

# Forest bird communities across a gradient of urban development

Emily Minor · Dean Urban

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**Abstract** This study examined native bird communities in forest patches across a gradient of urbanization. We used field data and multivariate statistical techniques to examine the effects of landscape context, roads, traffic noise, and vegetation characteristics on bird community composition in the North Carolina Piedmont (U.S.A.). Landscape-level variables, particularly those related to urbanization, were most important in structuring forest bird communities. Specifically, we found that road density and amount of urban land cover were the best predictors of species composition. We found that urban and rural bird communities were quite distinct from each other. Rural communities had more long-distance migrants and forest interior species but species richness did not differ between the communities. Our results suggest some specific guidelines to target bird species of interest both inside and outside of urban areas. For example, if increasing numbers of migratory species is of primary concern, then conservation areas should be located outside of urban boundaries or in areas with low road density. However, if maximizing species richness is the focus, location of the conservation area may not be as important if the conservation area is surrounded by at least 50 m of forest habitat in all directions.

**Keywords** Roads · Forest patch · Bird communities · Urbanization · Fragmentation · Management

## Introduction

Alteration or loss of native habitat to urbanization is a growing global phenomenon with important ecological implications. Species vary in their ability to adapt to human

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E. Minor (✉) · D. Urban  
Nicholas School of the Environment, Duke University, Box 90328, Durham, NC 27708, USA  
e-mail: [eminor@uic.edu](mailto:eminor@uic.edu)

*Present Address:*

E. Minor  
Department of Biological Sciences (M/C 066), University of Illinois at Chicago, 845 W. Taylor Street,  
Chicago, IL 60607, USA

development: some, such as rock doves (*Columba livia*), thrive (Ewins and Bazely 1995), while others, such as the ivory-billed woodpecker (*Campephilus principalis*), are driven out of the area or to extinction (Jackson 2006). Beyond these familiar examples, however, we have much to learn about the way that species respond to anthropogenic disturbance and how we can minimize the impacts of urbanization on native communities.

Several studies have described the differences between urban bird communities and those in native habitats. When native habitat is replaced by golf courses, residential neighborhoods, and business districts, the resulting change in bird communities is dramatic: species richness and abundance are altered and community composition shifts from predominantly native species to a set of urban-adapted species (often non-native) that are found in cities around the world (Blair 1996; Jokimäki et al. 1996; Blair 2004; Stratford and Robinson 2005), in a process called biotic homogenization (McKinney and Lockwood 1999; McKinney 2006). Common trends seen along the urban gradient include a peak in avian species richness at intermediate levels of urbanization (Tratalos et al. 2007) and higher densities of birds in urban areas (Palomino and Carrascal 2006). However, with some notable European exceptions (Jokimäki 1999; Mörtberg and Wallentinus 2000; Fernandez-Juricic and Jokimäki 2001), fewer studies have examined bird communities in native habitat patches surrounded by human development. Remnants of native vegetation are often left intact in areas of human development in the form of parks, reserves, or simply undeveloped parcels. Questions of ecological and conservation interest surround the bird communities on these remnants: Do they differ from other communities in similar habitat types, and, if so, how and why? Can these remnants be useful for conservation of native species? More work is needed to answer these questions and guide management of natural areas in urban settings.

It is well documented that forest bird communities are affected by both the amount of forest habitat (Renjifo 2001; Rodewald and Yahner 2001; Lee et al. 2002; MacFaden and Capen 2002; Mitchell et al. 2006) and the other land cover types (Dunford and Freemark 2005; Watson et al. 2005) in the surrounding landscape. For example, studies have shown that a matrix of human development adversely affects Neotropical migrants (Rottenborn 1999; Dunford and Freemark 2005; Rodewald and Bakermans 2006) and insectivores (Rottenborn 1999; Glennon and Porter 2005) while increasing total bird abundance (Fraterrigo and Wiens 2005). More specifically, density of and distance to roads (Brotos and Herrando 2001; Fraterrigo and Wiens 2005; Glennon and Porter 2005) and density of buildings (Friesen et al. 1995; Fraterrigo and Wiens 2005) have been shown to strongly affect avian community composition. Road proximity is thought to be important for abundance and diversity of birds as well (Brotos and Herrando 2001; Forman et al. 2002; King and DeGraaf 2002; Gutzwiller and Barrow 2003), although the effects appear to be species- and landscape-specific. Despite the excellent work on this topic to-date, our understanding of how bird communities respond to human disturbance is still insufficient to provide managers with specific guidelines for creating nature reserves both in and out of city limits.

The objective of this study is to better understand the effects of human development on forest bird communities across a gradient of urbanization. Specifically, this research examines the effects of varying landscape contexts, roads, traffic noise, and vegetation characteristics to address several questions: (1) does community composition of forest birds change across a gradient of urban development, (2) if so, what are the important variables driving these changes, and (3) from a management perspective, can urban forests be useful habitat for conservation of native species? Finally, we wish to use the results of our research to make some specific recommendations to planners and park managers in urban areas.

## Methods

### Study site

This research was conducted in the Triangle region of the North Carolina Piedmont, an area defined by the cities of Durham, Raleigh, and Chapel Hill. The dominant vegetation on relatively undisturbed locations is deciduous forest composed of oaks (*Quercus spp*) and hickories (*Carya spp*) along with other hardwood species. Recently disturbed locations often are dominated by loblolly pine (*Pinus taeda*), which gradually transition to hardwood over the years. In the last few decades, urban development has increased at a remarkable pace (Hess et al. 2000), and today the Triangle contains a heterogeneous mix of land uses and development intensity. In particular, it includes areas of intense development (metropolitan Raleigh) to the east, and largely agricultural areas to the west. At the time of the 2000 U.S. Census, the population in the Raleigh-Durham metropolitan area was 1,314,589 and population density was 930/km<sup>2</sup> within Raleigh city limits (U.S. Census Bureau). Despite the intensity of human development, the area remains fairly forested; satellite imagery from 2001 indicated that 52% of the landscape is covered by pine, hardwood, or mixed forest.

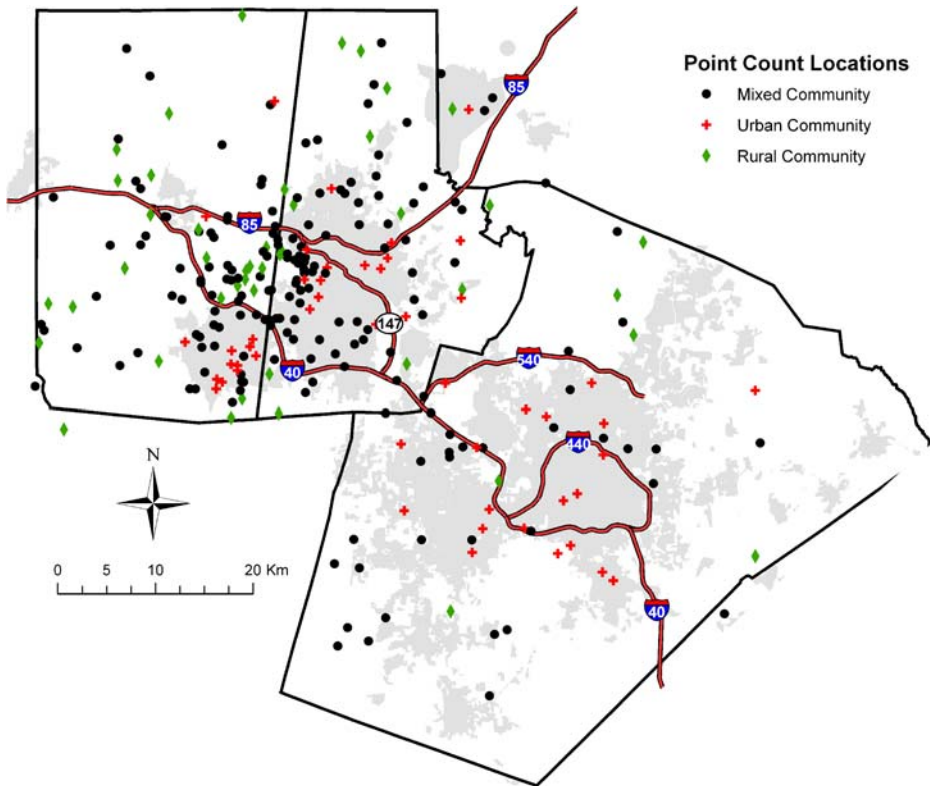
### Data collection

The data were collected from 272 point counts spread across the Triangle with a minimum separation distance of 300 m between points (Fig. 1). Study sites were located in city, county, and state parks, natural areas set aside by local conservation groups, state game lands and other state property, and privately owned woodlands. Sample locations were generally similar at the stand level; all were in mature, mixed pine and hardwood forests with a mostly closed canopy. Sites did vary in understory vegetation, topography, and proximity to rivers or streams. They also varied greatly in landscape context, proximity to a variety of roads, and size of forest patch (Table 1).

All points were surrounded by at least 50 m of forest in all directions. Most points were away from roads and foot trails, but about 20% were located either on footpaths or narrow, infrequently-used, unpaved roads. Footpaths were typically 1 m wide and were assumed not to alter forest structure. We measured distance to nearest road for every point and included this as a predictor variable in our analyses.

*Bird data* Point counts were carried out over four consecutive years, from 2002 to 2005. Because each point count location was censused during only 1 year to maximize sample number, we carefully sampled across the urban gradient each year to minimize bias from year-to-year variation in bird populations. Therefore, if bird populations were low during one year of sampling, that would be reflected in lower numbers across the study gradient and not simply in rural or urban areas.

Each point count location was visited two times during a single breeding season and individual sites were not visited over multiple years. The point counts were 10 min in duration and occurred 0–4 h after sunrise during the breeding season (mid-May to early July). We recorded the number of individuals of each species but subsequently converted abundance data to presence–absence data as we believed it was more reliable. Low visibility in our forested sample locations dictated that the vast majority of bird observations were made by ear rather than by eye; therefore, it was not always possible to distinguish between one very active or several sedentary conspecific individuals. Furthermore, although abundance is typically measured in number of breeding pairs, it was



**Fig. 1** Map of study area (North Carolina Piedmont, U.S.A.). The shaded areas and outer lines delineate municipal boundaries and county boundaries, respectively. Point count locations are shown as dots

difficult to distinguish sex and breeding status in some species in our study (e.g., Corvidae, Picidae). Using abundance or presence/absence data did not appreciably affect our results. Only birds observed within 50 m of the point count location were included, and presence/absence data were pooled for the two repeat visits such that if a species was present during either visit it would be counted as present.

Observed species (Table 2) were classified into various guilds—migratory, foraging strategy, and diet—according to Ehrlich et al. (1988) but modified when necessary based on personal knowledge or local information. Following Ehrlich et al. (1988), diet guild was assigned based on the primary type of food eaten during the breeding season. Additionally, species were assigned a conservation priority score from the Partners in Flight (PIF) species assessment database (Carter et al. 2000). This score, termed the Continental Combined Score (CCS), takes into account habitat vulnerability, population size, population trend, and extent of range, and ranges from four for widespread, numerous, and increasing species to 20 for a species of the highest conservation concern. Species with scores of 14 or higher are on the PIF Continental Watch List for North America.

*Local-scale environmental variables* Vegetation and other environmental variables (Table 1) were measured in the field at each point count location. Three 15-meter transects radiating from each point were used to estimate ground, shrub, and canopy cover for each location. Canopy cover was estimated using a densitometer at the central point and then again at the

**Table 1** Environmental variables measured at each sample location with data mean and range

| Environmental variable    | Description   | Data mean (range)                  |
|---------------------------|---|------------------------------------|
| Local-level variables     |   |                                    |
| BA hdwd                   | Total basal area of hardwoods, measured with a forester's prism                           | 27.1 (0–58 cm)                     |
| BA pine                   | Total basal area of pines, measured with a forester's prism                               | 14.0 (0–58 cm)                     |
| BA snag                   | Total basal area of dead trees (> _cm dbh), measured with a forester's prism              | 1.2 (0–24 cm)                      |
| Canopy                    | % canopy cover, measured with a densiometer   | 94% (67–98%)                       |
| Decid99                   | Deciduous NDVI (from 1999 satellite image) measured as average of four nearest neighbors  | 0.08 (0–0.23)                      |
| Ground veg                | % of ground covered by vegetation   | 58.2% (0–100%)                     |
| Ground wood               | % of ground covered by coarse woody debris  | 2.4% (0–20%)                       |
| Noise                     | Average noise level (in dB) at each location  | 54 dB (49–72 dB)                   |
| Pers99                    | Persistent NDVI (from 1999 satellite image) measured as average of four nearest neighbors | 0.80 (0.59–0.93)                   |
| Shrub                     | % shrub cover   | 43.3% (2.2–97.8%)                  |
| TCI                       | Topographic convergence index, measured as average of four nearest neighbors              | 4.9 (2.7–15.1)                     |
| Landscape-level variables |   |                                    |
| Ag5                       | % of agriculture in a 5 cell radius (7 ha)  | 13% (0–49%)                        |
| Ag20                      | % of agriculture in a 20 cell radius (113 ha)   | 20% (0–69%)                        |
| Ag100                     | % of agriculture in a 100 cell radius (2827 ha)   | 24% (11–51%)                       |
| Allrd500                  | Density of all roads in a 500 m radius  | 4.6 (0–14.2 km/km <sup>2</sup> )   |
| Allrd2000                 | Density of all roads in a 2 km radius   | 4.4 (0.9–13.0 km/km <sup>2</sup> ) |
| Dist.nonfor               | Distance to closest nonforested pixel (i.e., edge)  | 63 (2.5–254 m)                     |
| Dist.pri.road             | Distance to closest primary road  | 1300 m (20.5–7683 m)               |
| Dist.road                 | Distance to closest road of any type  | 87 m (0–656 m)                     |
| Dist.stream               | Distance to closest stream  | 165 m (0–499 m)                    |
| Edge.area                 | Edge:area ratio of patches defined as contiguous forested pixels (4-neighbor rule)        | 178 m (87–431 m)                   |
| For5                      | % of forest cover in a 5 cell radius (7 ha)   | 77% (11–100%)                      |
| For20                     | % of forest cover in a 20 cell radius (113 ha)  | 64% (15–95%)                       |
| For100                    | % of forest cover in a 100 cell radius (2827 ha)  | 59% (32–79%)                       |
| Patch.area                | Patch size, defined as contiguous forested pixels (4-neighbor rule)                       | 22, 072 ha (1.35–51,361 ha)        |
| Prird500                  | Density of primary roads in a 500 m radius  | 0.73 (0–4.5 km/km <sup>2</sup> )   |
| Prird2000                 | Density of primary roads in a 2 km radius   | 0.55 (0–2.1 km/km <sup>2</sup> )   |
| Urban5                    | % of urban cover in a 5 cell radius (7 ha)  | 9% (0–69%)                         |
| Urban20                   | % of urban cover in a 20 cell radius (113 ha)   | 14% (0–62%)                        |
| Urban100                  | % of urban cover in a 100 cell radius (2827 ha)   | 14% (1–45%)                        |
| Water5                    | % of water in a 5 cell radius (7 ha)  | 1% (0–17%)                         |
| Water20                   | % of water in a 20 cell radius (113 ha)   | 3% (0–23%)                         |
| Water100                  | % of water in a 100 cell radius (2827 ha)   | 3% (1–35%)                         |

**Table 2** Bird species included in analyses. Only species occurring in greater than 5% of samples (at least 14 observations) were included in the ordination and classification analyses; all species were included in the community comparisons ANOVA

| Common name              | Latin Name                      | # of obs. | Migratory status | CCS | Foraging guild | Diet                | Habitat use |
|--------------------------|---------------------------------|-----------|------------------|-----|----------------|---------------------|-------------|
| Acadian flycatcher       | <i>Empidonax vireescens</i>     | 47        | Ld               | 12  | Aerial         | Insect              | Interior    |
| American crow            | <i>Corvus brachyrhynchos</i>    | 38        | Resident         | 6   | Ground         | Omniv.              | Edge        |
| American goldfinch       | <i>Carduelis tristis</i>        | 55        | Sd               | 6   | Foliage        | Seeds               | Edge        |
| American redstart        | <i>Setophaga ruticilla</i>      | 3         | Ld               | 8   | Aerial         | Insect <sup>a</sup> | Gen         |
| American robin           | <i>Turdus migratorius</i>       | 54        | Sd               | 5   | Ground         | Insect              | Edge        |
| Black-and-white warbler  | <i>Mniotilta varia</i>          | 2         | Ld               | 9   | Bark           | Insect              | Interior    |
| Blue-gray gnatcatcher    | <i>Poliopitila caerulea</i>     | 98        | Sd               | 7   | Foliage        | Insect <sup>a</sup> | Gen         |
| Blue-headed vireo        | <i>Vireo solitarius</i>         | 6         | Sd               | 8   | Foliage        | Insect <sup>a</sup> | Gen         |
| Blue jay                 | <i>Cyanocitta cristata</i>      | 80        | Resident         | 9   | Ground         | Omniv.              | Gen         |
| Brown-headed cowbird     | <i>Molothrus ater</i>           | 48        | Sd               | 7   | Ground         | Insect              | Edge        |
| Brown-headed nuthatch    | <i>Sitta pusilla</i>            | 4         | Resident         | 14  | Bark           | Insect              | Gen         |
| Brown thrasher           | <i>Toxostoma rufum</i>          | 19        | Resident         | 12  | Ground         | Omniv.              | Edge        |
| Carolina chickadee       | <i>Poecile carolinensis</i>     | 106       | Resident         | 11  | Foliage        | Insect              | Gen         |
| Carolina wren            | <i>Thryothorus ludovicianus</i> | 226       | Resident         | 8   | Ground         | Insect              | Gen         |
| Chipping sparrow         | <i>Spizella passerine</i>       | 43        | Sd               | 7   | Ground         | Insect              | Edge        |
| Downy woodpecker         | <i>Picoides pubescens</i>       | 85        | Resident         | 7   | Bark           | Insect              | Gen         |
| Common grackle           | <i>Quiscalus quiscula</i>       | 2         | Sd               | 8   | Ground         | Omniv.              | Edge        |
| Common yellowthroat      | <i>Geothlypis trichas</i>       | 4         | Sd               | 8   | Foliage        | Insect <sup>a</sup> | Edge        |
| Eastern bluebird         | <i>Sialia sialis</i>            | 1         | Sd               | 7   | Ground         | Insect              | Edge        |
| Eastern phoebe           | <i>Sayornis phoebe</i>          | 3         | Sd               | 8   | Aerial         | Insect <sup>a</sup> | Edge        |
| Eastern towhee           | <i>Pipilo erythrophthalmus</i>  | 85        | Resident         | 11  | Ground         | Insect              | Edge        |
| Eastern wood-pewee       | <i>Contopus virens</i>          | 16        | Ld               | 10  | Aerial         | Insect <sup>a</sup> | Gen         |
| Fish crow                | <i>Corvus ossifragus</i>        | 4         | Resident         | 9   | Ground         | Omniv.              | Edge        |
| Gray catbird             | <i>Dumetella carolinensis</i>   | 26        | Sd               | 9   | Ground         | Insect              | Edge        |
| Great crested flycatcher | <i>Myiarchus crinitus</i>       | 23        | Ld               | 9   | Aerial         | Insect              | Gen         |
| Hairy woodpecker         | <i>Picoides villosus</i>        | 11        | Resident         | 6   | Bark           | Insect <sup>a</sup> | Gen         |
| Hooded warbler           | <i>Wilsonia citrina</i>         | 20        | Ld               | 13  | Foliage        | Insect <sup>a</sup> | Interior    |
| House finch              | <i>Carpodacus mexicanus</i>     | 6         | Resident         | 6   | Ground         | Seeds               | Edge        |
| House wren               | <i>Troglodytes aedon</i>        | 9         | Sd               | 6   | Foliage        | Insect              | Edge        |
| Indigo bunting           | <i>Passerina cyanea</i>         | 8         | Ld               | 11  | Foliage        | Insect              | Edge        |
| Kentucky warbler         | <i>Oporornis formosus</i>       | 3         | Ld               | 14  | Ground         | Insect <sup>a</sup> | Interior    |
| Louisiana waterthrush    | <i>Seiurus motacilla</i>        | 8         | Ld               | 13  | Ground         | Insect              | Interior    |
| Mourning dove            | <i>Zenaidra macroura</i>        | 20        | Resident         | 5   | Ground         | Seeds               | Edge        |
| Northern cardinal        | <i>Cardinalis cardinalis</i>    | 214       | Resident         | 5   | Foliage        | Insect              | Gen         |
| Northern flicker         | <i>Colaptes auratus</i>         | 7         | Sd               | 9   | Ground         | Insect <sup>a</sup> | Edge        |
| Northern mockingbird     | <i>Mimus polyglottos</i>        | 4         | Resident         | 8   | Ground         | Insect              | Edge        |
| Northern parula          | <i>Parula Americana</i>         | 17        | Ld               | 10  | Foliage        | Insect <sup>a</sup> | Gen         |
| Ovenbird                 | <i>Seiurus aurocapilla</i>      | 64        | Ld               | 10  | Ground         | Insect <sup>a</sup> | Interior    |
| Pileated woodpecker      | <i>Dryocopus pileatus</i>       | 2         | Resident         | 7   | Bark           | Insect <sup>a</sup> | Gen         |

**Table 2** (continued)

| Common name             | Latin Name                  | # of obs. | Migratory status | CCS | Foraging guild | Diet                | Habitat use |
|-------------------------|-----------------------------|-----------|------------------|-----|----------------|---------------------|-------------|
| Pine warbler            | <i>Dendroica pinus</i>      | 62        | Sd               | 9   | Foliage        | Insect              | Interior    |
| Prothonotary warbler    | <i>Protonotaria citrea</i>  | 1         | Ld               | 15  | Bark           | Insect <sup>a</sup> | Interior    |
| Red-bellied woodpecker  | <i>Melanerpes carolinus</i> | 118       | Resident         | 9   | Bark           | Insect              | Gen         |
| Red-eyed vireo          | <i>Vireo olivaceus</i>      | 169       | Ld               | 7   | Foliage        | Insect <sup>a</sup> | Gen         |
| Scarlet tanager         | <i>Piranga olivacea</i>     | 36        | Ld               | 12  | Foliage        | Insect              | Interior    |
| Song sparrow            | <i>Melospiza melodia</i>    | 4         | Sd               | 8   | Ground         | Insect              | Edge        |
| Summer tanager          | <i>Piranga rubra</i>        | 42        | Ld               | 10  | Foliage        | Insect              | Gen         |
| Tufted titmouse         | <i>Baeolophus bicolor</i>   | 185       | Resident         | 8   | Foliage        | Insect              | Gen         |
| White-breasted nuthatch | <i>Sitta carolinensis</i>   | 70        | Resident         | 6   | Bark           | Insect              | Gen         |
| White-eyed vireo        | <i>Vireo griseus</i>        | 2         | Sd               | 10  | Foliage        | Insect <sup>a</sup> | Edge        |
| Wood thrush             | <i>Hylocichla mustelina</i> | 69        | Ld               | 14  | Ground         | Insect              | Gen         |
| Yellow-billed cuckoo    | <i>Coccyzus americanus</i>  | 17        | Ld               | 11  | Foliage        | Insect              | Gen         |
| Yellow-breasted chat    | <i>Icteria virens</i>       | 5         | Ld               | 10  | Foliage        | Insect              | Edge        |
| Yellow-throated vireo   | <i>Vireo flavifrons</i>     | 10        | Ld               | 11  | Foliage        | Insect <sup>a</sup> | Edge        |
| Yellow-throated warbler | <i>Dendroica dominica</i>   | 3         | Sd               | 11  | Bark           | Insect <sup>a</sup> | Interior    |

CCS continental combined score, a conservation priority score from Partners in Flight; migratory status *Ld* long distance, *Sd* short distance (after Ehrlich et al. 1988)

<sup>a</sup> obligate insectivores

end of each 15-m transect. The four canopy estimates were averaged into a single estimate of mean canopy cover at each location. Presence or absence of shrub layer and ground cover (vegetation and coarse woody debris) was recorded at one-meter increments along all three transects, for a total of 45 observations. These observations were combined to estimate mean shrub cover, ground vegetation cover, and cover of coarse woody debris for each location. A forester's prism was used to estimate basal area of pine and hardwood trees and snags (standing dead trees > 20 cm dbh) at each location.

Traffic noise was also measured at each location because several recent studies have implicated traffic noise as an important variable for many bird species (Forman et al. 2002; Rheindt 2003; Peris and Pescador 2004). It was measured multiple times during each visit with a digital sound level meter, which was held horizontal to the ground at waist height (approximately 1 m high) and pointed outward in a random direction. The average noise level during a 5 s period was recorded, then the sound level meter was rotated 90° and the average sound in the new direction was recorded, and so on, until there were two measurements each from four different directions. This was followed by an interval of about 10 min during which no noise measurements were taken, and then the procedure was repeated. This resulted in a total of four readings in each direction, or 16 different readings. The readings were averaged to get a single value for each visit.

We were aware of the possibility of traffic noise affecting our ability to detect birds and tested for this effect in our data (manuscript in preparation). We found that we were able to detect birds with confidence if they were within 50 m of the observer, but beyond 50 m our ability to detect birds in noisy locations diminished. Therefore, we truncated our observations at 50 m away from the observer.

Using a geographic information system (ArcGIS 9.0, ESRI), we calculated deciduous and persistent NDVI (normalized difference vegetation index—a measure of “greenness”)

and TCI (topographic convergence index—a measure of “wetness” that calculates the upslope contributing area (Beven and Kirkby 1979)) for each point count location using bilinear interpolation. This method calculates a weighted average of the values of the four nearest pixels based on their relative distance from the point count. Deciduous and persistent NDVI, calculated using paired summer/winter Thematic Mapper images from 2001, should be correlated with pine and hardwood basal area for each plot. However, bilinear interpolation estimates stand composition over a slightly larger area than the field measurements allowed, more closely matching the scale sampled by the point counts. We did not ground truth our NDVI values.

*Landscape-scale environmental variables* Landscape-scale variables were also collected using ArcGIS 9.0 (ESRI). A land cover map was created from classified LANDSAT Thematic Mapper satellite imagery (30 m resolution) from May 2001. The image was classified into four discrete classes: urban, agriculture, water, and forest. Urban cover types include roads, parking lots, and buildings. “Agriculture” refers variety of sparse vegetation; this cover type is dominated by agricultural fields but also includes old fields, lawns, and sports fields. Forest cover includes pine, hardwood, and mixed forest types. The ArcGIS function *focalmean* was used to measure percent of each cover type around point count locations at three different buffer sizes: 7 ha (150 m or 5 cell radius), 113 ha (600 m or 20 cell radius) and 2827 ha (3 km or 100 cell radius). For each location, GIS data layers were used to measure distance to nearest stream, distance to the nearest nonforested pixel (i.e., edge), distance to nearest road, and distance to nearest primary road (interstates, U.S. routes, and state routes). Density of all roads and of only primary roads was calculated around each point for a 500 m and 2 km radius, using a roads layer obtained from the North Carolina Department of Transportation. Finally, habitat patches were defined by grouping contiguous pixels of forest using a 4-neighbor rule, in which two forested pixels are considered to be in the same patch only if they are touching in the horizontal or vertical direction. Size and edge-to-area ratio were calculated for each patch.

## Data analyses

To examine changes in community composition across our study site, we used a multivariate statistical approach that allowed us to (1) examine general relationships between bird species and environmental variables, (2) identify discrete bird communities and measure ecological differences between them, and (3) make spatially explicit predictions about where these communities would occur across a rural-to-urban gradient.

*Ordinations* Ordinations were used to sort samples (point count locations) and bird species, reduce dimensionality, and identify trends in the data. Nonmetric Multidimensional Scaling (NMS; Shepard 1962) was selected for this analysis because it does not make assumptions about the shape of species’ distributions or the relationships between species’ occurrences and the underlying environmental gradients. It is an indirect ordination technique, which means that the gradients underlying species distributions are inferred from the species data matrix itself without ancillary (environmental) data. Thus, the species and/or samples are ordinated based on internal patterns of association or similarity, and then the ordering of the species or samples is used to interpret and attach ecological labels to the axes. This approach does not require that the measured variables are the most relevant to explaining species distributions, which is a benefit when the majority of bird-habitat models have a



large portion of unexplained variance. NMS iteratively searches for the best smaller-dimensional solution that is the least different from the original multi-dimensional data space and seeks to minimize this difference or “stress”. A step-down procedure can first be performed to determine the best number of axes (i.e., dimensionality) for the dataset. Those dimensions are then used to determine a final ordination of the data.

NMS is based on pairwise sample dissimilarities; for this analysis, Sorensen’s (Bray-Curtis) similarity index was used to calculate species dissimilarity between all pairs of samples. Since NMS fits all axes simultaneously, they are displayed arbitrarily (i.e., the axis accounting for the most variation in the dataset is not necessarily labeled as 1); varimax rotation was used to maximize the loadings of individual variables on the dimensions of the reduced ordination space. NMS ordination analyses were conducted in PC-ORD 4.0 (McCune and Mefford 1999), using a random starting configuration and 500 iterations. The stability criterion was a standard deviation in stress of less than 0.0005.

*Cluster analysis* We used cluster analysis (Wishart 1969) to identify distinct bird communities in the study area. Clustering is a hierarchical agglomerative method of identifying groups of samples (or “communities”) in a multivariate data set. In this case, the groups are compositionally similar species assemblages at point count locations. Similar to NMS, clustering is based on a dissimilarity matrix and the objective is to group together those samples that are the most similar. Sorensen’s index was again used as the distance measure between pairs of points. Because the algorithm is hierarchical, large clusters are composed of smaller clusters, and groups can be defined at various levels ranging from a few high-level groups to a large number of low-level groups; the decision about the number of groups is left to the user. The flexible beta linkage method was used ( $\beta=-0.5$ ) to determine how samples were placed into groups.

Once different levels of clusters were identified, the task was to choose the best number of groups and classify each sample location according to community type. First, multi-response permutation procedures (MRPP; Mielke 1991) were used to statistically test group differences for each level of clustering. MRPP is a non-parametric procedure that uses the species occurrence matrix and the classification (grouping) variable from the cluster analysis to test the hypothesis that samples within the same groups are clumped in multivariate space, evaluated by permutation of the group memberships. Again, Sorensen’s index was used as the distance metric. For each level of clustering, sample plots were labeled according to their community type and viewed in ordination space to detect natural and ecologically interpretable groups in the data. Finally, the best number of groups was selected and each sample location was classified according to the type of bird community present.

*Community comparison* Once bird communities were defined from the cluster analysis, we tested for ecological differences between the communities. We began by calculating the number of species in each of the various functional groups at each site. We also calculated a conservation value for each site by counting the number of species on the PIF Continental Watch List at each location. Species richness, number of species in each of the functional groups, and site conservation value were compared between communities using one-way ANOVA, and differences between pairs of communities were tested with Tukey’s multiple comparisons procedure ( $p=0.05$ ). Statistics were computed with S-Plus 6.2 (Insightful Corp. 2003).

*Classification and regression tree (CART) models* CART models (Breiman et al. 1984) were used to identify the important environmental factors for each of the newly-defined

bird communities. CART models are nonparametric and make no assumptions about the nature of the response. They classify community types by subsetting the data and successively explaining smaller and smaller groups of the data. At each split in the tree, the process finds the variable that best distinguishes between groups. The recursive nature of the algorithm tends to produce models that are over-fitted to the data used to generate the model, limiting application to other datasets. For this reason, CART models are often simplified, by “pruning”, to yield a final model that attempts to balance accuracy with robustness to new data.

When interpreting model output, the first division of each tree shows the variable that can best distinguish among the groups, while variables that occur successively lower in the tree explain a smaller portion of the variation in the dataset. The tree is plotted according to a set of rules in which each branch is keyed by a condition (e.g., canopy < 90%); the “true” reaction to this condition is graphed to the left, while the “false” reaction goes to the right. Non-uniform spacing between splits also indicates importance; the more important the parent split, the further the children node pairs are spaced from their parents.

In this analysis, the response variable was community type and the predictor variables were the measured environmental variables (Table 1). Our goal was to determine whether bird community type could be predicted by environmental settings and, if so, which environmental variables best differentiated the groups.

The analysis was performed using the S-PLUS contributed library *rpart*. In *rpart*, tree pruning is accomplished by using cross-validation to estimate the standard error of the full tree; 10 random partitions of the data are defined and trees are created for each subset of nine partitions, with these trees used to predict the reserved partition. Classification accuracy is then averaged over each of the cross-validated trees. The final tree is the tree that results in residual deviance that is one standard error above the full tree. A minimum of 10 observations per node was required before attempting a split.

*Spatially-explicit community analysis* As a final analysis, sample locations were coded according to their bird community type at that site and mapped into geographic space, with the simple goal of visually identifying any interesting geographic trends.

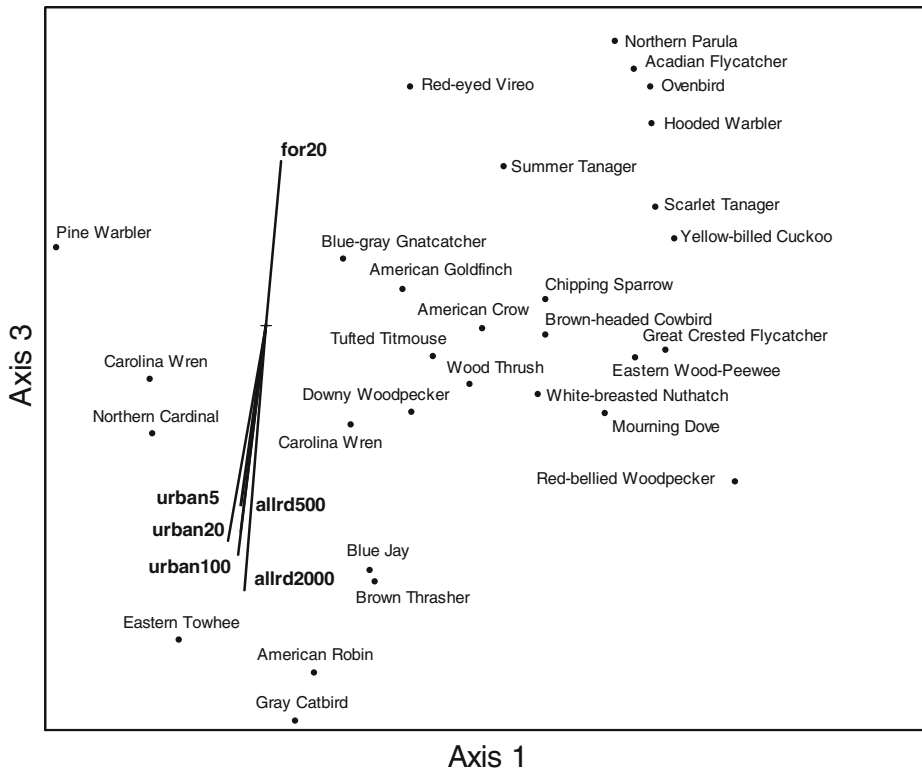
## Results

*Bird communities* There were a total of 69 species observed in the field, but 15 of them were flyovers and excluded from the analysis. Of the remaining 54 species (Table 2), 24 were observed at fewer than 5% of the point count locations; we removed these species from the ordination and cluster analysis to enhance the detection of multivariate relationships (McCune and Grace 2002). However, all 54 species were included in the community diversity comparisons. Species were split almost evenly among year-round residents, short-distance migrants, and long-distance migrants. More species preferred edge habitat or were habitat generalists than were forest interior specialists. Twenty-one species were ground foragers, 19 were foliage foragers, five were aerial foragers, and nine were bark foragers. The majority of species were classified as insectivores, although only 18 were considered obligatory insectivores. The conservation scores (CCS) of species ranged from 5 to 15. The prothonotary warbler had the highest score and only four species were on the PIF Continental Watch List.

**Ordinations** The results of the step-down procedure suggested a 3-dimensional solution with a stress of 24.0, due in part to the large sample size. A regression of the ordination scores against the original distance matrix showed that the ordination scores had a cumulative  $r^2$  of 0.585 (Table 3). Axis 3 accounted for the greatest portion of variation, followed by axis 1 and then axis 2. Environmental variables were overlaid on the ordination plot in order to visually assess their relationship with each axis (Fig. 2); only variables with  $r^2 > 0.4$  are shown. A correlation analysis between each environmental variable and the three axes (Table 3) confirmed the trends seen in Fig. 2: that species sort more strongly according to landscape-scale variables than local-scale variables. In addition, the significant landscape-scale variables were mostly variables related to urbanization and human development. Multiple variables were significantly, although weakly, correlated with each axis, and the few variables that were strongly correlated with any axis were all correlated with axis 3. The most important variables were density of roads, amount of urban cover, and amount of forest in the surrounding landscape. Density of roads in 500 m and 2 km radii, and the amount of urban cover at all three scales, were negatively correlated with axis

**Table 3** Correlations between environmental variables and NMS ordination axes. The last two rows indicate the amount of variation explained by each axis (incremental and cumulative). Only variables with a significant relationship ( $p=0.05$ ) are shown

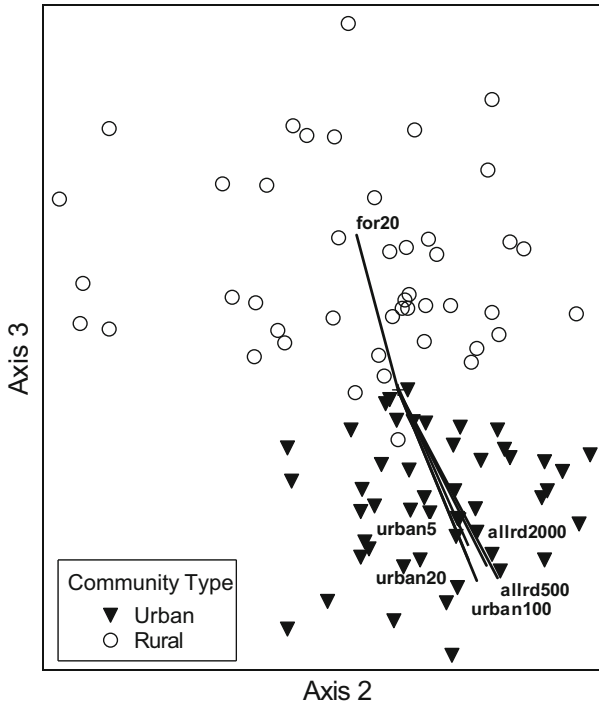
| Variable                  | Axis 1 | Axis 2 | Axis 3 |
|---------------------------|--------|--------|--------|
| Local-level variables     |        |        |        |
| BA hdwd                   | 0.229  | ns     | ns     |
| BA pine                   | -0.142 | ns     | ns     |
| Decid99                   | 0.138  | ns     | ns     |
| Noise                     | -0.287 | ns     | -0.235 |
| Shrub                     | ns     | -0.145 | ns     |
| Landscape-level variables |        |        |        |
| Allrd500                  | -0.176 | ns     | -0.489 |
| Allrd2000                 | -0.156 | ns     | -0.552 |
| Dist.nonfor               | ns     | ns     | 0.247  |
| Dist.pri.road             | 0.221  | ns     | 0.256  |
| Dist.road                 | ns     | ns     | 0.181  |
| Dist.stream               | ns     | ns     | 0.129  |
| Edge.area                 | ns     | ns     | -0.26  |
| For5                      | 0.23   | ns     | 0.372  |
| For20                     | 0.13   | ns     | 0.437  |
| For100                    | ns     | ns     | 0.296  |
| Patch.area                | ns     | ns     | 0.321  |
| Prird500                  | -0.17  | ns     | -0.151 |
| Prird2000                 | -0.221 | ns     | -0.288 |
| Urban5                    | -0.207 | ns     | -0.407 |
| Urban20                   | -0.213 | ns     | -0.5   |
| Urban100                  | -0.182 | ns     | -0.515 |
| Increment $r^2$           | 0.146  | 0.102  | 0.338  |
| Cumulative $r^2$          | 0.146  | 0.247  | 0.585  |



**Fig. 2** NMS ordination of bird species, with important environmental variables ( $r > 0.4$ ) overlaid. Trends in species composition appear to be driven by the amount of forest and urban cover and road density in the surrounding landscape

3, while the amount of forest cover in a 20 cell buffer was positively correlated with axis 3. Traffic noise was only weakly related to axes 1 and 3.

**Cluster analysis** The cluster analysis classified each point count location for all clustering levels from ten down to two. MRPP found every level of clustering to be statistically significant, so each grouping level was viewed against the NMS ordination axes to look for natural groupings in the data. The most ecologically appropriate number of groups was determined to be 3 ( $A=0.16$ ,  $p < 0.001$ ), based on the separation between groups on NMS axes (not shown). The difference between groups was greater when the first group was dropped ( $A=0.26$ ,  $p < 0.001$ ), meaning that groups 2 and 3 are more different from each other than group 1 is from either of them. This was also seen by plotting communities 2 and 3 on the NMS axis without community 1 (Fig. 3); there is very little overlap between the two communities. Group 1 is similar in species composition to both groups 2 and 3 and seems to represent an intermediate community between two end points. Because a vector representing forest cover is pointing toward community 3 and several vectors representing urbanization are pointing towards community 2, we will refer to them as rural and urban communities, respectively, from here forward. Community 1 will be called the mixed community.



**Fig. 3** NMS ordination of urban and rural communities. Communities are clearly separated along axis 3, which correlates with the amount of forest and urban cover and road density in the surrounding landscape

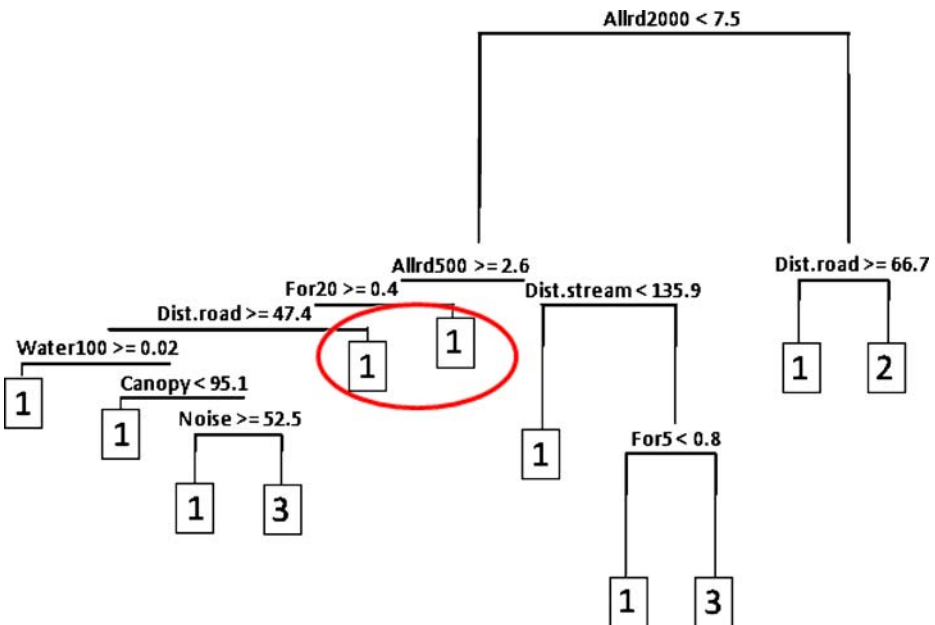
*Community comparison* Mean species richness over all sites was eight species and was not statistically different between the three community types (Table 4). The rural communities had the highest number of long-distance migrant species and urban communities had the lowest number of migrant species. Forest interior species were statistically more common in rural communities than in mixed or urban communities, and edge species were most common in urban communities. All communities had small but similar numbers of species on the Partners in Flight watch list.

When looking at foraging and diet guilds, there was no statistical difference between sites in numbers of aerial foragers (these numbers were  $< 1$  for all communities). However, urban communities were statistically higher in numbers of ground foraging species and lower in numbers of foliage foraging species than the other two community types. They had higher numbers of bark foraging species than mixed communities, but were not statistically different from rural communities. Urban communities also showed a significantly lower number of obligatory insectivores than mixed communities, which was significantly lower than rural communities. Urban communities had more omnivores than mixed communities but were no different than rural communities. There was no statistical difference in number of insectivores or seed-eaters between community types.

*CART model* The classification tree (Fig. 4) supported the results of the NMS analysis by indicating that landscape-scale variables related to urban development were primary in structuring bird communities across our study site. The first split in the tree was based on the density of roads in a 2 km radius and completely separated rural and urban

**Table 4** Summary of community composition in mixed, urban, and rural bird communities. Statistical differences were assessed with ANOVA and Tukey’s multiple comparisons procedure. Values in each community column are mean number of species (standard error) in that guild. Superscript letters indicate statistical differences between individual groups

|                      | Mixed                   | Urban                   | Rural                    | F value | Probability of F |
|----------------------|-------------------------|-------------------------|--------------------------|---------|------------------|
| Richness             | 8.1 <sup>a</sup> (0.23) | 8.9 <sup>a</sup> (0.30) | 8.5 <sup>a</sup> (0.51)  | 1.17    | ns               |
| Ld migrant species   | 2.1 <sup>a</sup> (0.12) | 0.9 <sup>b</sup> (0.15) | 3.3 <sup>c</sup> (0.24)  | 30.27   | <0.001           |
| Aerial forager       | 0.3 <sup>a</sup> (0.04) | 0.2 <sup>a</sup> (0.07) | 0.3 <sup>a</sup> (0.08)  | 0.73    | ns               |
| Foliage forager      | 4.1 <sup>a</sup> (0.12) | 3.0 <sup>b</sup> (0.17) | 4.3 <sup>a</sup> (0.29)  | 11.25   | <0.001           |
| Ground forager       | 2.8 <sup>a</sup> (0.12) | 4.2 <sup>b</sup> (0.17) | 2.6 <sup>a</sup> (0.25)  | 17.45   | <0.001           |
| Bark forager         | 0.9 <sup>a</sup> (0.07) | 1.5 <sup>b</sup> (0.14) | 1.2 <sup>ab</sup> (0.12) | 7.58    | <0.001           |
| Insectivore          | 7.4 <sup>a</sup> (0.21) | 7.8 <sup>a</sup> (0.30) | 7.6 <sup>a</sup> (0.43)  | 0.49    | ns               |
| Obligate insectivore | 1.7 <sup>a</sup> (0.09) | 0.7 <sup>b</sup> (0.11) | 2.5 <sup>c</sup> (0.19)  | 29.49   | <0.001           |
| Omnivores            | 0.4 <sup>a</sup> (0.04) | 0.8 <sup>b</sup> (0.18) | 0.6 <sup>ab</sup> (0.23) | 7.36    | <0.001           |
| Seed eaters          | 0.3 <sup>a</sup> (0.04) | 0.2 <sup>a</sup> (0.07) | 0.3 <sup>a</sup> (0.08)  | 0.37    | ns               |
| Forest interior      | 0.9 <sup>a</sup> (0.07) | 0.2 <sup>b</sup> (0.06) | 1.6 <sup>c</sup> (0.16)  | 28.6    | <0.001           |
| Forest generalist    | 5.7 <sup>a</sup> (0.15) | 5.8 <sup>a</sup> (0.26) | 5.8 <sup>a</sup> (0.36)  | 0.08    | ns               |
| Forest edge          | 1.5 <sup>a</sup> (0.10) | 2.8 <sup>b</sup> (0.19) | 1.1 <sup>a</sup> (0.15)  | 24.49   | <0.001           |
| Watch list species   | 0.3 <sup>a</sup> (0.05) | 0.2 <sup>a</sup> (0.06) | 0.3 <sup>a</sup> (0.10)  | 1.34    | ns               |



**Fig. 4** CART model predicting mixed (1), urban (2), and rural (3) bird communities. The tree is plotted according to a set of rules in which each branch is keyed by a condition (e.g., canopy < 90%); the “true” reaction to this condition is graphed to the left, while the “false” reaction goes to the right. The circled terminal nodes have a very high misclassification rate

communities; according to this model, any location with a road density higher or equal to  $7.5 \text{ km/km}^2$  in a 2 km radius would not contain a rural bird community. Conversely, if a site had a road density of less than  $7.5 \text{ km/km}^2$  then it would not contain an urban bird community. The distinction between mixed and urban communities was also fairly simple; if a location had road density higher than  $7.5 \text{ km/km}^2$  and was greater than 66.7 m from a road, it would be mixed; otherwise, it would be urban. The distinction between mixed and rural was less simple. While most variables separating the two communities were of the landscape-scale, urban-development type (e.g., amount of forest in surrounding landscape, distance to road), a few local-scale variables came into play as well. For example, mixed communities seemed to be wetter, either by proximity to streams or by the amount of water in the surrounding landscape (this could include lakes, ponds, streams, etc.). Mixed communities also had a more open canopy than rural communities, although the range of canopy cover across all the sites was not large.

The confusion matrix (Table 5) provides overall classification accuracy (79%) for each community type and identifies specific kinds of misclassifications. It reveals the difficulty in distinguishing between mixed and rural communities; 17 out of the 45 rural communities were misclassified as mixed. Conversely, no rural communities were incorrectly classified as urban communities. Twenty-three of the 49 urban communities were misclassified as mixed, while only three were misclassified as rural. Therefore, there was a large environmental distinction between rural and urban communities, while the mixed community was more difficult to predict.

Specific nodes on the tree where misclassification errors occur can be revealing. For example, the circle drawn on the tree identifies two nodes with high misclassification errors. Both of the terminal nodes were classified as mixed communities, but almost half (12/30) of the observations at these nodes were actually urban communities. These locations had a lower road density than the typical urban community but showed other kinds of anthropogenic disturbance: one node contained observations that were closer than 47 m from a road, and the other node contained observations with low forest cover in the surrounding landscape.

*Spatially-explicit community analysis* Mapping the community types in geographic space with other variables of interest revealed that rural and urban community types were closely aligned with municipal boundaries. Forty-two of the 49 (86%) urban communities were located within municipal boundaries, while 42 of the 45 (93%) rural communities fell

**Table 5** Confusion matrix shows classification accuracy of CART model (Fig. 4). Overall accuracy of classification for all communities was 79%

| Observed             | Predicted            |                      |                      |
|----------------------|----------------------|----------------------|----------------------|
|                      | Community 1<br>Mixed | Community 2<br>Urban | Community 3<br>Rural |
| Community 1<br>Mixed | 165                  | 5                    | 8                    |
| Community 2<br>Urban | 23                   | 23                   | 3                    |
| Community 3<br>Rural | 17                   | 0                    | 28                   |

outside of municipal boundaries (Fig. 1). One hundred and sixteen out of 178 (65%) of mixed communities fell within municipal boundaries. Overall, 59% of all point count locations were located within municipal boundaries.

Urban communities were statistically closer to roads than rural communities (mean distance to road: urban = 61 m, rural = 116 m,  $t=2.40$ ,  $p=0.01$ ), although distance to road did not define these communities. Urban sites ranged in distance from road from 21 m to 178 m, while rural sites ranged from 0 m to 655 m. In fact, more than one rural community was centered directly on a road and almost half (22/45) of rural sites were 50 m or less from road. On the other hand, road density in the surrounding landscape more cleanly defined the two communities. Road density was significantly lower for rural communities than for urban communities (mean road density in 2 km buffer: urban = 6.2 km/km<sup>2</sup>, rural = 2.6 km/km<sup>2</sup>,  $t=10.0$ ,  $p<0.001$ ; mean road density in 500 m buffer: urban = 7.5 km/km<sup>2</sup>, rural = 2.3 km/km<sup>2</sup>,  $t=11.0$ ,  $p<0.001$ ). Rural communities never occurred in locations with a road density greater than 6.4 km/km<sup>2</sup> at either measured scale.

## Discussion

In our study area, bird community composition was linked much more strongly with landscape-level variables than local-level environmental variables. Of particular importance to community composition were variables related to urbanization, such as road density and amount of urban land cover. Urbanization in the surrounding landscape has been shown to be important to native birds in other locations (Fernandez-Juricic and Jokimaki 2001; Dunford and Freemark 2005; Evans et al. 2009; Luther et al. 2008; Garaffa et al. 2009). However, our analyses allowed us to identify particular thresholds of road density and distance that were important predictors of the bird community in forest fragments.

We identified three different bird communities across the study area, which we have termed mixed, urban, and rural communities. As a whole, these three community types were not completely distinct (i.e., there is overlap in species), but community composition in rural and urban communities was quite different. Interestingly, species richness did not differ between communities. Rather than replacement of native species by exotics, as has been seen in other locations (Blair 1996; Crooks et al. 2004), we found a different set of native species in each community. Several species present in rural communities were never found in urban communities (Hooded Warbler, Northern Parula, Yellow-billed Cuckoo), and several of the common urban species were only rarely present in rural communities (American Robin, Eastern Towhee). Many of the species in urban forests were not strictly forest species. For example, both the American Robin and the Eastern Towhee are commonly found in open farmland, fields, and gardens, in addition to forests. These species may prefer urban forests over rural forests because of the unique habitat and supplementary resources found in urban forests, such as bird feeders, fruit trees, and water (Gaston et al. 2005, 2007). Other studies have found increased bird abundance in urban areas (Palomino and Carrascal 2007), which further suggests that urban areas offer increased resources to some bird species.

Road density was the most important factor driving community composition, as seen in both the NMS analysis and the CART model. Distance to road was of secondary importance to bird communities but appeared as two different splits in the CART model. Our observation that road density is more important than distance to road is supported by the research of Palomino and Carrascal (2007), who found the effect of roads on bird



communities depended on habitat, and in particular that birds in deciduous forests were not negatively affected by nearby roadsides. They did not examine the effect of road density, however. Other studies have found road density (van der Zande et al. 1980; Hennings and Edge 2003) or distance to road (Kuitunen et al. 1998; Brotons and Herrando 2001; Palomino and Carrascal 2007) to be important to bird communities, but our study is one of the few that has looked at both density and distance of different kinds of roads. Interestingly, type of road did not seem to be an important factor in determining bird communities; metrics for all roads combined were consistently selected over metrics for primary roads alone. This implies that road width and traffic volume are not important in structuring bird communities, but instead that the effect of roads may be related to fragmentation or the altered biophysical environments that accompany most roads. Research has shown that roads can have an effect on macroinvertebrates (Haskell 2000) and chemical contamination (Poszyler-Adamska and Czerniak 2007) in the soil, but more work is needed to understand how these soil characteristics might affect forest birds.

While road density was an important predictor of species composition, traffic noise did not have a large effect. This was unexpected, as several studies have suggested that traffic noise may have a negative effect on bird communities (Reijnen et al. 1996; Forman et al. 2002; Rheindt 2003). However, these previous studies did not directly measure noise but instead relied on distance to roads as an estimate of noise. An additional difficulty with examining the effects of traffic noise is its strong correlation with other road-related variables such as distance to road and road density. We believe this correlation may partially explain the weak relationship seen between noise and species composition in our ordination analysis and we examine the effect of traffic noise in greater detail in a forthcoming manuscript. In light of the capacity demonstrated by many birds species to communicate in noisy environments (Aubin and Jouventin 1998; Cynx et al. 1998; Slabbekoorn and Smith 2002; Slabbekoorn and Peet 2003), perhaps it is not surprising that birds are able to adjust their behavior in response to noise.

Most species common to urban communities are thought of as edge species, including the Carolina Wren, Northern Cardinal, American Robin, and Eastern Towhee. However, density of roads rather than distance to edge was the most important factor distinguishing these communities. This implies that edge may be more meaningful at larger scales (e.g., the amount of edge in the surrounding landscape) than in a local context. In other words, edge species prefer fragmented landscapes with a high proportion of edge but do not necessarily need to establish territories immediately adjacent to edges. Likewise, the forest interior species that were more common in rural communities do not necessarily avoid roads but seem to prefer landscapes with a smaller proportion of edges overall. This observation supports Villard's (1998) contention that many birds labeled forest interior are misclassified and observed habitat selection patterns are likely related to area-sensitivity rather than edge-avoidance.

A preference for or against edges might be related to resource availability in fragmented landscapes, as species seem to sort according to diet and foraging guilds. For example, urban communities had significantly higher numbers of ground feeding and bark foraging species than rural communities, although the mechanism behind this difference is not clear: these locations did not differ significantly in amount of ground vegetation, coarse wood debris, shrub cover, or pine or hardwood basal area. Rural communities, on the other hand, had significantly higher numbers of obligate insectivores than either urban or mixed communities. This result has been seen before (Rottenborn 1999; Glennon and Porter 2005), and the mechanism behind this trend is more apparent. Roads have been shown to significantly reduce the depth of the leaf-litter layer and depress both the abundance and

richness of macroinvertebrate soil fauna up to 100 m into the forest (Haskell 2000). The high density of roads surrounding urban communities may ensure that very little of the forest area is greater than 100 m from a road, resulting in reduced foraging success for obligate insectivores.

### Conservation & planning considerations

The fact that landscape-level variables were most important for predicting bird community composition in our study area suggests that where a forest patch is located in an urban landscape is more important than vegetation composition and structure within the patch. This concurs with other studies that have found landscape-level variables to be equally or more important than local-level variables to avian communities (Fauth et al. 2000; Golet et al. 2001; Cleary et al. 2005; Luther et al. 2008). However, other studies have found that local-scale vegetation variables are very important to bird communities (Jokimäki 1999; Lichstein et al. 2002; Fernandez-Juricic 2004; reviewed by Evans et al. 2009). The relative importance of landscape-level versus local-level habitat variables seems to depend greatly on species, landscape, and study approach. For example, it is difficult to compare results between studies such as ours, that sample only in native habitat, to studies that sample sites spanning a range of management and human disturbance. When sample locations differ greatly from each other (e.g., a manicured park versus a forest patch), it is not surprising that local vegetation variables outweigh landscape-level variables in importance. While our sample locations were all within forest patches, they were not identical in vegetation structure. Instead, the vegetation characteristics at each location did vary considerably (Table 1). Therefore, it doesn't appear that our results are an artifact of too little variation in local-scale vegetation variables. Rather, we believe that the urban gradient in our study area has a strong and dominating effect on the bird community that overshadows the influence of local vegetation.

There is a clear geographic division between the rural and urban bird communities in this study area, which is delineated quite well by municipal boundaries. Municipal areas are characterized by a high density of roads and a low density of forest cover, so it is not surprising that they do not contain rural communities. This provides a convenient rule of thumb for conservation planners in the Triangle: if birds common to rural communities (e.g., Neotropical migrants) are a conservation focus, reserves should be created outside of municipal boundaries. This does not mean that functional reserves cannot exist in urban areas, though; mixed communities are quite common within municipal boundaries, and proper placement on the landscape can help to encourage their prevalence over urban communities. In particular, forest reserves in urban areas should extend at least 67 m away from roads to encourage presence of most Neotropical migrant species. However, depending on the landscape context, reserves in closer proximity to roads may still be valuable habitat for resident species.

Our conclusions differ from those offered by Stratford and Robinson (2005), who found that urbanization had a strong effect on species richness. They conclude that “the conservation value of small woodlots in urban settings may be minimal and...that conservation of migratory birds will be best achieved by giving higher priority to sites where urban cover is still low.” While rural communities did contain more Neotropical migrants in our study site, species richness did not significantly differ between urban and rural settings, and mixed communities—many found within municipal boundaries—still contain many Neotropical migrant species. Additionally, all three communities supported similar numbers of species on the Partners in Flight Continental Watch List. Our results

indicate that forest patches in urban environments can be useful conservation sites for many species, in addition to the recreation and other climate services these forest patches provide to city dwellers (Chee 2004). Furthermore, a review of avian productivity in urban landscapes suggests that annual productivity and survival may be higher in urban settings (Chamberlain et al. 2009), providing additional motivation for maintaining or creating reserves in urban areas. If bird conservation is a goal in urban areas, our study provides guidelines that will allow planners to target the bird communities of interest both inside and outside urban areas.

**Acknowledgments** We are grateful for a wonderful group of field assistants, including D. Horkavy, K. Jensen, B. Keighton, M. McKown, and M. Skakuj.

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