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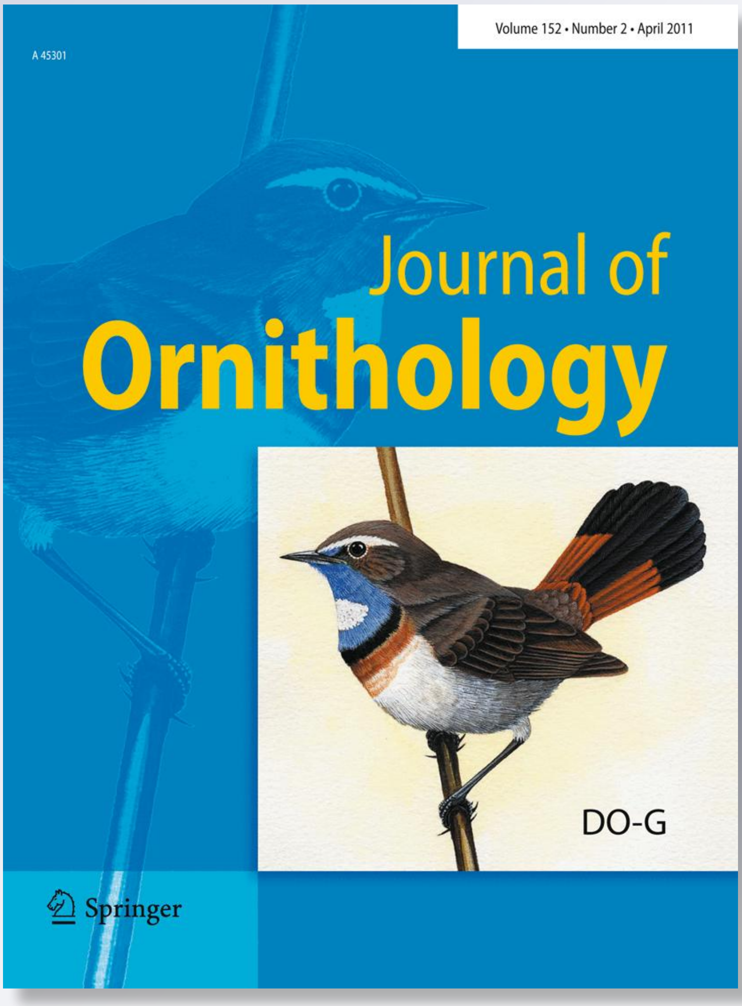

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ORIGINAL ARTICLE

Influence of exurban development on bird species richness and diversity

Marcela Suarez-Rubio · Peter Leimgruber · Swen C. Renner

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Abstract Exurban development is an accelerating land use trend in the United States with new housing units emerging in formerly closed forests. Conservation practitioners and planners suspect exurban development alters ecological processes and biodiversity to a considerable larger extent than suspected by inhabitants of exurban development areas, but empirical support for this assertion is lacking. To examine the consequences of exurban development, we studied forest bird communities in exurban development and forests located in and around Shenandoah National Park and Massanutten Mountain in northern Virginia, USA. We conducted point-count surveys for birds three times at 106 sample locations from April to July 2006. We recorded 44 species in total; 30 species were present in both exurban development and forests, 9 species were only found in exurban development, and 5 species only in forest. Bird species composition differed significantly between land-use types based on analysis in a multi-response permutation procedure (MRPP; $P < 0.01$). Relative bird abundance for forest specialist species changed significantly in exurban development versus forest (*t* test, $P < 0.05$). Three species, American Robin *Turdus migratorius*, Northern Cardinal *Cardinalis cardinalis*, and Common Grackle *Quiscalus quiscula* were indicators of exurban development. Indicators of forest were Carolina Chickadee *Poecile carolinensis*, Eastern Towhee *Pipilo erythrophthalmus*, and Wood Thrush *Hylocichla mustelina*. Our study demonstrates that exurban development alters bird community composition and relative abundance of forest specialist species.

Keywords Community response land cover · Land-use change · Rural sprawl · Urban fringe · Eastern deciduous forest

Zusammenfassung Exurbane Landentwicklung (engl.: *exurban development*) ist ein rasant zunehmender Landnutzungstyp in den Vereinigten Staaten von Amerika, bei dem Wohngebäude in zuvor geschlossenen und naturnahen Wäldern konstruiert werden. Naturschutzorganisationen und Landschaftsplaner vermuten, dass Exurbane Landentwicklung die ökologischen Prozesse und Biodiversität bedeutend verändern, allerdings fehlen bisher empirische Daten dies zu belegen. Um den Einfluss von Exurbaner Landentwicklung zu ermitteln, haben wir Vogelgemeinschaften in Exurbaner Landentwicklung mit Vogelgemeinschaften naturnaher Wälder im und um den Shenandoah Nationalpark und Massanutten Mountain im Norden des US Bundesstaates Virginia untersucht. An 106 Stellen wurden alle Vögel mit Punkt-Stopp-Zählungen insgesamt dreimal in der Zeit von April bis Juli 2006 aufgenommen. Insgesamt wurden 44 Arten erfasst; 30 Arten waren in beiden Habitattypen anzutreffen, während neun Arten nur

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in exurbaner Landentwicklung und fünf ausschließlich im naturnahen Wald anzutreffen waren. Die Zusammensetzung der Vogelgemeinschaft unterschied sich signifikant zwischen beiden Vogelgesellschaften (MRPP, $P < 0.01$). Ebenso änderte sich die Relative Abundanz für Waldvögel signifikant zwischen Exurbaner Landentwicklung und naturnahem Wald (t-test, $P < 0.05$; Exurbane Landentwicklung geht in der Regel aus naturnahem Wald hervor). Drei Arten, *Turdus migratorius*, *Cardinalis cardinalis*, und *Quiscalus quiscula* wurden als Indikatorarten für Exurbane Landentwicklung identifiziert, während *Poecile carolinensis*, *Pipilo erythrophthalmicus*, und *Hylocichla mustelina* als Indikatorarten für naturnahe Wälder gelten können. Die Studie belegt, dass Exurbane Landentwicklung die Vogelgemeinschaften in der Artenzusammensetzung und die relative Abundanz der Waldvogelarten deutlich beeinflusst.

Introduction

Global changes resulting from human activities are among the most pressing environmental challenges of the twenty-first century (Vitousek et al. 1997; Czech et al. 2000; Renner 2005; Chace and Walsh 2006; McKinney 2008). One challenge of global concern is the conversion or modification of natural habitats into urban development. Seventy percent of the world's population is projected to live in urban areas by 2050 (United Nations 2007). In addition, the number of households have increased more rapidly than the population growth in the last couple of decades (Liu et al. 2003). Rising demands of ever-growing human population is resulting in degrading ecosystem services, seriously threatening biodiversity, and increasing species extinctions (Dale et al. 2000; McKinney 2002; Chace and Walsh 2006).

Urban development is the major cause for federal listing of threatened and endangered species in the United States (Czech et al. 2000). As areas become increasingly urbanized, species richness and abundance are altered (reviewed by, e.g., Chace and Walsh 2006; McKinney 2008; Evans et al. 2009) and community composition changes. Forest-specialized species are lost rapidly (urban avoiders) and other species are gradually replaced by a few ubiquitous urban species (urban adaptors; Luniak 1994; Blair 2001; Marzluff 2001; McKinney 2002), a process called biotic homogenization (McKinney and Lockwood 1999; McKinney 2006).

In the United States, rural landscapes have changed dramatically in recent decades due to the rapid development of private rural lands into exurban development (i.e., land-use change beyond the urban fringe; Hansen et al. 2002; Theobald 2005). Exurban development is the fastest-growing type of development in the United States (Theobald 2001; Hansen et al. 2005; Radeloff et al. 2005a). Exurban development is defined as low-density residential development scattered outside suburbs, cities, and towns (Daniels 1999) but within the limits of commuting range to urban and suburban employment opportunities (Nelson 1992). Exurban development (in contrast to suburban sprawl) has low-density housing units and is often located adjacent to or nearby protected areas because of their attractive recreational and aesthetical amenities (Hansen et al. 2005; Radeloff et al. 2005a, b). However, existing definitions of exurban development are inconsistent in measurements and scale, and include: areas with 1–10 people/ha (Marzluff et al. 2001), 6–25 housing units/km^2 (0.06–0.25 units/ha or 0.08–0.17 ha/unit; Hansen et al. 2005), or 0.68–16.18 ha/unit (0.06–1.47 units/ha; Theobald 2005). Forests with low density of exurban development typically retain a closed canopy or at least canopy that appears many times to be closed if observed with medium-resolution satellite sensors. However, these forests experience significant changes in the understory resulting from maintained trails and lawns, and the landscape becomes increasingly fragmented by paved roads (Hansen et al. 2005). Recent studies have demonstrated that one-tenth to a quarter of the area (differing numbers result from different definitions and classifications, see above) and one-third of the housing units in the United States are already in exurban development areas where wild-land vegetation is interspersed by housing (USDA and USDI 2001). Exurban development also seems to be increasing more rapidly in areas of high conservation value (Hansen et al. 2002; Radeloff et al. 2005a, b), i.e. inside forests (Radeloff et al. 2005a, b), next to protected lands (Rasker and Hansen 2000), and along lakefronts (Radeloff et al. 2001; Schnaiberg et al. 2002).

In general, many United States citizens consider exurban development a valuable alternative to urban sprawl, because exurban development is considered to have less impact on biodiversity than urban sprawl (J. Buff, personal communication). However, the general view among conservationists is that exurban development alters ecological processes and biodiversity to a greater extent than forestry and agriculture (Marzluff 2001), and bird communities are suspected to be particularly sensitive (Hansen et al. 2005). Exurban development may also have a profound influence on adjacent protected lands that may include the loss of native species, changes in disturbance regimes, and the spread of invasive organisms (Hansen et al. 2002; Theobald 2004). Other concerns regarding urban sprawl and exurban development in particular are patterns of resource consumption, effects on air and water quality, and pollution (Dale et al. 2005; Hansen et al. 2005).

Exurban development affects large geographic areas (Brown et al. 2005), but the effects of this development on wildlife and biodiversity are little known especially in the eastern deciduous forest region where exurbanized areas have increased since the 1950s (Brown et al. 2005; Theobald 2005). Birds' response to urbanization has in general been well documented. Several studies have focused on bird diversity in and around cities (e.g., Emlen 1974; Beissinger and Osborne 1982; Fernández-Juricic and Jokimäki 2001; Palomino and Carrascal 2005) and along a rural to urban gradient (e.g., Blair 1996; Clergeau et al. 1998; Crooks et al. 2004; Blair and Johnson 2008; Ortega-Alvarez and MacGregor-Fors 2009). However, those studies do not clearly distinguish exurban areas from suburbia. Some studies have addressed the effects of exurban development on birds in the western US (e.g., Odell and Knight 2001; Fraterrigo and Wiens 2005; Bock et al. 2008; Merenlender et al. 2009) and a few have addressed these effects in eastern deciduous forest (Friesen et al. 1995; Nilon et al. 1995; Kluza et al. 2000). These studies provide general insights into the negative consequences of exurban development on bird communities, but little is known about exurban bird communities in eastern deciduous forest, whether exurban bird communities have a composition similar to communities of forested areas in this ecoregion, and whether modification of forest understory, typical in these areas, affects forest specialist species and ground-breeding birds.

The aim of our study is to assess the impact of exurban development on bird communities in northern Virginia, eastern United States, and contribute empirical data and analysis of exurban development on wildlife. In particular, we addressed whether species composition differs between exurban areas and forests, and if forest specialists and near-ground breeding birds decrease in exurban areas. Our presented results are relevant for conservation planning and contribute to the understanding of the impact of less intensive land-use activities (i.e., exurban development) on species distribution and species richness.

Methods

Study area

Our study area covered six sites around Front Royal, Warren County, northern Virginia (Fig. 1). Front Royal is the northern gateway to the Shenandoah National Park. It is linked to the Washington, DC, metropolitan area via Interstate 66 (about 110 km). The area experienced rapid exurban expansion between 2000 and 2006, and the population increased by almost 13% (U.S. Census Bureau 2007).

Three of our study sites were used as a reference for forests and were located in the Shenandoah National Park, on Massanutten Mountain (part of George Washington and

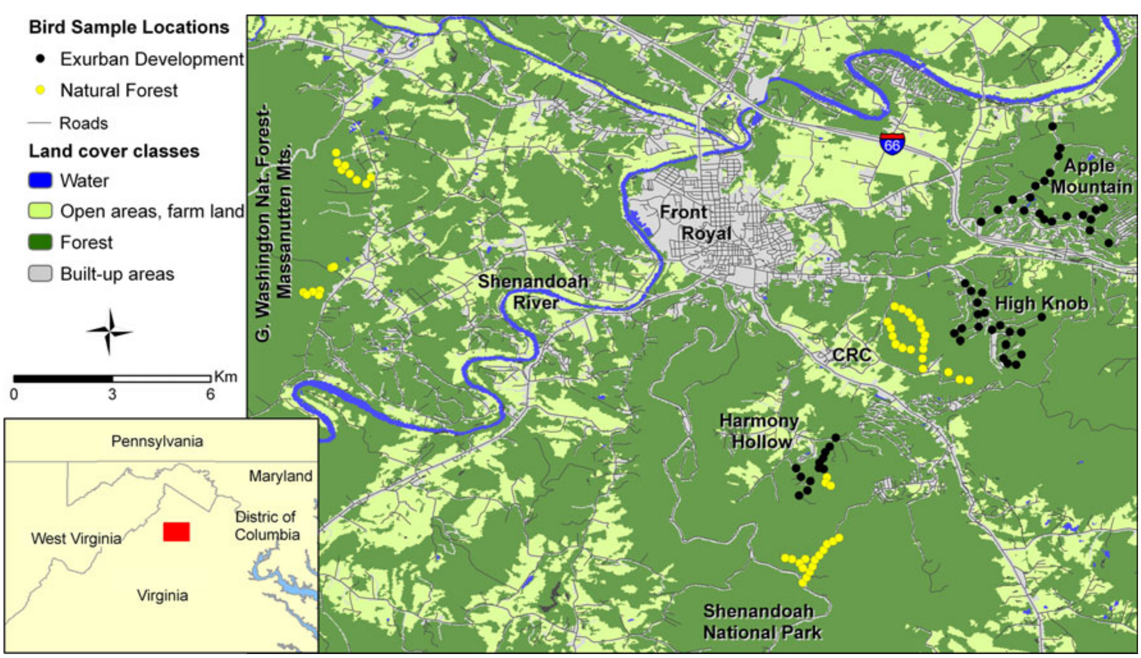

Fig. 1 Point count locations and land cover of Warren County, northern Virginia (source land cover: Huang et al. 2001; Homer et al. 2004). Exurban development localities (*black dots*) included Apple Mountain, High Knob, and Harmony Hallow; forest localities (*yellow dots*) are Massanutten Mountain, Shenandoah National Park, and the Smithsonian Conservation and Research Center (CRC)

Jefferson National Forests), and in Poesy Hollow at the Smithsonian Institution's Conservation and Research Center (Fig. 1). The other three sites were under exurban development and were placed in local communities including High Knob, Harmony Hallow, and Apple Mountain. All sites had similar vegetation characteristics and elevation (400–500 m a.s.l.). Exurban development in the study area was located in forests. The mean housing density in our exurban development sites was 0.23, 0.25, and 0.77 ha/units in High Knob, Apple Mountain, and Harmony Hollow, respectively.

Bird surveys

Six major localities were selected based on whether exurban development or forest was present. Then, we established 53 point-count localities in each of the two land-use types, exurban development and forest (106 point counts in total; Fig. 1). Point-count localities were randomly placed at least 150 m apart (maximum distance: 19.25 km). To increase comparability of forests and exurban development areas, we purposely choose our point-count localities on unpaved, narrow roads in exurban development and trails in forested areas. In addition, we choose exurban development point-count localities only with a well-retained canopy cover. Thus, differences in point-count localities between the two land-use types were minimal and should not have biased our results.

Two observers collected abundance data for birds at each sample location using fixed-radius point counts (50 m radius) from late April to July 2006, the peak of the breeding season for passerines at our study sites (Kingery 1998). We assumed each singing bird represented an adult and potentially as breeding during our surveying period (same year birds are rarely displaying if at all before the post-breeding period). Surveys were performed from sunrise until 1000 hours on days without rain and when wind was less than 15 km/h. Each sample location was surveyed three times during the surveying period for 5 min to maximize count efficiency (Petit et al. 1995), and efforts were made to avoid double-counting individuals moving among points (Bibby et al. 1992). We visited a maximum of 15 points per day, and changed sampling sequence of point counts every visit. We used the maximum detection per all three repetitions of each point-count locality as relative abundance.

Data analysis

We determined detectability of birds using the 'single-season occupancy model' in the program PRESENCE 2.4 (Hines 2006; with assumptions by Mackenzie et al. 2002, 2003). We determined detectability for all species in all 106 sample locations for the first survey plus two consequent repetitions (i.e. each sample location was visited three times). Patch occupancy was high for 37 species (out of 44 in total), i.e. these species were detected in at least 60% of all the point-count localities (Table 1).

Point-count data were used to calculate species diversity (EstimateS 8.0; Colwell 2006). We used these diversity statistics as indices and to establish whether or not our data sampling effort was sufficient. For species richness, species accumulation curves of the Abundance-based Estimator of Species Richness (ACE) was most suitable; the requirement to apply ACE and not other estimators of species richness are medium species numbers and medium to high sample sizes (Colwell 2006).

We analyzed differences in bird composition between the two land-use types using a multi-response permutation procedure (MRPP; McCune and Grace 2002). MRPP is a nonparametric procedure and we used it to test the hypothesis of no difference between the two land-use types. Prior to MRPP analyses, we log-transformed relative abundance values to compress high values, spread low values, and express the values as orders of magnitude. We searched for outliers among sample locations, using Sørensen (Bray–Curtis) distance with two standard deviations from the mean as cutoff value (McCune and Grace 2002). To identify community composition differences, we also used Sørensen (Bray–Curtis) distance measure and a natural group weighting factor $n_i/\Sigma\ n_i$ (where n_i is the number of sample locations in each group). The MRPP test statistic (T) describes the separation between the groups: stronger separations have more negative values of T, and the chance-corrected within-group agreement (A) describes the within-group homogeneity, compared to the random expectation. If the items are identical within groups, then $A = 1$. If the groups are heterogeneous and have less agreement than expected by chance, then $A < 0$ (McCune and Grace 2002).

To assess the impact of exurban development on relative abundance of forest birds, we classified birds into two groups and analyzed subsets of the entire bird community. The classification for both subsets was based on Poole's (2005) breeding habitat and nest placement information and classification. The first group (forest specialists) included birds occurring mainly in closed forest and breeding rarely if ever outside forests (class values are listed in Table 1). The second group (understory breeders) included birds breeding mainly in understory below 5 m and on the ground (values listed in Table 1). Both groups should be affected especially by exurban development because the structure of the forests changed and the understory is diminished in exurban development. We compared relative abundance for both groups (subsets) of species with a t test (relative abundance of birds in exurban

Table 1 Species detected in forest and exurban development in Warren County, northern Virginia, USA, including subsets used for analysis of impact of exurban development on forest species and understory breeders; sorted by maximum total detections

English name	Scientific name	Forest specialist[a]	Understory breeder[b]	Forest[c] ($t = 0$)	Exurban development[c] ($t = 1$)	Total detections[c]	Probability of detection (P)[d]	Proportions of sites occupied (ψ)[e]
Northern Cardinal	*Cardinalis cardinalis*		X	50	117	167	0.482	0.855
Wood Thrush	*Hylocichla mustelina*		X	81	64	145	0.473	0.818
Carolina Chickadee	*Poecile carolinensis*			84	59	143	0.409	0.891
Tufted Titmouse	*Baeolophus bicolor*			52	60	112	0.428	0.801
Eastern Wood-Pewee	*Contopus virens*			54	45	99	0.296	1.000
American Crow	*Corvus brachyrhynchos*			39	59	98	0.387	0.773
Blue Jay	*Cyanocitta cristata*			36	54	90	0.362	0.765
Swainson's Thrush	*Catharus ustulatus*	X	X	49	39	88	0.239	0.775
American Robin	*Turdus migratorius*			18	54	72	0.271	0.801
Scarlet Tanager	*Piranga olivacea*			35	29	64	0.201	1.000
Red-eyed Vireo	*Vireo olivaceus*		X	28	24	52	0.219	0.918
Eastern Towhee	*Pipilo erythrophthalmus*		X	25	11	36	0.210	0.688
Mourning Dove	*Zenaida macroura*			17	19	36	0.146	0.775
Hairy Woodpecker	*Picoides villosus*			17	17	34	0.177	0.746
Worm-eating Warbler	*Helmitheros vermivorus*	X	X	19	10	29	0.104	0.911
Common Grackle	*Quiscalus quiscula*			2	25	27	0.177	0.213
Pileated Woodpecker	*Dryocopus pileatus*	X		15	9	24	0.085	1.000
Cerulean Warbler	*Dendroica cerulea*	X		13	10	23	0.072	1.000
American Redstart	*Setophaga ruticilla*			9	8	17	0.310	0.183
Sharp-shinned Hawk	*Accipiter striatus*	X		11	5	16	0.354	0.891
Acadian Flycatcher	*Empidonax virescens*	X	X	5	10	15	0.109	0.547
Downy Woodpecker	*Picoides pubescens*			10	4	14	0.123	0.436
Hooded Warbler	*Wilsonia citrina*	X	X	10	4	14	0.035	1.000
Eastern Phoebe	*Sayornis phoebe*			7	4	11	0.079	0.518
Red-bellied Woodpecker	*Melanerpes carolinus*	X		3	4	7	0.047	1.000
Indigo Bunting	*Passerina cyanea*		X	3	3	6	0.242	0.117
Northern Flicker	*Colaptes auratus*			1	5	6	0.016	1.000
Alder Flycatcher	*Empidonax alnorum*		X	0	5	5	0.009	1.000
Canada Goose[f]	*Branta canadensis*			2	3	5	0.009	1.000
Common Raven	*Corvus corax*			1	2	3	0.009	1.000
Ovenbird	*Seiurus aurocapilla*	X	X	2	1	3	0.006	1.000
Blue-gray Gnatcatcher	*Polioptila caerulea*			0	2	2	0.006	1.000
Carolina Wren	*Thryothorus ludovicianus*			2	0	2	0.177	0.639

Table 1 continued

English name	Scientific name	Forest specialist[a]	Understory breeder[b]	Forest[c] ($t = 0$)	Exurban development[c] ($t = 1$)	Total detections[c]	Probability of detection (P)[d]	Proportions of sites occupied (ψ)[e]
Gray Catbird	*Dumetella carolinensis*		X	0	2	2	0.006	1.000
Northern Mockingbird	*Mimus polyglottos*		X	0	2	2	0.006	1.000
Tree Swallow[f]	*Tachycineta bicolor*			0	2	2	0.003	1.000
American Goldfinch	*Carduelis tristis*		X	0	1	1	0.006	1.000
Brown Thrasher	*Toxostoma rufum*		X	0	1	1	0.003	1.000
Brown-headed Cowbird	*Molothrus ater*			1	0	1	0.382	0.025
European Starling	*Sturnus vulgaris*			0	1	1	0.003	1.000
House Sparrow	*Passer domesticus*			0	1	1	0.003	1.000
Kentucky Warbler	*Oporornis formosus*	X	X	1	0	1	0.006	1.000
Red-winged Blackbird	*Agelaius phoeniceus*		X	1	0	1	0.003	1.000
Summer Tanager	*Piranga rubra*		X	1	0	1	0.003	1.000
Grand Total	44	10	18	704	775	1,479		

[a] Habitat mainly forest and rarely if at all found outside closed forest; data adapted from Poole (2005)

[b] Bird breeding on or near ground below 5 m; data adapted from Poole (2005)

[c] Relative abundance derived from maximum detection per point count

[d] Probabilities of detection (P of PRESENCE results protocol) for each species, calculated with PRESENCE 2.4

[e] Proportion of sites occupied (106 sites in total, default model parameters), calculated with PRESENCE 2.4; $\psi = 1.000$ indicates that species S probably occupied all sites

[f] Over-flying

Table 2 Observed species richness and diversity of bird communities in Warren County, northern Virginia, USA; statistics calculated applying Colwell (2006)

Indicator	Variable name as in Colwell (2006)	Overall	Exurban development	Forest
Sample points	–	106	53	53
Observed species (*S*)	–	44	39	35
Detections (*n*)	–	1,479	775	704
S_{obs}	Sobs (Mao Tau)	44	39	35
Individuals	Individuals (computed)	1,470	772	704
Jackknife (±SD)	Jack 1 mean	54.83 (2.39)	47.67 (1.76)	42.33 (1.76)
Bootstrap (±SD)	Bootstrap mean	48.76 (0.00)	43.22 (0.00)	38.41 (0.00)
Michaelis–Menten (±SD)	MMRuns mean	48.52 (48.43)	49.47 (49.75)	41.92 (41.08)
α of log-series (±SD)	Alpha mean	8.54 (0.58)	8.67 (0.69)	7.74 (0.65)
Shannon–Wiener (±SD)	Shannon mean	3.03 (0.01)	2.98 (0.00)	2.99 (0.00)
Simpson (±SD)	Simpson mean	15.98 (0.00)	14.75 (0.00)	15.94 (0.00)

development vs forest), because exurban development can be regarded as change from forest ($t = 0$) to development ($t = 1$).

We conducted indicator species analysis following the method of Dufrêne and Legendre (1997) to find representative species for the different land-use types. The procedure combines a species' relative abundance with its relative frequency of occurrence in each sample location to provide an indicator value for the particular species for each land-use type. The indicator value of a given species is independent of other species values. The index ranges from 0 to 100, the latter indicating all individuals of a species in a single land-use type and in all sample locations of that land-use type. We used the Monte Carlo technique with 1,000 permutations to test for significance of indicator values (McCune and Mefford 1999). The outlier analysis, MRPP, and the indicator species analysis were performed using PC-ORD 5 for Windows (McCune and Grace 2002).

Results

Species richness

We recorded 44 species in 1,479 detections; 30 of these species were present in both land-use types; we found 9 species only in exurban development and 5 only in forest (Table 1). Species with the highest relative abundance were Northern Cardinal, Wood Thrush, Carolina Chickadee, and Tufted Titmouse (Table 1). We detected Brown-headed Cowbird, Carolina Wren, Kentucky Warbler, Red-winged Blackbird, and Summer Tanager only in forest, and American Goldfinch, Brown Thrasher, European Starling, House Sparrow, Blue-gray Gnatcatcher, Gray Catbird, Northern Mockingbird, Tree Swallow, and Alder Flycatcher only in exurban development.

Accumulative species estimates (i.e., ACE; Fig. 2) indicated that our sampling effort was appropriate, capturing most species in the system. Similarly, standard

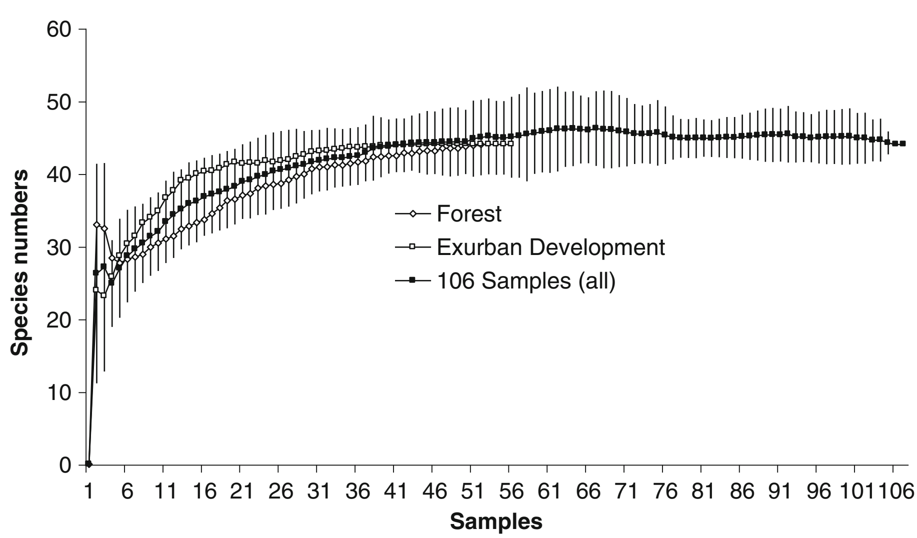

Fig. 2 Accumulative species-sample curve of estimated species numbers of the Abundance-based Estimator of Species Richness (ACE) for forest, exurban development, and 106 samples combined (the latter with ±SD *error bars*) of Warren County, northern Virginia, USA

deviations were low (>0.01 for the maximum sample) for all the accumulated diversity indices we calculated (Table 2; Fig. 2). This demonstrated that our surveys effectively sampled the bird community and that there was only a small chance that we missed additional species.

Differences on bird composition between forest and exurban development

Three point-count localities were outliers and excluded in further analyses because the weather conditions in these sample locations turned too windy to appropriately detect all the species. In addition, their average Sørensen (Bray–Curtis) distances were high (0.91, 0.91, and 0.82) compared to all other locations (mean ± SD: 0.62 ± 0.07). Bird species composition differed significantly between the two land-use types, i.e. forest and exurban development (MRPP: $T = -8.51$, $A = 0.02$, $P < 0.01$).

Impact of exurban development on relative abundance of forest birds

Exurban development significantly affected relative abundance of forest-specialist species (as classified in Table 1). Ten forest species had significantly different relative abundance in exurban development versus forest ($t = -2.437$, $df = 9$, $P = 0.038$). Eight of these ten forest species showed lower relative abundance in exurban development (vs forest; e.g., Worm-eating Warbler, Hooded Warbler), while only two have slightly increasing relative abundance (Acadian Flycatcher and Red-bellied Woodpecker; Table 1). Relative abundance of 18 understory-breeding birds was not significantly different between the two land-use types ($t = 0.255$, $df = 17$, $P = 0.8$).

Indicator species

Three species were identified as indicators of forest (Carolina Chickadee, Eastern Towhee, and Wood Thrush; Table 3), and three species as indicators of exurban development (American Robin, Northern Cardinal, and Common Grackle; Table 3).

Table 3 Species identified as indicators of exurban development and forest in Warren County, northern Virginia. All indicator values were significantly larger than random values based on Monte Carlo tests (1,000 permutations, $P < 0.05$)

Species by land-use type	Indicator value		
	Observed	Random	±SD
Exurban development			
American Robin	44.7	27.0	3.45
Northern Cardinal	61.7	40.8	3.22
Common Grackle	13.5	7.2	2.29
Forest			
Carolina Chickadee	45.7	38.2	3.18
Eastern Towhee	26.1	18.0	3.27
Wood Thrush	42.6	36.5	3.28

Discussion

Our results show that exurban development significantly alters bird community composition and changes relative abundance of forest specialists (as classified in Table 1). The number of species in our forests (35; Table 2) is comparable to other studies in forests of the eastern United States (Holmes and Sturges 1975; Kluza et al. 2000). Although the species richness between forest and exurban development in our study sites were similar (35 vs 39 species), the species composition differed between land-use types. Species commonly associated with humans (i.e., urban adaptors) were only present in exurban areas (e.g., European Starling, House Sparrow, Northern Mockingbird), whereas forest-specialist species were only found in forests (Kentucky Warbler, Summer Tanager). These findings show that exurban development is changing bird community composition, even though canopy cover is largely retained. Previous studies have also demonstrated changes in species composition in exurban areas of Missouri (Nilon et al. 1995), Oklahoma (Engle et al. 1999), Colorado (e.g., Odell and Knight 2001; Fraterrigo and Wiens 2005), and California (Merenlender et al. 2009), where (as a general trend) the numbers of urban adapter species increased while urban avoiders decreased. For instance, low human densities (<0.07 people/ha) favored open-habitat species, while higher human density areas (>0.12 people/ha) favored species associated with human activities (Engle et al. 1999). Most notably, forest and edge species were replaced by species associated with human development, especially in higher housing density rural areas. Changes in bird species assemblages have frequently been linked to diminished habitat patch size (e.g., Tilghman 1987; McIntyre 1995; Park and Lee 2000; Fernández-Juricic and Jokimäki 2001; Suarez-Rubio and Thomlinson 2009) or modification of vegetation structure (e.g., Germaine et al. 1998; Miller et al. 2003; Renner et al. 2006; Croci et al. 2008). Alterations in habitat structure can have a marked impact on breeding species either by providing well-hidden nesting sites and decreasing predation by visually oriented predators, or increasing predation through reduced ability of parents to detect predators and defend the nest (Jokimäki and Huhta 2000; Jokimäki et al. 2005; Weidinger 2002; Evans et al. 2009). Therefore, housing development is detrimental for natural bird communities (Lepczyk et al. 2008), even at low housing densities.

Our results reveal how groups of species respond differently to exurban development. Relative abundance of forest-specialist species was significantly different in forests versus exurban development, but that was not the case for relative abundance of understory breeders. Changes in relative abundance of forest specialists support the general finding of alterations in species composition as discussed above. However, we also expected a significant difference in relative abundance of near-ground breeding birds because ground vegetation within exurban development areas is often removed for housing construction, while canopy trees need to be retained (High Knob Owners Association, personal communication). Also, the adverse impact of feral cats and domestic dogs in these areas is well documented (Coleman et al. 1997; Odell and Knight 2001; Gillies and Clout 2003; Lenth et al. 2006). The lack of detectable effect for understory breeders may represent an extinction debt which may lead to the loss of understory breeders over time (Tilman et al. 2002). However, the bird community needs to be monitored over longer time periods to assess this assertion.

Bird communities are frequently used as indicators of environmental quality (Mayer and Cameron 2003; Lepczyk et al. 2008) and are considered a useful proxy for assessing the human influence on biodiversity (Garson et al. 2002; Lepczyk et al. 2008; Evans et al. 2009). Our results identified species as indicators of both, exurban development and forest. For example, the American Robin typically prefers open areas and frequents forests and woodlands with lighter understory (Sallabanks and James 1999). Other indicators of exurban development were Northern Cardinal and Common Grackle. These results suggest that exurban development is being perceived by birds more as an open habitat although the canopy is maintained. Species indicative of forest were Carolina Chickadee, Eastern Towhee, and Wood Thrush. The Wood Thrush inhabits the interior of deciduous and mixed forests, especially well developed with moderate sub-canopy and shrub density (Roth et al. 1996). Exurban development is jeopardizing Wood Thrush populations by altering the forest structure, as their relative abundance decreases. Wood Thrushes responded dramatically to development in Waterloo, Ontario, where they practically disappeared from residential areas (Friesen et al. 1995).

Conclusion

Our fine-scale study of bird communities demonstrates that exurban development in the eastern deciduous forest region is changing bird community composition and affecting forest-specialist species. At broader spatial scales, such alterations will have significant impacts on bird species persistence, entire bird populations, and biodiversity. Our results hence show that, despite the general perception of exurban development as environmentally preferable to urban sprawl, this is not necessarily correct. Given that exurban development is differentially impacting bird species, it would be valuable to keep monitoring these bird communities. In addition, educating residents of these exurban communities about the impacts of exurban development might encourage the management of these areas to provide suitable habitat for native bird species.

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References

Beissinger SR, Osborne DR (1982) Effects of urbanization on avian community organization. Condor 84:75–83

Bibby CJ, Burgess ND, Hill DA (1992) Bird census techniques. Neumann, Radebeul

Blair RB (1996) Land use and avian species diversity along an urban gradient. Ecol Appl 6:506–519

Blair RB (2001) Birds and butterflies along urban gradients in two ecoregions of the US. In: Lockwood JL, McKinney ML (eds) Biotic homogenization. Kluwer, Norwell, pp 33–56

Blair R, Johnson E (2008) Suburban habitats and their role for birds in the urban-rural habitat network: points of local invasion and extinction? Landsc Ecol 23:1157–1169

Bock CE, Jones ZF, Bock JH (2008) The oasis effect: response of birds to exurban development in a southwestern savanna. Ecol Appl 18:1093–1106

Brown DG, Johnson KM, Oveland TR, Theobald DM (2005) Rural land-use trends in the conterminous United States, 1950–2000. Ecol Appl 15:1851–1863

Chace JF, Walsh JJ (2006) Urban effects on native avifauna: a review. Landsc Urban Plan 74:46–69

Clergeau P, Savard JPL, Mennechez G, Falardeau G (1998) Bird abundance and diversity along a urban-rural gradient: a comparative study between two cities on different continents. Condor 100:413–425

Coleman JS, Temple SA, Craven SR (1997) Cats and wildlife: a conservation dilemma. http://www.fw.vt.edu/extension/fiw/wildlife/damage/Cats.pdf. Accessed 10 January 2010

Colwell RK (2006) EstimateS: statistical estimation of species richness and shared species from samples. Version 8.00. User's guide and application. http://purl.oclc.org/estimates. Accessed 10 January 2010

Croci S, Butet A, Georges A, Aguejdad R, Clergeau P (2008) Small urban woodlands as biodiversity conservation hot-spot: a multi-taxon approach. Landsc Ecol 23:1171–1186

Crooks KR, Suarez AV, Bolger DT (2004) Avian assemblages along a gradient of urbanization in a highly fragmented landscape. Biol Conserv 115:451–462

Czech B, Krausman PR, Devers PK (2000) Economic associations among causes of species endangerment in the United States. Bioscience 50:593–601

Dale VH, Brown S, Haeuber RA, Hobbs NT, Huntly N, Naiman RJ, Riebsame WE, Turner MG, Valone TJ (2000) Ecological principles and guidelines for managing the use of land. Ecol Appl 10:639–670

Dale V, Archer S, Chang M, Ojima D (2005) Ecological impacts and mitigation strategies for rural land management. Ecol Appl 15:1879–1892

Daniels T (1999) When city and country collide: managing growth in the metropolitan fringe. Island Press, Washington

Dufrêne M, Legendre P (1997) Species assemblages and indicator species: the need for a flexible asymmetrical approach. Ecol Monogr 67:345–366

Emlen JT (1974) An urban bird community in Tucson, Arizona: derivation, structure, regulation. Condor 76:184–197

Engle DM, Criner TL, Boren JC, Masters RE, Gregory MS (1999) Response of breeding birds in the Great Plains to low density urban sprawl. Gt Plains Res 9:55–73

Evans KL, Newson SE, Gaston KJ (2009) Habitat influences on urban avian assemblages. Ibis 151:19–39

Fernández-Juricic E, Jokimäki J (2001) A habitat island approach to conserving birds in urban landscapes: case studies from southern and northern Europe. Biodivers Conserv 10:2023–2043

Fraterrigo JM, Wiens JA (2005) Bird communities of the Colorado Rocky Mountains along a gradient of exurban development. Landsc Urban Plan 71:263–275

Friesen LE, Eagles PFJ, Mackay RJ (1995) Effects of residential development on forest-dwelling neotropical migrant songbirds. Conserv Biol 9:1408–1414

Garson J, Aggarwal A, Sarkar S (2002) Birds as surrogates for biodiversity: an analysis of a data set from Southern Quebec. J Biosci 27:347–360

Germaine SS, Rosenstock SS, Schweinsburg RE, Richardson WS (1998) Relationships among breeding birds, habitat and residential development in Greater Tucson, Arizona. Ecol Appl 8:680–691

Gillies C, Clout M (2003) The prey of domestic cats (*Felis catus*) in two suburbs of Auckland city, New Zealand. J Zool Lond 259:309–315

Hansen AJ, Rasker R, Maxwell B, Rotella JJ, Johnson JD, Wright Parmenter A, Langner U, Cohen WB, Lawrence RL, Kraska MPV (2002) Ecological causes and consequences of demographic change in the New West. Bioscience 52:151–168

Hansen AJ, Knight RL, Marzluff JM, Powell S, Brown K, Gude PH, Jones K (2005) Effects of exurban development on biodiversity: patterns, mechanisms, and research needs. Ecol Appl 15:1893–1905

Hines JE (2006) PRESENCE 2.4—Software to estimate patch occupancy and related parameters. USGS-PWRC. http://www.mbr-pwrc.usgs.gov/software/presence.html. Accessed 10 January 2010

Holmes RT, Sturges FW (1975) Bird community dynamics and energetics in a northern hardwoods ecosystem. J Anim Ecol 44:175–200

Homer C, Huang C, Yang L, Wylie B, Coan M (2004) Development of a 2001 national land-cover database for the United States. Photogramm Eng Remote Sens 70:829–840

Huang C, Yang L, Wylie B, Homer C (2001) A strategy for estimating tree canopy density using Landsat 7 ETM+ and high resolution images over large areas: national land cover database mapping zone 60. Third International Conference on Geospatial Information in Agriculture and Forestry. Sioux Falls, SD, USA. CD-ROM, 1 disk. US Environmental Protection Agency, US Dept of Agriculture Forest Service (Forest Inventory and Analysis Program), USGS EROS Data Center

Jokimäki J, Huhta E (2000) Artificial nest predation and abundance of birds along an urban gradient. Condor 102:838–847

Jokimäki J, Kaisanlahti-Jokimäki ML, Sorace A, Fernández-Juricic E, Rodriguez-Prieto I, Jimenez MD (2005) Evaluation of the 'safe nesting zone' hypothesis across an urban gradient: a multi-scale study. Ecography 28:59–70

Kingery HE (1998) Colorado breeding bird atlas. Colorado Bird Atlas Partnership and Colorado Division of Wildlife Denver, Denver

Kluza DA, Griffin CR, Degraaf RM (2000) Housing developments in rural New England: effects on forest birds. Anim Conserv 3:15–26

Lenth BA, Knight RL, Gilgert WC (2006) Conservation value of clustered housing developments. Conserv Biol 20:1445–1456

Lepczyk CA, Flather CH, Radeloff VC, Pidgeon AM, Hammer RB, Liu JG (2008) Human impacts on regional avian diversity and abundance. Conserv Biol 22:405–416

Liu J, Daily GC, Ehrlich PR, Luck GW (2003) Effects of household dynamics on resource consumption and biodiversity. Nature 421:530–533

Luniak M (1994) The development of bird communities in new housing estates in Warsaw. Memorab Zool 49:257–267

Mackenzie DI, Nichols JD, Lachman GB, Droege S, Royle JA, Langtimm CA (2002) Estimating site occupancy rates when detection probabilities are less than one. Ecology 83:2248–2255

Mackenzie DI, Nichols JD, Hines JE, Knutson MG, Franklin AB (2003) Estimating site occupancy, colonization, and local extinction when a species is detected imperfectly. Ecology 84:2200–2207

Marzluff JM (2001) Worldwide urbanization and its effects on birds. In: Marzluff JM, Bowman R, Donnelly R (eds) Avian ecology and conservation in an urbanizing world. Kluwer, Boston, pp 19–47

Marzluff JM, Bowman R, Donnelly R (2001) A historical perspective on urban bird research: trends, terms and approaches. In: Marzluff JM, Bowman R, Donnelly R (eds) Avian ecology and conservation in an urbanizing world. Kluwer, Boston, pp 1–17

Mayer AL, Cameron GN (2003) Landscape characteristics, spatial extent, and breeding bird diversity in Ohio, USA. Divers Distrib 9:297–311

McCune B, Grace JB (2002) Analysis of ecological communities. MjM Software Design, Gleneden Beach

McCune B, Mefford MJ (1999) PC-ORD. Multivariate analysis of ecological data. Version 4. MjM Software Design, Gleneden Beach

McIntyre NE (1995) Effects of forest patch size on avian diversity. Landsc Ecol 10:85–99

McKinney ML (2002) Urbanization, biodiversity, and conservation. Bioscience 52:883–890

McKinney ML (2006) Urbanization as a major cause of biotic homogenization. Biol Conserv 127:247–260

McKinney ML (2008) Effects of urbanization on species richness: a review of plants and animals. Urban Ecosyst 11:161–176

McKinney ML, Lockwood JL (1999) Biotic homogenization: a few winners replacing many losers in the next mass extinction. Trends Ecol Evol 14:450–456

Merenlender AM, Reed SE, Heise KL (2009) Exurban development influences woodland bird composition. Landsc Urban Plan 92:255–263

Miller JR, Wiens JA, Hobbs NT, Theobald DM (2003) Effects of human settlement on bird communities in lowland riparian areas of Colorado (USA). Ecol Appl 13:1041–1059

Nelson AC (1992) Characterizing exurbia. J Plan Lit 6:350–368
Nilon CH, Long CN, Zipperer WC (1995) Effects of wildland development on forest bird communities. Landsc Urban Plan 32:81–92
Odell EA, Knight RL (2001) Songbird and medium-sized mammal communities associated with exurban development in Pitkin County, Colorado. Conserv Biol 15:1143–1150
Ortega-Alvarez R, MacGregor-Fors I (2009) Living in the big city: effects of urban land-use on bird community structure, diversity, and composition. Landsc Urban Plan 90:189–195
Palomino D, Carrascal LM (2005) Birds on novel island environments: a case study with the urban avifauna of Tenerife (Canary Islands). Ecol Res 20:611–617
Park CR, Lee WS (2000) Relationship between species composition and area in breeding birds of urban woods in Seoul, Korea. Landsc Urban Plan 51:29–36
Petit DR, Petit L, Saab VA, Martin TE (1995) Fixed-radius point counts in forests. USDA For Serv Tech Rep 149:49–56
Poole AE (2005) The birds of North America online. Cornell Laboratory of Ornithology, Ithaca. http://bna.birds.cornell.edu.bnaproxy.birds.cornell.edu/BNA/. Accessed 10 January 2010
Radeloff VC, Hammer RB, Voss PR, Hagen AE, Field DR, Mladenoff DJ (2001) Human demographic trends and landscape level forest management in the northwest Wisconsin Pine Barrens. For Sci 47:229–241
Radeloff VC, Hammer RB, Stewart SI (2005a) Rural and suburban sprawl in the US Midwest from 1940 to 2000 and its relation to forest fragmentation. Conserv Biol 19:793–805
Radeloff VC, Hammer RB, Stewart SI, Fried JS, Holcomb SS, Mckeefry JF (2005b) The wildland-urban interface in the United States. Ecol Appl 15:799–805
Rasker R, Hansen AJ (2000) Natural amenities and population growth in the Greater Yellowstone region. Hum Ecol Rev 7:30–40
Renner SC (2005) Biodiversity: there's a role to be played by museum-keepers' too. Nature 438:914
Renner SC, Waltert M, Mühlenberg M (2006) Comparison of bird communities in primary versus young secondary tropical montane cloud forest in Guatemala. Biodivers Conserv 15:1545–1575
Roth RR, Johnson MS, Underwood TJ (1996) Wood thrush (*Hylocichla mustelina*). The Birds of North America, no. 246. The Birds of North America, Philadelphia
Sallabanks R, James FC (1999) American Robin (*Turdus migratorius*). The Birds of North America, no. 462. The Birds of North America, Philadelphia
Schnaiberg J, Riera J, Turner MG, Voss PR (2002) Explaining human settlement patterns in a recreational lake district: Vilas County, Wisconsin, USA. Environ Manag 30:24–34
Suarez-Rubio M, Thomlinson JR (2009) Landscape and patch-level factors influence bird communities in an urbanized tropical island. Biol Conserv 142:1311–1321
Theobald DM (2001) Land use dynamics beyond the American urban fringe. Geogr Rev 91:544–564
Theobald DM (2004) Placing exurban land-use change in a human modification framework. Front Ecol Environ 2:139–144
Theobald DM (2005) Landscape patterns of exurban growth in the USA from 1980 to 2020. Ecol Soc 10:32–66
Tilghman NG (1987) Characteristics of urban woodlands affecting breeding bird diversity and abundance. Landsc Urban Plan 14:481–495
Tilman D, May RM, Lehman CL, Nowak MA (2002) Habitat destruction and the extinction debt. Nature 371:65–66
U.S. Census Bureau (2007) State and county quickfacts. Last revised: Friday, 12th January 2007 16:06:43 EST. http://quickfacts.census.gov/qfd/states/51/51107.html. Accessed 7 January 2010
United Nations, Department of Economic and Social Affairs, Population Division (2007) World population prospects: the 2007. http://esa.un.org/unup, Accessed 2 October 2010
USDA and USDI (2001) Urban wildland interface communities within vicinity of Federal lands that are at high risk from wildfire. Fed Regist 66:751–777
Vitousek PM, Mooney HA, Lubchenco J, Melillo JM (1997) Human domination of earth's ecosystems. Science 277:494–499
Weidinger K (2002) Interactive effects of concealment, parental behaviour and predators on the survival of open passerine nests. J Anim Ecol 71:424–437