Research Article

The Effects of Exurbanization on Bird and Macroinvertebrate Communities in Deciduous Forests on the Cumberland Plateau, Tennessee

Jordan M. Casey,[1] Marie E. Wilson,[1] Nicholas Hollingshead,[2] and David G. Haskell[1]

[1] *Department of Biology, University of the South, 735 University Avenue, Sewanee, TN 37383-1000, USA*
[2] *Landscape Analysis Lab, University of the South, 735 University Avenue, Sewanee, TN 37383-1000, USA*

Correspondence should be addressed to Jordan M. Casey, jcasey508@gmail.com

To investigate the potential causes of changes to bird communities in exurban areas, we examined the relationship between bird and macroinvertebrate communities in exurbanized forest. We randomly located sampling points across a gradient of exurbanization. We used point counts to quantify bird communities and sweep netting, soil cores, pitfalls, and frass collectors to quantify macroinvertebrates. Bird communities had higher richness and abundance in exurban areas compared to undeveloped forests, and lost some species of conservation concern but gained others. The macroinvertebrate community was slightly more abundant in exurban areas, with a slight shift in taxonomic composition. The abundance of macroinvertebrates in soil cores (but not pitfalls) predicted the abundance of ground-foraging birds. The abundance of macroinvertebrates in sweep nets was not associated with the abundance of aerial insectivore birds. Exurbanization therefore appears to change bird and macroinvertebrate communities, but to a lesser extent than agricultural forest fragmentation or intensive urbanization.

1. Introduction

Exurbanization is the conversion of native or agricultural vegetation into low density housing development [1]. Exact definitions of "exurban" are inconsistent across previous literature [2], but exurban areas are most often characterized by housing densities between 0.06 and 0.25 houses per hectare, and they retain some of the previous vegetation, albeit in modified form [1, 3]. In the United States, exurban development has expanded fivefold since 1950 and occupies nearly 25% of the lower 48 states [1, 4].

The effects of exurbanization on biodiversity are complex and depend on the regional context, the type of housing development, and the taxon being studied [1, 5, 6]. In general, exurban areas experience significant shifts in community composition relative to undeveloped habitat, but these shifts are less severe than those in more heavily urbanized areas. Depending on the region and taxon, the overall richness of native species can either increase or decrease in exurban areas relative to undeveloped habitat [5–7].

Of all the taxa and regions studied to date, birds in the United States are the best understood in relation to exurbanization [6, 8]. Bird species richness is often higher in exurban areas compared to other habitat types. This is true in regions as varied as coastal chaparral forest scrub in California [5], broadleaf forests in Ohio [9], Colorado ranch land [10], Tennessee oak-hickory forest [7], and Arizona grassland and mesquite-oak savannah [11]. However, as the density of housing increases, species richness drops, especially the richness of species that inhabit native vegetation in each region. Once development reaches suburban or urban densities, bird communities experience substantial declines in richness and increases in spatial homogenization [12, 13]. It appears that similar patterns are found in other regions of the world such as "periurban" areas in Australia [14] and Europe [15].

Although we have a fairly good understanding of how bird communities change in exurban areas, our understanding of the causes of these changes is limited. Among the possible causes are alterations in exotic plants [10, 16], forest structure [17], nest parasitism [18], mesopredator abundance and nest predation [9, 10, 16], or subsidies in the form of waste food, feeders, gardens, or water sources [1, 11, 19]. These possible causes either have not been quantified in exurban areas or have been quantified in a small number of locations. Recent reviews conclude that a better understanding of these mechanisms should be a priority for future research in both urban and exurban areas [1, 8].

Here we examine whether the abundance of macroinvertebrates during the bird breeding season is associated with changes in bird communities in exurbanized deciduous forest. Macroinvertebrates form the majority of the diet of most forest birds during the breeding season, and changes in the availability of these food sources is known to change the success of bird reproduction [20–22]. Despite the central role of macroinvertebrates in the functioning of forest ecosystems, we know very little about how macroinvertebrates respond to urban development and even less about their responses to exurbanization [23].

The few published studies of macroinvertebrates in exurban and urban areas have been conducted in different taxa and ecosystems, making generalities difficult to draw. Butterfly richness in Arizona was not different in exurban compared to undeveloped areas, although there were statistically significant interactions between development and the type of habitat (grass or mesquite) [24]. Likewise, the extent of development seemed mostly unrelated to the richness of wasps near Sydney, Australia [25], the richness of leaf-miners in California [26], and the richness of native ant species in the Florida Keys, although nonnative species were more abundant in developed areas [27]. In contrast, butterfly diversity in coastal chaparral forest scrub in California peaked with intermediate levels of development [5]. Arthropod communities in the Arizona Sonoran desert were altered in urban settings, as were the trophic processes that regulate community structure [28–31]. Fragmentation of native habitats in coastal southern California reduced arthropod diversity in a complex manner dependent on fragment size, area, and the presence of nonnative species [32]. In forests of the eastern U.S., arthropods are known to be less abundant and diverse in forest fragments [33] and near roads [34], but it is not clear how these changes translate in exurban areas.

Our study area comprised of a mix of forested exurban and undeveloped areas on the southern Cumberland Plateau in Tennessee, USA. The study area is located in the Cumberland Plateau and the Southern Appalachian region, which have been identified as areas of high conservation priority [35, 36]. Native forests on the southern Cumberland Plateau have been declining at a rate of about 1% per year for several decades, with the primary causes of loss being conversion to pine plantations and exurbanization [37, 38]. Exurbanization in this area is predicted to continue into the foreseeable future [39]. A previous study in this region found that the richness and composition of bird communities differed in exurban areas compared to the surrounding forest [7]. We build on this study first by reexamining bird communities using randomly located sampling points. The previous study was conducted from roads or trails which do not provide a random sample across the landscape. Second, we use these same randomly located sampling points to sample the macroinvertebrate community. Specifically, we tested the following hypotheses: (1) bird richness and abundance increase as the degree of exurbanization increases, as found in a previous work in this region; (2) macroinvertebrate diversity and abundance will change across an exurban gradient (given the variability of previous studies we made no specific prediction about the direction of change); (3) across undeveloped and exurban areas, ground-feeding bird diversity is positively associated with abundance of leaf litter macroinvertebrates; (4) across undeveloped and exurban areas, insectivorous bird diversity is positively associated with abundance of flying macroinvertebrates; (5) community composition of birds and macroinvertebrates (as measured by ordination methods) is associated with the degree of exurbanization.

2. Materials and Methods

2.1. Study Sites. Our study took place in and around Sewanee, Tennessee, USA on the Cumberland Plateau (35.20°N, 85.92°W). The forests in this region are mostly composed of oaks (*Quercus*) and hickories (*Carya*), with some maple (*Acer*) and pine (*Pinus*). Soils in the region are derived from sandstone and are generally welldrained and nutrient poor [38].

2.2. Point Selection. We used a random number generator in Manifold 8.0 (Manifold Net Ltd., Carson City, NV), a geographical information system (GIS) software, to generate a stratified random set of points within our study area. The study areas were defined as the town of Sewanee and the surrounding forest, an area approximately 4000 ha area in extent. Each point was at least 400 m away from any other point and 100 m from the escarpment of the plateau (where the plateau drops about 275 m in elevation). Because housing developments are likely nonrandomly located on the landscape with respect to streams and the plateau escarpment, random point selection was stratified by distance from streams and distance from the edge of the plateau. We therefore obtained randomly positioned points in undeveloped forest and exurban areas, but the distance from streams and the escarpment did not differ significantly between points in undeveloped forest and points in exurban areas ($P > .05$ and df = 1,27 for all regressions comparing either distance from sampling points to streams or distance from sampling points to the edge of the escarpment with the proportion of impervious or canopy cover around each point; see below for details on these proportions). In addition, using a more coarse measure of exurbanization and defining "undeveloped" points ($n = 15$) as those with no houses within 200 m and "exurban" points ($n = 14$) as those with one or more houses within 200 m, undeveloped

and exurban points did not differ in distance to the nearest stream (*t*-test P =.51) and distance to escarpment (*t*-test P =.86). We obtained thirty points across the landscape, but discarded one that was in a golf course, resulting in a sample size of 29 points. We discarded the golf course point because our study was not designed to examine golf course ecology.

2.3. Quantification of Exurbanization. We used digital aerial photography to quantify the degree of exurbanization within a 200 m radius circle around each sample point, using Manifold 8.0. The 200 m radius ensured that circles from sampling points did not overlap. Within these circles, we digitized tree canopy cover using summer leaf-on 2008 United States Department of Agriculture Imagery Program (NAIP) orthorectified aerial imagery. Canopy cover was defined as any mature tree cover within the circle. Impervious surfaces were digitized from orthorectified leaf-off aerial imagery, with 6 inch pixel resolution. The imagery was collected by the Franklin County Tennessee GIS Users Group (Franklin county, TN) and captured in March 2008. Impervious surfaces were defined as all impermeable surfaces such as roads, buildings, and gravel parking areas. We digitized canopy cover and impervious surfaces at a scale of 1: 1700. After digitizing, we calculated the proportion coverage of canopy and impervious surfaces for each point.

2.4. Bird Point Counts. Bird counts were conducted between 5:00 and 8:30 AM from 27 May to 2 June 2008. At each point, we recorded all birds seen and heard during a five minute point count. Five minutes is the recommended optimal sampling period for bird point counts in our region [40]. One observer made all detections and identifications at all sites. Bird counts were not conducted during rain or while wind force was higher than a three on the Beaufort scale.

For the analyses that examined associations between the abundance of aerial and soil macroinvertebrates and birds, we divided birds into "ground-feeding" and "aerial insectivore" foraging groups. These classifications were based on Birds of North America species accounts [41]. "Ground feeders" were those species that performed >10% of their breeding season foraging on the ground. "Aerial insectivores" were those species that performed >10% of their breeding season foraging by hunting insects on the wing.

2.5. Aerial Macroinvertebrates: Sweep Netting. Sweep netting occurred between 2:00 and 5:00 PM from 3 June to 24 June 2008. At each point, we used sweep netting at four locations 10 m away from the point in each cardinal direction. For each of these four locations, we took one sample near the ground and one sample in the air three feet off the ground. We moved the net in the shape of a figure eight six times for each sample. Macroinvertebrate diversity and abundance were quantified to the level of order in the field. We did not sweep net when the temperature was below 21 degrees Celsius, during rain, or with wind force higher than a three on the Beaufort scale.

2.6. Ground-Dwelling Macroinvertebrates: Soil Core Samples and Pitfall Traps. Soil core samples were taken from 24 June

to 22 July 2008. Samples were taken at 5 m and 10 m for each cardinal direction at every point (i.e., 8 cores per point). We used a corer to obtain samples, and we placed our samples in a stack of two soil sieves (4 mm and 2 mm mesh sizes). We shook the stack of soil sieves for 30 seconds, and then we searched for 60 seconds at the top layer (particles > 4 mm), 120 seconds at the middle layer (4 mm > particles > 2 mm), and 180 seconds at the bottom layer (particles < 2 mm). Macroinvertebrates were identified in the field to the level of order (in the case of Araneae, Coleoptera, Dermaptera, Diplura, Hemiptera, Hymenoptera, Isopoda, Isoptera, Orthoptera, Protura, Pulmonata, and Thysanura), superorder (for Acariformes and Parasitiformes), subclass (Collembola and Oligochaeta), or class (Diplopoda and Chilopoda).

We used pitfall traps from 2 to 24 July 2008. We created pitfall traps using waxed paper cups with a diameter of 7.5 cm and a volume of 266 mL. We filled each with 120 mL of water and approximately 6 mL of Dial handsoap. We used the holes created by the soil core samples to place the cups flush to the ground. Pitfall traps were placed at five and ten meters in each cardinal direction at every point (i.e., 8 pitfall traps per point). The pitfall traps were left for 46–50 hours. Upon collection, macroinvertebrates were stored in 95% ethyl alcohol. Macroinvertebrates were identified in the lab to the levels listed above for soil cores. In the case of heavy rain that caused the traps to overflow, the trap contents were discarded and traps were reset for 48 hours. To obtain biomass data, the pitfall traps were replicated from 7 to 12 July 2009 at each point using the same field protocol as in 2008, except that four instead of eight pitfalls were used at each point (at 10 m from each point). The contents of each of these pitfalls were drained through a paper coffee filter, macroinvertebrates were counted, then the contents were dried (after removing all extraneous plant matter) at 50 degrees Celsius for 72 hours then weighed to the nearest thousandth gram using an Ohaus TS400D scale.

2.7. Tree Canopy Macroinvertebrates: Frass Collection. To quantify the abundance of caterpillars and other canopy-dwelling macroinvertebrates, we assessed the amount of frass (feces) falling from the canopy at each point from 3 to 25 June 2008. We placed eight plastic containers with a 16.5 cm diameter under trees at five and ten meters in each cardinal direction for 24–28 hours at every site. After collecting the containers, we emptied the frass in each container into envelopes and dried the frass in an oven at 48 degrees Celsius for 46–50 hours, following the methods of Fischbacher et al. [42]. We weighed the dried frass to the nearest thousandth of a gram using a Denver Instrument Company A-160 scale.

2.8. Community-Level Analyses for Birds and Invertebrates. We assessed bird species richness (number of species detected per point) by examining the number of species and individuals found per point. We also compared species richness at a larger spatial extent by pooling all the data from exurban areas and comparing this to the pooled data from all undeveloped areas (see "Point Selection" section for

definitions) then running rarefaction curves in EcoSim 7.0 [43] to analyze how species richness increases as the number of individuals sampled increases. Rarefaction curves control for both sampling effort and the density of individuals. We assessed species evenness by calculating the probability of interspecific encounter (PIE). PIE controls for both sampling effort and bird density, and uses repeated resampling of the data to calculate the probability that the next bird sampled will be of a different species [43]. High PIE values indicate high species evenness. We used detrended correspondence analysis (DCA) to assess how similar sampling points were in their bird and invertebrate communities. DCA is an ordination technique that uses reciprocal averaging of species abundance data to place samples in an ordination space defined by a small number of dimensions. DCA places samples in the ordination space so that distances between points are equivalent across the entire ordination space and points close to each other share similar communities.

3. Results

3.1. Metrics of Exurbanization. The mean housing density measured within 200 m radius areas around each sample point was 0.26 houses/ha, with a range of 0 to 0.96 houses/ha. These houses were embedded in several thousand hectares of undeveloped forest. The proportion of impervious surface around each point was a very strong predictor of the proportion of canopy cover (linear regression: P <.0001, $R^2 = 0.92$, df = 1,27). Because these two measures of exurbanization were highly correlated to each other, in subsequent analyses we use the proportion of impervious surface around each point as our continuous measure of exurbanization. Where an analysis requires not a continuous measure of exurbanization, but a simple exurban/undeveloped categorization, we used the definitions of exurban and undeveloped forest from Section 2.2.

3.2. Bird Communities. Bird species richness (number of species detected per point) increased as the proportion of impervious surface around each point increased. This was true both for the subsample of birds detected within 50 m of each point (Figure 1; linear regression: P =.010, $R^2 = 0.22$, df = 1,27) and for all birds detected at each point regardless of the distance from the point (linear regression: P =.031, $R^2 = 0.16$, df = 1,27). At a larger scale (pooling all the data from exurban areas and comparing this to the pooled data from all undeveloped areas) rarefaction curves indicated that exurban areas had slightly higher richness than did undeveloped areas, although the 95% confidence intervals for each overlapped, indicating that the difference was slight (Figure 2).

Bird abundance (number of individuals detected per point) also increased across the exurbanization gradient, for birds detected within 50 m of each point (Figure 3; linear regression: P =.0003, $R^2 = 0.38$, df = 1,27) and for all birds detected at each point (linear regression: P =.002, $R^2 = 0.29$, df = 1,27).
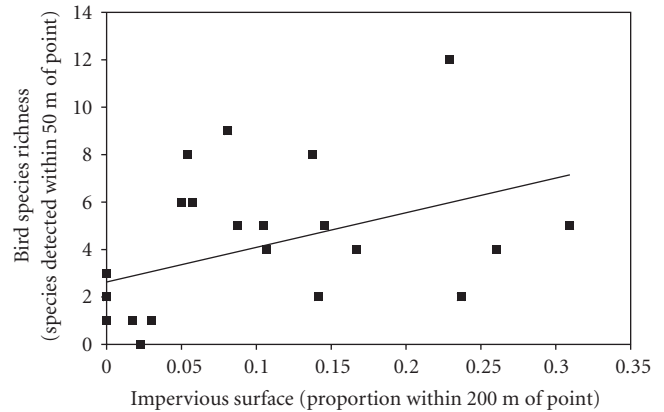

FIGURE 1: Bird species richness measured at the per-point scale increased with increasing exurbanization. The number of bird species detected during 5 minute point counts was higher at points that had higher proportions of impervious cover around them (linear regression: P =.010, $R^2 = 0.22$, df = 1,27).
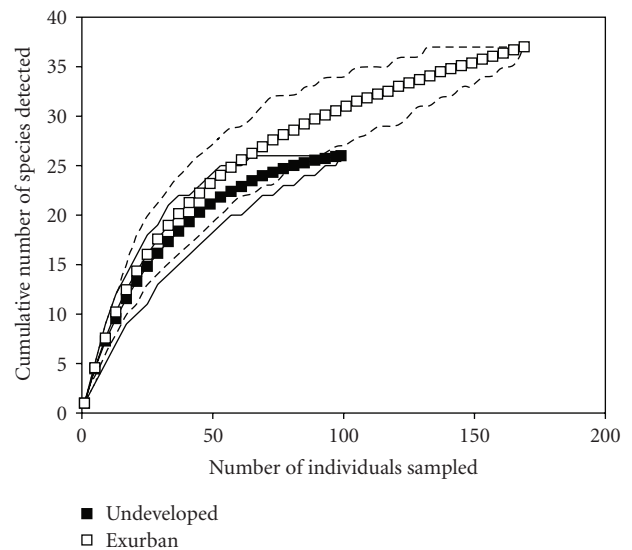

FIGURE 2: Bird species richness in each habitat class measured with rarefaction curves at the scale of habitat class. Rarefaction curves describe how the number of species changes with the number of individuals sampled, thus controlling for both sampling effort and bird density. Thick lines indicate species richness (open points: exurban areas; filled points: undeveloped areas) and thin lines indicate 95% confidence intervals (dashed thin line: exurban areas; solid thin line: undeveloped areas).

Species evenness, as measured by the probability of interspecific encounter (PIE), was higher in exurban areas compared to undeveloped areas, although there is a small overlap in the 95% confidence intervals of PIE (Figure 4).

The composition of bird communities was strongly related to the surrounding habitat. In a detrended correspondence analysis (DCA) of all the points sampled, the exurban and undeveloped points clustered in different places
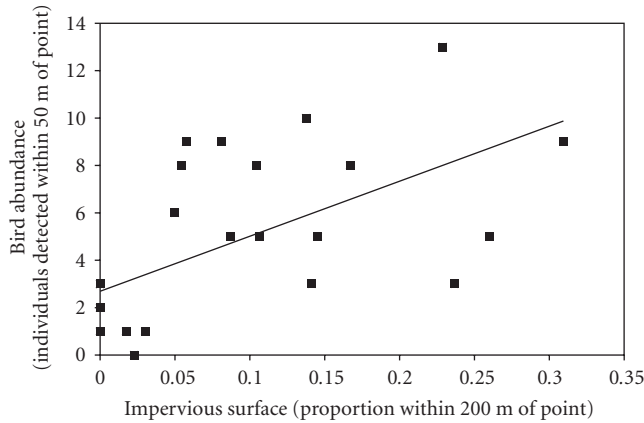
FIGURE 3: Abundance of birds increased with increasing exurbanization. The number of individual birds (regardless of species) detected during 5 minute point counts was higher at points that had higher proportions of impervious cover around them (linear regression, $P =.0003$, $R^2 = 0.38$, df = 1,27).
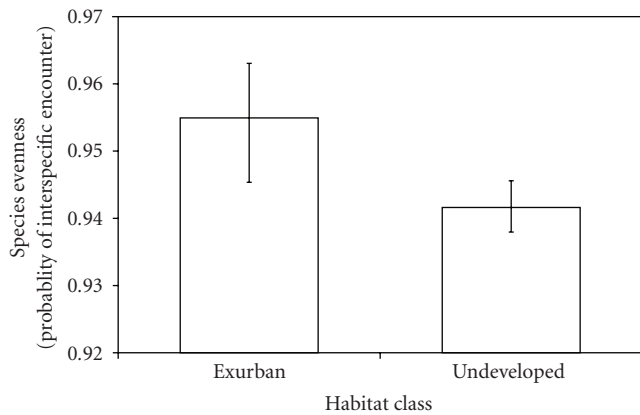

FIGURE 4: Mean and 95% confidence intervals of bird species evenness in each habitat class. Evenness is shown by the probability of interspecific encounter (PIE; calculated in EcoSim using 95 individuals in each habitat class; [43]). PIE controls for both sampling effort and bird density, and it uses repeated resampling of the data to calculate the probability that the next bird sampled will be of a different species. Therefore, high PIE values indicate high species evenness.

in ordination space, indicating that the species composition of communities differed between these two habitats (Figure 5). A summary of detections of birds in exurban and undeveloped areas gives a general ranking of which species where found in which areas (Table 1).

3.3. Macroinvertebrate Diversity and Abundance.

There was no significant relationship between richness or abundance and impervious cover for sweep nets or for pitfall traps (linear regressions: sweep net richness $R^2 = 0.07$, $P =.14$, df = 1,27; sweep net abundance $R^2 = 0.08$, $P =.13$, df = 1,27; pitfall richness $R^2 = 0.04$, $P =.30$, df = 1,27; pitfall abundance
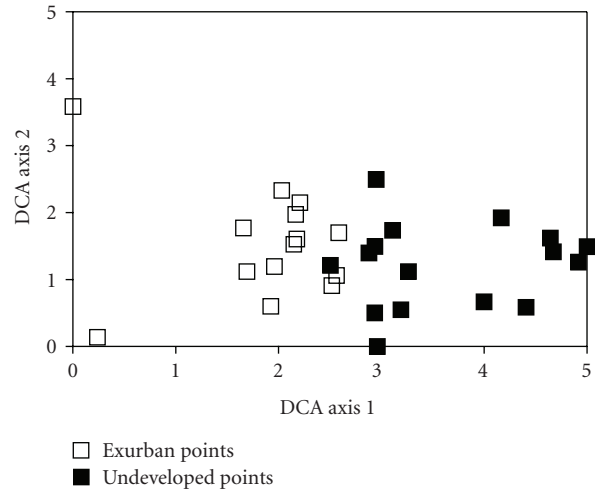

FIGURE 5: Detrended correspondence analysis of bird communities. Each point represents the position in ordination space of the bird community detected at one sampling point. The two axes show the relative position of each point in the multidimensional space defined by the species found at each point. Thus, points with similar bird communities cluster together on the graph. The first axis is the one along which most of the variation in the ordination space is arranged (eigenvalue = 0.67) the second axis is the second most important axis through the ordination space (eigenvalue = 0.35).

$R^2 = 0.04$, $P =.29$, df = 1,27). However, both the richness and the abundance of macroinvertebrates sampled in soil cores increased as the proportion of impervious surface around each point increased (linear regressions: richness $R^2 = 0.50$, $P <.0001$, df = 1,27; abundance $R^2 = 0.16$, $P =.034$, df = 1,27).

A detrended correspondence analysis of the data from the soil core samples showed that exurban and undeveloped areas differed somewhat in the composition of the macroinvertebrate communities (Figure 6), although there was more overlap than the DCA for bird communities. Note that the bird data assessed diversity at the level of species and the macroinvertebrate data assessed diversity at a much coarser scale (mostly orders; see Methods). Nonetheless, macroinvertebrate communities in exurban and undeveloped areas differed significantly in their position along the first DCA axis (t-test: $P =.018$). A summary of macroinvertebrates in soil core samples in exurban and undeveloped areas gives a general ranking of which taxa where found in which areas (Table 2).

In 2009, the dry biomass of macroinvertebrates in pitfall traps at each point increased significantly with the degree of impervious surface at each point (linear regression: $R^2 = 0.306$, $P =.002$, df = 1,27). In addition, there was a significant relationship between the abundance of macroinvertebrates in pitfall traps and the dry biomass of these macroinvertebrates (linear regression: $R^2 = 0.317$, $P =.001$, df = 1,27).

The dry mass of frass collected was at or below the limit of the detection ability of the scales that we used (mean and median dry mass were 0.001 g); therefore, we could not use this information to assess the relationship between frass and exurbanization.

TABLE 1: Bird species detected during point counts. Species are ranked according to the number of detections per sample point in undeveloped areas ($n = 15$) minus the number of detections per sample point in exurban areas ($n = 14$ points). Species with positive values of this difference were found mostly undeveloped forests and not in exurban areas, species with values near zero were found in both undeveloped forest and in exurban areas, and species with negative values were found mostly in exurban areas and not in undeveloped forest.

Common name	Scientific name	Detections per point		
		Exurban	Undeveloped	Undeveloped minus exurban
Red-eyed Vireo	Vireo olivaceus	0.14	1.00	0.86
Ovenbird	Seiurus aurocapilla	0.00	0.73	0.73
Scarlet Tanager	Piranga olivacea	0.00	0.53	0.53
Hooded Warbler	Wilsonia citrina	0.00	0.40	0.40
Blue-gray Gnatcatcher	Polioptila caerulea	0.00	0.20	0.20
Black-and-white Warbler	Mniotilta varia	0.00	0.20	0.20
Kentucky Warbler	Oporornis formosus	0.00	0.13	0.13
Ruby-throated Hummingbird	Archilochus colubris	0.00	0.13	0.13
Eastern Wood-Pewee	Contopus virens	0.21	0.33	0.12
White-eyed Vireo	Vireo griseus	0.00	0.07	0.07
Hairy Woodpecker	Picoides villosus	0.07	0.13	0.06
Indigo Bunting	Passerina cyanea	0.07	0.13	0.06
Mourning Dove	Zenaida macroura	0.07	0.07	0.00
Red-shouldered Hawk	Buteo lineatus	0.07	0.00	−0.07
Eastern Bluebird	Sialia sialis	0.07	0.00	−0.07
Gray Catbird	Durmetella carolinensis	0.07	0.00	−0.07
Summer Tanager	Piranga rubra	0.07	0.00	−0.07
Pileated Woodpecker	Dryocopus pileatus	0.07	0.00	−0.07
Northern Flicker	Colaptes auratus	0.07	0.00	−0.07
Pine Warbler	Dendroica pinus	0.07	0.00	−0.07
Yellow-throated Warbler	Dendroica dominica	0.07	0.00	−0.07
Purple Martin	Progne subis	0.07	0.00	−0.07
House Sparrow	Passer domesticus	0.07	0.00	−0.07
Wood Thrush	Hylocichla mustelina	0.29	0.20	−0.09
House Finch	Carpodacus mexicanus	0.14	0.00	−0.14
Eastern Phoebe	Sayornis phoebe	0.14	0.00	−0.14
Downy Woodpecker	Picoides pubescens	0.21	0.07	−0.15
American Goldfinch	Carduelis tristis	0.29	0.13	−0.15
Brown-headed Cowbird	Molothrus ater	0.36	0.13	−0.22
Red-bellied Woodpecker	Melanerpes carolinus	0.43	0.20	−0.23
White-breasted Nuthatch	Sitta carolinensis	0.43	0.20	−0.23
Great Crested Flycatcher	Myiarchus crinitus	0.29	0.00	−0.29
American Robin	Turdus migratorius	0.29	0.00	−0.29
European Starling	Sturnus vulgaris	0.29	0.00	−0.29
American Crow	Corvus brachyrhynchos	0.50	0.20	−0.30
Eastern Towhee	Pipilo erythrophthalmus	0.36	0.00	−0.36
Song Sparrow	Melospiza melodia	0.43	0.00	−0.43
Chipping Sparrow	Spizella passerine	0.43	0.00	−0.43
Northern Cardinal	Cardinalis cardinalis	0.57	0.13	−0.44
Blue Jay	Cyanocitta cristata	0.64	0.20	−0.44
Carolina Chickadee	Poecile carolinensis	0.79	0.20	−0.59
Common Grackle	Quiscalus quiscula	0.64	0.00	−0.64
Carolina Wren	Thryothorus ludovicianus	0.93	0.20	−0.73
Tufted Titmouse	Baeolophus bicolor	1.43	0.60	−0.83
Chimney Swift	Chaetura pelagica	0.93	0.07	−0.86

TABLE 2: Macroinvertebrate taxa detected from soil cores. Taxa are ranked according to the number of captures per sample point in undeveloped areas (n = 15) minus the number of captures per sample point in exurban areas (n = 14 points). Taxa with positive values of this difference were found mostly undeveloped forests and not in exurban areas taxa with values near zero were found in both undeveloped forest and in exurban areas, and taxa with negative values were found mostly in exurban areas and not in undeveloped forest.

| Taxon | Captures/sample | | Captures/sample: |
	Exurban	Undeveloped	Undeveloped minus exurban
Acari	0.07	0.13	0.06
Isoptera	0.36	0.40	0.04
Dermaptera	0.07	0.00	−0.07
Ixodida	0.07	0.00	−0.07
Pulmonata	0.07	0.00	−0.07
Protura	0.14	0.07	−0.08
Thysanura	0.14	0.07	−0.08
Hemiptera	0.14	0.00	−0.14
Orthoptera	0.21	0.00	−0.21
Diplopoda	0.43	0.07	−0.36
Araneae	0.79	0.40	−0.39
Chilopoda	2.14	1.73	−0.41
Gastropoda	0.50	0.07	−0.43
Diplura	0.57	0.07	−0.50
Collembola	1.93	1.13	−0.80
Hymenoptera	2.21	1.40	−0.81
Coleoptera	2.43	1.40	−1.03
Oligochaeta	1.43	0.27	−1.16
Isopoda	1.43	0.07	−1.36

3.4. Associations between Birds and Macroinvertebrates. When compared across all sampling points, the abundance of macroinvertebrates in soil core samples was positively associated with the abundance of ground-foraging birds at point counts (linear regression: richness R^2 = 0.30, P =.002, df = 1,27; 23 out of the 45 bird species that we detected were classified as "ground-foragers"). However, there was no relationship between the abundance of macroinvertebrates in pitfall traps and the abundance of ground-foraging birds (linear regression: richness R^2 < 0.01, P =.68, df = 1,27). In addition, the abundance of macroinvertebrates in sweep nets was not associated with the abundance of aerial insectivore birds (linear regression: richness R^2 < 0.01, P =.91, df = 1,27; 16 out of the 45 bird species that we detected were classified as "aerial insectivores").

4. Discussion and Conclusions

We found that bird richness and abundance increased across the exurban gradient in our study area. A previous study of birds in our region obtained similar results [7]. The sampling points in this earlier study were, however, located along existing roads and trails and were not placed using a randomization process. Roads in this region, and beyond, are known to be nonrandomly located on the landscape [44], meaning that roadside samples give potentially biased results. In contrast, all sampling points in the present study were placed using randomization methods over the entire study area. Our finding that richness and abundance of birds increased as the intensity of exurbanization increased suggests that the previous results were not an artifact of the roadside sampling method used. Our results also conform to patterns found elsewhere in North America, where low density exurban areas have higher species richness than the surrounding habitat [5, 9–11]. Note that the mean impervious surface cover within 200 m of our sample points was 7% (with a maximum of 30%), so our study area did not include the more heavily urbanized areas (which have impervious cover of 50% and more) in which bird diversity usually declines [45].

The composition of the bird community shifted with exurbanization. A detrended correspondence analysis (DCA) showed that exurban and undeveloped areas had different bird communities, with sample points in each habitat type clustering together (Figure 5). A ranking of species according to the number of detections in exurban and undeveloped areas shows that some species are strongly associated with undeveloped forest. Presumably these are the species that will fare poorly if exurbanization expands in the future. This group of species includes several on the Partners in Flight Species of Continental Importance list of priority species for conservation action (Hooded Warbler and Kentucky Warbler) [46] (Partners in Flight is a scientific group that assesses the conservation status of North American landbirds) as well
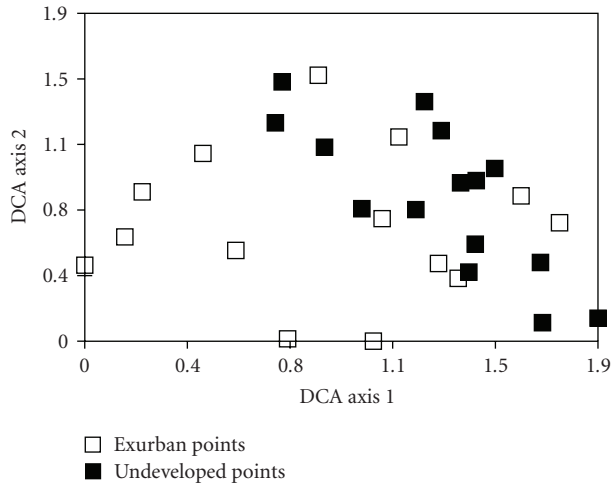
FIGURE 6: Detrended correspondence analysis of macroinvertebrates from soil core samples. Each point represents the position in ordination space of the macroinvertebrate community detected at one sampling point. The two axes show the relative position of each point in the multidimensional space defined by the macroinvertebrate orders found at each point. Thus, points with similar macroinvertebrate taxa cluster together on the graph. The first axis is the one along which most of the variation in the ordination space is arranged (eigenvalue = 0.30); the second axis is the second most important axis through the ordination space (eigenvalue = 0.165).

as species in population decline (Black-and-white Warbler) [47]. At the other end of the spectrum, several species were strongly associated with exurban areas (e.g., Chimney Swift, Tufted Titmouse), including two exotic species (House Sparrow and European Starling), but also species that are on the Partners in Flight Species of Continental Importance priority list (Wood Thrush and Eastern Towhee). Exurban areas in our region maintain most of their forest canopy, with some interspersed openings and shrubby vegetation. These habitat conditions evidently attract numerous native species. The exotic species in our study area were restricted to one sampling point—the point with the highest proportion of impervious surface around it (30%). The presence of species of conservation concern in exurban areas confirms the results of a previous study in this region [7], which found that exurban areas had the highest numbers of Partners in Flight species of conservation concern, although native forest had more of these species at high densities.

There are numerous potential causes for the changes in richness and diversity of birds in exurban areas [1, 8]. Here, we investigated one of these: the abundance and diversity of macroinvertebrates (potential food sources for birds) during the breeding season. Unlike the very clear patterns in the bird data, results for the macroinvertebrate data were mixed. The richness and the abundance of macroinvertebrates in soil core samples increased as the proportion of impervious surface around sampling points increased. The soil core samples also showed some clustering in a DCA, although much less distinctly than the bird data (perhaps unsurprisingly, given that birds were identified to species and macroinvertebrates

to order or above). However, there was no significant relationship between the extent of exurbanization and the abundance and richness of macroinvertebrates in 2008 pitfall traps or in sweep nets.

Our results are interesting in light of previous work that has shown that macroinvertebrate biomass is an order of magnitude or more lower in small forest fragments compared to large fragments [33]. Here, we studied forested areas that have been perforated by small openings. This contrasts with "fragmentation" where forests are cut into block-like fragments surrounded by agriculture or urban areas. Our results suggest that scattered exurban development may have a very different effect than fragmentation of forests, with exurban development having a smaller effect on macroinvertebrate communities. Studies of butterflies in Arizona also found that richness was similar in exurban and undeveloped areas [24]. The generality and robustness of this conclusion requires further testing in our study region and beyond, especially because "perforation" of forest by small openings appears to cover up to 20% of the eastern North American forest, making it an important source of change in forest communities [48]. To this end, we repeated pitfall traps in 2009, this time measuring the abundance and dry biomass of macroinvertebrates (in 2008 we did not measure biomass). We found that the biomass of macroinvertebrates increased across the exurban gradient and that the abundance of macroinvertebrates in the traps predicted the dry biomass of the samples (thus the 2008 abundance data also may be informative about biomass). This additional set of data suggests that the results from 2008 were not an anomaly—looking across both years, exurban areas in our region host macroinvertebrate communities that are either broadly similar in richness, abundance, or biomass as the communities in undeveloped areas, or exurban areas have somewhat higher levels of richness, abundance, or biomass. We emphasize, however, that more work in other regions is needed to test the generality of this finding. Studies of macroinvertebrates in urban areas have found very different patterns in different ecosystems, suggesting that the effects of development are context dependent [25, 27, 30–32].

The availability of macroinvertebrate food during the breeding season is known to be an important predictor of the breeding productivity of bird populations [20–22]. Therefore, it is possible that the slightly higher numbers of macroinvertebrates that we found in exurban areas may be partly responsible for the increased abundance and diversity of birds. However, two factors moderate the strength of this conclusion. First, our study was correlational, not experimental. Exurban and undeveloped areas differ in many ways, so without experimental manipulations it is hard to tease out the effect of macroinvertebrates from the confounding effects of predators, parasites, vegetation, water, and other variables [8]. Second, we found limited relationships between foraging groups of birds and the abundance of ground and aerial macroinvertebrates. The abundance of macroinvertebrates in soil core samples did predict the abundance of ground-foraging birds, but the abundance of macroinvertebrates in pitfall traps did not. The abundance

of macroinvertebrates in sweep nets was not associated with the abundance of aerial insectivore birds. Thus, there was no strong relationship between macroinvertebrate food availability and the abundance of birds, at least at the scale at that we measured. This suggests that macroinvertebrate food may be only one of many factors that interact to produce changes in bird communities in exurban areas.

We recommend that future studies quantify macroinvertebrate communities in other exurban areas. Expanding both the taxonomic depth and the range of microhabitats examined would help explore the responses of macroinvertebrates in more detail. In particular, our canopy frass-sampling methods did not yield enough material to provide meaningful information, yet the forest canopy is home to much of the diversity and biomass of macroinvertebrates. Given the rapid rate of the expansion of exurban areas [1], understanding how macroinvertebrates respond to low-density housing development will be an important component of understanding the ecology of an exurbanized world.
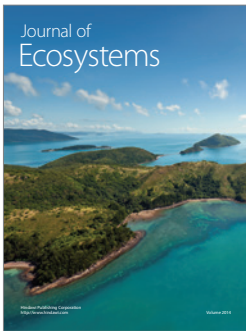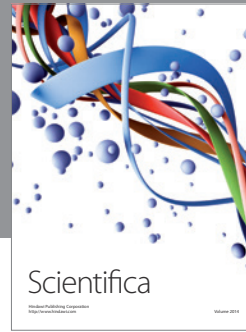
Acknowledgment

References

[1] A. J. Hansen, R. L. Knight, J. M. Marzluff, et al., "Effects of exurban development on biodiversity: patterns, mechanisms, and research needs," *Ecological Applications*, vol. 15, no. 6, pp. 1893–1905, 2005.

[2] D. M. Theobald, "Placing exurban land use change in a human modification framework," *Frontiers in Ecology and Environment*, vol. 2, no. 3, pp. 139–144, 2004.

[3] D. M. Theobald, "Land-use dynamics beyond the American urban fringe," *Geographical Review*, vol. 91, no. 3, pp. 544–564, 2001.

[4] D. G. Brown, K. M. Johnson, T. R. Loveland, and D. M. Theobald, "Rural land-use trends in the conterminous United States, 1950–2000," *Ecological Applications*, vol. 15, no. 6, pp. 1851–1863, 2005.

[5] R. B. Blair, "Birds and butterflies along an urban gradient: surrogate taxa for assessing biodiversity?" *Ecological Applications*, vol. 9, no. 1, pp. 164–170, 1999.

[6] M. L. McKinney, "Effects of urbanization on species richness: a review of plants and animals," *Urban Ecosystems*, vol. 11, no. 2, pp. 161–176, 2008.

[7] D. G. Haskell, J. P. Evans, and N. W. Pelkey, "Depauperate Avifauna in plantations compared to forests and exurban areas," *PLoS ONE*, vol. 1, no. 1, article e63, 2006.

[8] D. E. Chamberlain, A. R. Cannon, M. P. Toms, D. I. Leech, B. J. Hatchwell, and K. J. Gaston, "Avian productivity in urban landscapes: a review and meta-analysis," *Ibis*, vol. 151, no. 1, pp. 1–18, 2009.

[9] R. B. Blair, "The effects of urban sprawl on birds at multiple levels of biological organization," *Ecology and Society*, vol. 9, no. 5, pp. 1–21, 2004.

[10] J. D. Maestas, R. L. Knight, and W. C. Gilgert, "Biodiversity across a rural land-use gradient," *Conservation Biology*, vol. 17, no. 5, pp. 1425–1434, 2003.

[11] C. E. Bock, Z. F. Jones, and J. H. Bock, "The oasis effect: response of birds to exurban development in a southwestern savanna," *Ecological Applications*, vol. 18, no. 5, pp. 1093–1106, 2008.

[12] J. M. Marzluff, R. Bowman, and R. Donnelly, Eds., *Avian Ecology and Conservation in an Urbanizing World*, Kluwer Academic Publishers, Norwell, Mass, USA, 2001.

[13] R. B. Blair and E. M. Johnson, "Suburban habitats and their role for birds in the urban-rural habitat network: points of local invasion and extinction?" *Landscape Ecology*, vol. 23, no. 10, pp. 1157–1169, 2008.

[14] F. Yeoman and R. Mac Nally, "The avifaunas of some fragmented, periurban, coastal woodlands in south-eastern Australia," *Landscape and Urban Planning*, vol. 72, no. 4, pp. 297–312, 2005.

[15] P. Clergeau, S. Croci, J. Jokimäki, M.-L. Kaisanlahti-Jokimäki, and M. Dinetti, "Avifauna homogenisation by urbanisation: analysis at different European latitudes," *Biological Conservation*, vol. 127, no. 3, pp. 336–344, 2006.

[16] K. L. Borgmann and A. D. Rodewald, "Nest predation in an urbanizing landscape: the role of exotic shrubs," *Ecological Applications*, vol. 14, no. 6, pp. 1757–1765, 2004.

[17] K. E. Heckmann, P. N. Manley, and M. D. Schlesinger, "Ecological integrity of remnant montane forests along an urban gradient in the Sierra Nevada," *Forest Ecology and Management*, vol. 255, no. 7, pp. 2453–2466, 2008.

[18] J. Phillips, E. Nol, D. Burke, and W. Dunford, "Impacts of housing developments on Wood Thrush nesting success in hardwood forest fragments," *The Condor*, vol. 107, no. 1, pp. 97–106, 2005.

[19] G. D. Daniels and J. B. Kirkpatrick, "Does variation in garden characteristics influence the conservation of birds in suburbia?" *Biological Conservation*, vol. 133, no. 3, pp. 326–335, 2006.

[20] L. Zanette, P. Doyle, and S. M. Trémont, "Food shortage in small fragments: evidence from an area-sensitive passerine," *Ecology*, vol. 81, no. 6, pp. 1654–1666, 2000.

[21] S. W. Seagle and B. R. Sturtevant, "Forest productivity predicts invertebrate biomass and ovenbird (*Seiurus aurocapillus*) reproduction in Appalachian landscapes," *Ecology*, vol. 86, no. 6, pp. 1531–1539, 2005.

[22] M. E. Visser, L. J. M. Holleman, and P. Gienapp, "Shifts in caterpillar biomass phenology due to climate change and its impact on the breeding biology of an insectivorous bird," *Oecologia*, vol. 147, no. 1, pp. 164–172, 2006.

[23] N. E. McIntyre, "Ecology of urban arthropods: a review and a call to action," *Annals of the Entomological Society of America*, vol. 93, no. 4, pp. 825–835, 2000.

[24] C. E. Bock, R. A. Bailowitz, D. W. Danforth, Z. F. Jones, and J. H. Bock, "Butterflies and exurban development in southeastern Arizona," *Landscape and Urban Planning*, vol. 80, no. 1-2, pp. 34–44, 2007.

[25] F. J. Christie and D. F. Hochuli, "Responses of wasp communities to urbanization: effects on community resilience and species diversity," *Journal of Insect Conservation*, vol. 13, no. 2, pp. 213–221, 2009.

[26] J. K. Rickman and E. F. Connor, "The effect of urbanization on the quality of remnant habitats for leaf-mining Lepidoptera on *Quercus agrifolia*," *Ecography*, vol. 26, no. 6, pp. 777–787, 2003.

[27] E. A. Forys and C. R. Allen, "The impacts of sprawl on biodiversity: the ant fauna of the lower Florida Keys," *Ecology and Society*, vol. 10, no. 1, pp. 1–14, 2005.

[28] N. E. McIntyre, J. Rango, W. F. Fagan, and S. H. Faeth, "Ground arthropod community structure in a heterogeneous

urban environment," *Landscape and Urban Planning*, vol. 52, no. 4, pp. 257–274, 2001.

[29] E. Shochat, W. L. Stefanov, M. E. A. Whitehouse, and S. H. Faeth, "Urbanization and spider diversity: influences of human modification of habitat structure and productivity," *Ecological Applications*, vol. 14, no. 1, pp. 268–280, 2004.

[30] J. J. Rango, "Arthropod communities on creosote bush (*Larrea tridentata*) in desert patches of varying degrees of urbanization," *Biodiversity and Conservation*, vol. 14, no. 9, pp. 2185–2206, 2005.

[31] S. H. Faeth, P. S. Warren, E. Shochat, and W. A. Marussich, "Trophic dynamics in urban communities," *BioScience*, vol. 55, no. 5, pp. 399–407, 2005.

[32] D. T. Bolger, A. V. Suarez, K. R. Crooks, S. A. Morrison, and T. J. Case, "Arthropods in urban habitat fragments in southern California: area, age, and edge effects," *Ecological Applications*, vol. 10, no. 4, pp. 1230–1248, 2000.

[33] D. M. Burke and E. Nol, "Influence of food abundance, nest-site habitat, and forest fragmentation on breeding Ovenbirds," *Auk*, vol. 115, no. 1, pp. 96–104, 1998.

[34] D. G. Haskell, "Effects of forest roads on macroinvertebrate soil fauna of the southern Appalachian mountains," *Conservation Biology*, vol. 14, no. 1, pp. 57–63, 2000.

[35] A. P. Dobson, J. P. Rodriguez, W. M. Roberts, and D. S. Wilcove, "Geographic distribution of endangered species in the United States," *Science*, vol. 275, no. 5299, pp. 550–553, 1997.

[36] D. M. Olson and E. Dinerstein, "The global 200: priority ecoregions for global conservation," *Annals of the Missouri Botanical Garden*, vol. 89, no. 2, pp. 199–224, 2002.

[37] J. P. Evans, N. Pelkey, and D. G. Haskell, *An Assessment of Forest Change on the Cumberland Plateau in Southern Tennessee*, Small Area Assessment Forestry Demonstration Project for the Southern Forest Resource Assessment, Landscape Analysis Lab, Sewanee, Tenn, USA, 2002.

[38] D. A. McGrath, J. P. Evans, C. K. Smith, et al., "Mapping land-use change and monitoring the impacts of hardwood-to-pine conversion on the southern Cumberland Plateau in Tennessee," *Earth Interactions*, vol. 8, no. 9, pp. 1–24, 2004.

[39] D. N. Wear and J. G. Greis, Eds., "Southern forest resource assessment," General Technical Report SRS-53, U S Department of Agriculture, Forest Service, Southern Research Station, Asheville, NC, USA, 2002.

[40] C. J. Ralph, S. Droege, and J. R. Sauer, "Managing and monitoring birds using point counts: standards and applications," in *Monitoring Bird Populations by Point Counts*, C. J. Ralph, S. Droege, and J. R. Sauer, Eds., pp. 161–169, US Department of Agriculture, Forest Service, Pacific Southwest Research Station, Albany, Calif, USA, 1995, General Technical Report PSW-GTR-149.

[41] BNA, Birds of North America, July 2009, http://bna.birds.cornell.edu/bna.

[42] M. Fischbacher, B. Naef-Daenzer, and L. Naef-Daenzer, "Estimating caterpillar density on trees by collection of frass droppings," *Ardea*, vol. 86, no. 1, pp. 121–129, 1998.

[43] N. J. Gotelli and G. L. Entsminger, "Entsminger. EcoSim: null models software for ecology. Version 7," Acquired Intelligence Inc. & Kesey-Bear, Jericho, Vt, USA, 2009, http://garyentsminger.com/ecosim/index.htm.

[44] J. B. C. Harris and D. G. Haskell, "Land cover sampling biases associated with roadside bird surveys," *Avian Conservation and Ecology*, vol. 2, no. 2, p. 12, 2007.

[45] J. M. Marzluff, D. J. McGowan, R. E. Donnelly, and R. L. Knight, "A historical perspective on urban bird research: trends, terms, and approaches," in *Avian Conservation in an Urbanizing World*, J. M. Marzluff, R. Bowman, and R. E. Donnelly, Eds., pp. 1–17, Kluwer Academic Publishers, Norwell, Mass, USA, 2001.

[46] T. D. Rich, C. J. Beardmore, H. Berlanga, et al., *Partners in Flight North American Landbird Conservation Plan*, Cornell Lab of Ornithology, Ithaca, NY, USA, 2004.

[47] J. R. Sauer, J. E. Hines, and J. Fallon, *The North American Breeding Bird Survey, Results and Analysis 1966–2007, Version 5.15.2008*, USGS Patuxent Wildlife Research Center, Laurel, Md, USA, 2008.

[48] K. H. Riitters and J. W. Coulston, "Hot spots of perforated forest in the eastern United States," *Environmental Management*, vol. 35, no. 4, pp. 483–492, 2005.