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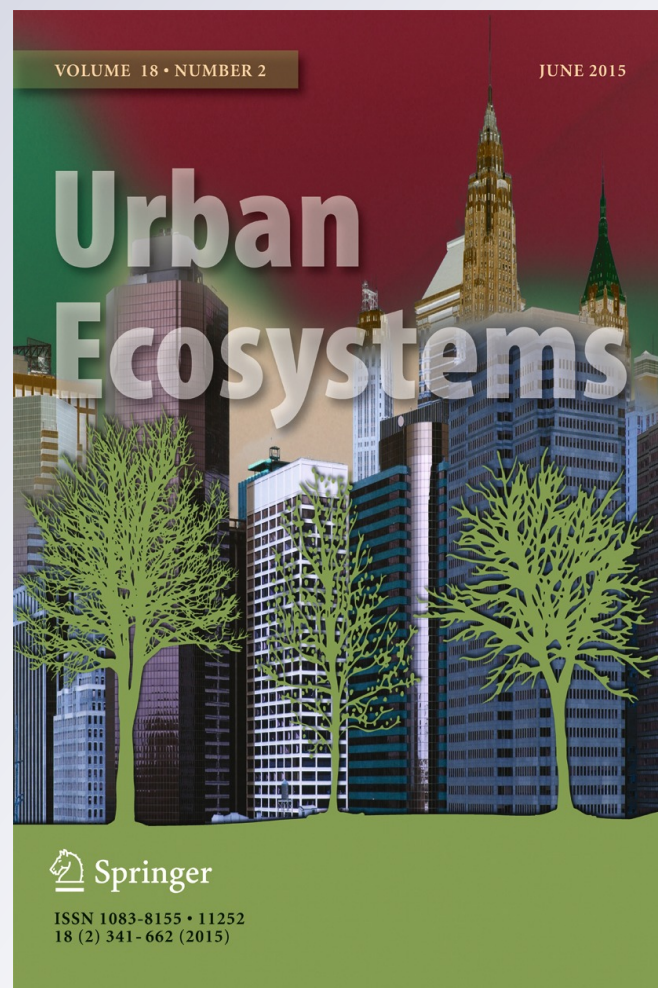
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Two-sided edge responses of avian communities in an urban landscape

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Abstract Impacts of habitat edges on wildlife populations have received considerable attention, yet few researchers have quantified changes in animal community structure on both sides of an interface between distinct habitats. To gain a better understanding of the ways in which species-specific responses scale up to produce community patterns across habitat boundaries, we examined the response of avian communities to forest-suburb edges in northeastern Illinois, USA. We surveyed bird assemblages using replicated point-transects ($n=21$) that crossed boundaries between remnant forest patches and suburban residential areas in order to compare differences in community composition, species distributions, and densities. Forest and suburban bird communities were distinct, and community composition changed with distance-from-edge in forests but not suburbs. Abundances of many species that were common in the forest increased with distance-from-edge in the forest, whereas numbers of common species in the suburbs were largely unaffected by distance-from-edge. Using a new metric that we termed “tolerance,” we found many forest species avoided the edge and suburbs, and suburban species were present near the edge but did not venture far into forest. Overall, distance to the forest-suburb boundary was more influential in structuring avian communities in the forest. Some species of conservation concern crossed edges into the suburbs, suggesting that management activities may improve suburban biodiversity. Many other imperiled forest species, however, will only be retained in urban environments through the protection of forest interior habitat.

Keywords Avian communities · Edges · Species richness · Tolerance · Urbanization

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Introduction

Biodiversity conservation has emerged as a priority in urban areas (Miller and Hobbs 2002). Urbanization results in habitat loss and fragmentation of remnant patches, phenomena that have been implicated in the decline of many species (Fahrig 2003; Pereira et al. 2004). Fragmentation dramatically increases habitat edge, which exposes organisms in remnants to altered biotic and abiotic conditions (Murcia 1995). These altered conditions, collectively known as edge effects, result in diverse patterns of response for many biological traits of interest that have yet to be satisfactorily explained despite decades of research (Ries et al. 2004).

Edge effect studies often fail to detect a meaningful response in biological traits of interest (Ries et al. 2004), suggesting that many species are unaffected by edges (Ries and Sisk 2010). Nonetheless, numerous studies have demonstrated that habitat edges can have both positive and negative impacts on animal diversity (Johnston 1947; Campi and Mac Nally 2001), abundance (Lidicker 1999; Kristan et al. 2003), behavior (Haddad 1999; Ries and Debinski 2001), and fitness (Gates and Gysel 1978; Flaspohler et al. 2001). Perhaps this discrepancy results from a mismatch between the mechanism driving the response and the scale of the investigation (Laurance 2004). Another possible explanation is that most workers have taken a one-sided approach, in which ecological patterns and processes are examined from the edge toward the interior of only one of the adjacent habitats (Fonseca and Joner 2007). Because species and communities from different habitats may not respond to edges in similar ways, a two-sided approach has the potential to foster a more complete understanding of the ecological processes associated with habitat boundaries (Ries and Sisk 2004; Fonseca and Joner 2007).

A two-sided approach could be particularly informative for biodiversity conservation in urban landscapes where hard edges between urban and natural areas are pervasive. The ability of species to move through or utilize human-dominated areas is a major determinant of functional connectivity at landscape scales (Tischendorf and Fahrig 2000; Walting et al. 2010). Whereas some species specialize on resources provided in urban environments (urban exploiters) and some are able to adapt and use resources in modified habitats (urban adapters), other species are extirpated or are restricted to habitat remnants (urban avoiders; Blair 1996). In order to mitigate the loss of native biodiversity associated with urbanization (McKinney 2006), we must gain a better understanding of how avoiders are lost from remnants, how adapters are able to spread from remnants, and how nonnative exploiters invade remnants. This will require a detailed examination of edge effects between remnants and modified habitats, and identification of mechanisms that produce observed patterns of response.

The first step in this process is using a two-sided approach to document community responses to edge effects in urban environments. To our knowledge, only three studies—all conducted in Australia—have attempted to do so. Catterall et al. (1991) concluded that there was little movement of either suburban or forest bird species across an edge, Hodgson et al. (2007) reported that the behavioral responses of birds differed by feeding guild, and Ikin et al. (2013) found that native street trees promoted bird richness and diversity in suburbs and adjacent reserves. Each of these studies was conducted in a single year along relatively short transects (ranging from 100 to 500 m in total length) across edges separating remnants and developed areas. The investigation by Catterall et al. (1991) was restricted to one large forest. Multi-year examinations over broader spatial scales are clearly needed, particularly outside of Australia.

The objective of our research was to document two-sided responses of avian communities to boundaries between forest and suburban habitats over an extensive area in a major metropolitan region. Specifically, we addressed the following questions: (1) how does bird

species richness change across forest-suburb edges? (2) how does the composition of avian communities differ across edges? (3) can particular species be classified as edge-avoiders? We believe that this study, replicated and conducted over landscape scales, extends what has been learned from previous work by using a two-sided approach, investigating responses to a common edge type that has rarely been examined, focusing both on community patterns and on the response of individual species, and applying a new metric (termed tolerance) to quantify community responses across edges.

Methods

Study area and site selection

We focused on forest remnants in the Chicago metropolitan area, a region in the Midwestern USA that encompasses northeastern Illinois, northwestern Indiana, southwestern Michigan, and southeastern Wisconsin with a population totaling more than 9.8 million people (U.S. Census Bureau 2012). Population density within the city of Chicago is 4,447 people per km² (U.S. Census Bureau 2012). However, large tracts of remnant vegetation have been preserved in the Chicago metropolitan area, totaling more than 220,500 ha (Chicago Wilderness 2014).

Our study design comprised 21 transects of six avian survey points each, three points in each forest fragment and three in the adjacent suburb (Fig. 1). Points were located 75, 225, and 375 m from the edge separating the two habitat types, with all suburban points placed on roads that were perpendicular to the edge. Points were spaced 150 m apart to reduce the possibility that the same birds would be recorded at multiple points. Surveys were not conducted at the edge itself because this would have necessitated placing adjacent points 150 m into the forest and suburb, limiting our ability to make inferences about near-edge changes. We used ArcGIS 10 (Environmental Systems Research Institute, Redlands, CA) to select study sites based on two criteria. First, a fragment had to be large enough to accommodate a transect (i.e., the 375-m point in the forest had to be at least 375 m from any other edge). Second, the forest remnant had to be adjacent to a residential area. Overall, 21 sites in the metropolitan region met these criteria (Fig. 1). All transects were at least 1 km apart, and sites were distributed across a wide geographic area encompassing approximately 400,000 ha.

The forest fragments included in our study were dominated by oak (*Quercus* spp.) and the invasive European buckthorn (*Rhamnus cathartica*), although hickory (*Carya* spp.), elm (*Ulmus* spp.), and ash (*Fraxinus* spp.) were also common. These fragments ranged in size from 54 to 619 ha and were mostly surrounded by residential areas, but also open green space (i.e. parks, cemeteries, and golf courses), small bodies of water, and commercial areas such as shopping centers, factories, and shipping facilities.

Bird surveys

Birds were surveyed three times annually during the breeding season between late May and early July in 2010 and 2011. We used a fixed-radius point count protocol with the radius set at 50 m to avoid double-counting individuals moving among points (Bibby et al. 2000). We conducted 10-min counts on clear mornings between sunrise and 0930 h (Bibby et al. 2000). During each survey, we recorded all birds seen or heard and distance from the survey point in

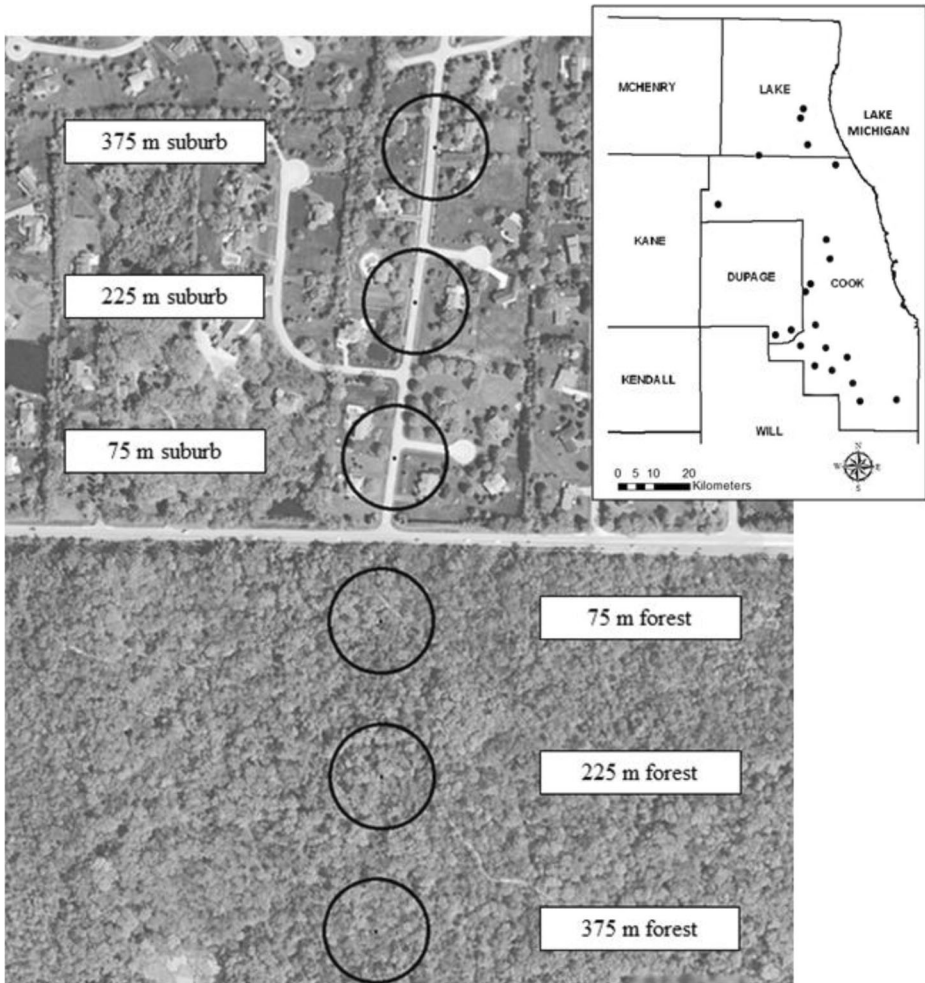


Fig. 1 Representative point transect ($n=21$) illustrative of the study design and the location of all study sites in northeastern Illinois (inset map with counties labeled)

10-m increments. Fly-overs and detections outside the 50-m radius were not recorded. Each year surveys were conducted by two observers who rotated among points to minimize potential bias. Prior to each field season, observers underwent a week-long training session to sharpen bird identification and distance estimation skills.

Aerial photographs of the area within 50 m of suburban points were utilized during surveys to identify landmarks and improve distance estimates. Though concerns have been raised regarding potential biases associated with surveys near roads (Hanowski and Niemi 1995), roadside counts can generate bird lists that are similar to those generated from off-road counts within the same habitat type (Hutto et al. 1994). Roadside point counts were used because of the logistical challenges of working on the properties of numerous homeowners. If continuous loud noise (i.e. lawnmowers or garbage trucks) interrupted a survey, observers stopped and returned to the location at a later time. No roads had particularly high traffic volume during surveys.

Habitat characteristics

To determine if edge effects led to dramatic changes in vegetation structure among survey points, we measured a variety of habitat features at each point. Given limited access in suburban areas, we took a number of coarse habitat measurements along the point transects. We visually estimated percent shrub cover to the nearest 5 % and the number of trees (>2 m in height and 8 cm diameter-at-breast-height) within 50 m of every point. We inspected aerial photographs to increase the accuracy of these estimates. At forest points, we measured canopy cover using a spherical densiometer and quantified the degree of invasion by non-native plants (e.g., buckthorn, honeysuckle [*Lonicera* spp.], and multiflora rose [*Rosa multiflora*]) within the 50-m radius on a scale of 0–2, with 0 representing relatively “un-invaded areas”, 1 representing “moderately invaded” areas (i.e. locations that were characterized by the presence of some invasives), and 2 representing “heavily invaded” areas (i.e. locations with extremely dense invasive woody vegetation and many buckthorn trees). Areas receiving a score of 1 had typically undergone some form of management in the past, whereas areas receiving a score of 2 had clearly received no such attention and were physically difficult to maneuver through. Densiometer measurements from the suburbs were not included in the analyses because they were strongly affected by the presence of trees over point count locations rather than the canopy cover of the properties surrounding a point. This was not an issue in forest fragments where canopy cover was more uniform. Lastly, we recorded the number of bird feeders and buildings within the 50-m radius of suburban points. Buildings that were only partially within the 50-m radius were included in this tally. All buildings in the study were single-family residences, except for one commercial structure.

Data analyses

Environmental variables

We determined whether shrub cover, tree density, canopy cover, and building density differed among the three survey points within each habitat type using analysis of variance (ANOVA) in SAS version 9.2 (SAS Institute 1999). We used Fisher’s Exact Test to determine if the discrete environmental variables (degree of invasion and number of bird feeders) differed among habitat-specific distance categories.

Birds

We restricted analyses to bird species that typically breed in the area based on a review of the literature (Poole 2005). Gulls, raptors, shorebirds, and waterfowl were excluded because point counts are not considered a suitable survey method for these taxa (Bibby et al. 2000). To determine if species richness differed along the point-transects, we used a general linear mixed model. Distance category was included as a fixed effect and site and year as random effects. If distance category was significant, pairwise comparisons between distance categories were made with Bonferroni corrections.

To further investigate the impact of edges on species richness, we examined how the presence of forest and suburban species was affected by distance-to-edge. Species were labeled as forest or suburban birds if they occupied more distance categories in one habitat than the other. For this analysis, a category was considered occupied if a species was detected at that distance on more than one transect. Species that were present at an equal number of distance categories in both habitats or that were detected only near the edge (i.e. the 75 m category)

were not included in this analysis. We conducted separate logistic regressions for forest and suburban birds to model changes in the proportion of species with distance from the edge. Distance categories in the habitat of origin were negative, and probabilities of occurrence were modeled to “1”.

To quantify the response of forest and suburban birds to edge, we calculated a metric that we term “tolerance” (T) using parameter estimates from the logistic regressions. At some distance from the edge, species classified as forest or suburban were no longer detected due to abiotic and biotic changes associated with the edge and adjacent habitat type. “Tolerance” indicates the sensitivity of a group of organisms to these changes, as measured by the distance from the edge at which half of the species from a particular habitat are no longer detected. It is calculated by solving a form of the logistic regression function (Ott and Longnecker 2001) for $F(x)=0.5$:

$$0.5 = \frac{1}{1 + e^{-(\beta_0 + \beta_1 x)}}$$

which simplifies to:

$$x_{0.5} = T = -\beta_0 / \beta_1$$

where β_0 and β_1 are logistic parameter estimates for the intercept and distance, respectively. The standard deviation of T was calculated using the delta method (Powell 2007):

$$SD_T = \sqrt{T^2 \left[\frac{VAR_{\beta_0}}{\beta_0^2} + \frac{VAR_{\beta_1}}{\beta_1^2} - \frac{2COV(\beta_0, \beta_1)}{\beta_0 \beta_1} \right]}$$

where VAR is the variance of a parameter estimate and COV is the covariance between the estimates. We tested whether T values were significantly different from 0 using a Wald Chi-square test. Negative tolerance values indicate that the species from one habitat are highly intolerant of the second habitat, so much so that the majority of species are not detected there. Positive values mean that most species are present beyond the edge into the second habitat (though they are ultimately extirpated from the second habitat with sufficient distance from the edge), suggesting that they can tolerate the abiotic and biotic changes that occur at the edge.

To determine if the composition of bird assemblages differed significantly along the point-transect, we conducted a permutational analysis of variance (PERMANOVA; Anderson 2001, 2005) with presence-absence data for both years using PC-ORD version 6 (McCune and Mefford 2011). This analysis relies on an F -test to assess differences in mean Bray-Curtis distances among groups and derives a p -value via permutations (Anderson 2001). If the overall test was significant, we used *posteriori* pair-wise comparisons to examine differences among particular distance categories. We also used a two-level nested PERMANOVA to determine if there were differences in community composition within each habitat type and site.

To determine if there were differences in the relative abundances of individual species among distance categories within a particular habitat type, we used general linear mixed models (PROC MIXED, SAS). Analyses were conducted separately for forests and suburbs because detectability may have differed between the habitats, which could have biased comparisons between habitats had they been modeled together. Models were derived for each species detected at more than a third of the point counts per habitat ($n=21$ of 63). Two model sets were run. In the first, relative abundance was pooled across all surveys per point and modeled against distance categories from the edge with site included as a random variable. In the second, a year by distance interaction term was used to determine if edge responses varied

between 2010 and 2011. In all cases, models with data pooled across years were better supported so only results from these models are reported. Models were also run using non-normal distributions (i.e., Poisson and negative binomial) with PROC GLIMMIX to determine if they were a better fit for our count-based data; model residuals indicated the normal distribution was most appropriate so only results from PROC MIXED are reported. We tested the null hypothesis of equal abundances among distance categories using a Type III F test. For models with a significant F test, mean abundances were compared for pairs of distance categories using a least squares mean test adjusted with a Bonferroni correction for multiple comparisons.

Results

Environmental variables

None of the environmental variables differed among distance categories within either habitat (forest: shrub cover, $F=0.48$, $p=0.619$; tree density, $F=0.72$, $p=0.491$; canopy cover, $F=0.10$, $p=0.908$; degree of invasion, Fisher's exact test, $p=0.317$; suburb: shrub cover, $F=1.06$, $p=0.353$; tree density, $F=0.23$, $p=0.797$; building density, $F=0.08$, $p=0.928$; number of bird feeders, Fisher's exact test, $p=0.120$). These results confirm that each habitat type was relatively homogenous with respect to these measures. We therefore assumed that differences in bird distributions along transects were due to distance from the edge within each habitat type rather than changes in environmental variables.

Birds

We detected 8,103 birds during the course of the study. Of these detections, 5,043 were in the suburban habitat and 3,060 were in forest fragments. We detected a total of 65 species: 20 exclusively in forest, five exclusively in suburbs, and 40 in both habitats. The American robin (*Turdus migratorius*) was the most abundant species in both habitats, representing 19.2 % of all forest observations and 29.3 % of all suburban observations. Less than 1 % of the observations in the forest were nonnative birds, compared to 27.2 % in the suburbs.

After accounting for variation among sites and years, species richness differed among distance categories ($F=4.45$, $p<0.001$; Fig. 2). This metric was highest in the forest interior and in the suburbs near the edge, and lowest at points furthest into suburbs. Within each habitat species richness declined with distance from the forest interior, though only the comparisons between 375 and 75 m were significant. At 75 m, species richness was higher in suburbs than in forest, although this difference was not statistically significant.

For the logistic regressions, 21 species were classified as “forest” birds and 9 as “suburban” species. Logistic regression models fit the data well for both forest and suburban bird communities (forest: Deviance=0.6924, maximum rescaled $R^2=0.5581$; suburb: Deviance=0.2459, maximum rescaled $R^2=0.6668$). Forest and suburban birds responded differently to the edge (Fig. 3). Tolerance for forest birds was negative ($\beta_0 = -0.7920$, $\beta_1 = -0.0081$, $\text{COV} = 0.0002$, $T = -97.8 \text{ m} \pm 30.8$, $X^2_1 = 10.06$, $p = 0.0015$), indicating that the majority of these species are habitat specialists that are highly edge sensitive. Tolerance for suburban birds was positive, but not significantly different from 0 ($\beta_0 = 0.7011$, $\beta_1 = -0.0103$, $\text{COV} = 0.0004$, $T = 68.1 \text{ m} \pm 30.8$, $X^2_1 = 2.79$, $p = 0.0949$). This suggests that within suburbs, most species were edge-tolerant at 75 m from the edge, but the majority did not penetrate the forest to a distance of 75 m. Because we did not survey the bird community at the edge, it is unclear whether most

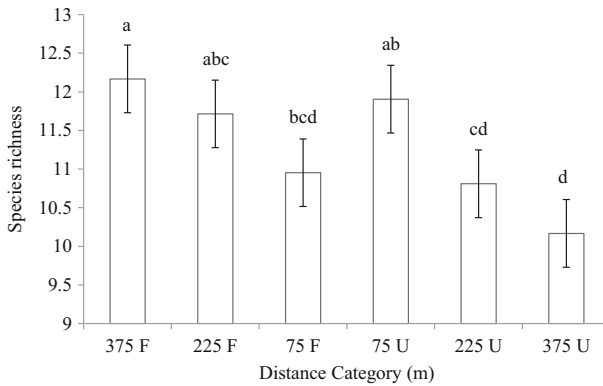


Fig. 2 Species richness (mean±S.E.) across distances categories for forest points (F) and suburban points (U). Means that have the same superscript are not significantly different from one another (Bonferroni correction)

suburban species were present at the edge or absent between the edge and 75 m into the suburbs.

Avian assemblages differed by habitat type but not site ($F=6.84, p<0.001$; $F=0.47, p=0.99$ respectively). Composition of avian assemblages differed significantly among distance categories ($F=15.74, p<0.001$; Table 1). Bird assemblages did not differ significantly with distance-from-edge in the suburbs, but did in forested habitat. The composition of the forest bird assemblage 375 m from the edge differed significantly from that at 75 m. While not statistically significant, there was also a notable difference between the composition of forest bird assemblages at 75 and 225 m.

A total of 19 species were detected in both habitats at all distance categories (Online Resource 1). Three abundant exotic species were encountered in this study; house sparrows (*Passer domesticus*) and house finches (*Carpodacus mexicanus*) ventured 75 m into forested habitat and the European starling (*Sturnus vulgaris*) was detected exclusively in suburban

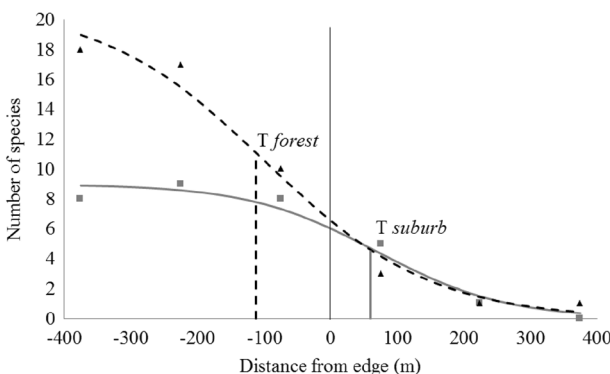


Fig. 3 Logistic regression analysis of the decline in cumulative forest and suburban species richness along the point transect. The edge is represented by a vertical line (distance=0). Observed suburban values are represented by gray squares (i.e., richness for species observed at more distance categories in the suburbs than the forest), and observed forest values are represented by black triangles (i.e., richness for species observed at more distance categories in the forest than the suburbs). The solid gray line represents the predicted logistic curve for the suburb, whereas the dashed black line represents that of forest. Tolerance (T) values are marked with vertical gray (suburb) and dashed black (forest) lines

Table 1 Test statistic (*t*-value) and associated significance (*p* value) derived from pair-wise comparisons of bird assemblages based on occurrence at the six distance categories in 2010–2011

Distance category	375 m Forest	225 m Forest	75 m Forest	75 m Suburb	225 m Suburb
225 m Forest	1.07 (0.35)				
75 m Forest	1.80 (<0.01)	1.38 (0.06)			
75 m Suburb	6.62 (<0.01)	5.57 (<0.01)	5.05 (<0.01)		
225 m Suburb	5.73 (<0.01)	4.86 (<0.01)	4.34 (<0.01)	0.97 (0.45)	
375 m Suburb	4.96 (<0.01)	4.22 (<0.01)	3.83 (<0.01)	1.29 (0.12)	0.65 (0.86)

Boldface entries indicate within-habitat comparisons, and significant differences ($p < 0.05$) in avian composition are italicized

p-values are not corrected for multiple comparisons

habitat. Two other common suburban species, the mourning dove (*Zenaida macroura*) and chipping sparrow (*Spizella passerina*), were detected only once in forest.

Twenty-six species were detected at enough points within each habitat type to analyze changes in relative abundance (forest $n = 18$, suburb $n = 17$; Table 2). In forest, the abundance of half of the species analyzed differed significantly among distance categories. Of these, all except the northern cardinal (*Cardinalis cardinalis*) and American robin experienced declines in numbers as distance-to-edge decreased (Table 2). In suburbs, relative abundance was similar among distance categories for all species except the blue jay (*Cyanocitta cristata*) and downy woodpecker (*Picoides pubescens*), which were significantly less numerous farther from the edge.

Discussion

In this study, forest-suburban edges clearly exerted a strong influence on bird communities. The most notable difference in community structure and composition was between bird assemblages of the two habitat types. Typically, urban bird communities differ substantially from those in remnant habitats in that there are fewer native species and a few highly abundant nonnative species (Beissinger and Osborne 1982; Blair 1996; McKinney 2006; Catterall et al. 2010). Our results also showed richness was lower in the interior of suburbs than in the interior of forest fragments and that nonnatives were a much larger component of the avifauna in the suburbs, though the most abundant species in the suburbs was native (American robin). However, multiple metrics also confirmed that distance-from-edge played a role in shaping avian communities, though more so in forest bird communities than in those of the suburbs. We detected larger differences in avian assemblages among forest points compared to suburbs. These differences were likely due to the fact that forests contained rare habitat-specialists that avoided edges, as indicated by the forest's negative tolerance value. This suggests that the maintenance of core forest interior habitat may be crucial for the urban conservation of Neotropical migrants such as the ovenbird (*Seiurus aurocapilla*) and hooded warbler (*Setophaga citrina*), which were only detected at the 225- and 375-m forest points.

Unlike forest birds, the suburban bird community responded less strongly to edges. We found no significant differences in species composition among any of the suburban distance categories—a result similar to findings from an Australian study that showed urban sites both near and far from a large forest had similar bird communities (Catterall et al. 1989). However, we did find that species richness declined in suburbs as distance-to-forest-edge increased. We

Table 2 Mean estimates of abundance (\pm S.E.) of common birds (detected at >21 of 63 points). Separate models in forest and suburban habitat were run for each species

Common name (<i>Scientific name</i>)	375 m Forest	225 m Forest	75 m Forest	75 m Suburb	225 m Suburb	375 m Suburb	
Blue-gray gnatcatcher (<i>Poliopitila caerulea</i>)	0.67 (0.26)	0.76 (0.26)	1.10 (0.26)	NS			NS
Eastern towhee (<i>Pipilo erythrophthalmus</i>)	1.57 (0.47)	a 1.29 (0.47)	ab 0.62 (0.47)	b **			NS
Eastern wood-pewee (<i>Contopus virens</i>)	3.05 (0.42)	a 2.29 (0.42)	ab 1.33 (0.42)	b **			NS
Gray catbird (<i>Dumetella carolinensis</i>)	1.67 (0.46)	1.43 (0.46)	1.43 (0.46)	NS			NS
Great crested flycatcher (<i>Myiarchus cineritus</i>)	2.90 (0.33)	a 2.00 (0.33)	a 0.67 (0.33)	b *			NS
Indigo bunting (<i>Passerina cyanea</i>)	2.33 (0.49)	1.52 (0.49)	1.86 (0.49)	NS			NS
Northern flicker (<i>Colaptes auratus</i>)	1.33 (0.25)	a 0.57 (0.25)	ab 0.52 (0.25)	b **			NS
Red-bellied woodpecker (<i>Melanerpes carolinus</i>)	2.62 (0.38)	1.81 (0.38)	1.67 (0.38)	**			NS
Red-eyed vireo (<i>Vireo olivaceus</i>)	3.62 (0.54)	3.57 (0.54)	2.29 (0.54)	**			NS
American robin (<i>Turdus migratorius</i>)	8.43 (1.11)	a 8.52 (1.11)	a 10.95 (1.11)	b **	22.12 (1.54)	23.90 (1.53)	24.48 (1.53)
Black-capped chickadee (<i>Parus atricapillus</i>)	2.43 (0.55)	3.10 (0.55)	3.14 (0.55)	NS	3.30 (0.6)	2.95 (0.59)	2.43 (0.59)
Brown-headed cowbird (<i>Molothrus ater</i>)	1.19 (0.32)	1.29 (0.32)	1.19 (0.32)	NS	3.39 (0.82)	3.24 (0.81)	4.14 (0.81)
Blue jay (<i>Cyanocitta cristata</i>)	3.81 (0.74)	3.62 (0.74)	3.43 (0.74)	NS	1.89 (0.4)	a 1.14 (0.4)	ab 0.62 (0.4)
Downy woodpecker (<i>Picoides pubescens</i>)	2.67 (0.34)	a 2.10 (0.34)	ab 1.57 (0.34)	b **	1.33 (0.27)	a 0.86 (0.27)	ab 0.33 (0.27)
House wren (<i>Troglodytes aedon</i>)	1.43 (0.56)	1.76 (0.56)	1.52 (0.56)	NS	2.31 (0.44)	2.57 (0.44)	2.33 (0.44)
Northern cardinal (<i>Cardinalis cardinalis</i>)	3.05 (0.61)	a 3.43 (0.61)	a 5.33 (0.61)	b *	5.46 (0.64)	5.43 (0.63)	4.43 (0.63)
Red-winged blackbird (<i>Agelaius phoeniceus</i>)	1.00 (0.41)	0.48 (0.41)	1.43 (0.41)	NS	1.95 (0.56)	1.10 (0.56)	1.33 (0.56)
White-breasted nuthatch (<i>Sitta carolinensis</i>)	2.33 (0.35)	1.90 (0.35)	1.29 (0.35)	NS	0.91 (0.25)	0.76 (0.25)	0.52 (0.25)
American goldfinch (<i>Spinus tristis</i>)				NS	3.55 (0.62)	2.52 (0.62)	3.76 (0.62)
Cedar waxwing (<i>Bombycilla cedrorum</i>)				NS	1.39 (0.33)	1.52 (0.33)	1.19 (0.33)
Chipping sparrow (<i>Spizella passerina</i>)				NS	2.26 (0.61)	2.67 (0.6)	3.57 (0.6)
Common grackle (<i>Quiscalus quiscula</i>)				NS	1.83 (1.03)	3.43 (1.02)	2.48 (1.02)
European starling (<i>Sturnus vulgaris</i>)				NS	2.52 (0.82)	2.57 (0.82)	2.57 (0.82)
House finch (<i>Haemorhous mexicanus</i>)				NS	1.65 (0.5)	1.67 (0.5)	2.05 (0.5)
House sparrow (<i>Passer domesticus</i>)				NS	16.78 (3.76)	18.10 (3.74)	17.81 (3.74)
Mourning dove (<i>Zenaidura macroura</i>)				NS	1.03 (0.41)	1.81 (0.4)	1.81 (0.4)

Differences among distance categories (Type III F test) are indicated with an asterisk while letters show significant differences among estimates (least squares mean test adjusted with Bonferroni correction)

** $P \leq 0.05$; * $P \leq 0.01$; NS, not significant ($P \geq 0.05$)

believe these patterns were produced by edge tolerant forest species that were present 75 m into the suburbs. Others have also demonstrated that proximity to habitat remnants enhances avian richness in urban developments (Loss et al. 2009), which underscores the importance of retaining remnants in metropolitan areas to sustain native diversity. Our data also revealed a pattern of lower species richness in the interior of suburban areas relative to the interior of remnant habitats, as has been noted in other studies (Beissinger and Osborne 1982; Catterall et al. 2010; Shochat et al. 2010). Taken together, our findings suggest that the suburban bird community is relatively homogenous and less diverse than forest bird assemblages.

The patterns of species' abundance further support our assertion that forest birds respond more strongly to edges than suburban birds. The relative abundance of many species common in these forests increased with distance-from-edge, whereas numbers of birds varied little among distance categories for nearly all species in the suburbs. These data reinforced what our presence-absence data suggested—that many forest species, such as the red-eyed vireo (*Vireo olivaceus*), are sensitive to forest-suburban edges. Several studies have found that the red-eyed vireo and other forest species are significantly more abundant in forest interiors than in edge habitats (Germaine et al. 1997; King et al. 1997). Edge-avoiding birds are often insectivorous Neotropical migrants that have experienced severe population declines in recent decades (Hagan and Johnston 1992), though we also found evidence of reduced numbers of short-distance migrants (e.g., eastern towhee (*Pipilo erythrophthalmus*) and residents (e.g., downy woodpecker) near the edge. Avoidance could reflect decreased food availability (Báldi 1999; Fernández-Juricic 2001), increased probability of nest predation (Gates and Gysel 1978), human disturbance (e.g., anthropogenic noise and pedestrian traffic; Fernández-Juricic 2000), or changes in vegetation structure (Villard 1998) or composition that we did not measure.

We observed a more pronounced spillover effect of forest species into suburbs than in the reverse direction. Some forest-dwelling birds appear to utilize anthropogenic resources in suburban habitats and could be nesting there (Loss et al. 2009). We observed the scarlet tanager (*Piranga olivacea*) and Acadian flycatcher (*Empidonax virescens*) 75 m from the edge, species such as the Baltimore oriole (*Icterus galbula*), yellow warbler (*Setophaga petechia*), and great-crested flycatcher (*Myiarchus crinitus*) at 225 m, and the wood thrush (*Hylocichla mustelina*), hairy woodpecker (*Picoides villosus*) and northern flicker (*Colaptes auratus*) as far as 375 m into the suburbs. Some species traditionally considered urban avoiders were actually detected at all distance categories in the suburbs: blue-gray gnatcatcher (*Poliophtila caerulea*), common yellowthroat (*Geothlypis trichas*), eastern wood-pewee (*Contopus virens*), and red-eyed vireo (Johnston 2001). Even a few species that are not typically associated with either deciduous upland forests or suburbs were found in both habitats (e.g., field sparrow; *Spizella pusilla*). Several of these are species of regional conservation concern (e.g., wood thrush and northern flicker; Ruth 2006). These observations underscore the potential of management actions to augment biodiversity in built environments. For example, suburban streets with trees planted along the roadside (particularly natives) have higher avian richness than streets without trees (Fernández-Juricic 2000; Ikin et al. 2013). On the other hand, suburban birds were rarely detected in forests beyond 75 m. Similarly, Catterall et al. (1991) found that suburban species reached high densities in suburbs, lower densities at forest-suburb edges, and were not detected in a large adjacent eucalypt forest. These findings suggest that there may be limited competition from nonnatives within remnants.

Our study represents a key step in understanding avian community dynamics across suburban-forest edges. Our tolerance metric offers a simple means of summarizing responses of multiple organisms to edges and facilitating comparisons of community response from different habitats. We believe that this is an advancement over past studies that were limited to

species-specific responses (Campi and Mac Nally 2001) and changes in overall species richness (Ikin et al. 2013). Our metric can also be used to quantify the impact of management actions on community responses to edges in future studies (e.g., whether planting street trees in suburbs shifts tolerance values of forest and suburb birds). Using the tolerance metric in conjunction with other measures of community and single-species responses to edges, we have shown that edges act like a biotic filter that removes edge-sensitive species near the edge, limits how far edge-tolerant species penetrate into adjacent habitats, and affects the abundance of species present at all measured distances from the edge. This filtering effect likely interacts with landscape composition and configuration to shape patterns of urban biodiversity such as the number of edge specialists retained in remnants and the magnitude of the spillover effect from remnants to adjacent developed habitats. Thus, a thorough understanding of how species respond to edges will be key in managing urbanized landscapes to maximize biodiversity conservation.

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