch shape could not significantly affect our results. However, the information about the relationship between patch shapes and a proper patch size could be valuable in developing better forest management plans. For future study, we suggest exploring how patch size interacts with matrix, habitat connectivity, and patch shape. It will provide crucial information on determining the optimal patch size required for avian conservation in this region.

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Table 4.1. Summary (X^2, *P*) of Kruskal-Wallis test conducted to examine the effect of basal area on avian richness (number of bird species) and RCS (Partners In Flight Regional Combined Score, RCS-b). See Figures (Fig. 4.3 – 4.10) for actual richness and RCS.

	Richness		RCS	
Guild	X^2 (2 df)	*P*	X^2 (2 df)	*P*
Total	17.64	< 0.001	19.59	< 0.001
Nest placement				
Cavity	3.43	0.180	4.89	0.087
Tree	1.34	0.512	1.00	0.606
Shrub	24.39	< 0.001	23.15	< 0.001
Ground	8.56	0.013	10.76	0.005
Migratory status				
Resident	10.85	0.004	12.72	0.002
Migrant	12.77	<0.002	14.08	< 0.001
Habitat preference				
Forest interior	0.27	0.872	0.17	0.919
Forest edge	10.17	0.006	10.04	0.007
Pine-grassland	28.15	< 0.001	28.03	< 0.001

Table 4.2. Summary (F, *P*) of the analysis of covariance results. Statistical significance: * $P < 0.05$; **, $P < 0.01$. See Figures (Fig. 4.3 – 4.10) for actual richness (number of bird species) and RCS (Partners In Flight Regional Combined Score, RCS-b).

Guild	Richness			RCS		
	BA Class (2 df)	Area (1 df)	Interaction (2 df)	BA Class (2 df)	Area (1 df)	Interaction (2 df)
Total	12.69**	4.22*	3.71*	15.03**	5.38*	3.37*
Nest placement						
Cavity	1.40	0.12	0.41	2.06	0.18	0.32
Tree	1.14	0.59	3.63*	1.20	0.51	3.36*
Shrub	20.28**	5.41**	1.85	21.76**	6.64*	2.02
Ground	4.69*	8.49**	1.37	6.10**	8.68**	1.20
Migratory status						
Resident	6.71**	1.61	2.12	8.32**	2.16	1.59
Migrant	8.68**	3.95*	2.35	10.24**	5.10*	2.86
Habitat preference						
Forest interior	0.12	0.51	2.00	0.16	0.80	2.08
Forest edge	5.26**	2.26	0.94	5.23**	2.39	0.98
Pine-grassland	26.74**	5.48*	8.68**	28.53**	5.28*	7.53**

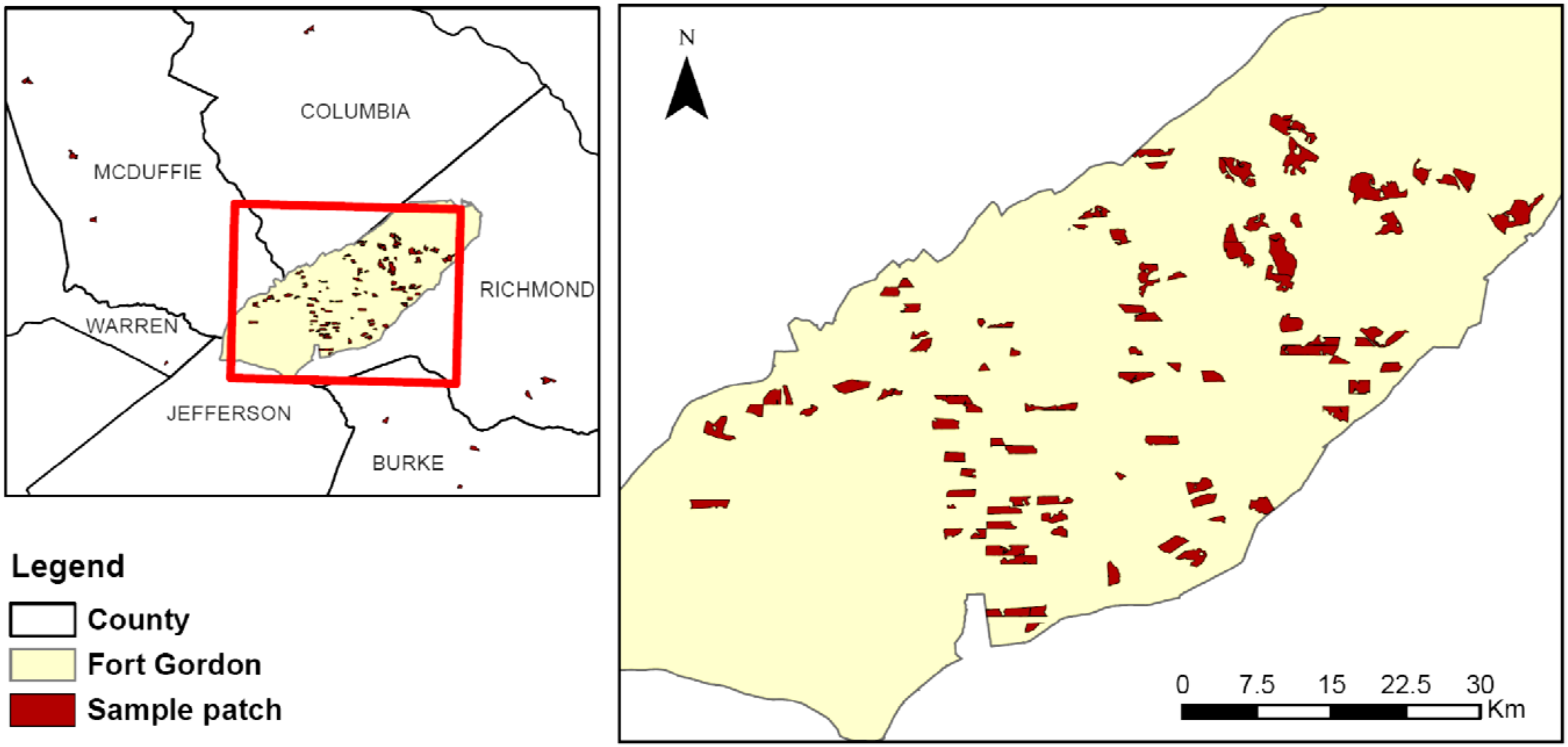


Figure 4.1. Map of study areas (central east Georgia) and locations of sample pine patches surveyed in 2011. Sample patches included both loblolly pine patches and longleaf pine patches. Of 99 sample patches, 11 patches were located outside of Fort Gordon (left map) and the rest of the patches were located in Fort Gordon (right map).

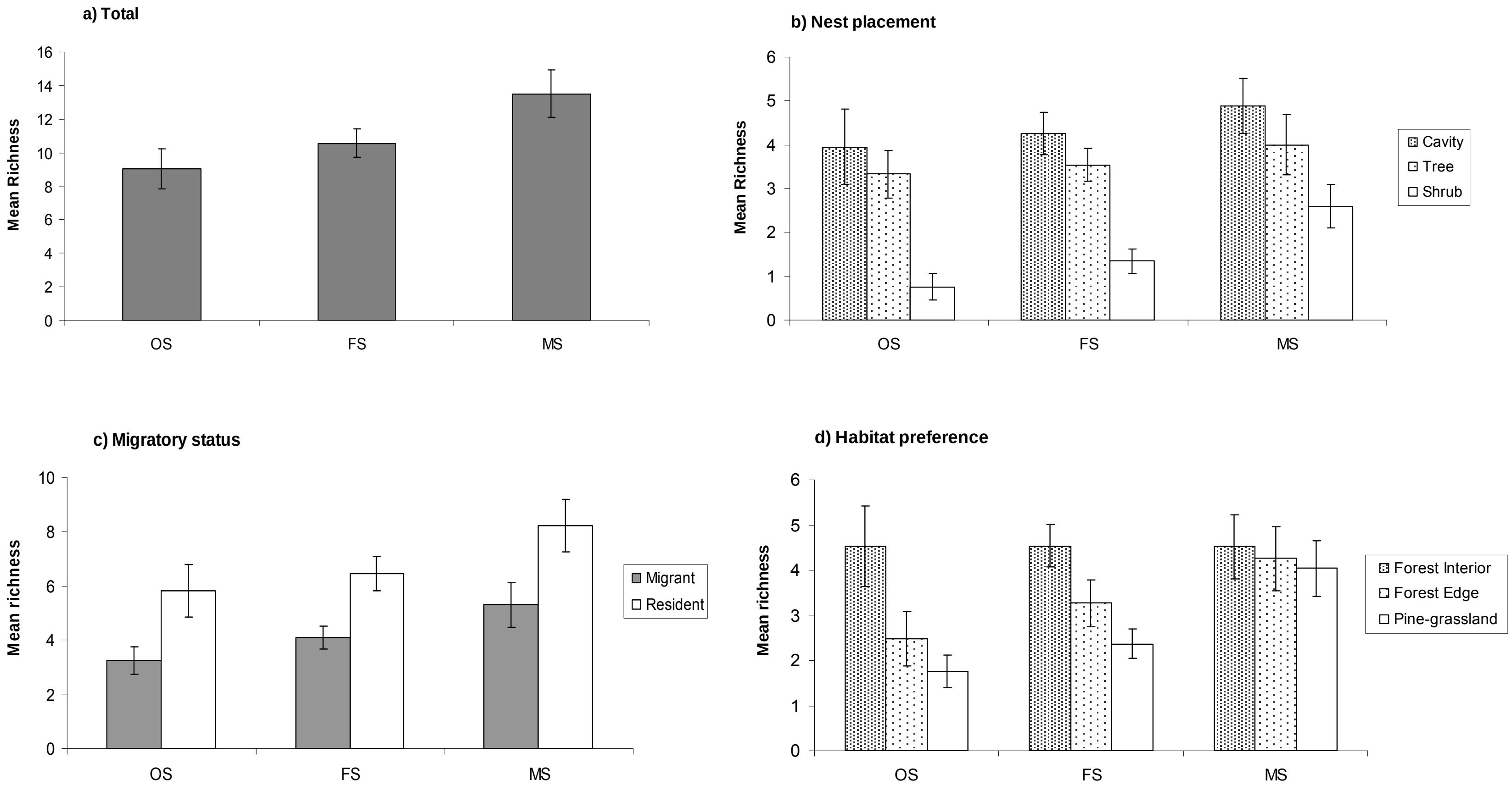


Figure 4.2. Relationship between basal area (BA) and (a) mean total richness (number of species) and (b-d) mean richness of each guild. Abbreviations: OS, overstocked (BA > 23m^2/ha, n=20); FS, fully/densely stocked (13.8 m^2/ha ≤ BA < 23m^2/ha, n=52); MS, moderately stocked (2.3m^2/ha ≤ BA < 13.8m^2/ha, n=27). Bars represent 95% CI. Note that non-overlap of 95% CI between MS and OS in total richness and richness of most guilds.

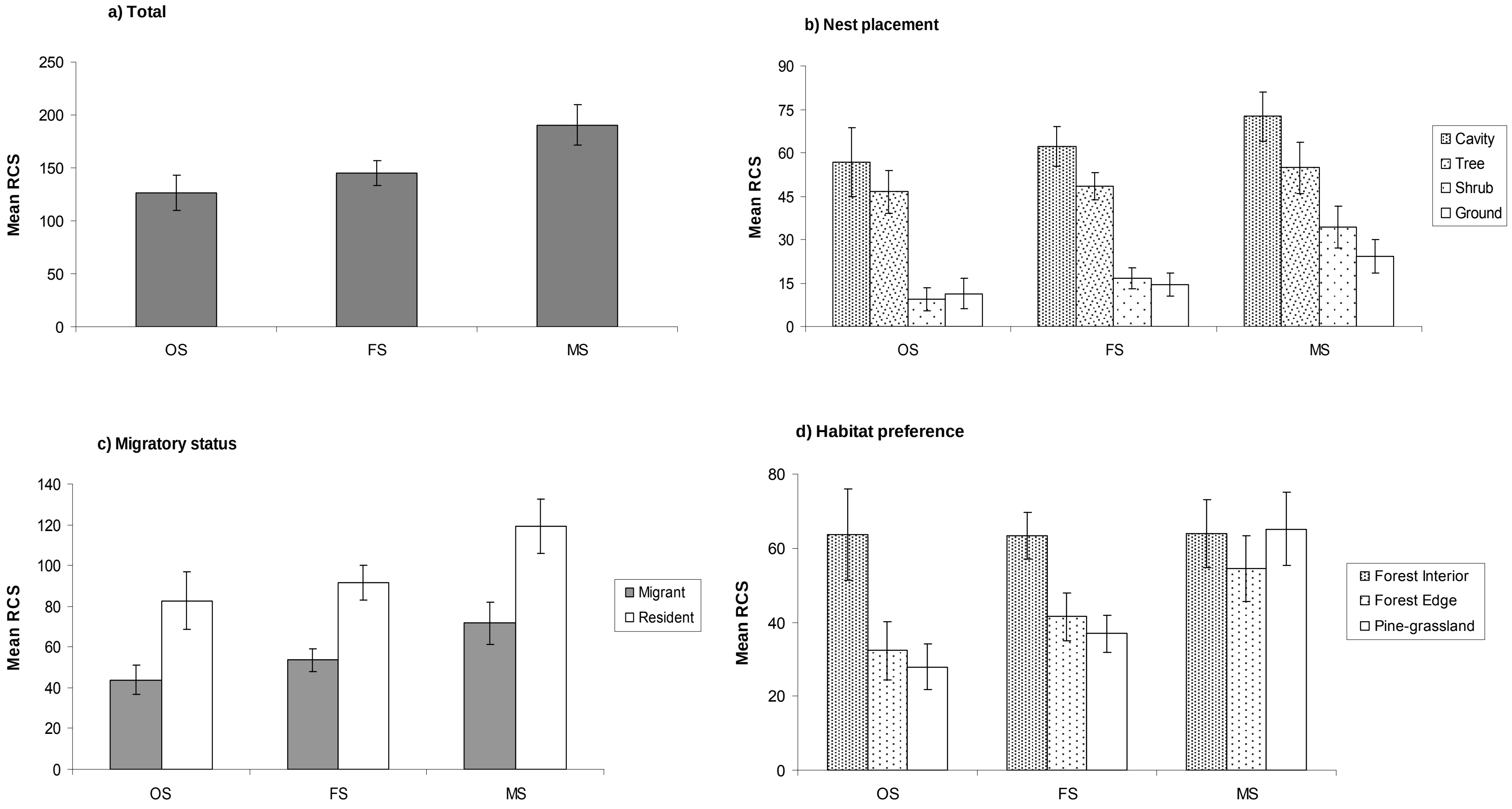


Figure 4.3. Relationship between basal area (BA) and mean total RCS (Regional Combined Score from Partners in Flight) and mean RCS of each guild. Abbreviations: OS, overstocked (BA > 23m^2/ha, n=20); FS, fully/densely stocked (13.8 m^2/ha ≤ BA < 23m^2/ha, n=52; MS, moderately stocked (2.3m^2/ha ≤ BA < 13.8m^2/ha, n=27). Bars represent 95% CI. Note that non-overlap of 95% CI between MS and OS in total RCS and RCS of most guilds.

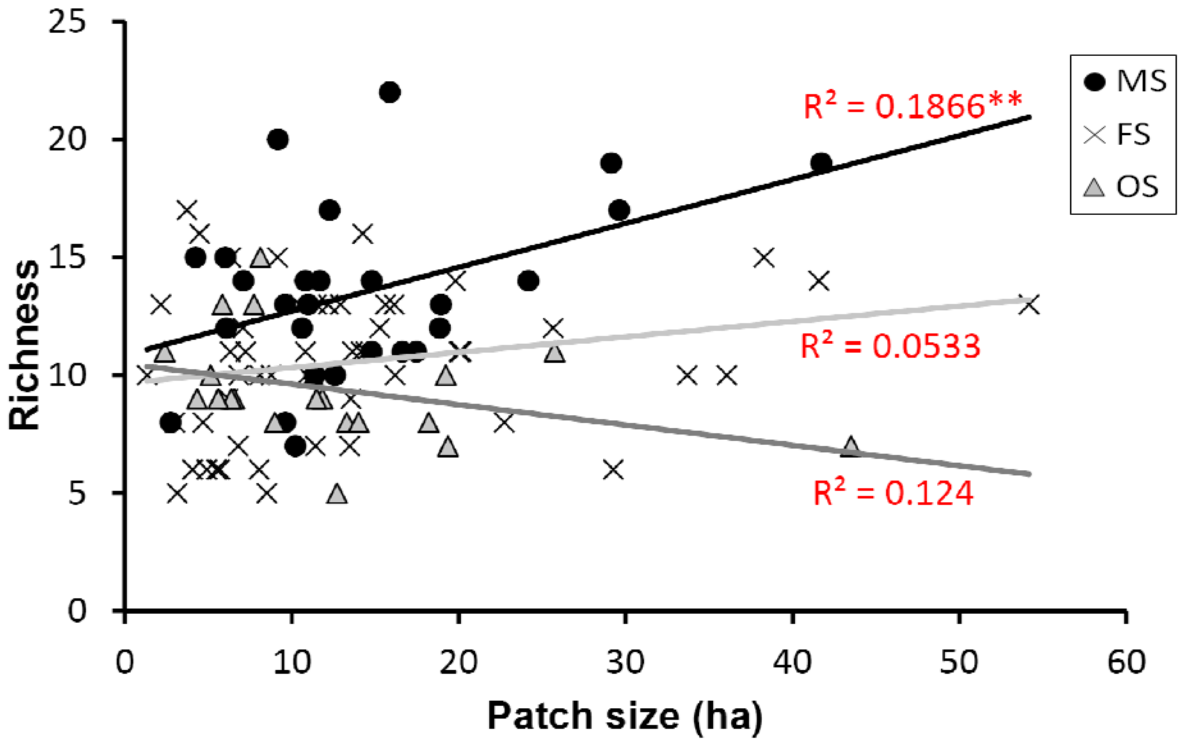
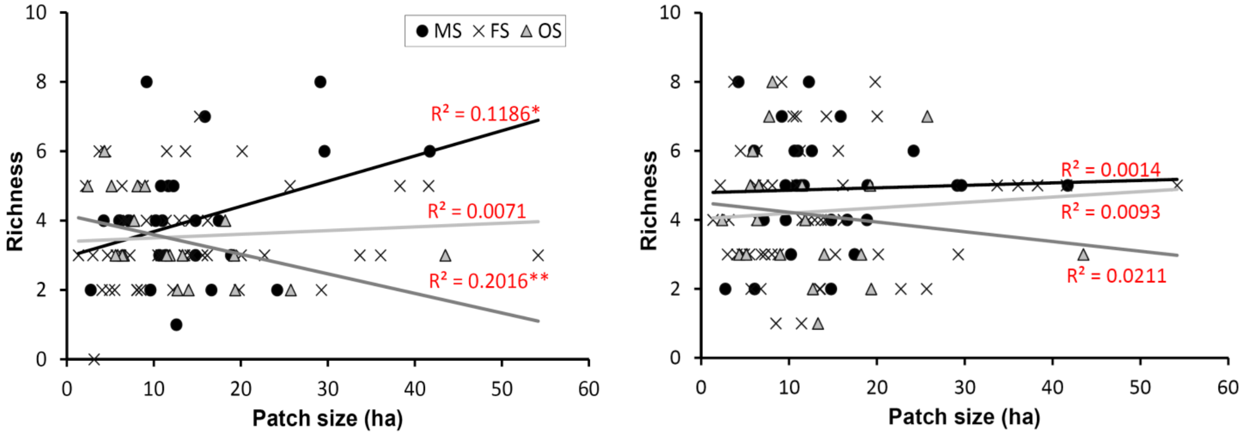
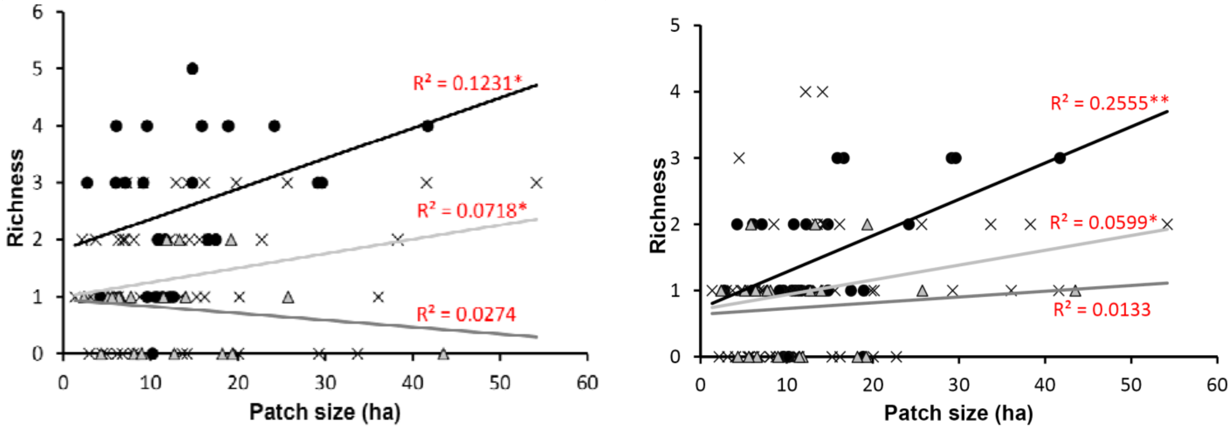


Figure 4.4. Regression plot of total richness (number of species) with patch size at each of 3 basal area classes. Abbreviations: OS, overstocked (BA > 23m^2/ha, n=20); FS, fully/densely stocked (13.8 m^2/ha ≤ BA < 23m^2/ha, n=52; MS, moderately stocked (2.3m^2/ha ≤ BA < 13.8m^2/ha, n=27). ** denotes *P* < 0.05.



a) Tree

b) Cavity

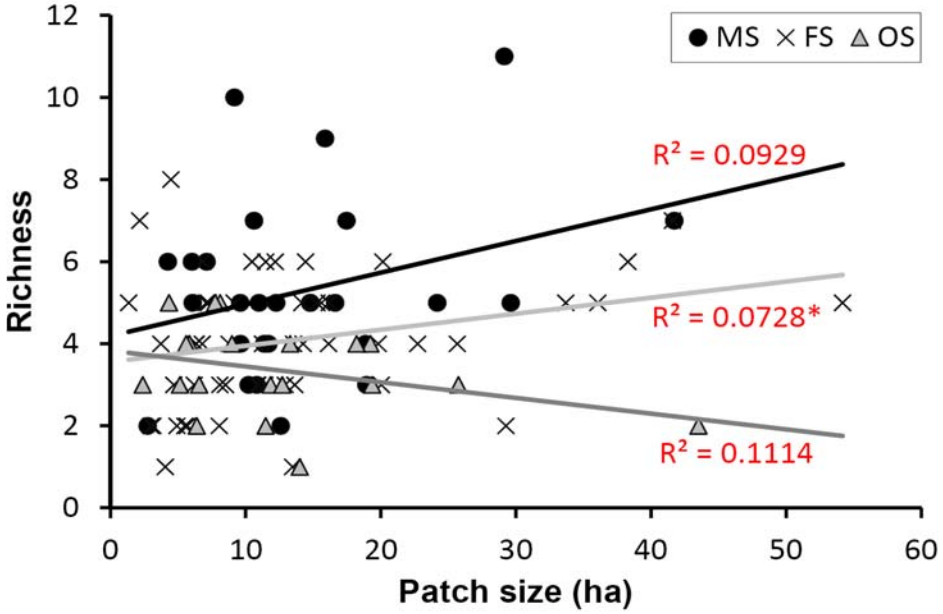


c) Shrub

d) Ground

Figure 4.5. Regression plot of richness (number of species) of 4 guilds (a, Tree; b, Cavity; c, Shrub; d, Ground) based on nest placement with patch size at each of 3 basal area classes. Abbreviations: OS, overstocked (BA > 23m^2/ha, n=20); FS, fully/densely stocked ($13.8 \text{ m}^2/\text{ha} \leq$ BA < 23m^2/ha, n=52; MS, moderately stocked ($2.3\text{m}^2/\text{ha} \leq \text{BA} < 13.8\text{m}^2$/ha, n=27). * denotes *P* < 0.1; **, 0.05 < *P*.

a) Migrant



b) Resident

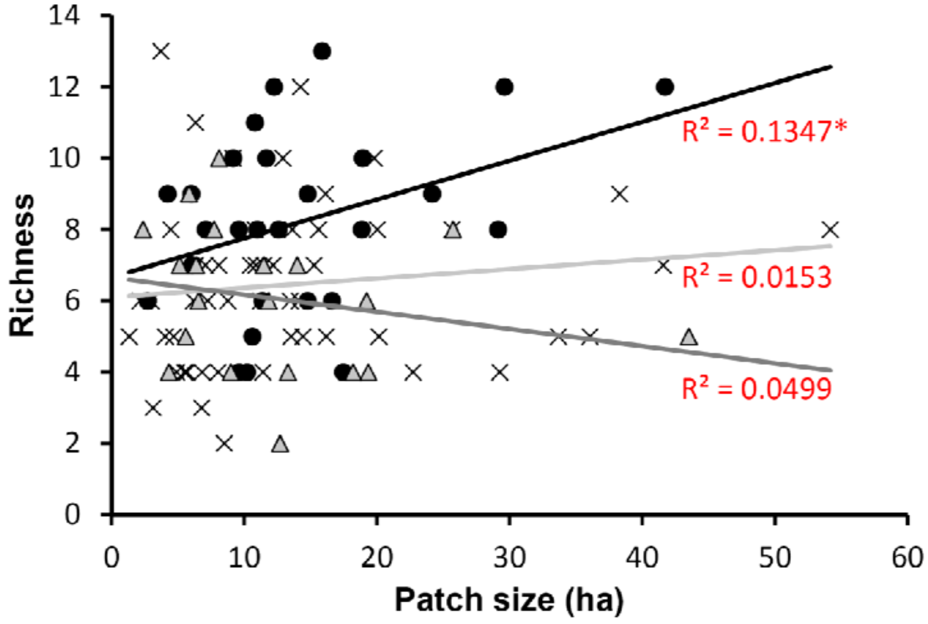
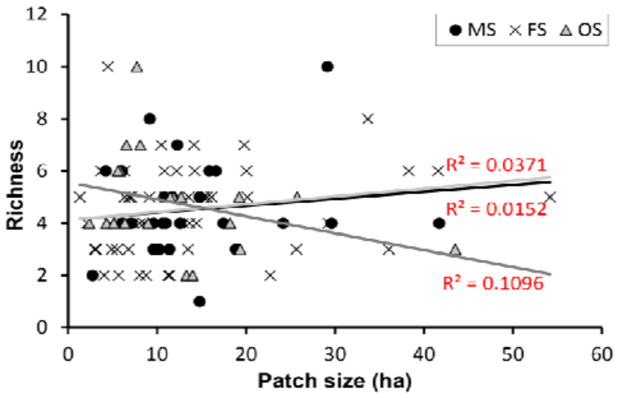
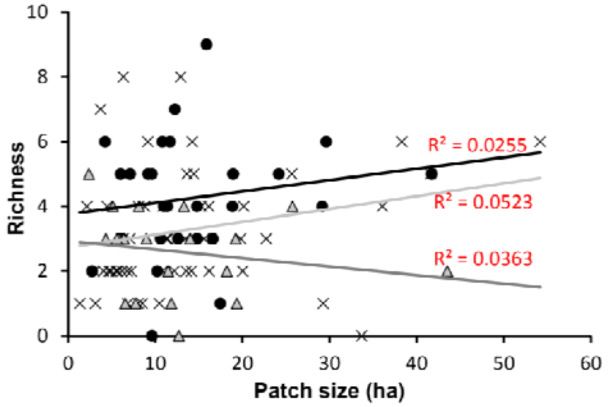


Figure 4.6. Regression plot of richness (number of species) of 2 guilds (a, Migrant; b, Resident) based on migratory status with patch size at each of 3 basal area classes. Abbreviations: OS, overstocked (BA > 23m^2/ha, n=20); FS, fully/densely stocked (13.8 m^2/ha ≤ BA < 23m^2/ha, n=52; MS, moderately stocked (2.3m^2/ha ≤ BA < 13.8m^2/ha, n=27). * denotes $P < 0.05$.

a) Forest interior



b) Forest edge



c) Pine-grassland

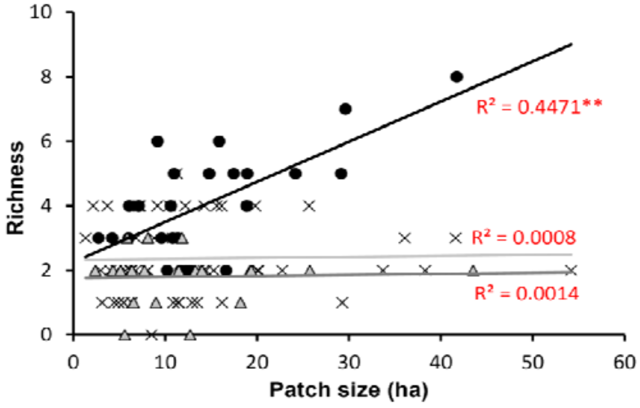


Figure 4.7. Regression plot of richness (number of species) of 3 guilds (a, Forest interior; b, Forest edge; c, Pine-grassland) based on nest placement with patch size at each of 3 basal area classes. Abbreviations: OS, overstocked (BA > 23m^2/ha, n=20); FS, fully/densely stocked (13.8 m^2/ha ≤ BA < 23m^2/ha, n=52; MS, moderately stocked (2.3m^2/ha ≤ BA < 13.8m^2/ha, n=27). ** denotes $P < 0.05$.

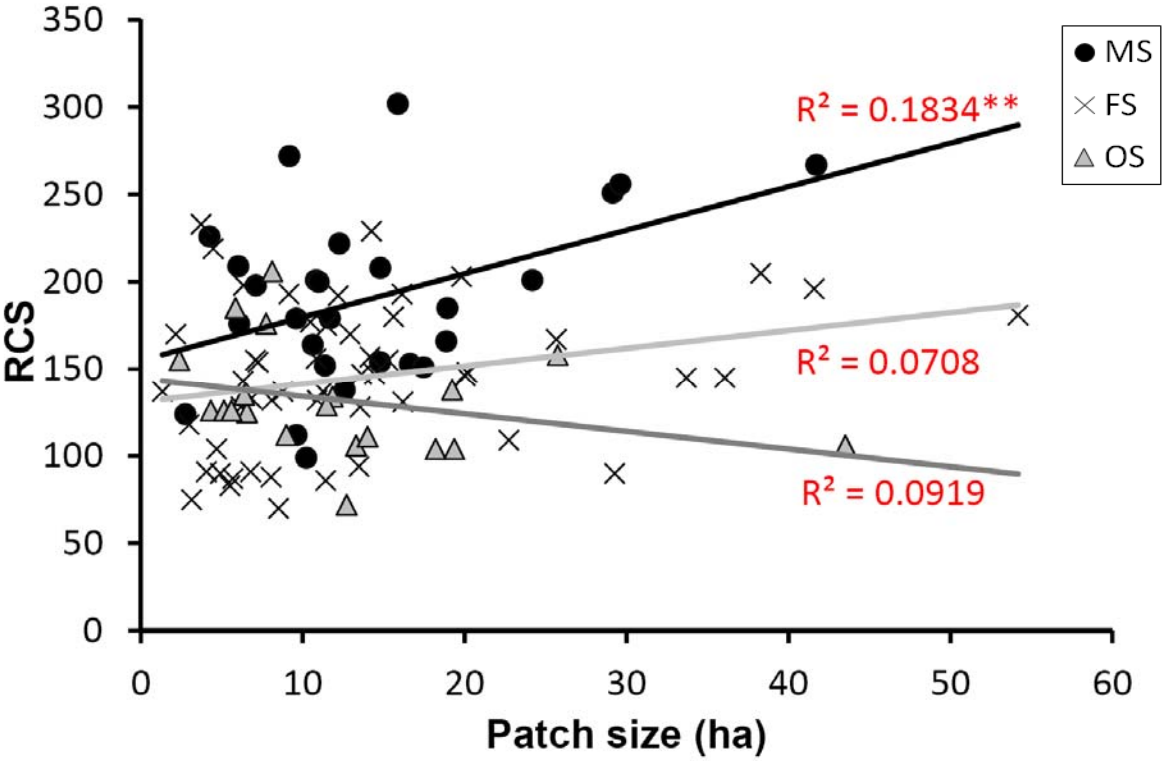
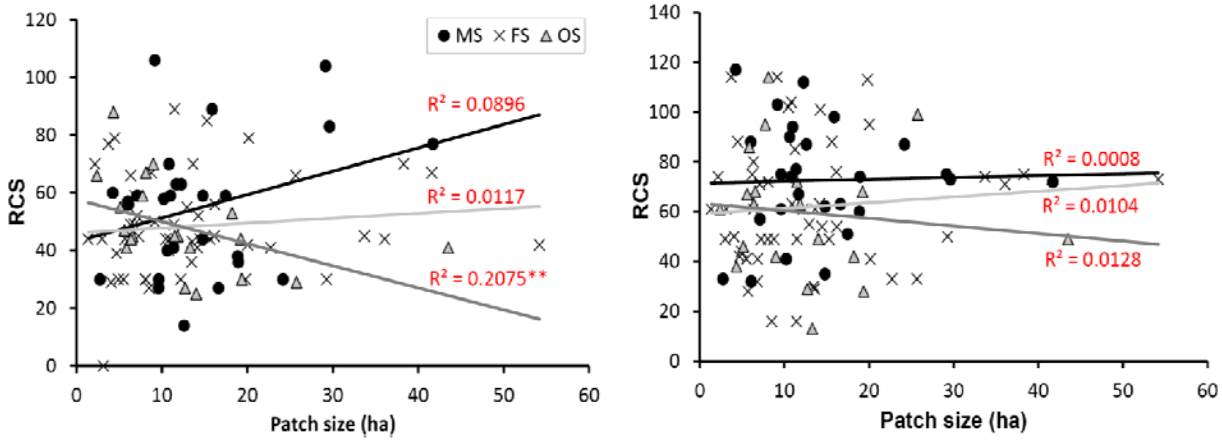


Figure 4.8. Regression plot of total RCS (Regional Combined Score from Partners in Flight) of all species with patch size at each of 3 basal area classes. Abbreviations: OS, overstocked (BA > 23m^2/ha, n=20); FS, fully/densely stocked (13.8 m^2/ha ≤ BA < 23m^2/ha, n=52; MS, moderately stocked (2.3m^2/ha ≤ BA < 13.8m^2/ha, n=27). ** denotes $P < 0.05$.

a) Tree b) Cavity



c) Shrub d) Ground

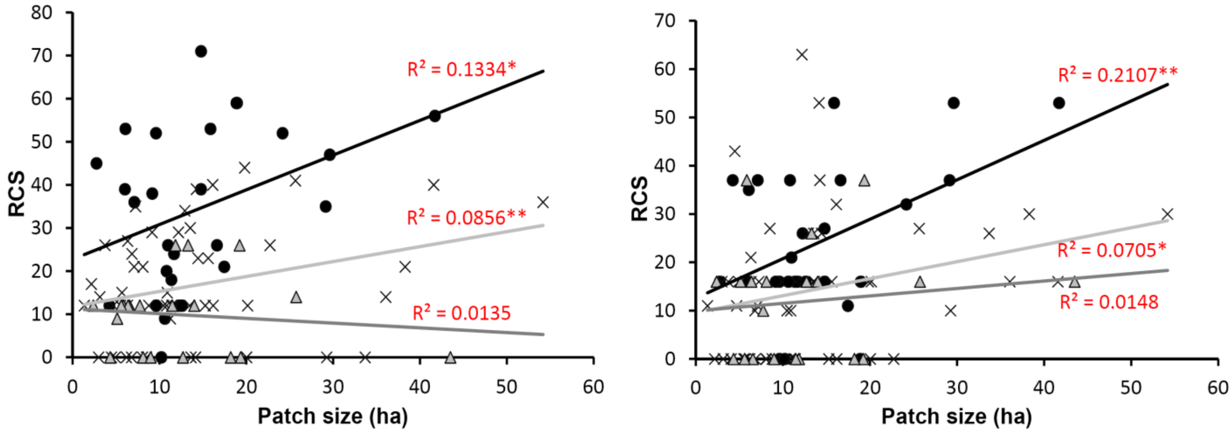
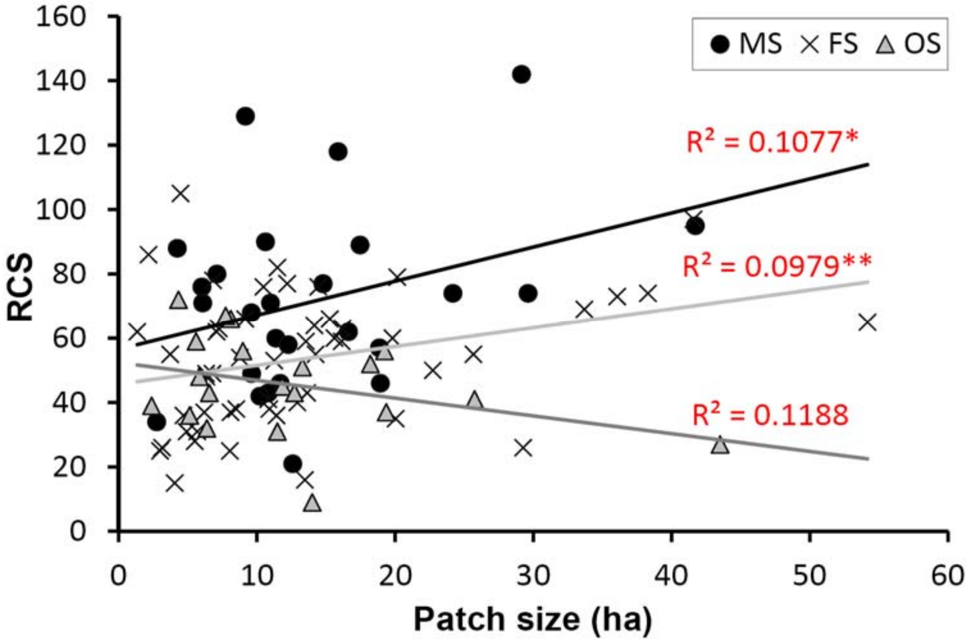


Figure 4.9. Regression plot of RCS (Regional Combined Score from Partners in Flight) of 4 guilds (a, Tree; b, Cavity; c, Shrub; d, Ground) based on nest placement with patch size at each of 3 basal area classes. Abbreviations: OS, overstocked (BA > 23m^2/ha, n=20); FS, fully/densely stocked (13.8 m^2/ha ≤ BA < 23m^2/ha, n=52; MS, moderately stocked (2.3m^2/ha ≤ BA < 13.8m^2/ha, n=27). * denotes $P < 0.1$; **, $P < 0.05$.

a) Migrant



b) Resident

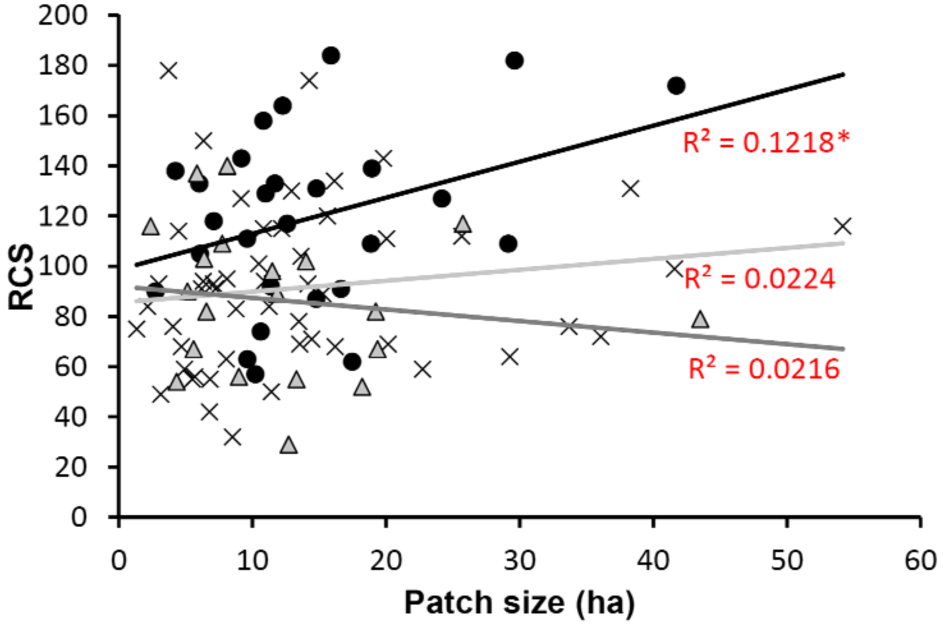
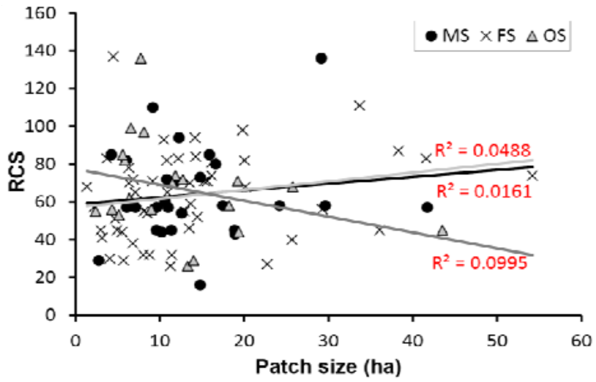
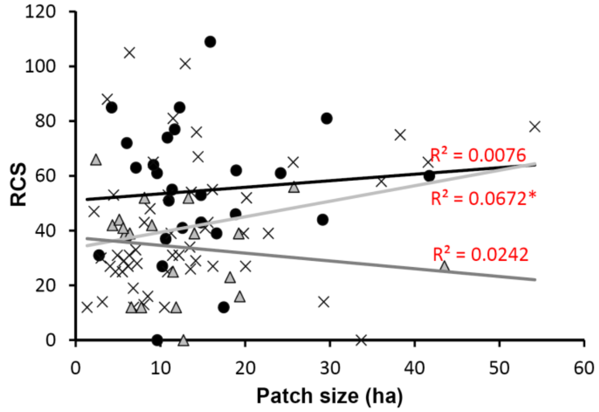


Figure 4.10. Regression plot of RCS (Regional Combined Score from Partners in Flight) of 2 guilds (a, Migrant; b, Resident) based on migratory status with patch size at each of 3 basal area classes. Abbreviations: OS, overstocked (BA > $23 m^2/ha$, n=20); FS, fully/densely stocked ($13.8 m^2/ha \leq BA < 23 m^2/ha$, n=52; MS, moderately stocked ($2.3 m^2/ha \leq BA < 13.8 m^2/ha$, n=27).
* denotes $P < 0.1$; **, $P < 0.05$.

a) Forest interior



b) Forest edge



c) Pine-grassland

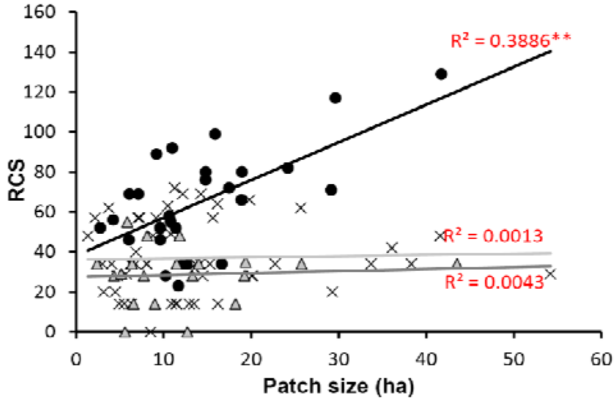


Figure 4.11. Regression plot of RCS (Regional Combined Score from Partners in Flight) of 3 guilds (a, Forest interior; b, Forest edge; c, Pine-grassland) based on nest placement with patch size at each of 3 basal area classes. Abbreviations: OS, overstocked (BA > 23m^2/ha, n=20); FS, fully/densely stocked ($13.8\ \text{m}^2$/ha ≤ BA < 23m^2/ha, n=52; MS, moderately stocked (2.3m^2/ha ≤ BA < 13.8m^2/ha, n=27). * denotes $P < 0.1$; **, $P < 0.05$.

CHAPTER 5

SUMMARY AND CONCLUSION

With rapid expansion of urban development, it is expected that fragmentation and loss of southern forests which are already highly modified by timber harvest and agricultural land uses will be accelerated (Wear and Gries 2011). Biodiversity loss is expected to continue. In this situation, forest management plans relying on natural habitats at wildland may not guarantee long-term biodiversity conservation. We need to develop other types of management plans, considering the availability of semi-natural habitats such as planted pine forests and other forest remnants in a matrix of urban development and/or agricultural lands. Planted pine forests managed for timberland often form large tracks of pine forest, containing more interior patches embedded in forest matrix. If they are managed properly, they can play an important role in biodiversity conservation (e.g., Melchiors 1991). However, even a matrix surrounding some planted pine forests is currently changing due to urbanization, adding another component to the landscape where agriculture is a dominant form of human land-use other than the timberland. Planted pine forests for non-timber and natural pine forest remnants are also experiencing development pressures. Pine forests are increasingly interfaced with urban areas or both urban and agricultural lands. Therefore, for sound management plans for biodiversity conservation, it is critical to understand how the matrix of urban development and/or agricultural lands influences biodiversity-habitat relationship and to identify important habitat characteristics, which requires exploring landscape-level characteristics as well as local or patch level characteristics.

By considering habitat characteristics at both scales, our study demonstrated importance of landscape-level habitat characteristics, potential role of pine patches in a matrix of urban development and/agricultural lands to improve avian biodiversity, and significance of habitat heterogeneity for biodiversity conservation. Occupancy of more species was associated with habitat characteristics at landscape scale. Among the characteristics, percent cover of the two dominant human land-uses, especially of agricultural land-uses strongly influenced species occupancy. Species tended to positively respond to the human land-use. In particular, pine patches in low level of a mixture of urban development and agricultural land-uses (sum of percent cover of urban development and agriculture within a 1 km circular landscape is 5-20%) and in low level of agricultural land-uses (percent cover of agriculture land is 5-20%) showed greater species richness, whereas richness was lowest at patches in wildland than any other levels of urban development and agricultural land use. Our results suggested that the pattern was associated with variation in vegetation structure, structural diversity within a patch. Patterns may also relate to other types of potential habitats or resources (e.g., open space, planted vegetation, water, etc) created by the human land-use. In a landscape where human land-use is very low (i.e., wildland) and pine forest is a dominant component, structural diversity determined by basal area was a significant factor affecting richness: richness was high at moderate or low level of basal area (2.3-13.8 m^2/ha), but low at high level of basal area (> 23m^2/ha). Level of basal area also influenced effect of patch sizes on species richness. While patch size effect was insignificant when basal area was high, richness tended to increase with patch size when basal area was moderate or low level. Large sized patch (presumably >10 ha) with moderate or low level of basal area was appropriate for promoting avian biodiversity in pine forests. However, some of our results demonstrated that species responses to spatial scale, urban development and agricultural land-uses, and other habitat characteristics could vary depending on species and ecological or functional guild of the species, particularly, guild types based on habitat preference (forest interior, forest edge, and pine-grassland). For example, while landscape scale habitat characteristics were better to explain the variations in occupancy of forest interior species (and forest edge species), local scale habitat characteristics were more important to pine-grassland species. Pine-grassland species were also more dominant at wildland and agricultural matrix where there are open-pine forests. They strongly responded level of basal area and patch size. This suggests that we need to have a clear objective of forest management, whether the objective is to improve biodiversity of a specific group of species (e.g., forest interiors, pine-grassland species, or migrant) or to improve total biodiversity of avian species. If the goal of forest management is to conserve forest interior species, the management needs to focus on landscape scale characteristics. If the goal is the conservation of pine-grassland species, management needs to focus on local (or patch) scale characteristics, particularly, maintaining basal area of pine patches to moderate or low level and preserving large patches. If management aims to increase total avian biodiversity, habitat characteristics at both local and landscape scale should be considered.

Overall, our study firstly suggests that pine patches in wildland landscapes (i.e., Fort Gordon) are crucial habitats for conservation-related species which are mostly pine-grassland species; however, current condition of pine patches at wildland is not sufficient to conserve total avian biodiversity. We need to develop management plans to enhance avian biodiversity in wildland landscapes in this region. Plans should focus on increasing habitat heterogeneity more than current level both at patch and landscape scale. Reduction of basal area is required to improve habitat quality, increasing vegetation structural diversity within a patch. Creation of low disturbance such as small open space and diversification of age structure of pine patches can increase habitat diversity at landscape scale. Secondly, more importantly, our study suggests that pine patches in urban development and/or agricultural lands can contribute enhancing avian biodiversity. It is a traditional view of ecologists to consider remnant habitats in urban matrix and agricultural matrix unsuitable because of negative impacts of the human land-uses on biodiversity. As urbanization continues unabated, it becomes one of the most major threats to biodiversity loss worldwide (e.g., Czech et al. 2000; Ricketts and Imhoff 2003), some ecologists recently start to recognize the limitation of depending on wild habitats for biodiversity conservation and pay attention to potential positive effects of the human land-uses on biodiversity. They begin to consider remnant habitats in urban or urban itself (or urban ecosystem) not only a threat but also another type of habitats or new opportunity we can use for conservation (e.g., Marzluff and Rodewald 2008; Faeth et al. 2011). Our study supports this view. Pine patches in urban matrix (and agricultural matrix) can be valuable habitats. They may play a key role for future biodiversity conservation, depending on how we manage them. As a matter of fact, improvement of quality of habitat in urban matrix can also enhance sustainability of development by providing diverse ecosystem services. For example, if we remove invasive plant species (e.g., English Ivy, *Hedera helix*) in pine patches in urban matrix and increase grass ground cover with some reduction of shrub cover, the pine patches become open (or at least semi-open) forests. This forest can attract pine-grassland species and other animals and thus increase biodiversity. It is also a forest type which was historically prevalent in southern regions. It can be a powerful tool for education. Moreover, the forest can improve an aesthetic value of the city and provide recreational activities such as bird watching, photographing, and natural walk. However, managing pine patches in urban and/or agricultural matrix will be challenging because land ownership tends to be in small parcels, with many stakeholders such as land owners or homeowners, land managers, developers, planners, and policy makers. We need to educate and convince them that enhancement of biodiversity in the landscape increases sustainability of development and human well-being. State and Federal policy mechanisms such as "tax incentives, subsidies and cost-share programs, conservation easements, fee-simple purchases, tradable development rights, and regulations restricting land use" may encourage land owners' participation (Notman et al. 2006). We should also provide guidelines about how their lands can be managed for biodiversity conservation. However, one of the most effective practices managing pine forests, prescribed fire is almost impossible to apply in urbanized areas (especially densely populated areas) and adjacent to the areas. We need to develop other types of practices which can surrogate prescribed fire and other methods that cannot be implanted in the areas.

Although we emphasize the potential positive role of pine patches in anthropogenic landscape for biodiversity conservation, there is a need of further studies to verify the role and to promote a sound conservation management plan. Firstly, we need to examine avian demographics along an urban-rural/agriculture-wildland gradient. Our study focused on richness as an indicator of biodiversity and of habitat quality. However, higher richness does not always mean that the habitat is suitable. In spite of relatively higher richness, it is possible that the habitats in high or moderate urban and agricultural matrix may function as ecological traps, as opposed to supplementary habitats, which could jeopardize long term persistence of the species (e.g., Purcell and Verner 1998; Boal and Mannan 1999; Robertson and Hutto 2006). It is important to know annual productivity and survival of avian species in the matrix before we make any final management plan. A study estimating demographic parameters such as annual productivity rate and survival rate of avian species can clarify the possibility, help re-evaluating the value of the habitats, and develop more proper management plans. Secondly, the habitat characteristics associated with positive or negative responses of birds in the matrix should be thoroughly and clearly identified. We could determine important habitat characteristics within a patch and we could indirectly understand a mechanism behind the pattern (richness) using the characteristics. However, we did not directly investigate what characteristics of urban or agricultural matrix and how they affected species richness. Future research, combined with demographic studies, needs to focus on mechanism-oriented understanding by identifying the characteristics.

Thirdly, we should explore the relationship between spatial configuration of landscape features (urban development, agricultural lands, and other land covers) and avian biodiversity. Increasing human land-uses causes reduction in amount of habitats available in a landscape. As available habitats declines, configuration of landscape elements becomes a major landscape feature affecting species distribution and persistence (e.g., Fahrig 1998; Flather and Bevers 20002). We could not incorporate configurations of landscape elements due to relatively small sample size. Given that our study region is experiencing not only centralized urbanization but also suburban and exurban type of urbanization, habitat fragmentation as well as habitat loss is increasing. In this landscape, a study incorporating configuration features can provide better information in understanding avian species response to human land-uses, improving habitat connectivity, and determining an optimum land mosaic that enhance biodiversity and sustainability of development. For doing so, we may need to consider larger landscape scales than the scale used in our study (a 1 km circular landscape) if there are significant variations in landscape features with increasing landscape size. Lastly, for future forest management plans, we stress a need of considering establishment of a habitat network by increasing connectivity between remnant patches in urban or agricultural matrix and patches at wildland. “Connectivity,” whether it is called ecological, habitat, or landscape connectivity, is known to be one of crucial factors influencing species persistence in fragmented habitats and its importance is emphasized in numerous conservational studies and managements (e.g., Taylor et al. 1993; Forman 1995;Bennett 2003;Lindenmayer and Fischer 2006; Kindlmann and Burel 2008). As discussed previously (in Chapter 3), we can consider first increasing connectivity between patches in low level of human land-uses (especially agricultural lands) close to wildlands and those at wildlands and then expand the connectivity to patches in other levels of human land-uses. In the network, we may manage pine patches at wildland as primary habitats for conservation-related species and species sensitive to human disturbances, and pine patches in urban and agricultural matrix as secondary or supplementary habitats for the species and as primary habitats for other species.

In conclusion, we acknowledge the limitation of conserving biodiversity by relying on habitats at wildlands and the potential values of habitats in urban and/or agricultural matrix for future conservation. Also, to minimize biodiversity loss and promote future species persistence and biodiversity in fragmented landscapes, we recommend forest managements combining local or patch-level managements (e.g., maintaining structural diversity within a patch and preserving or increasing patch size) with landscape-level managements (e.g., creating different successional habitats and improving connectivity).

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Appendix A

Reclassification of land cover used in digitization

Class	Description (NLCD land cover code)
Pine Forest	Forest covered by > 75% pine trees (17)
Hardwood Forest	Forest covered by > 75% hardwoods (18)
Mixed Forest	Forest where neither hardwood nor pine species are > 75% of total tree cover (19)
Shrub Vegetation	True shrubs and young trees in an early successional stage (16)
Agriculture	Crop field and hay/pasture (9, 10)
Urban Development	Residential and commercial/industrial areas, areas with > 30% impervious surface, railroad, and roads (1-5, 7, 12)
Open Area	Park/golf/recreational areas, power line, any grass/herbaceous vegetation, and semi-open areas (6, 8, 11, 13)
Open Water	Ponds, lakes, streams (15)
Disturbed Areas	Quarry/mine and barren lands. Also, some of intensive military training areas in Ft. Gordon (14)

Appendix B
List of bird species detected during 2010-2011

COMMON NAME	SCIENTIFC NAME	SPECIES (Alpha code)	RCS[1]	HABITAT PREFERENCE[2]	NEST PLACEMENT[3]	MIGRATORY STATUS[3]
Acadian Flycatcher	*Empidonax virescens*	ACFL	15	Forest Interior	Tree	Migrant
American Crow	*Corvus brachyrhynchos*	AMCR	11	Forest Edge	Tree	Resident
American Goldfinch	*Spinus tristis*	AMGO	8	Forest Edge	Shrub	Resident
American Kestrel	*Spinus tristis*	AMKE	13	Forest Edge	Cavity	Resident
American Redstart	*Setophaga ruticilla*	AMRE	11	Forest Interior	Tree	Migrant
American Robin	*Turdus migratorius*	AMRO	6	Forest Edge	Tree	Resident
Bachman's Sparrow	*Aimophila aestivalis*	BACS	21	Pine-grassland	Ground	Resident
Barn Swallow	*Hirundo rustica*	BARS	9	Others	Others	Migrant
Black-and-white Warbler	*Mniotilta varia*	BAWW	11	Forest Interior	Ground	Migrant
Blue-gray Gnatcatcher	*Polioptila caerulea*	BGGN	11	Forest Edge	Tree	Migrant
Brown-headed Cowbird	*Molothrus ater*	BHCO	8	Forest Edge	Tree	Resident
Brown-headed Nuthatch	*Sitta pusilla*	BHNU	20	Pine-grassland	Cavity	Resident
Blue Grosbeak	*Passerina caerulea*	BLGR	12	Pine-grassland	Shrub	Migrant
Blue Jay	*Cyanocitta cristata*	BLJA	14	Forest Edge	Tree	Resident
Brown Thrasher	*Toxostoma rufum*	BRTH	15	Forest Edge	Shrub	Resident
Carolina Chickadee	*Poecile carolinensis*	CACH	16	Forest Interior	Cavity	Resident
Carolina Wren	*Thryothorus ludovicianus*	CARW	13	Forest Edge	Cavity	Resident
Chipping Sparrow	*Spizella passerina*	CHSP	9	Pine-grassland	Shrub	Migrant
Common Grackle	*Quiscalus quiscula*	COGR	11	Forest Edge	Tree	Resident
Common Nighthawk	*Chordeiles minor*	CONI	13	Others	Ground	Migrant
Chuck-will's-widow	*Caprimulgus carolinensis*	CWWI	16	Forest Edge	Ground	Migrant

COMMON NAME	**SCIENTIFC NAME**	**SPECIES (Alpha code)**	**RCS**[1]	**HABITAT PREFERENCE**[2]	**NEST PLACEMENT**[3]	**MIGRATORY STATUS**[3]
Downy Woodpecker	*Picoides pubescens*	DOWO	14	Forest Interior	Cavity	Resident
Eastern Bluebird	*Sialia sialis*	EABL	11	Forest edge	Cavity	Resident
Eastern Kingbird	*Tyrannus tyrannus*	EAKI	15	Pine-grassland	Tree	Migrant
Eastern Phoebe	*Sayornis phoebe*	EAPH	9	Forest Edge	Others	Resident
Eastern Towhee	*Pipilo erythrophthalmus*	EATO	16	Forest Edge	Ground	Resident
Eastern Wood-Pewee	*Contopus virens*	EAWP	14	Pine-grassland	Tree	Migrant
Fish Crow[1]	*Corvus ossifragus*	FICR	14	Forest Edge	Tree	Resident
Great Crested Flycatcher	*Myiarchus crinitus*	GCFL	12	Forest Interior	Cavity	Migrant
Gray Catbird	*Dumetella carolinensis*	GRCA	11	Forest edge	Shrub	Migrant
Hairy Woodpecker	*Picoides villosus*	HAWO	13	Forest Interior	Cavity	Resident
Hooded Warbler	*Wilsonia citrina*	HOWA	14	Forest Interior	Shrub	Migrant
Indigo Bunting	*Passerina cyanea*	INBU	14	Pine-grassland	Shrub	Migrant
Kentucky Warbler	*Oporornis formosus*	KEWA	16	Forest Interior	Ground	Migrant
Mourning Dove	*Zenaida macroura*	MODO	11	Forest Edge	Tree	Resident
Northern Bobwhite	*Colinus virginianus*	NOBO	16	Pine-grassland	Ground	Resident
Northern Cardinal	*Cardinalis cardinalis*	NOCA	12	Forest Edge	Shrub	Resident
Northern Flicker	*Colaptes auratus*	NOFL	15	Forest Edge	Cavity	Migrant
Northern Mockingbird	*Mimus polyglottos*	NOMO	12	Others	Shrub	Resident
Northern Parula	*Parula americana*	NOPA	15	Forest Interior	Tree	Migrant
Orchard Oriole	*Icterus spurius*	OROR	16	Forest Edge	Tree	Migrant
Ovenbird	*Seiurus aurocapilla*	OVEN	10	Forest Interior	Ground	Migrant
Pine Warbler	*Dendroica pinus*	PIWA	14	Pine-grassland	Tree	Resident
Pileated Woodpecker	*Dryocopus pileatus*	PIWO	14	Forest Interior	Cavity	Resident
Prairie Warbler	*Dendroica discolor*	PRAW	18	Pine-grassland	Shrub	Migrant
Purple Martin	*Progne subis*	PUMA	14	Forest Edge	Cavity	Migrant

COMMON NAME	SCIENTIFC NAME	SPECIES (Alpha code)	RCS[1]	HABITAT PREFERENCE[2]	NEST PLACEMENT[3]	MIGRATORY STATUS[3]
Red-bellied Woodpecker	*Melanerpes carolinus*	RBWO	13	Forest Interior	Cavity	Resident
Red-cockaded Woodpecker	*Picoides borealis*	RCWO	23	Pine-grassland	Cavity	Resident
Red-eyed Vireo	*Vireo olivaceus*	REVI	11	Forest Interior	Tree	Migrant
Red-headed Woodpecker	*Melanerpes erythrocephalus*	RHWO	15	Pine-grassland	Cavity	Migrant
Red-shouldered Hawk	*Buteo lineatus*	RSHA	12	Forest Edge	Tree	Resident
Red-tailed Hawk	*Buteo jamaicensis*	RTHA	9	Forest Edge	Tree	Resident
Ruby-throated Hummingbird	*Archilochus colubris*	RTHU	12	Forest Edge	Tree	Migrant
Summer Tanager	*Piranga rubra*	SUTA	16	Forest Interior	Tree	Migrant
Tufted Titmouse	*Baeolophus bicolor*	TUTI	13	Forest Interior	Cavity	Resident
White-eyed Vireo	*Vireo griseus*	WEVI	14	Forest Edge	Shrub	Migrant
Worm-eating Warbler	*Helmitheros vermivorum*	WEWA	14	Forest Interior	Ground	Migrant
Wild Turkey	*Meleagris gallopavo*	WITU	11	Forest Edge	Ground	Resident
Wood Thrush	*Hylocichla mustelina*	WOTH	15	Forest Interior	Tree	Migrant
Yellow-billed Cuckoo	*Coccyzus americanus*	YBCU	15	Forest Interior	Tree	Migrant
Yellow-breasted Chat	*Icteria virens*	YBCH	13	Forest Edge	Shrub	Migrant
Yellow-throated Vireo	*Vireo flavifrons*	YTVI	15	Forest Edge	Tree	Migrant
Yellow Warbler	*Dendroica petechia*	YWAR	9	Forest Edge	Shrub	Migrant

[1] Regional combined score for the breeding season (RCS-b) from Partners in Flight.

[2] Wilson et al. 1995

[3] Ehrlich et al. 1988; Harmel 1992