THE RELATIONSHIP BETWEEN BREEDING BIRD COMMUNITY STRUCTURE IN URBAN FOREST PATCHES AND THE HUMAN-MEDIATED RESOURCES IN THE SURROUNDING RESIDENTIAL MATRIX

by

CHRISSA ERIN CARLSON

(Under the Direction of Gary W. Barrett)

ABSTRACT

Urban forest patches function as habitat fragments within a landscape matrix dominated by human development. Features of both the forest patch itself and the surrounding landscape matrix influence avian habitat selection. In residential areas, the resource-base available to forest birds is augmented by the decisions of individual homeowners. Breeding bird communities in 15 small forest patches (2-8 ha) in Baltimore, Maryland were surveyed during the 2005 breeding season. An information-theoretic approach was used to select models that explain avian diversity in these patches, including variables describing forest patch characteristics, land-cover in the surrounding neighborhoods, and the availability of feeders, baths, and nest boxes provided by neighborhood residents. Abundant tree cover surrounding the forest patches increased the number of species selecting the forest patch as breeding habitat. This was observed within a narrow buffer from the forest edge, indicating that individual land-owners can manage their property to enhance adjacent forest habitats.

INDEX WORDS: urban ecology, birds, habitat fragmentation, landscape ecology

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DEDICATION

This thesis is dedicated to my entire family, which includes my biological relationships, as well as those non-genetic ties which have shaped me as a thinker, a scientist, and a human. My parents, Eugene and Berlyn Carlson, have provided me with boundless love and support through my every endeavor, and have never passed judgment on any learning experience that I chose, even those that did not fall on the path towards traditional models of success. Growing up with Erika Carlson-Hiles and Kevin Carlson has made me who I am today, and has kept me grounded in where I am from. And while not an exhaustive list, I must mention the names of a few of the friends that I have gathered about me over the years that have continually inspired me to challenge myself in the way I think about and create my place in the world. Some of these include: Cary Pirone, Chris Cummings, Laura Brams, Lisy Holloway, Sigalle Rosner, Jackie, Jim, Mark, and Taki Melonas, Brittan Hallar, Krista Jacobsen, Jason Mann, Jeffrey Stoike, Matt Bonds, Gretchen Heilman, Jessica Geoghegan, and Charlotte Swatek.

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Introduction and Literature Review

1.1 Urban Ecosystems and Landscape Ecology

As the world's human population continues to grow, an increasing proportion of the land is becoming urbanized (McDonnell and Pickett, 1990). However, the ecological structure and function of urban ecosystems remains poorly understood. Urbanization, defined here as the process by which areas of human habitation and commerce expand and transform the landscape, provides a unique setting in which to answer basic scientific questions regarding ecosystem change (McDonnell and Pickett, 1990), as well as opportunities to investigate the effects of anthropogenic landscape alteration on ecological processes.

Humans impact the ecology of cities by introducing exotic species, altering the spatial arrangement of habitats, and creating large- and small-scale disturbances (Germaine et al., 1998). As a result, the biotic communities of an urban area are often drastically different from those typical of the natural habitats of the region (Jokimaki and Kaisanlahti-Jokimaki, 2003). Urbanization can be considered a grand experiment in which the ecology of areas in different stages of urbanization can be investigated within a relatively small area (McDonnell and Pickett, 1990), allowing ecologists to analyze the relationship between human land use and ecological processes at multiple spatial and temporal scales.

Urban areas are complex landscape mosaics; habitat patches and corridors are scattered across a background matrix of development, often creating abrupt transitions between habitats (Barrett et al., 1999; Gilbert, 1989). These landscape elements exist in a wide variety of land uses under different management regimes. The large spatial extent of human-influence and tremendous spatial heterogeneity inherent in urbanized areas make a landscape-scale approach appropriate for studying urban ecosystems (Pickett and Cadenasso, 1995). Landscape ecology attempts to elucidate the effects of spatial heterogeneity on ecological processes at a variety of scales (Risser et al., 1984; Turner et al., 2001). A landscape ecological approach can include broad-scale studies of the behavior and dynamics of a large mosaic, or fine-scale analyses of the interactions between patch and matrix elements in order to reveal mechanisms driving the ecological functioning of those landscape elements (Pickett and Cadenasso, 1995).

Urbanized landscapes provide ideal opportunities for integrative science (Barrett and Barrett, 2001). Human decisions, both individual and institutional, are the driving force behind environmental conditions within cities (Alberti et al., 2003). The cumulative effect of public policies and individual decisions shape the structure and function of urban ecosystems. Cities are sustained by the flow of critical resources (biophysical, socio-economic, and cultural), and the allocation of these resources among various social groupings (Grove and Burch, 1997) is reflected in how humans interact with their environment (Machlis et al., 1997). Continued research is necessary to provide data on how urban residents and policy makers can create, manage, and restore urban landscapes that sustain both humans and native biotic communities.

1.2. Birds in Urban Landscapes

Much research on the effect of urbanization on faunal communities has focused on birds. Birds are highly mobile, and many species are adapted to edge habitats, which are common in a fragmented landscape (Odum and Barrett, 2005). Birds are therefore able to persist in urban areas where most other vertebrate species are extirpated. Bird distribution and abundance can be used to investigate population- and community-level responses to landscape alteration (Palomino and Carrascal, in press). Hence, many landscape-scale studies have attempted to detect common patterns in avian community structure among cities (e.g. Clergeau, Jokimaki et al., 2001; Fernandez-Juricic and Jokimaki, 2001; Jokimaki et al., 2002). A few generalizations have been made: urban bird communities have long been described as having a greater biomass than less developed environments, but greatly reduced species evenness, due to a few abundant, non-native species dominating the community (Beissinger and Osborne, 1982; Emlen, 1974). In a meta-analysis of urban bird community studies, Marzluff (2001) found that a high density of individuals is common across urban areas worldwide. Although trends in diversity are less clear, most studies reported decreased richness in urban areas.

The cultural setting of the landscape is often an important driver of ecological processes within urban areas (Grove et al., in press), and can be observed at multiple scales. The ecology of residential areas, in particular, reflects the past and present choices of residents, developers, and municipal planners. Human culture shapes the vegetation structure and built architecture of residential neighborhoods, which in turn structures bird communities using the neighborhood as habitat.

Interspersed among patches of urbanized cover types (e.g. buildings, roads) exist remnant natural vegetation patches. This juxtaposition of highly managed and unmanaged patches brings into question the relative importance of the qualities of the habitat patch (e.g. vegetation structure and patch area; Blake and Karr, 1987; Erdelen, 1984; James and Wamer, 1982) and the qualities of the matrix that are assessed by breeding forest birds during habitat selection. Adding additional complexity to managing landscapes for biodiversity is the fact that land management happens at multiple scales, ranging from government and institutional policies to the individual property owner decisions.

The extent to which the effects of residential land-management occurring at the scale of individual land parcels permeates remnant forest patches and influence habitat selection by breeding birds remains uncertain. The central question of the present study is whether the resources provided by residential areas contribute to the determination of breeding bird community structure in embedded forest patches.

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CHAPTER 2

The Relationship Between Breeding Bird Community Structure in Urban Forest Patches and Fine-Scale Management of the Surrounding Residential Matrix

2.1 Introduction

2.1.1. Urban Forest Patches as Avian Habitat

While urban habitats exclude most vertebrate species, birds are one taxonomic group that persists. Due to their high mobility, many species of birds, both native and exotic, are able to exploit habitats in a landscape fragmented by urban development. Urbanization, defined here as the process by which landscapes are transformed by expanding residential, commercial, and industrial development (sensu Alig and Healy, 1987), selects for distinct avian communities. Some species thrive while others diminish in response to changes in food quality and availability, habitat structure, predation pressure, and disturbance (Marzluff, 2001). Understanding the mechanisms structuring urban avian communities allows ecologists to make recommendations regarding the adaptation and design of land use practices that support native bird species, enhance biodiversity, and provide opportunities for human-wildlife interaction (Nilon and Pais, 1997).

Habitat patches are embedded in multiple land use types within urbanized landscapes (Nowak, 1994). In forested ecoregions, forest patches in urban landscapes tend to have richer bird diversity than patches of other landcover types (Jokimaki and Suhonen, 1998; Tilghman, 1987). As the landscape becomes increasingly fragmented, wooded patches in urban and suburban areas can increase the persistence of species at regional scales (Fernandez-Juricic, 2004). However, habitat patches within urban landscapes have been likened to isolated islands in an "urban ocean" (Fernandez-Juricic and Jokimaki, 2001). Indeed, island biogeography theory (Macarthur and Wilson, 1963) has been applied to the study of avian communities in remnant habitat fragments, and positive species-area relationships have been observed (Donnelly and Marzluff, 2004; Fernandez-Juricic and Jokimaki, 2001; Mortberg, 2001; Robbins et al., 1989). In addition to patch area, the spatial configuration of habitat patches impacts species occupancy. However, studies have shown that habitat patch isolation does not decrease the retention of native forest bird species until suitable habitat becomes rare within the region (Andren, 1994; Donnelly and Marzluff, 2006). When the proportion cover of native habitat drops below critical thresholds (Andren (1994) suggests 30%), the landscape context in which the fragment is embedded may influence habitat patch suitability. Land –use and –cover data describing the surrounding landscape may explain species occurrence in forest patches better than internal habitat features or patch spatial characteristics taken alone (Nilon and Pais, 1997; Park and Lee, 2000).

Vegetation structure and food resources of a given habitat interact in determining which bird species may potentially occupy that habitat (Chace and Walsh, 2006 and references therein; Robinson and Holmes, 1982). The habitat value of an urban forest fragment is therefore limited by the ability of birds to either find necessary resources within the patch, or negotiate the inhospitable matrix. Diverse land uses surrounding forest patches are of varying quality for biota and may impact patch suitability. The urban matrix can modify the capacity of species to disperse through the landscape, and the movement of individuals between source and sink populations (Opdam et al., 1985; Pulliam 1988). The urban matrix may provide food, shelter, or other resources that are limiting within the patch, and modify biotic interactions (e.g. predation, disturbance, colonization by exotics), particularly at patch edges (Bennett et al., 2004; Watson et al., 2005). Therefore, the value of a forest patch as bird habitat depends on both internal patch factors such as tree species composition and vegetation structure (Blake and Karr, 1987; Erdelen, 1984; James and Wamer, 1982; Mortberg, 2001) and the character of the landscape matrix within which the fragment exists (i.e. the landscape context). In urban landscapes, the landscape context is shaped by human decisions at multiple scales.

2.1.2. Human Influences on Urban Avian Communities

Recent studies have investigated bird communities within wooded habitat patches along a gradient of increasing urbanization (Bennett et al., 2004; Donnelly and Marzluff, 2004; Melles et al., 2003). In addition, most studies describe the landscape context of the patch in terms of broad-scale metrics such as patch configuration, edge length, and land cover composition (Gutzwiller and Anderson, 1992; Mortberg, 2001). Other studies have investigated relationships between bird communities and various land use types, finding that land use alone is a poor predictor of bird occurrence (Hostetler and Knowles-Yanez, 2003), because different areas constituting a single land use type often vary greatly in structure (Blair, 2004; Palomino and Carrascal, in press). However, these studies assume that the behaviors and decisions of the human population inhabiting urban areas are of little consequence (Kinzig et al., 2005), and fail to account for the diversity of human-mediated resources found within the landscape matrix (Barrett and Barrett, 2001). Adding data on the variation in the resources managed by the humans may explain variation in bird communities in addition to what has been explained by coarse-scale data. Residential areas are of particular interest, where dense human populations dwelling on small land parcels, combined with a diversity of household land-management practices, create fine-scale heterogenity within the urban matrix (Grove et al., 2006). The diverse cultural backgrounds and socioeconomic status of urban populations influence their preference for different landscaping types, as well as the proportion of economic resources that can be devoted to shaping outdoor surroundings (Grove et al., in press; Kinzig et al., 2005). This mosaic of culturally-influenced land management shapes the resource base available to the biotic communities that utilize residential areas as habitat (Melles, 2005; Pickett et al., 2001); we henceforth refer to resources managed by urban residents as cultural resources.

Determining which variables best capture the characteristics of residential landscapes that are driving bird community structure in embedded forest patches is a topic requiring investigation. For example, neighborhood age can be used as an indicator of time since disturbance (Martin et al., 2004), and can serve as an indicator of the stage of cultural succession (Barrett et al., 1999), a parameter complementary to the seral stage of succession of a forest patch. As neighborhoods age, vegetation matures and the biotic communities occupying the neighborhood subsequently transform (Grimm et al., 2000; Hope et al., 2006). For example, in Alberta, Canada, Edgar and Kershaw (1994) observed greater breeding bird diversity in the oldest suburban subdivision than in newer developments. The degree of contrast between the patch and the matrix is an important component of landscape effects (Lichstein et al., 2002; Watson et al., 2005), and it may be expected that a forest surrounded by a mature neighborhood will have less edge contrast than a forest/young neighborhood edge, mitigating the isolating effects of urban development (White et al., 2005). However, alternative metrics describing other aspects of matrix structure (e.g., building type, lawn cover) may also be useful in explaining bird diversity in embedded forest fragments.

In addition to modifying and creating habitats through vegetation change, humans modify traditional resource availability-biodiversity relationships (Hope et al., 2006) by providing birds with direct resource subsidies. The availability of bird feeders, bird baths, and nest boxes is likely to differ among neighborhoods (Hostetler and Knowles-Yanez, 2003), influenced by various aspects of human culture, such as level of education, socio-economic status, and lifestyle choices. These subsidies can alter avian community structure by selecting for species that are tolerant of human presence and therefore able to exploit these resources (e.g. Lauro and Tanacredi, 2003; Marzluff et al., 2001). The tendency for avian diversity to decrease and density to increase along a gradient of increasing urbanization (Marzluff, 2001) results from the over-abundance of a few, dominant, often exotic species with life histories that allow them to exploit the structural and trophic resources provided by urban development.

Although large habitat patches (> 40 ha; Donnelly and Marzluff, 2004) embedded in urban matrices can be valuable to breeding birds; urban forest patches are often small, and the potential of small fragments to serve as avian habitat deserves increased attention. While development practices which maximize the retention of trees and native canopy composition can assist in the conservation of birds at broad scales (Donnelly and Marzluff, 2006), these decisions are often made by city planners and developers. It remains uncertain whether cultural resources managed at the scale of the individual land parcel can contribute to the conservation value of small forest patches. Empirical investigation of individual property owner capacity to modify bird habitat through land-management decisions are particularly relevant to wildlife conservation in urban areas, since models have suggested that backyard habitat creation is the best approach to creating habitat connectivity in urban landscapes (Rudd et al., 2002). In spite of this potential, few empirical studies have attempted to relate the quality of an unmanaged habitat patch to the variation in the fine-scale variation in cultural resources in the surrounding urban matrix. The relationships between bird diversity and biophysical variables describing forest fragments (e.g. fragment area, vegetation structure) have been well-established (Blake and Karr, 1987; Erdelen, 1984; James and Wamer, 1982); here we attempt to determine whether variables describing cultural resources surrounding the fragment provide additional information in explaining patterns of avian diversity in forest fragments.

2.1.3. Hypothesized relationships between bird community structure and cultural resources

Bird species richness and density show opposite trends in response to urbanization (Marzluff, 2001), and were investigated as response variables in this study. In order to assess differences in community composition with respect to sensitive species (i.e. species not associated with residential development), Neotropical migrant species richness was also treated as a response variable (Dunford and Freemark, 2005). Many forest-dwelling Neotropical migrant bird species occur infrequently in small forest patches (Askins et al., 1987; Lynch and Whigham, 1984; Robbins et al., 1989; Whitcomb et al., 1981); conservation of these species is therefore an important and challenging planning target in increasingly fragmented landscapes. Furthermore, Neotropical migrants serve as an ecologically distinct indicator guild (Blake and Karr, 1987), as opposed to other groupings (e.g. foraging guild, edge versus interior species) for which assignment of species to a particular group is often subjective, as reported life history characters of individual species vary across the literature.

These three response variables (total bird species richness, Neotropical migrant species richness, and total avian density) can be expected to relate to different suites of explanatory variables. We investigated which variables describing cultural resources in residential neighborhoods can explain patterns in breeding bird communities, beyond what can be explained by forest patch characteristics alone. The justification for the specific hypothesized relationships investigated in this study follows:

(i) *Total Species Richness*: Variation in breeding bird richness in urban forest patches may relate to coarse-scale structure of the surrounding residential neighborhoods.

Neighborhoods containing high proportions of tree-cover and lower density housing may be more permeable to birds moving among patches to assess breeding habitat quality. Alternatively, heavily treed neighborhoods could increase the effective patch size, and presumably, species richness within the patch (Degraaf and Wentworth, 1986). However, there are alternative metrics that may capture the aspects of the matrix driving habitat selection: Neighborhood age reflects mature tree cover, time since disturbance (Martin et al., 2004), and occurrence of non-native plant species (Clemants and Moore, 2003). Forest patches in older neighborhoods may therefore be expected to have more species rich bird communities; more species may colonize as the surrounding canopy develops, species extirpated by the disturbance of development may recolonize, and new species exploit the novel vegetation types created through the continued addition of ornamental exotic species. However, explicit land cover data (including additional information on built structures, pavement, and grass cover) reflects additional aspects of neighborhood structure to which species may be attracted or deterred.

(ii) *Neotropical Migrant Species Richness:* Migrant richness is expected to be primarily predicted by forest patch features; most forest-dwelling Neotropical migrants are sensitive to human disturbance and do not typically include forest edges and adjacent residential areas in their territory (Blake, 1983). However, while habitat selection is primarily based on characteristics of the habitat itself, abundant tree cover adjacent to the forest patch may increase the perceived core area of the patch, making it more attractive to area-sensitive species. Additionally, migrant richness may have a negative relationship with subsidy density, as highly subsidized forest patches may be saturated with individuals of more human-tolerant bird species (Blake, 1983), including nest predators (e.g. Blue Jay, *Cyanocitta cristata*) and brood parasites (e.g. Brown-headed Cowbird, *Molothrus ader*). We also investigated the relationship between Neotropical migrant species richness and neighborhood age. Community relaxation (Gonzalez, 2000) occurs when local populations of sensitive species go extinct and a more limited cohort of urban-adapted species colonize following disturbance of the habitat. Urban forest bird communities are thus expected to be composed of progressively fewer Neotropical migrant species over time since neighborhood construction.

(iii) *Total Density*: Density of bird resource subsidies in the surrounding neighborhood may explain variation in avian density in forest patches beyond what can be explained by features of forest patches (Morneau et al., 1999). Density of forest birds is often primarily determined by the availability of appropriate resources per unit area (e.g. Blewett and Marzluff, 2005; Shochat et al., 2002); therefore, the density of birds in woodlots might be expected to have a positive relationship with resources available in the surrounding urban matrix, as many species of birds may include the surrounding neighborhood in their territories or home ranges (Blake, 1983). The proportion of urban land cover in the matrix, represented by proportion cover of building and pavement within 100 m of the forest edge, was also hypothesized to have a positive relationship with avian density in forest patches, corresponding to broad-scale trends in avian density along gradients of urbanization (Marzluff, 2001; Palomino and Carrascal, in press).

2.2. Materials and Methods

2.2.1. Study site

This study was conducted in the Baltimore metropolitan area, Maryland, USA (76^{o}60’W, 39^{o}40’N) during the 2005 bird breeding season in cooperation with the Baltimore Ecosystem

Study (BES) Long Term Ecological Research program (http://www.beslter.org). The Gwynns Falls Watershed (GFW) (Fig. 1), one of Baltimore City's four major drainage basins, extends from west Baltimore City north into Baltimore County, and includes recently suburbanized areas, established suburbs, and dense urban areas. The watershed is comprised of residential, commercial, agricultural, and recreational land-uses. This 17,150-ha watershed, which spans gradients in topography, human population density, socio-economic characteristics, and land use, has served as the focal landscape for BES research. The GFW was primarily forested before European settlement, after which it was largely converted to agriculture. No virgin forest remains in the watershed; secondary forest cover now constitutes approximately 19% of the landscape (Baltimore Ecosystems Study, 2004a). Forests in the upper watershed are dominated by chestnut oak (*Quercus prinus*) associations, transitioning to tulip poplar (*Liriodendron tulipifera*) associations in the lower watershed. Riparian areas are characterized by box elder (*Acer negundo*)-green ash (*Fraxinus pennsylvanica*)-sycamore (*Plantanus occidentalis*)-silver maple (*Acer saccharinum*) associations (Brush et al., 1980).

2.2.2. Site selection

Individual forest patches constitute the unit of replication in this study. The National Landcover Dataset 2001 (NLCD) (see Homer et al. 2004 for a description of land cover classification methodology) was used as the base layer for identifying potential study sites. Grid cells (30 x 30 m resolution) within the GFW containing forested cover-types were identified, and discrete patches (using an 8-neighbor rule; Turner et al. 2001) between 2-10 ha were extracted. Patches were eliminated from the site pool if they were not surrounded by developed land cover types (high-, medium-, and low-intensity development). Each candidate patch was examined

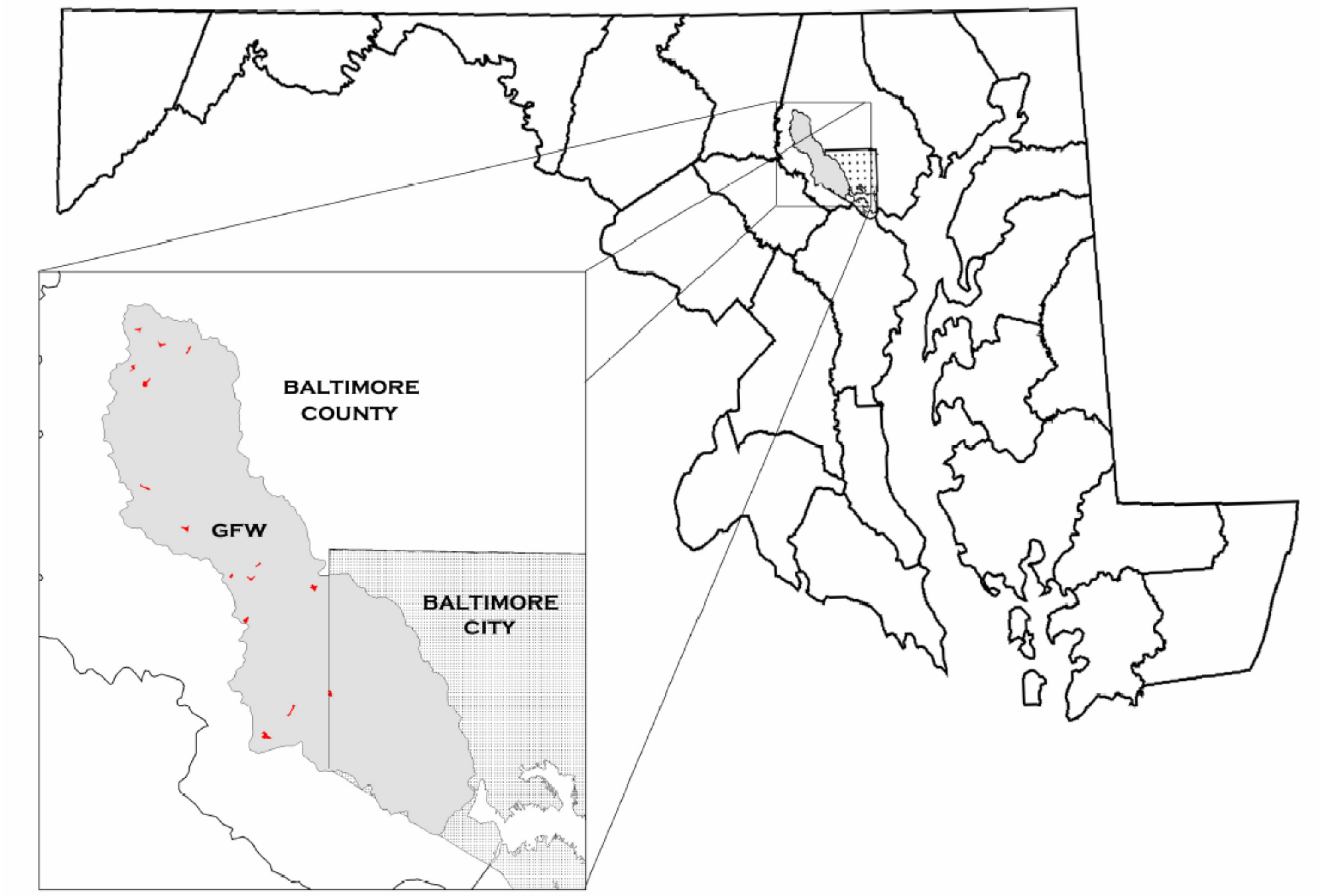

Fig. 1: Location of GFW within Baltimore City and County, and distribution of study sites throughout the watershed (red patches).

against aerial imagery (Baltimore Ecosystems Study, 2004b) to confirm that the surrounding landscape matrix was primarily residential. Twenty-one sites met all criteria and were visited to determine final candidacy as a study site; six sites were eliminated due to low accessibility (e.g. fences, extremely steep banks). Final sample size was n=15 (Figure 1).

Within the final set of study sites, area ranged from 2.1-8.3 ha ([Mean] 4.3 ha ± 1.9 [S.D.]), and proportion of forest edge intersecting with residential land use ranged from 75.0-100% (86.5% ± 8.2). Due to their small size, each patch had a high edge-to-area ratio, ranging from 189.0-386.3 m/ha (297.7 m/ha ± 72.2). Although not part of site selection criteria, each site had an intermittent stream bed or a perennially flowing stream. Most sites were intact because they were protected riparian or floodplain areas, receiving stormwater drainage from the surrounding neighborhoods. The study sites spanned the watershed, starting at the boundary of Baltimore City, and extending approximately 21 km into Baltimore County. Although one site was within Baltimore City limits, all of the neighborhoods surrounding the study sites were typical of suburban development: single-family housing was the most common housing type and multifamily housing (apartments and townhomes) was located in complexes that included large areas of lawn (sensu Marzluff et al. 2001).

Patch boundaries were determined from polygons extracted from the NLCD grid layer. In some cases, forest patches were continuous with other patches connected by narrow corridors of trees. The determination of a discrete patch from a raster dataset is influenced by the alignment of the grid overlay comprising the land cover map; narrow corridors may not be classified as forest if the majority of that cell is comprised of other land covers (e.g. development, agriculture). In these cases, the area of the forest was regarded as that which was extracted from the NLCD layer, and bird surveys were limited to these boundaries (Fig. 2, in yellow). Study site selection, and all subsequent landscape analyses were completed using ArcGIS 9.0 software (Environmental Sciences Research Institute, 2004).

2.2.3. Avian Community Surveys

Breeding bird communities were surveyed between 6 May and 22 July 2005. Surveys were conducted between sunrise and 1000 hours on days of fair weather. Using a territory mapping method (Bibby et al., 2000), each forest patch was traversed along a route composed of parallel transects located along edges and through the interior patch approximately 50 m apart (Fig. 2). The entire forest patch was therefore surveyed from a distance of no greater than 25 m, a distance from which most bird vocalizations are regarded as equally detectable (Schieck, 1997). Individuals of each species seen or heard were recorded at their approximate location on a datasheet containing the footprint of the forest patch, route lines, and reference waypoints. Observer location within the patch was estimated relative to waypoints using a Garmin eTrex Vista C handheld GPS receiver. Behavioral observations related to breeding status (e.g. singing, male-male aggression, carrying food or nest material) were also recorded. Two sites were visited per day, and sites were paired by geographic location in the watershed to reduce travel time between sites. The order in which the paired sites were surveyed (i.e. first versus second) was reversed between each round of visits. Each visit lasted between one and three hours depending on patch size, intensity of bird activity, and vegetation complexity; travel speed was not held constant, as maintaining speed while negotiating dense understory vegetation would have reduced the ability to detect birds at some sites. Rather, the observer paused at regular distance intervals (approximately every 10 m) to listen and look for birds that may have been missed while in motion. Each site was visited six times, with the order of visits randomized between

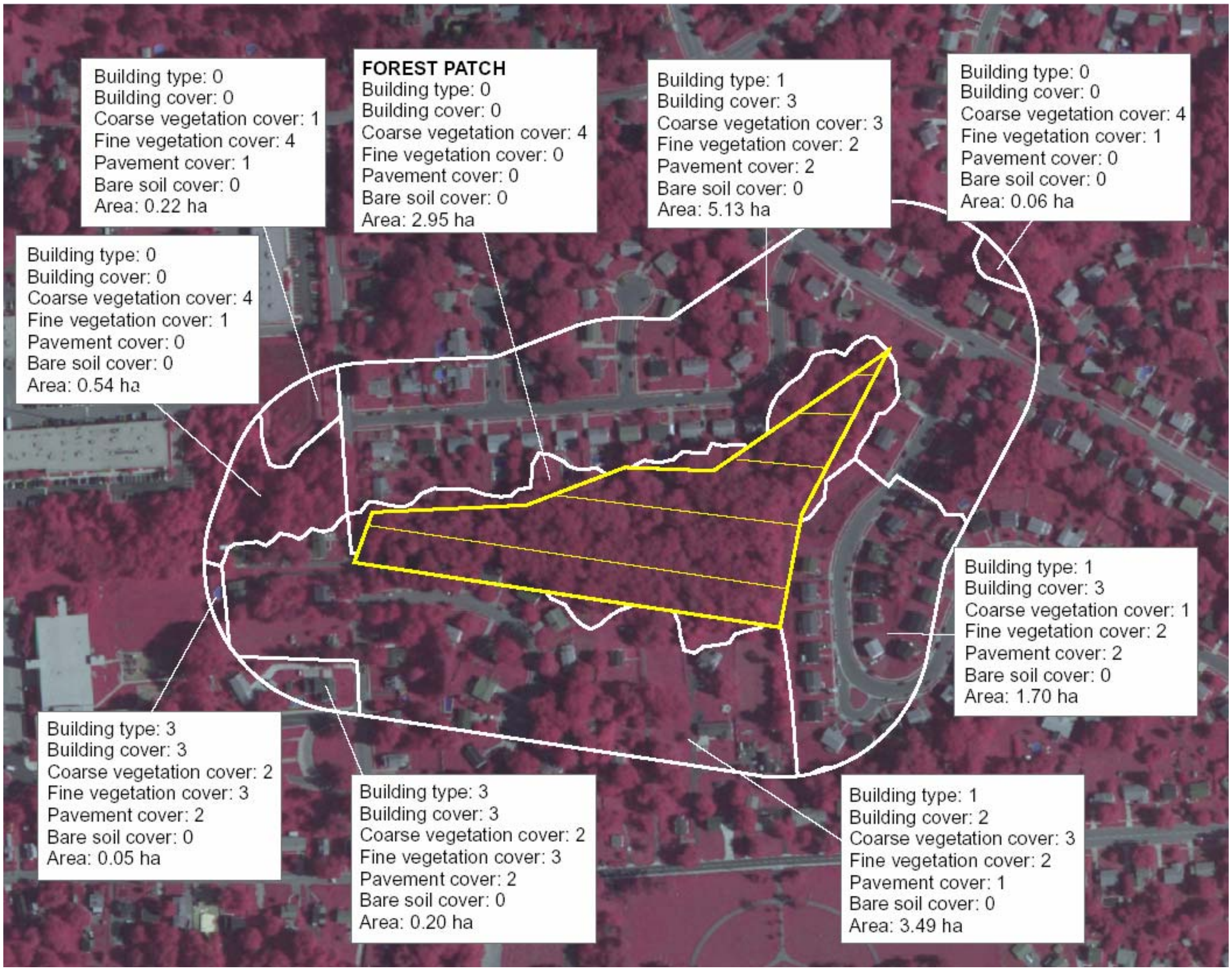

Fig. 2: Orthophoto of a representative study site, showing patch boundaries extracted from NLCD data and approximate location of bird survey transects (yellow), boundaries of HERCULES patches intersecting the 100 m buffer (white), and the data matrix associated with the HERCULES patch classification. Categorical HERCULES variables are designated as follows: Building type: 0= none, 1= single, 2= attached, 3= complex footprint; All cover variables: 0= none, 1= present-10%, 2= 11-35%, 3= 6-75%, 4= >75%

rounds of visits to reduce bias due to variation in singing patterns among species across the breeding season. All surveys were completed by a single observer (CC).

A species was considered to have bred in the forest patch if: (i) it was detected on at least three visits; (ii) it was detected on two-consecutive visits separated by at least 10 days outside of migration dates for the species (taken from the literature, as summarized in Birds of North America species accounts (Cornell Lab of Ornithology, 2005)); (iii) territorial behavior (e.g. singing, male-male aggression) was observed on at least two occasions; (iv) evidence of breeding was observed on any visit (e.g. active nests, nest building, food carrying, or newly fledged young) (sensu Bellamy et al., 1996; Bibby et al., 2000). Because this method is only appropriate for territorial birds, certain non-territorial or colonial species, and species with very large territories (e.g. raptors) were eliminated from the dataset because detections within the forest patch could not reliably ensure a pair was breeding in the habitat unless an active nest was detected, or that their habitat assessment was closely linked to the immediate neighborhoods surrounding the forest edge. Eliminated species included: American Crow (*Corvus brachyrhynchos*), American Goldfinch (*Carduelis tristis*), Blue Jay (*Cyanocitta cristata*), Common Grackle (*Quiscalus quiscula*), Cooper's Hawk (*Accipiter cooperii*), Fish Crow (*Corvus ossifragus*), and Red-shouldered Hawk (*Buteo linneatus*). All remaining species determined to be breeding were classified as resident, short-distance migrant, or Neotropical migrant using the Birds of North America species accounts. Neotropical migrant species richness was the total count of species detected in a site whose breeding populations in Maryland migrate exclusively from Central or South America; mixed classifications (i.e. species whose populations in Maryland migrate from within or outside the continent) were not included in the count of Neotropical migrants.

The number of territories held by each species in each forest patch was determined by analysis of composite maps created for each species at each site. While absolute densities cannot be calculated via the described territory mapping method, reliable estimates of relative densities can be approximated if a consistent approach is used (Bibby et al., 2000). A set of a priori rules for delineating territories based on clusters of observations was created to reduce bias in density estimates. If one-half or more of the detections comprising a cluster were recorded at the forest edge, that territory was counted as 0.5 (i.e. the forest patch served as only half of the territory of the individual bird). All density estimates were made by examinations of maps by a single observer (CC).

2.2.4. Forest Patch Characterization

To account for patch-level variation in vegetation structure, vegetation data were collected at random points within each forest patch using techniques modified from the Urban Forest Effects model data collection protocol (Nowak, 2000). The number of vegetation surveys was proportional to forest patch size, such that approximately 2% of the area of each forest patch was surveyed. A circular plot with a radius of 5 m was centered on each point. For each woody plant greater than 2.5 cm diameter at breast height (dbh) with at least one-half of its basal area within the plot, species name, dbh, height-to-crown, and total height were recorded. Tree heights were measured using an electronic clinometer. Based on these survey data, indices of forest structure were calculated, pooling data from all trees at all points within each site (Table 1). Foliage Height Diversity (FHD) was calculated using the Shannon-Weaver diversity index (Shannon and Weaver, 1949) for cover at each canopy level (0-1m, 1-2m, 2-4m, 4-16m, 16-32m, >32m; sensu Prodon and Lebreton, 1981), using height-to-crown and total height to determine the proportion of trees with vegetation intersecting each level. Stem Size Diversity (SSD) was

Table 1
Variables describing vegetation structure of forest patches and HERCULES classification of the 100m buffer surrounding forest patches. Percent cover variables are classified as follows: 0= absent, 1= present to 10%, 2= 11-35%, 3= 36-75%, 4= >75%.

Vegetation structure variables

Tree species richness: Number of tree species/m^2
Stem density: Number of stems >2.5 cm dbh/m^2
DBH_{max}: Maximum recorded diameter at breast height (cm)
FHD: Foliage Height Diversity; Shannon-Weaver diversity index of tree and shrub (dbh>2.5 cm) cover at six discreet canopy levels
SSD: Stem Size Diversity; Shannon-Weaver diversity index of tree and shrub stem sizes in four DBH ranges

Categorical variables describing structure of landcover in each HERCULES patch.	
Building type:	0 = no building, 1 = single structures, 2 = connected structures, 3 = mixed footprint
Percent cover of buildings:	0-4 as in legend
Percent cover of coarse vegetation (tree and shrubs):	0-4 as in legend
Percent cover of fine vegetation (grass and herbaceous):	0-4 as in legend
Percent cover of pavement:	0-4 as in legend
Percent cover of bare soil:	0-4 as in legend

calculated by determining the proportion of stems of woody plants whose dbh fell within standard class intervals (<10cm, 10-30cm, 30-50cm, >50cm; sensu Fernandez-Juricic, 2000).

2.*2.5. Neighborhood Characterization*

A 100 m buffer around each forest patch (Fig. 2) was characterized based on both land cover composition and age of residential development. This narrow buffer width was selected to ensure that only resources provided by the immediate residential neighborhoods were assessed as explanatory variables; a larger buffer width may have captured the influence of other adjacent land uses (e.g. commercial, institutional) and confounded the interpretation of results. The High Ecological Resolution Classification of Urban Landscapes and Environmental Systems (HERCULES) classification system (Cadenasso et al., submitted) was used to classify the structure of the landscape surrounding the study sites within a 100 m buffer. HERCULES is a new classification of land cover that integrates built and non-built components of the landscape. The basic elements of the urban landscape are buildings, surface materials and vegetation (Ridd, 1995). HERCULES recognizes the independent variation in the type, density and arrangement of each of these elements: the landscape is broken down into discrete units (patches) delineated from their neighbors at boundaries drawn where the type, density, or arrangement of landscape elements changes. As a result, the biophysical structure of the system is emphasized. HERCULES is applied to false-color, infrared aerial photography of submeter resolution, in which the user systematically delineates patch boundaries based on visual inspection of land cover composition ("heads-up" digitizing). Patches must be 20 m in two orthogonal directions to be recognized by the system. This rule was selected to prevent patches containing only a single city lot or residential street. Within each patch the relative cover of coarse vegetation (trees and shrubs), fine vegetation (grass and herbs), bare soil, pavement, and buildings is recorded. An additional source of variation is building type which includes: single structures in rows or clusters, connected structures with shared walls, and clusters of buildings of mixed sizes and dimensions. HERCULES variables are summarized in Table 1.

The HERCULES land cover approach is unique in that it is designed specifically to incorporate the ecological characteristics of urban heterogeneity. For example, standard classifications, such as the NLCD data set and others like it that are derived from the original Anderson et al. (1976) scheme identify land uses such as high, medium, and low intensity residential. These classes give some indication of the density of buildings on the landscape but no indication of other elements. In addition to building density, HERCULES also distinguishes the relative cover of coarse and fine vegetation, pavement and bare soil. These additional elements may influence the ecological functioning of the landscape. Ancillary data useful for a specific research question can easily be added in a GIS as an additional data layer on top of HERCULES. The power of HERCULES is its flexibility in describing land cover not only in terms of building density but also in terms of other elements that may be critically important for ecological understanding.

Neighborhood age was calculated from the Maryland Property View Assessors and Taxation database. For each HERCULES patch, median age was calculated for all structures. Median age reflects the age of the majority of the houses in the patch, and is not heavily influenced by extreme observations. Because housing density varied around each forest patch, such that many data points for housing age may exist in a small portion of the buffer, and vice versa, area-weighted median age was calculated. Median age of housing within each HERCULES patch was multiplied by the proportion of residential area within the 100 m buffer occupied by that patch. These weighted medians were summed to provide the area-weighted median age of neighborhoods surrounding each forest patch. This index best reflects the time since the majority of the development occurred within the buffer.

2.2.6. Bird Resource Subsidies

We quantified the extent to which birds are subsidized by homeowners in different neighborhoods by estimating the density of bird feeders, bird baths or other artificial water sources, and nest boxes within each 100 m buffer. HERCULES patches of the same building type and density around a single forest patch were pooled for resources subsidy sampling (henceforth, subsidy patch), in order to enable the extrapolation of resource subsidy density from the proportion of homes offering subsidies. In subsidy patches containing attached buildings, visual surveys were completed of all residential structures (i.e. apartments, townhomes) within the subsidy patch. Because backyards frequently could not be viewed from public rights-of-way in subsidy patches containing single family homes, the proportion of homeowners providing resources subsidies was estimated from verbal surveys. All surveys were completed between 10am and 6pm; first visits to homes within the subsidy patch were on weekdays; however, if the target sample size (n=20) was not reached, second visits were made on Saturdays. Homeowners were asked how many of each subsidy they provided in their yard during the bird breeding season. In very small subsidy patches or in areas of low housing density, the number of surveys was limited by the number of residences within the patch and the number of residents at home. In these situations, additional surveys were completed by visually surveying lots within the subsidy patch that were fully visible from public rights-of-way (e.g. corner lots without fences) to obtain the largest sample size possible.

For subsidy patches comprised of attached housing, we calculated absolute densities by dividing the number of subsidies observed by the area of the subsidy patch. However, for single-family homes, we first estimated of the number of households offering at least one subsidy by multiplying the proportion of homeowners surveyed that offered subsidies by the total number of homes in the patch. Homeowners who did provide artificial resources to birds frequently offered multiple subsidies; however, it was felt that calculating the mean number of subsidies per household and multiplying this by the estimated number of households offering subsidies would give an inflated estimate of resource density heavily influenced by whether any bird "enthusiasts" were surveyed in the random sample. Rather, if were any surveyed households offered multiple subsidies, the additional number of subsidies recorded was added to the estimate of the number of households offering at least one subsidy. This value was summed for all subsidy patches within the buffer, and then divided by the sum of the area of the subsidy patches to provide an estimate of subsidy density for each 100 m buffer.

2.2.7. Data Analysis

An information-theoretic approach (Burnham and Anderson, 1998) was used to investigate the relationship between total species richness (TSR), Neotropical migrant species richness (MSR), and total density (TD) and characteristics of the forest patch and the surrounding neighborhood. This approach allows one to select the best model from a suite of a priori candidate models that are based on previous evidence from the literature and/or sound logic. Rather than rejecting a null hypothesis at an arbitrary significance level, this strategy weighs multiple working hypotheses based on both the fit of model to the data, and parsimony (Burnham and Anderson, 1998); the best model is the model with "...the smallest possible number of parameters for adequate representation of the data." (Box and Jenkins, 1970). Thus, information-theoretic methods attempt to achieve a balance between under- and over-fitted models, and are appropriate for observational studies (Burnham and Anderson, 1998).

2.2.7.1. Variable Reduction

2.2.7.1.1 Patch Structure

To reduce the number of explanatory variables being entered into analysis, a principle components analysis (PCA) was performed on the correlation matrix of vegetation variables collected within each forest patch. Site scores along PCA axis one (PCA_{veg}) were entered into analysis as a means of accounting for patch-level variation in vegetation structure (James and Wamer, 1982).

2.2.7.1.2. Landscape Context

HERCULES patch classification was used to calculate an area-weighted mean for five of the six categorical variables describing the HERCULES patches within each 100 m buffer (Table 1). Building type was not included in this analysis because we believed that variation in housing cover, rather than type, better reflected the aspect of landscape structure to which birds were likely to respond. This resulted in a single value for each proportion cover variable for each buffer; a continuous variable between zero and four. A PCA was performed on the area-weighted means, reducing the number of variables describing the composite land cover of the neighborhoods to a single value on each resulting axis. These orthogonal axes also reduced colinearity among the explanatory variables, which otherwise may have been problematic, because the individual proportion cover variables could be expected to have inverse relationships with one another. Models for total species richness included landcover PCA score as predictors because species richness in the forest patches was expected to be related to overall landscape structure surrounding the patches. Total density and migrant richness, however, were expected to respond to individual aspects of the landscape context surrounding the forest patches (urban landcover and coarse vegetation cover, respectively), and these individual area-weighted means, rather than PCA scores, were tested as predictors.

Correlation coefficients were calculated for each pair-wise correlation between all hypothesized explanatory variables. If pairs were highly correlated ($|r|>0.7$), only the more logical variable in the relationship was selected to include in models. The total density of resource subsidies (SUBDEN) was correlated with the individual densities of feeders, artificial water sources, and nest boxes (i.e. no one type of subsidy dominated); therefore, SUBDEN was the only subsidy variable used in further analysis. Table 2 summarizes all explanatory variables used in model selection analyses.

2.2.7.2. Model Selection

The Akaike Information Criteria for small sample sizes (AIC_c) (Sugiura, 1978) was used to weight multiple linear regression models constructed for each response variable. The alternative models contain various subsets of variables that, based on previous research, are thought to be related to the response variable, and are derived from the a priori verbal hypotheses outlined in the introduction (section 1.3.) (Table 3). Every possible subset of explanatory variables was not included in the suite of candidate models; the models represent alternative hypotheses that make biological sense and are of interest to the research question. The alternative models represented hypothesized relationships between the response variable and characteristics of the forest patch and surrounding neighborhood, as well as simpler models containing only variables describing characteristics of the forest patch itself. The various combinations of cultural resource variables appearing in candidate models reflect variables

Table 2
Description of response (**boldface**) and explanatory variables appearing in the suite of linear regression models.

Variable	Description
TSR	**Total Species Richness**, total number of breeding bird species detected within each forest patch
MSR	**Neotropical Migrant Species Richness**, number of exclusively Neotropical migrant bird species detected within each forest patch
TD	**Total Density**, total number of breeding territories detected per ha within each forest patch
AREA	Patch area (ha), log transformed
PCA_{veg}	Score of each forest patch along the first axis constructed from a PCA on vegetation structure variables
CV	Area-weighted mean of coarse vegetation (tree and shrub) cover, calculated for each 100m buffer by multiplying the HERCULES patch score for percent cover of coarse vegetation times the proportion of the buffer occupied by the HERCULES patch, and summing for all HERCULES patches within the buffer, square root transformed
URBAN	Area-weighted mean urban cover, calculated for each 100m buffer by multiplying the sum of the scores for building and pavement cover times the proportion of the buffer occupied by the HERCULES patch, and summing for all HERCULES patches within the buffer
PCA_{HERC}	Score of each forest patch along the axes resulting from a PCA performed on the area-weighted means of the five variables describing landcover in the HERCULES patches comprising the 100m buffer
AGE	Area-weighted median neighborhood age of all residential structures in the 100m buffer, years
SUBDEN	Total density of all pooled subsidies within the 100m buffer, no. subsidies/ha

Table 3

The suite of a priori linear regression models ranked in descending order by Akaike weights (ω_m). The global model is an overfitted model containing all variables included in the list of candidate models for the response variable, and is used to confirm linear regression produces an acceptable fit to the data, not for inference. K is the number of parameters in the model (including intercept and error terms); Δ_i describes the deviation of each model from the model with the lowest AIC_c.

Model Variables	R^2	**K**	AIC_c	Δ_i	ω_m
Total Species Richness					
Global Model	0.74	8	78.95	18.48	0.00
AREA, PCA_{HERC1}	0.68	4	60.47	0.00	0.42
AREA, AGE, AGE^2	0.71	5	62.26	1.79	0.17
AREA	0.54	3	63.22	2.75	0.11
AREA, PCA_{veg}, PCA_{HERC1}	0.68	5	63.43	2.96	0.10
AREA, PCA_{HERC1}, PCA_{HERC2}	0.68	5	63.60	3.13	0.09
AREA, PCA_{veg}	0.55	4	65.40	4.93	0.04
AREA, AGE	0.55	4	65.53	5.06	0.03
AREA, PCA_{veg}, AGE, AGE^2	0.71	6	66.40	5.93	0.02
AREA, PCA_{veg}, PCA_{HERC1}, PCA_{HERC2}	0.69	6	67.74	7.27	0.01
AREA, PCA_{veg}, AGE	0.56	5	68.28	7.81	0.01
Neotropical Migrant Species Richness					
Global Model	0.48	7	58.60	9.25	0.00
AREA, CV	0.30	4	49.35	0.00	0.42
AREA§, PCA_{veg}, CV	0.38	5	51.02	1.67	0.18
AREA	0.04	3	51.50	2.16	0.14
AREA, PCA_{veg}	0.16	4	52.08	2.73	0.11
AREA, SUBDEN	0.08	4	53.48	4.13	0.05
AREA, AGE	0.05	4	53.96	4.61	0.04
AREA, PCA_{veg}, SUBDEN	0.21	5	54.49	5.14	0.03
AREA§, PCA_{veg}, AGE	0.19	5	54.96	5.62	0.03
Total Density					
Global Model	0.74	6	75.42	17.26	0.00
AREA	0.73	3	58.16	0.00	0.76
AREA, URBAN§	0.74	4	62.19	4.04	0.10
AREA, SUBDEN§	0.73	4	63.11	4.96	0.06
AREA, PCA_{veg}	0.73	4	63.16	5.00	0.06
AREA, PCA_{veg}, URBAN§	0.74	5	68.16	10.00	0.01
AREA, PCA_{veg}, SUBDEN§	0.73	5	69.07	10.92	0.00
SUBDEN§	0.06	3	76.61	18.45	0.00
URBAN	0.00	3	77.55	19.39	0.00

§ Sign (+/-) of the parameter estimate in the fitted model is opposite what was explicitly predicted in a priori hypotheses. These models have limited value for inference. See Discussion for justification of expected directionality of relationships, and discussion of violations of these expectations.

hypothesized to have the strongest influence on the response variable, or represent alternative means of quantifying cultural resource variables to which birds may be responding.

Based on ample evidence from the literature, forest patch area was assumed to be of primary importance in explaining richness, and therefore appeared in all TSR and MSR models. The relationship between forest patch area and avian density was less certain; area was therefore not included in every candidate model for TD. Avian density may relate more directly to landscape-level urbanization processes (Marzluff, 2001) than to local habitat variables, justifying the inclusion of models containing only buffer characteristics in the subset.

Vegetation structure of the forest patch was hypothesized to explain less variation in avian community structure than forest patch area, and therefore appeared in only some of the models that contained cultural resources variables. This allowed us to compare the relative ability of forest patch vegetation structure and neighborhood cultural resources to explain response variables (i.e. to compare habitat quality versus matrix quality in their explanatory power). In general, it was expected that species richness and density would increase with vegetation complexity (Blake and Karr, 1987; Erdelen, 1984; Macarthur and Macarthur, 1961) (but see James and Wamer (1982) for a more specific description of this relationship).

Least-squares regression was used to fit multiple linear regression models corresponding to the a priori hypotheses. Prior to fitting models, histograms of each explanatory variable were examined; AREA and CV were transformed to normalize their distributions (log and square-root transformations, respectively). Residual versus predicted plots from each model were examined to confirm assumptions of homogeneous variance; no violations of this assumption were found. A global model (i.e. an over-fitted model containing all of the explanatory variables appearing in various combinations in the suite of candidate models) was fit for each response variable before proceeding with analysis. R^2 values of the global models were used to confirm that linear regression produced an acceptable fit to the data (Table 3) before beginning model selection routines.

AIC_c values were derived from the maximum likelihood estimator of variance, calculated from the residual sum of squares from least squares regression. Akaike model weights (ω_m) were used to rank models according to their usefulness in predicting total species richness, Neotropical migrant species richness, and total density. Model weights describe the probability that a given model within the set of alternative models is the best representation of reality (Burnham and Anderson, 1998), and was used to assess whether the inclusion of data describing cultural resources in the buffer provided enough additional information to warrant including additional parameters (i.e. in addition to parameters describing the forest patch) in the models.

Post hoc tests were conducted to test for possible unexpected correlations between response variables and explanatory variables not appearing in the suite of candidate models. A correlation matrix was constructed post hoc to examine the strength and direction of relationships between the response variables and the full range of explanatory variables explored in this study, including the individual variables entered into the vegetation and HERCULES PCAs. When there was evidence that an explanatory variable was correlated with one of the response variables ($|r| \geq 0.4$), a simple linear regression line was fit to investigate the strength of the relationship within this data set. This exploratory data dredging was performed to provide preliminary evidence for future investigations, not as a means of making strong inference.

2.3. Results

2.3.1. Avian Community

A total of 26 species were detected and determined to be breeding, six of which are exclusively Neotropical migrants in Maryland (Table 4). Total species richness varied between eight and 17 species ([Mean] 12.47 ± 2.70 [S.D.]) across the 15 study sites. Neotropical migrant species richness varied between zero and five species detected at a site (2.40 ± 1.24). Total avian density ranged from 4.76 to 14.06 territories/ha (9.08 ± 2.50). American Robin, Carolina Wren, Gray Catbird, and Northern Cardinal were detected in all sites. Gray Catbird and Northern Cardinal were the most abundant species, with mean densities of 2.87 and 1.55 territories/ha respectively.

2.3.2. Vegetation Principle Components Analysis

PCA_{veg} accounted for 53.49% of the variation in vegetation structure data, and was the only axis with an eigenvalue greater than one. PCA_{veg} expresses the trend for stem size diversity, foliage height diversity, and DBH_{max}, to increase together (Table 5). Stem density and tree species richness/m^2 are negatively correlated with this axis.

2.3.3 HERCULES Landscape Analysis

The 100-m buffers surrounding the 15 forest patches were classified into 127 patches of 72 distinct types (i.e. distinct combinations of the six categorical descriptor variables delineating each patch from its neighbors). The number of HERCULES patches comprising an individual buffer ranged from four to 12 (8.47±2.47). The distribution of the values for each of the variables across all 127 HERCULES patches comprising the buffers is shown in Fig. 3.

The area-weighted means calculated for each of the HERCULES proportion cover variables summarize the relative importance of each land cover type for each buffer (Fig. 3).

Table 4:
List of bird species detected and determined to be breeding across the study sites. For each species, migratory status in Maryland (R=resident, SD=short-distance, N=Neotropical), number of sites in which it was detected, and the mean density of territories and mean area of sites in which the species was present is given.

Species name	Migratory status	No. of sites	Mean density (terrritories/ha)	Mean patch area (ha)
Acadian Flycatcher (*Empidonax virescens*)	N	3	0.35	4.21
American Robin (*Turdus migratorius*)	R/SD	15	0.88	4.12
Blue-gray Gnatcatcher (*Polioptila caerulea*)	SD/N	3	0.26	5.21
Brown Creeper (*Certhia americana*)	R	1	0.32	3.10
Brown Thrasher (*Toxostoma rufum*)	SD	2	0.19	5.32
Carolina Chickadee (*Poecile carolinensis*)	R	11	0.26	4.64
Carolina Wren (*Thryothorus ludovicianus*)	R	15	0.63	4.12
Common Yellowthroat (*Geothlypis trichas*)	SD/N	3	0.36	2.90
Downy Woodpecker (*Picoides pubescens*)	R	12	0.28	4.42
Eastern Towhee (*Pipilo erythrophthalmus*)	R/SD	7	0.34	5.19
Eastern Wood-pewee (*Contopus virens*)	N	5	0.23	4.26
Great-crested Flycatcher (*Myiarchus crinitus*)	N	3	0.29	4.71
Gray Catbird (*Dumetella carolinensis*)	SD	15	2.87	3.92
House Wren (*Troglodytes aedon*)	SD	9	0.28	4.12
Northern Cardinal (*Cardinalis cardinalis*)	R	15	1.55	4.16
Northern Flicker (*Colaptes auratus*)	R	7	0.20	4.12
Ovenbird (*Seiurus aurocapillus*)	SD/N	1	0.12	5.42
Pileated Woodpecker (*Dryocopus pileatus*)	R	1	0.20	8.30
Red-bellied Woodpecker (*Melanerpes carolinus*)	R	14	0.42	4.97
Red-eyed Vireo (*Vireo olivaceus*)	N	12	0.54	4.19
Red-shouldered Hawk (*Buteo lineatus*)	R	1	0.27	4.32
Scarlet Tanager (*Piranga olivacea*)	N	1	0.27	3.68
Song Sparrow (*Melospiza melodia*)	R	1	0.16	3.68
Tufted Titmouse (*Parus bicolor*)	R	14	0.45	3.20
White-breasted Nuthatch (*Sitta carolinensis*)	R	4	0.19	5.92
Wood Thrush (*Hylocichla mustelina*)	N	12	0.66	4.27

Table 5

Results of principle components analysis (PCA) performed on vegetation and area-weighted means of HERCULES proportion cover variables

A. Vegetation structure	Principle components appearing in regression models
Correlation between original variables and principle component	I (PCA$_{veg}$)
Tree spp/m^2	-0.40
Stem density	-0.54
DBH$_{max}$	+0.40
FHD	+0.35
SSD	+0.51
Eigenvalue	2.67
Percent of variance accounted for	53.49

B. HERCULES analysis		
Correlation between original variables and principle component	I (PCA$_{HERC1}$)	II (PCA$_{HERC2}$)
Building cover	+0.42	+0.14
Coarse vegetation cover	-0.55	+0.15
Fine vegetation cover	+0.39	-0.59
Pavement cover	+0.53	+0.05
Bare soil cover	+0.29	+0.78
Eigenvalue	2.20	1.02
Percent of variance accounted for	43.95	20.47

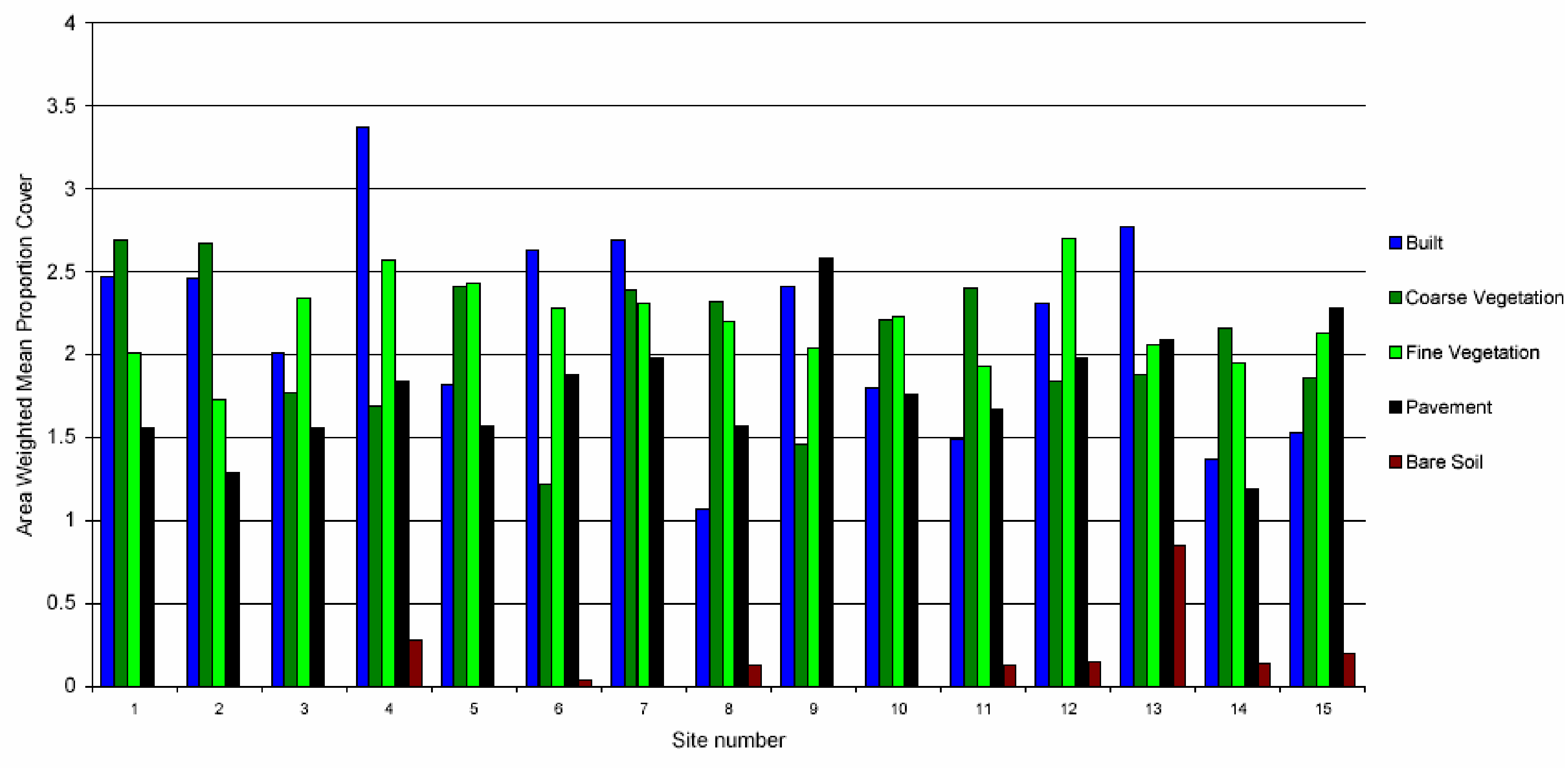

Fig. 3: Area-weighted mean proportion cover of the five land cover variables defining HERCULES patches constituting the 100 m buffers surrounding the study sites.

The first axis constructed from the PCA on these area-weighted means (PCA_{HERC1}) accounted for 43.95% of the variation in the data, and axis two (PCA_{HERC2}) accounted for an additional 20.47% (Table 5); these axes were the only two with eigenvalues greater than one. The interpretation of PCA_{HERC2} is difficult because bare soil cover was the primary source of variation in this axis, but there is very little bare soil cover among the sites. The construction of this axis was strongly influenced by an outlier (site 13), which had a much higher value for area-weighted mean bare soil cover in the buffer than other sites. However, when the PCA was performed excluding this data point, bare soil cover continued to be the dominant factor loading, although a negative relationship with building cover became strongly correlated with this axis. Re-fitting the regression models using the scores on the PCA_{HERC2} axis created by omitting site 13 did not change the conclusions of model selection; therefore, this data point was retained. Fig. 4 shows the relative position of the study sites along the two PCA axes.

HERCULES patch classification was used to calculate area-weighted median neighborhood age. The time elapsed since the majority of residences surrounding the study sites were constructed varied between 6.46 and 60.02 years (32.49±14.73).

2.3.4 Bird Resource Subsidies

The density of bird resources subsidies (SUBDEN) varied between 0.43 and 10.00 subsidies/ha (4.39±2.97) among the buffers surrounding the study sites. Highest densities of subsidies were observed at both extremes of the geographic range covered by the study sites, with lowest values of SUBDEN found at sites in the middle of the watershed (Fig. 5, low site numbers correspond to sites most distant from the city, while high numbers are closest to or within city limits).

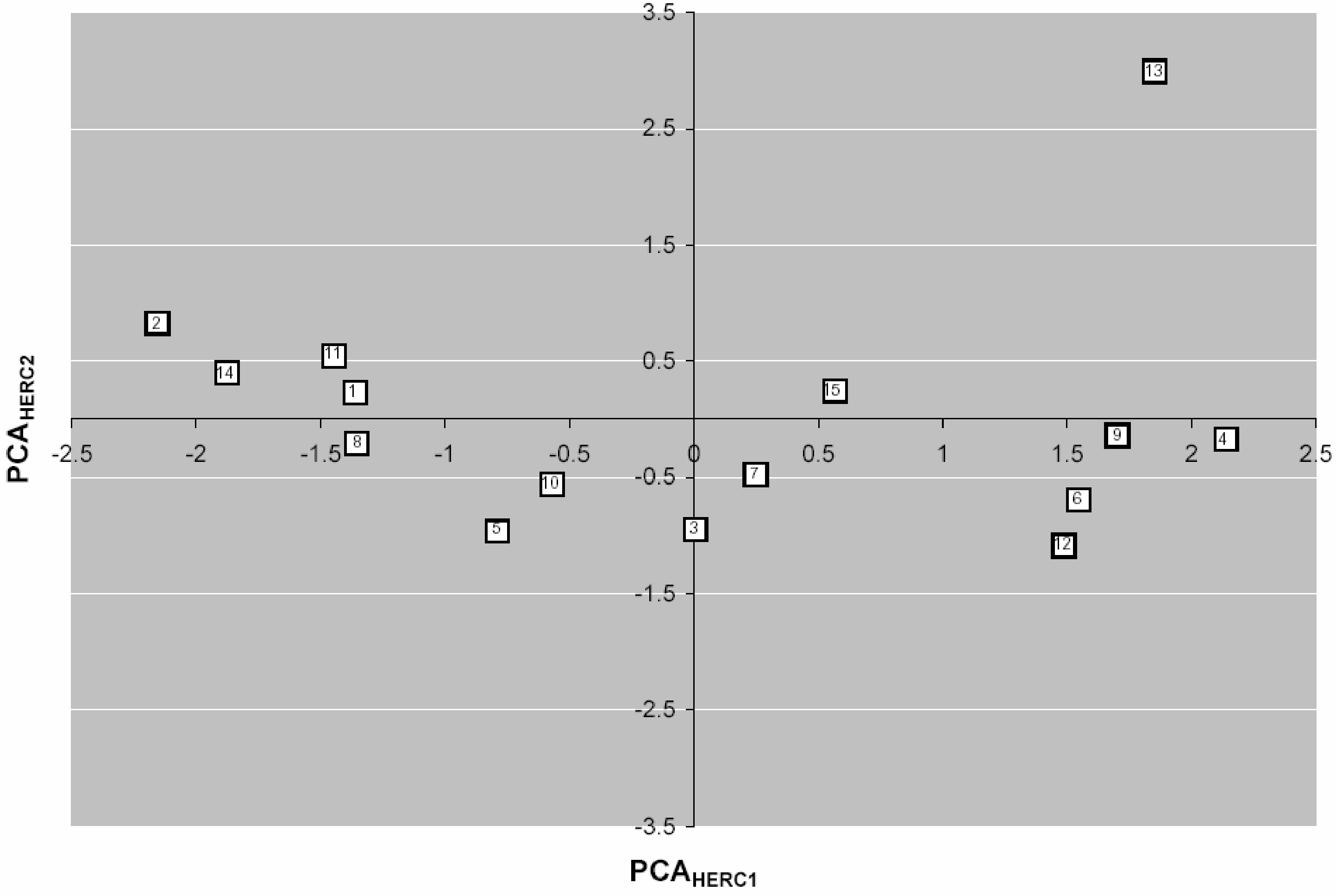

Fig. 4: Position of study sites along the two PCA axes describing proportion cover of various landcover types in the 100 m buffer, with site numbers shown inside data points.

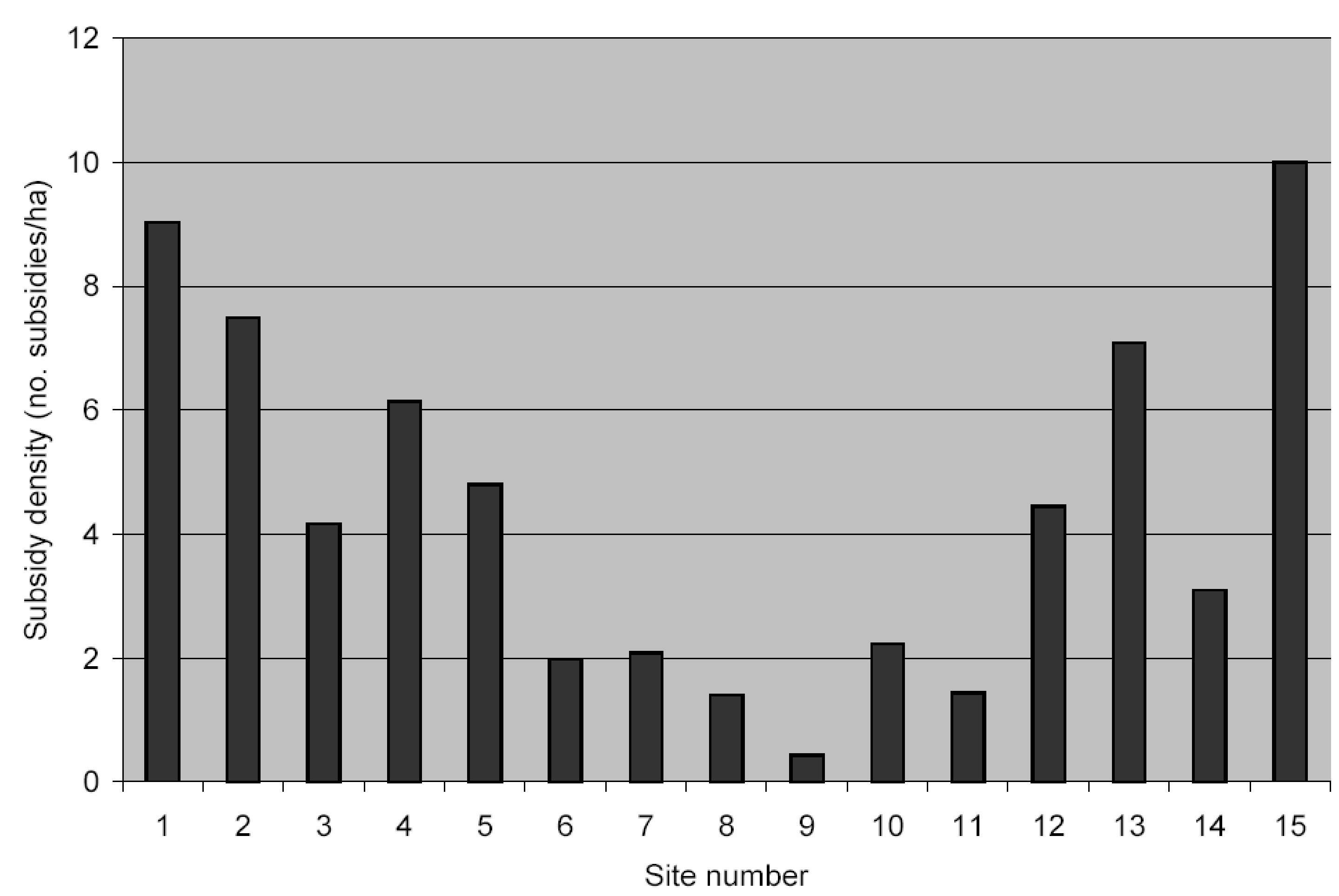

Fig. 5: Variation in estimated density of bird resource subsidies (feeders, baths, and nest boxes) among the 100 m buffers surrounding the study sites.

2.3.5 Model Selection

2.3.5.1 Total Species Richness

Akaike model weights (ω_m) indicate that about 47% of the information contained in the data supports the model containing forest patch area and PCA_{HERC1} as the best model for Total species richness (TSR) (Table 3). There was a negative relationship with PCA_{HERC1}, indicating that TSR decreased with increasing pavement cover, and increased with increasing coarse vegetation cover. PCA_{HERC1} also appeared in two of the next three competing models, all of which had similar values of ω_m, further supporting the inclusion of this variable describing matrix landscape structure in models explaining TSR. The second best model, however, included forest patch area as well as the AGE – AGE^2, indicating that TSR has a concave-down parabolic relationship with neighborhood age (i.e. TSR is greatest in large forest patches surrounded by intermediate-aged neighborhoods). Parameter weights, calculated by summing ω_m for all models containing that parameter, support AREA and PCA_{HERC1} as the most useful variables among those included in the set of candidate models in predicting TSR (Table 6). PCA_{veg}, which describes variation among forest patches in vegetation structure, was less useful in explaining TSR than was the structure of the surrounding neighborhood.

2.3.5.2. Neotropical Migrant Species Richness

The best model for Neotropical migrant species richness (MSR) ($\omega_m = 0.38$) included forest patch area and area-weighted coarse vegetation cover of the 100 m buffer (CV). MSR had a positive relationship with both variables (Table 3), although the relationship to forest patch area was extremely weak, and subject to change directions depending on what other variables were included in the model. CV also appeared in the second best model, which added PCA_{veg} as a predictor. Based on parameter weights, PCA_{veg}, which appeared in three of the top five models,

Table 6

Parameter weightings based on summed Akaike weights (ω_m) of all models containing that parameter. Higher weights indicate support for the inclusion of that parameter in models explaining the response variable.

Parameter	$\sum\omega_m$	Parameter	$\sum\omega_m$	Parameter	$\sum\omega_m$
TSR models		**MSR models**		**TD models**	
AREA	1.00	AREA	1.00	AREA	1.00
PCA_{HERC1}	0.62	CV	0.60	URBAN	0.11
AGE	0.24	PCA_{veg}	0.34	PCA_{veg}	0.07
AGE^2	0.19	SUBDEN	0.08	SUBDEN	0.07
PCA_{veg}	0.17	AGE	0.07		
PCA_{HERC2}	0.10				

was relatively useful in predicting MSR; in all models containing $\mathrm{PCA}_{\mathrm{veg}}$, the number of Neotropical migrant species increased with $\mathrm{PCA}_{\mathrm{veg}}$, implying that MSR was higher in structurally complex forest patches. Neighborhood age and subsidy density both had limited utility in explaining Neotropical migrant species richness (Table 6), and the direction of the relationship with neighborhood age differed among models. Any relationship between MSR and neighborhood age suggested by the individual models is suspect, as the relationship changed if there were other, minimally collinear variables included in the model. It should be noted, however, that none of the candidate models produced a particularly good fit to the data; even the highly parameterized global model had an R^2 of only 0.48 (Table 3).

2.3.5.3. Total Density

Total density (TD) had a strong negative relationship with forest patch area; the best model selected included only AREA as a parameter. The weight of this model ($\omega_m = 0.76$) far exceeded any of the other competing models, implying that no other explanatory variable added sufficiently enough information to justify the inclusion of additional parameters in models predicting avian density (Table 3). Interestingly, TD had (weak) negative relationships with subsidy density and degree of urbanization, which is opposite what was predicted by a priori hypotheses. Therefore, even if these variables appeared in the selected best model, the inference that could be drawn from those models is limited, as the fitted model parameters did not align with the justification for including the variable in the models.

2.3.6. Post hoc Analyses

For each response variable, there were two correlated explanatory variables not explicitly tested in the model selection procedures. Fitted linear regression models of these unexpected relationships are shown in Fig. 6.

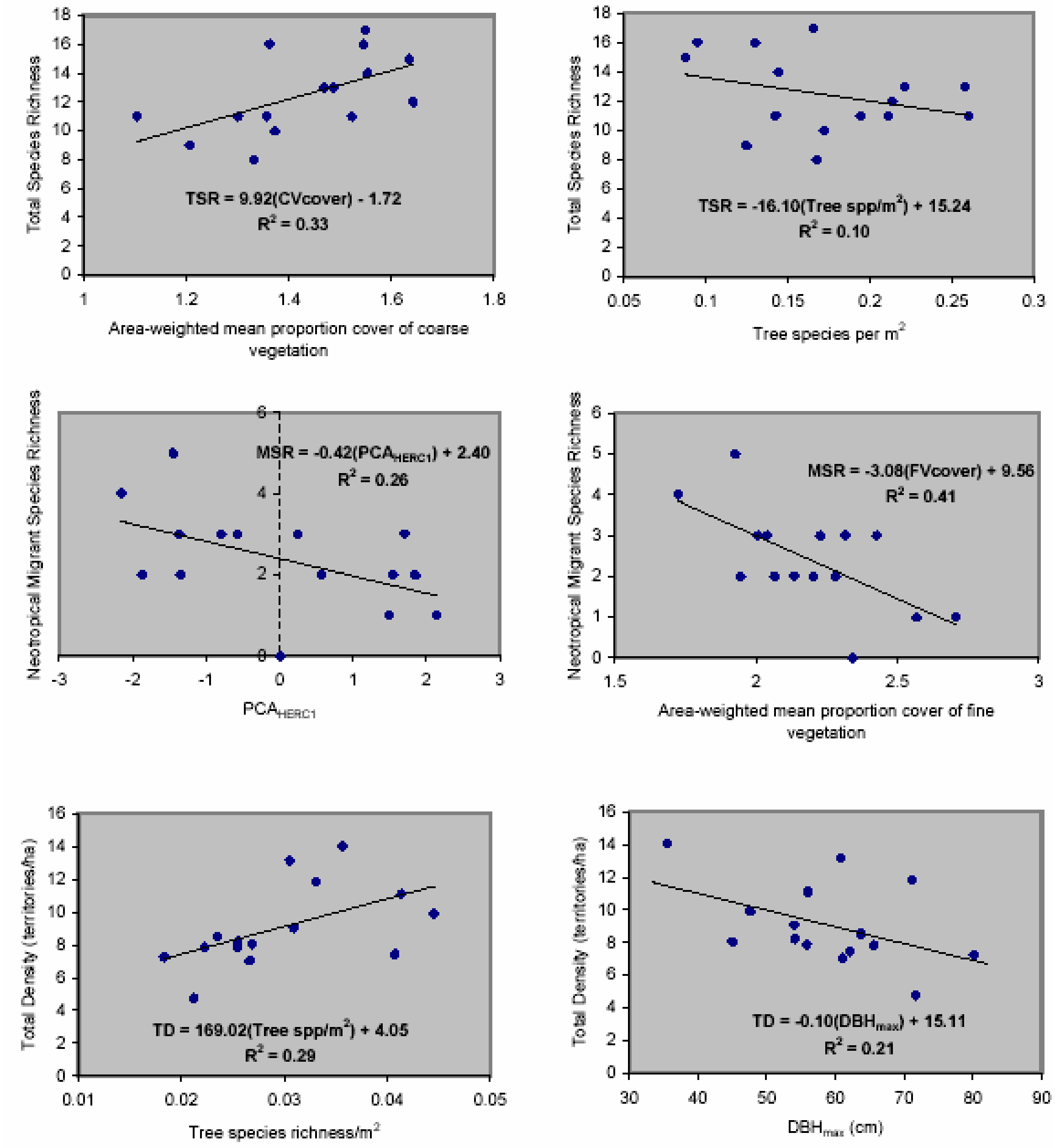

Fig. 6: Fitted regression models from post hoc analyses, showing unexpected relationships between explanatory variables and response variables revealed in a correlation matrix constructed for each response variable.

The direction of the relationships between the response variables and the individual vegetation and HERCULES cover variables were examined in a correlation matrix to determine if they were consistent with other research and made biological sense. For TSR, we wanted to compare using the most highly correlated HERCULES proportion cover variable as an explanatory variable to using the PCA axes to determine if including a measure of composite measure of variation in landscape structure performs better than data on one specific cover type. We fit linear regression models for TSR using CV, PCA_{HERC1} (alone), and PCA_{HERC1} and PCA_{HERC2} as predictors (Table 7). Coarse vegetation cover in the 100 m buffer performed better as a predictor of species richness in embedded forest patches than composite indicators of landscape structure. Because two individual HERCULES variables (area-weighted proportion cover of fine-vegetation and coarse-vegetation) correlated with MSR, a similar analysis was performed for this response variable. Once again, the individual cover variables performed better than the composite landscape structure data contained in the PCA_{HERC} axes.

2.4. Discussion

A distinction between ecology *in* the city to ecology *of* the city has been made with respect to empirical ecological studies in urban landscapes (Grimm et al., 2000). The first focuses on patterns and processes within specific patch and land use types; the second takes a systems approach to investigating the flow of critical resources through the entire urban landscape, operating as a subsystem of the regional landscape. However, these designations are not mutually exclusive; they represent a spectrum of approaches to urban ecological research. While the present study describes patterns of biodiversity within a single land cover type (forest), the integration of data concerning adjacent, highly-managed patches can contribute to a holistic understanding of landscape function (Pickett et al., 2001). Our bird community models

Table 7

Results of post hoc analyses investigating direction and strength of relationships between response and predictor variables.

A. Direction of relationship between response original variables and variables entered into PCAs

Variable	Direction of relationship		
	TSR	MSR	TD
HERCULES area-weighted proportion cover			
Buildings	-	-	+
Coarse vegetation (CV)	+	+	+
Fine vegetation (FV)	-	-	-
Pavement	-	-	-
Bare soil	-	-	-
Vegetation structure			
Tree spp/m^2	-	-	+
Stem density	-	-	+
DBH$_{max}$	+	+	-
FHD	+	+	-
SSD	+	+	-

B. Fitted regression models comparing the use of individual highly correlated HERCULES cover variables to using PCA$_{HERC}$ axes as explanatory variables. CV=area-weighted mean proportion cover of coarse vegetation (square root transformed), FV=area-weighted mean proportion cover of fine vegetation.

	P	R^2
$TSR = -1.72 + 9.92(CV) + \varepsilon$	0.03	0.33
$TSR = 12.47 - 0.88(PCA_{HERC1}) + \varepsilon$	0.07	0.23
$TSR = 12.47 - 0.88(PCA_{HERC1}) + 0.18(PCA_{HERC2}) + \varepsilon$	0.19	0.24
$MSR = 9.16 - 3.08(FV) + \varepsilon$	0.01	0.41
$MSR = -3.73 + 4.29(CV) + \varepsilon$	0.04	0.29
$MSR = 5.48 - 2.38(FV) + 1.04(CV) + \varepsilon$	0.01	0.52
$MSR = 2.40 - 0.42(PCA_{HERC1}) + \varepsilon$	0.04	0.26
$MSR = 2.40 - 0.42(PCA_{HERC1}) + 0.32(PCA_{HERC2}) + \varepsilon$	0.10	0.32

incorporated variables in a hierarchical form, first accounting for patch-level variation before considering local matrix variation. This is consistent with the modeling framework suggested by Grimm et al. (2000). Incorporating variables reflecting the behavior and culture of the human residents occupying the landscape matrix adds to the understanding of the flow of critical resources between and among patches (Grimm et al., 2000), increasing our ability to decipher how individual environmental decision-making shapes residential areas. Our findings about patterns of biodiversity within this urban landscape suggest inferences regarding the complex, interacting ecological and sociological processes controlling biological communities across the landscape as a whole.

It is worth noting that distinct relationships between breeding bird communities in forest patches and the neighborhoods surrounding the patches were indeed observed at the spatial scale used in this study (100 m). Other studies have detected relationships between forest-dwelling bird community structure and urbanization variables quantified within this narrow buffer width (e.g. Dunford and Freemark, 2005; Friesen et al., 1995). Lending additional credence to these findings is the fact that all of the correlations between the response variables and HERCULES land cover variables were in the direction that would be expected based on previous research (e.g. Friesen et al., 1995; Tilghman, 1987), with the exception of total density, which we expected to have a positive relationship with pavement cover.

We found that forest patch vegetation structure was not particularly useful in explaining variations in bird community structure among study sites. While the principle components axis describing variation in vegetation structure among patches (PCA_{veg}) appeared in one of the top three models for both total species richness and Neotropical migrant species richness, vegetation structure added less information to the models than variables describing the 100 m buffer.

PCA_{veg} also added very little information to models of total avian density. The post hoc analyses showed that density could be explained by individual aspects of habitat structure (i.e. TD increased with tree species richness per unit area, and decreased with DBH_{max}), but overall variation in vegetation structure, as described by the PCA_{veg} axis, did not explain avian density.

It appears that, for small forest patches (<10 ha) in this landscape, the interaction across forest edges with the surrounding mosaic of urban development is more important in structuring forest bird communities than the structure of the habitat itself. This contrasts the recent work of Donnelly and Marzluff (in press), who contend that habitat structure is as important as habitat quantity in explaining bird community structure. However, their larger sample size enabled them to test and detect relationships to a larger suite of variables explicitly describing vegetation structure, rather than representing variation in vegetation structure with a single PCA axis value. Also, the narrow range of patch sizes in this study meant that all sites were edge-rich, and prone to disturbance, which may have limited variation in vegetation structure. Earlier studies (Blake and Karr, 1987) found little relationship between species richness and habitat structure in isolated woodlots. Although there exists some debate among studies, it can be generalized that even if species richness does increase with vegetation complexity, early successional forest patches will conserve different bird species than mature forests. Many species that prefer early successional forest are common, suburban adaptable species that are not of particular conservation interest.

2.4.2. Avian community modeling

2.4.2.1. Total Species Richness

As expected, total species richness (TSR) increased with increasing forest patch area. This finding agrees with the species-area relationships incorporated into island biogeography theory models predicting species richness on islands. However, island biogeography theory also incorporates isolation as a determinant the equilibrium number of species. Truly isolated habitat islands (from a bird's perspective) are rare in urban landscapes, compared to agricultural landscapes (Watson et al., 2005). For birds using habitat islands in urban landscapes, the balance of colonization and extinction may be a function of area and landscape heterogeneity (Blair, 2004), rather than distance between islands. This study confirmed that the number of bird species selecting forest patches as breeding habitat increases with coarse vegetation cover within 100 m of the forest edge. Tree cover immediately surrounding forest patches may be a direct cue in forest bird habitat selection, presumably because it makes patches appear larger, or perhaps by mitigating the isolating effects of fragmentation. It is worth noting that coarse vegetation cover in the 100 m buffer was not correlated with forest patch size, indicating that large forest patches weren't habitat for more bird species simply because they were in a more heavily forested portion of the landscape.

Neighborhood age alone was not a good indicator of bird species richness. The number of bird species breeding in the forest patch could not be explained by the amount of time that had elapsed since the forest was disturbed by construction of the surrounding neighborhood, indicating that time since disturbance is not a good predictor of the number of species accumulation. Recent studies have also failed to detect a relationship between neighborhood age and bird species richness (e.g. Melles, 2005); however, these studies did not include the quadratic form of age in their models. In our study, the quadratic transformation of age (i.e. including AGE and AGE^2) improved models substantially. This finding provides further evidence that forest birds are assessing cover of mature vegetation in the neighborhood in selecting breeding habitat; tree cover peaks at intermediate ages and then decreases as trees die or are removed (Grove et al., in press). To confirm this relationship, we fit a regression model predicting coarse vegetation cover in the 100m buffers using AGE and AGE^2 as predictors. The model produced a good fit (R^2=0.60, P=0.0039).

Choices at time of development (e.g. trees cleared versus left intact, number and species of trees and shrubs installed as landscaping) impact eventual coarse vegetation cover as much as, if not more, than neighborhood age. Total species richness would probably have shown a stronger relationship with neighborhood age if the study design had been stratified by development type or socioeconomic status (Melles, 2005). However, this was not possible due to the fine-scale interspersion of suburban neighborhoods in Baltimore's landscape. Even if bird diversity in forest patches does increase with the maturation of the surrounding residential development, this may reflect succession of the avian community toward suburban adaptable species, and the transition toward assemblages increasingly distinct from the native community occupying the patch prior to fragmentation and development (Chace and Walsh, 2006 and references therein).

While the relation of vegetation structure within the patch to species richness was not as important as the relationship to coarse-scale structure of the surrounding neighborhood, there was a consistent, positive relationship with the vegetation structure PCA axis in all but one low-ranked model. This indicates that more species were found in forests with greater diversity of stem sizes and vertical distribution of foliage, a long-established relationship concerning forest bird species diversity (Macarthur and Macarthur, 1961). Other studies have shown that bird species richness is greatest in disturbed, early succesional forests which, in this study, would have been represented by low scores on the axis (James and Wamer, 1982); however, none of our sites were truly mature forests. Our results indicate that, within a set of early successional forests, vegetation complexity, rather than stem density, may cue more species to select a given forest patch as breeding habitat, although avian species composition can be expected to differ along this axis.

2.4.2.2. Neotropical Migrant Species Richness

Models for Neotropical migrant species richness (MSR) produced the poorest fit to the data of any of the response variables, largely influenced by the limited number of migrant species detected among the sites. We predicted that patch area was of primary importance in predicting the number of Neotropical migrant species selecting a forest patch as habitat; therefore, we included it in all the models. Previous studies have had at least moderate success in predicting the occurrence of long-distance migrants in forest fragments using only patch area (e.g. Blake and Karr, 1987; Friesen et al., 1995). However, our study differed in that the range of forest patch sizes investigated was narrower than previous studies, and may have been perceived as equal in size by migrant species. We found that Neotropical migrant species richness had a very weak relationship with patch area, so weak, in fact, that the direction of the relationship changed depending on what other variables were included in the model. Post hoc analyses revealed that coarse- and fine-vegetation cover in the 100 m buffer had a much stronger relationship with MSR than patch area. The inclusion of area in all the models biased the selection of the best model, because models containing other, more highly correlated variables were penalized for having AREA as an additional term. Future studies using a model selection approach should not bias their results by assuming that area will explain the diversity of Neotropical migrant forest birds in small urban forest patches; none of the migrant species detected in this study are highly area-sensitive (Whitcomb et al., 1981), and their occurrence is therefore inherently unpredictable using forest patch area.

Another possible explanation for the poor fit of the models is that migrants were not intentionally selecting these small habitat fragments, but were being forced into suboptimal territories when they could not establish a territory in a larger fragment (e.g. they were first year males). Another possibility is that inexperienced breeders landed in the small habitat, and stayed in it because the surrounding matrix was hostile and there was no other suitable habitat in sight (Shochat et al., 2002). If either of these explanations were true, it would be impossible to predict the occurrence of migrant species with any of the explanatory variables used in this study.

While adult migrants tend to show high site fidelity following initial establishment of a breeding territory, for many species, natal dispersal distance (i.e. the distance between birth site and first breeding site, established upon returning from the Neotropics their first spring) is largely unknown (Villard et al., 1995). Selection of a poor quality forest fragment due to limited ability to disperse away from natal sites is an unlikely explanation, considering that first season migrants are returning from wintering grounds thousands of kilometers away (Villard et al., 1995). Furthermore, vegetation structure was more useful in predicting migrant richness than any of the other response variables; suggesting that migrant birds are intentionally selecting habitat with desirable qualities (i.e. greater stem size diversity and vertical vegetation complexity). Understanding the relative importance of direct habitat assessment versus innate fidelity to natal sites when selecting territories would assist in drawing conclusions from future studies of the occurrence of Neotropical migrant breeding birds in urban landscapes.

Post hoc analyses revealed that, in addition to a positive relationship with tree and shrub cover in the surrounding neighborhood, migrant species richness had a negative relationship with fine vegetation (i.e. grass and herbaceous) cover. This relationship was stronger than the relationship to tree cover; this suggests that migrant forest birds have a stronger aversion to forest patches surrounded by large expanses of lawn, than an attraction to forest patches surrounded by ample tree cover. It is also interesting that the negative correlation between migrant species richness and building cover (r= -0.18) was not as strong as the negative correlation with fine vegetation cover (r= -0.64)

Although the study sites spanned a large geographic range, the residential land use surrounding all of the sites was typical of suburban areas, and not highly variable in the proportion cover of urban surfaces (e.g. buildings and pavement). If there had been more variation in landscape characteristics among the sites, particularly in building density (Friesen et al., 1995) we may have seen a stronger relationship to landscape variables (Weyrauch and Grubb, 2004), and could have confirmed broad-scale urban avoidance (Blair, 1996) by Neotropical migrant bird species.

A few migrant species were fairly common in this urban landscape. Whitcomb et al. (1981) noted that, out of the 30 species documented to commonly breed in small- to medium-sized forest patches, six were restricted to forest interior (Acadian Flycatcher and Wood Thrush) or forest interior and edge (Eastern Wood-pewee, Great-crested Flycatcher, Red-eyed Vireo, and Wood Thrush). Their list of species exactly matches the list of Neotropical migrants detected among our study sites. It is worth noting that we failed to detect any of the edge-adapted Neotropical migrant species that they reported breeding in small forest patches (e.g. Indigo Bunting). In our study, forest patches <10 ha did provide interior habitat to migrant birds, and perhaps the positive relationship between MSR and coarse vegetation cover in the surrounding neighborhood indicates that a buffer zone with ample tree cover expands the perceived core-area of these forest fragments.

Some of our results do not agree with other studies of Neotropical migrant forest birds in urban landscapes. Most notably is the occurrence of the Wood Thrush, which was among the most common long-distance migrant species detected. Whereas previous studies in the mid-Atlantic states have shown that this species is tolerant of fragmentation (Robbins et al., 1989; Roth and Johnson, 1993), Freisen et al. (1995) observed that this species disappeared from woodlots as development surrounding the forest increased; the contrast with their results is especially dramatic when you consider that their methods would have classified the buffers surrounding all of our sites as high-development. However, their study was conducted in Ontario, Canada, which is at the extreme edge of the breeding range for this species. Other conflicts with previous research include the common occurrence of Red-eyed Vireos, reported to prefer larger forest patches in Maryland (Whitcomb et al., 1981), and the Eastern Wood-Pewee, reported to prefer large forest fragments surrounded by low- or no- development (Friesen et al., 1995; Tilghman, 1987), but occurring in 80% and 33% of sites in this study, respectively.

It was thought that neighborhood age would give some indication as to whether community relaxation occurred in these woodlots, as sensitive species went extinct and suburban-adapted species colonized following development (Blair, 2001 and sources therein). However, the age of surrounding neighborhoods had a negligible relationship with MSR, and the sign of the relationship changed depending on what other variables were included in the model, rather than being negative, as predicted by a priori hypotheses. However, if community relaxation does occur, it can be expected to happen over fairly short time-scales, comparable to the breeding life-span of migratory songbirds (<10 years), as individuals return to breeding territories after development, but then aren't replaced by new immigrants after they die. Time-series data on bird communities, before and immediately following development could confirm over what time scales community relaxation occurs.

We found a negative relationship between migrant species richness and the density of resource subsidies. However, it is unwise to draw inferences from this result, due to the poor fit of the models, and the fact that total density also had a negative relationship with subsidy density. The justification for predicting that migrant species richness would have an inverse relationship with subsidy density was because highly subsidized forest patches would be saturated with individuals of more human-tolerant species, including generalist predators. Since this relationship was not observed, we can offer no mechanistic explanation for the decrease in MSR with increased subsidy density. We conclude that this relationship was an artifact of the small sample size.

Even though the occurrence of long-distance migrants holding breeding territories was limited, that does not negate the value of these forest patches to Neotropical migrant birds. Small woodlots in landscapes where natural habitat is rare are probably more important for migrants as stopover points than as breeding habitat (Blake, 1986). Several migrant species were detected in the study sites on single occasions early in the study period, including, American Redstart (*Setophaga ruticilla*), Chestnut-sided Warbler (*Dendroica pennsylvanica*), Northern Parula (*Parula americana*), and Veery (*Catharus fuscescens*).

2.4.2.3. Total Density

The strong negative relationship between patch area and avian density was unexpected. We believe that this can best be explained by the high edge-to-area ratios of these small woodlots (Suhonen and Jokimaki, 1988; Whitcomb et al., 1981); in the smallest study sites, this ratio was highest (especially in the many linear sites), providing abundant edge habitat for dense populations of suburban adaptable birds (e.g. Northern Cardinal). The smallest forest patches were therefore acting as an extension of the neighborhood, rather than the neighborhood acting as an extension of the forest.

Other studies have found that urban landcover and habitat quality does little to explain variation in avian density in forest patches (e.g. Tilghman, 1987), which justifies inclusion of additional variables, such as availability of resource subsidies in the surrounding neighborhood. An increase in the number of bird feeders was used to explain change in abundance over time in urban parks (Morneau et al., 1999). We hypothesized that this variable might be useful in explaining variation beyond what can be explained by forest patch characteristics and urban land cover alone. Apparently, direct resource subsidies provided by neighborhood residents are not as important as indirect subsidies provided to suburban adaptable birds by fragmentation (forest edge). Density of breeding bird territories within the forest patch did not increase with urban land cover (pavement and buildings) surrounding the forest. Apparently, the tendency for avian density to increase with urbanization did not appear to permeate the forest, although there may not have been enough variation in urban land cover across the sites to detect this broad-scale trend.

While these data show that small habitat fragments in residential developments can provide habitat for dense populations of urban birds, this should not be interpreted as advocating smaller fragments as valuable conservation reserves. Although their was very little relationship between total density and PCA_{veg}, post hoc analyses revealed that density had opposite relationships with the individual vegetation variables when compared to richness or migrant richness. Among the study sites, forests in very early stages of regeneration served as breeding habitat to only a few synathropic, over-abundant species. Density has little relevance to bird conservation planning (Palomino and Carrascal, in press), as the birds inhabiting these densely packed habitats are not conservation targets. Rather, small habitat fragments facilitate the development of homogenous avian communities (Blair, 2001).

2.4.3. Suggestions for future research

While the best models selected by the AIC_c statistic for total species richness and total density produced a fairly good fit to the data ($R^2 = 0.68$ and 0.73, respectively), the ability to predict the number of Neotropical migrant species selecting a given forest patch based on the variables assessed was limited ($R^2 = 0.30$ for the best model). Synthesis of research on birds utilizing habitat patches in urban landscapes can enable planners to use models to predict effects of development on forest bird richness and abundance (Palomino and Carrascal, in press), but more research is clearly necessary to determine if we can manage for sensitive species in urban environments.

The density of resource subsidies has been infrequently explored as an explicit determinant of urban bird community structure (Bolger, 2001; but see Johnsen and VanDruff, 1987), in spite of the fact that shifts in trophic structure and density of bird communities along an urban gradient are often explained by the abundance of supplementary food resources provided by humans (Marzluff, 2001). Subsidies such as bird feeders, nest boxes, and water sources are interesting variables that should be incorporated into future research designs, because they represent cultural resources directly and actively managed at the scale of the individual land parcel. We failed to detect a definitive relationship between the density of bird resource subsidies and bird community metrics; variation in subsidy density may be unimportant among these study sites, but may be important in different urban landscapes, or across sites imbedded in more variable matrices. Future studies should also focus on improved methods for quantifying the degree to which the resource base available to birds is supplemented by homeowners. Making generalizations about variation in management of private property is a major challenge for working in urban landscapes. In single family neighborhoods, management of backyard vegetation and amenities is often drastically different from frontyard landscaping, making it difficult to estimate the occurrence of bird feeders, baths, and nest boxes without gaining access to numerous private properties (Melles, 2005). We believe that the method used in this study to estimate subsidy density (i.e. verbal and visual surveys) provides more conservative estimates than would be achieved using mailed surveys (sensu Lepczyk et al., 2004) for which the sample of respondents may be biased toward those that put effort into attracting and observing birds in their yard.

An alternative strategy for improving the understanding of the relationship between bird resource subsidies and bird community structure could involve looking for strong relationships between easily measured variables and the occurrence of subsidies, and then testing these variables in future studies as surrogates for subsidy occurrence. We thought there may be a relationship between subsidy density and neighborhood age, as older neighborhoods are often home to many senior-aged residents, for which bird feeding and watching is a common pastime. However, we found no correlation with neighborhood age. Housing type (single versus attached) and socio-economic status predict the proportion of resources that can be devoted to shaping outdoor surroundings (Hope et al., 2006; Kinzig et al., 2005; Martin et al., 2004). If consistent relationships with these variables were established through detailed studies of subsidy occurrence, possible mechanistic explanations of variation in bird communities among neighborhoods of varying structure and socioeconomic status (e.g. Kinzig et al., 2005) could be offered.

While this study focused on beneficial bird subsidies, we are not unaware of the fact that there are direct harmful subsidies managed by homeowners, such as allowing domestic cats (*Felis catus*) to roam outdoors and potentially hunt birds. Cat ownership and the decision to allow cats outside is probably the strongest determinate of cat predation, which is influenced by socioeconomics, culture, and education. Additionally, suburban areas, and specifically bird feeders, attract gray squirrels (*Sciurus carolinensis*), which may be important nest predators of forest passerines (Leimgruber et al., 1994), although this has not been explored in urban landscapes.

This study investigated characteristics of suburban neighborhoods that influence avian habitat selection, but we have made no conclusions regarding whether these patches are sources or sinks. This can only be determined by habitat-specific demographic rates, as the assemblage of species in a given habitat patch may be the consequence of populations in neighboring habitats having growth rates greater than one, and does not necessarily reflect the resources and conditions of the habitat itself (Pulliam, 1988). Because the cultural resource variable with the strongest positive correlation with bird diversity in this study (tree and shrub cover in the surrounding neighborhood) is also positively correlated with abundance of nest predators (Sinclair et al., 2005), assessing breeding success is crucial to understanding whether small urban forest patches can actually improve the likelihood of species persistence at a landscape scale.

Careful analysis of socioeconomic variables may improve understanding of ecological patterns that are generated by the culture of human residents inhabiting urban landscapes (Kinzig et al., 2005). Socioeconomic factors such as race, education and income have been used as predictors of ecological phenomena; however, complex aspects of culture (e.g. behavior) aren't quantified by socioeconomics alone (Grove et al., in press) and social scientists have questioned the assumptions or bias that would predict such a relationship between socioeconomics and behavior. Instead, social scientists are beginning to turn toward datasets such as PRIZM (Potential Rating Indicators for Zip Markets) (Claritas, 1999) that focus on the people's choices as consumers. This data set incorporates the traditional socio-economic descriptors but also includes information on point of purchase receipts such as food, home and garden, and media choices. This additional information is used in an ordination analysis to develop the lifestyle clusters. In other BES investigations, PRIZM clusters have proven to be better predictors of vegetation cover on both private lands and public right-of-ways than standard socioeconomic variables (Grove et al., in press). A similar analysis could be used with bird data, comparing the efficacy of different suites of predictor variables (e.g. explicit socioeconomic data versus lifestyle clusters) in explaining the structure of bird communities in urban forest fragments.

Of course, any "snapshot" study needs to be complemented by data collected across greater temporal and spatial scales (Hostetler and Knowles-Yanez, 2003). Landscape-scale studies which involve the collection of field data often have a limited sample size; in this study, the inability to explain the occurrence of migrants was affected by the limited number of migrant territories detected among the study sites. Whenever possible, a larger sample size will decrease the chance of detecting spurious relationships.

2.4.4. Recommendations for design and management

An abundance of research, including the results of this study, suggests that larger natural areas in urban landscape will better conserve avian species. The urban woodlots examined in this study are much smaller than what would be recommended as a reserve, but small forest patches have the advantage of being abundant, and are often already protected from development as riparian areas. A network of small forest patches embedded in residential matrices can be an important component of urban bird conservation strategy, particularly if the surrounding neighborhoods are managed as buffers (Watson et al., 2005).

Maintaining tree cover in neighborhoods appears to be the most direct method of increasing bird diversity in remnant forest patches. This suggests that broader-scales of management (subdivision or city planning level) may be more efficient means of improving forest bird habitat from outside of the forest boundary than working at the scale of the individual land parcel, because canopy retention is largely determined by subdivision design and development practices (Donnelly and Marzluff, 2006). Kinzig et al. (2005) and Melles (2005) both concluded that top-down management plays an important role in structuring urban bird habitat. However, the small buffer width used in this study indicates that tree maintenance at fine scales can affect bird habitat selection of embedded forest patches. Reducing open lawn size and maintaining tree cover can be achieved by individual homeowners, and can contribute to broad-scale landscape heterogeneity (Grimm et al., 2000; Hostetler and Knowles-Yanez, 2003; Melles, 2005). Maintaining heterogeneous interspersion of forest and development, while maximizing the retention of tree canopy, can mitigate the deleterious effects of urbanization on native faunal communities (Blair, 2004; Donnelly and Marzluff, 2006; Palomino and Carrascal, in press; Sodhi et al., 1999). There exist many challenges to effecting this change at the level of individual properties, including confronting the culture of status in suburban neighborhoods associated with neatly manicured, open lawns (Bormann et al., 2001; Grove et al., 2006). New strategies are needed to convince homeowners, particularly those living adjacent to forest patches, of the multiple advantages to having a well-shaded yard. Incentives toward shifting yard management practices could include certification of yards as bird-friendly (Donnelly and

Marzluff, 2006), constituting an attempt to shift the attachment of prestige from the manicured lawn to the multilayered, complex yard habitat.

While we have focused on the quality of cultural resources managed outside of remnant forest patches, there was ample evidence that residents are impacting the quality of resources in the forest patch itself. It was not uncommon to observe homeowner land management extending into the woods: adjacent to residential lawns, understory and herbaceous vegetation was often cleared. This decision could be based on a desire for a neatly organized appearance to the boundaries of the yard, or a concern for safety in maintaining a clear view of the wooded edge. This presents yet another aspect of culturally-influenced land management which needs to be addressed (Blewett and Marzluff, 2005), so that homeowners are comfortable with, and appreciate the aesthetic value of, living adjacent to an unmanaged natural habitat.

The impact of neighborhood residents also extended into the core of the woods: almost all sites had trails or other evidence of human use, even though none of the sites were managed for recreation. Many sites were highly degraded. Residents used the woods to dump landscaping and household refuse (see also Tilghman, 1987), and less obvious damage was facilitated in the form of damage to regeneration (i.e. trampling), and facilitation of invasion by exotics along foottrails (Pickett et al., 2001). We suggest that community associations could adopt embedded forest fragments as reserves, stewarding them to avoid degradation due to litter, fires set by youth (observed once during the study period), and blazing of additional trails. Most of these sites existed as intact woodland only because they were riparian or floodplain areas; since the county already recognizes them as protected areas, the infrastructure exists to assign stewardship responsibilities to local residents. Such a program could foster wildlife interaction, and increase the aesthetic and economic value of having natural habitat close to private property

(Hale et al., 2005). However, increased visitation can cause decreased reproductive success (Chace and Walsh, 2006 and references therein); therefore, guidance for proper, low-impact management could be provided by local environmental and ornithological societies.

Due to their small size, remnant forest patches embedded in the matrix of suburban neighborhoods will probably never support the full range of native bird species. In fact, it is probably desirable that sensitive species do not select these small fragments as habitat due to high levels of nest failure in small forest fragments due to predation, brood parasitism (Robinson et al., 1995), and nest abandonment (Blair, 2004). Efforts to conserve bird diversity in urban landscapes must consider what are the most relevant and reasonable conservation targets. Perhaps the most realistic management goals in urban landscapes are those that allow residents to experience a diversity of birds in their surroundings, without unrealistic ambitions of restoring native biotic communities or conserving species. It is reasonable to manage for a diverse community of birds, even if this community is made up primarily of common, suburban adaptable species.

Bird diversity often peaks at intermediate levels of development (e.g. in suburban areas), as landscape heterogeneity is greatest at this range of the urban-to-rural gradient (Blair, 2004). Fifty percent of the U.S. population lives in the suburbs (U.S. Census Bureau, 1999) creating an enormous occasion for resident engagement in environmental observation and conservation in urban landscapes. Suburban development is a recent phenomenon, bringing people into daily contact with habitats not present in urban centers (Pickett et al., 2001); these opportunities for environmental orientation of suburban residents should not be missed. A diverse avian community increases human perception and appreciation of birds more so than the simple abundance of birds (Clergeau, Mennechez et al., 2001). Experiencing biodiversity in the local environment can improve quality of life for urban residents (Fernandez-Juricic, 2004) and influence individual decisions about the environment at broad scales (Middleton, 1994). Therefore, creating a human habitat which supports a diverse avifauna stands to increase environmental awareness among urban residents.

As summarized by Nilon and Pais (1997), wildlife conservation efforts in urban landscapes can serve two broad purposes: to serve as integrated components of regional planning for species conservation, or to increase opportunities for human-wildlife interactions. The results of this study suggest that the historic SLOSS (Single Large or Several Small) debate (Diamond et al., 1976) should consider the relative importance of these two purposes when approaching the question of conservation area design in urban landscapes. Large habitat reserves are likely the only real way to provide habitat for intact native bird communities, which include sensitive species, in urban landscapes. The sum of many small habitat fragments in urban areas will probably not have greater gamma diversity than a single large reserve, as they will likely be dominated by similar suites of urban- and surburban-adapted edge species. However, the several small approach still has conservation value, as experiencing a diverse avifauna, even if it is composed of common species, can affect valuation of biodiversity, and therefore indirectly benefit broader conservation goals.

Environmental education and outreach efforts directed at suburban residents are perhaps most important in less affluent neighborhoods, where residents are less likely to experience and appreciate biodiversity (Kellert, 1984; Kinzig et al., 2005); they are raised in "biological poverty" and are therefore unable to assess ecological health of their surroundings (Melles, 2005). If increasing attention is not paid to managing wildlife in economically depressed areas, the environment will continue to erode (Melles, 2005), and residents will have no base-line experience against which to compare deteriorating conditions, further dissociating them from nature (Turner et al., 2004).

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