

Do birds and beetles show similar responses to urbanization?

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Abstract. To date, the vast majority of studies in urban areas have been carried out on birds, yet it is not known whether the responses of birds to urbanization are congruent with those of other taxa. In this paper, we compared the responses of breeding birds and carabid beetles to urbanization, specifically asking whether the emerging generalizations of the effects of extreme levels of urbanization on birds (declines in total species richness and the richness of specialist species, increases in total abundance and the abundances of native generalist and introduced species, and community simplification, including increasing similarity) could also be applied to ground beetles. We also directly tested for congruence between birds and ground beetles using correlations between variables describing bird and beetle community structure and correlations between bird and beetle distance matrices describing community dissimilarity between pairs of sampling locations. Breeding bird and carabid beetle community data were collected in Ottawa, Ontario, and Gatineau, Quebec, Canada, in two groups of sites: developed sites representing the predictor variable within-site housing density, and forested sites adjacent to development representing the predictor variable neighboring housing density (each site was 0.25 km²). Breeding birds and carabid beetles do not respond similarly to increasing within-site housing density but do exhibit some similar responses to increasing neighboring housing density. Birds displayed strong declines in diversity, compositional changes, and community simplification in response to increasing within-site housing density. Forest and introduced species of birds and beetles responded similarly to increasing housing density within a site, but responses of overall diversity and open-habitat species richness and patterns of community simplification differed between birds and beetles. Increasing neighboring housing density resulted in increases in the abundances of introduced birds and introduced beetles and similar patterns of community simplification in both taxa. To better understand and mitigate the effects of urbanization on biodiversity, we suggest that, in addition to the responses of birds, future research should focus on the responses of other taxa in the urban matrix.

Key words: *biodiversity congruence; breeding birds; Carabidae; edge effect; forest remnant; Gatineau, Quebec, Canada; ground beetle; housing density; indicator taxon; Ottawa, Ontario, Canada; residential development; urban gradient.*

INTRODUCTION

The generality of ecological results, especially the consistency of findings across taxa (biodiversity congruence [Murphy and Wilcox 1986]) may determine the efficacy of broad conservation strategies such as the creation of reserves. Previous studies have documented modest congruence in how species diversity responds to environmental change, with the greatest congruence at large spatial scales (Wolters et al. 2006), although correlation strength is context dependent (Hess et al. 2006). Despite such results, there will remain many taxa for which little to no information is available, highlighting the importance of determining congruence between

well- and little-known taxa to biodiversity conservation. This has rarely been done in human-dominated environments, particularly urban areas. Urbanization is proceeding rapidly in many parts of the world with important consequences for biodiversity (McDonald et al. 2008). However, it is unclear whether different taxa respond similarly to urbanization. To date, the vast majority of studies in urban areas have been carried out on birds (McDonnell and Hahs 2008). Thus, birds have become a de facto indicator taxon for urbanization due to their inherent appeal, conspicuousness, mostly diurnal habits and well-known natural history, and the extensive development of research techniques with which to study them. In terms of understanding and mitigating the effects of urbanization on biodiversity, it is important to determine whether the responses of birds correlate with the responses of other taxa.

Several generalizations are emerging from the literature of the effects of urbanization on birds. Studies have reported a decrease in bird species richness with

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increasing urbanization (e.g., housing density, amount of urban land cover) (Germaine et al. 1998, Miller et al. 2003). A humped-shaped response has also been observed, with species richness initially increasing to intermediate levels of urbanization and then decreasing at high levels (Blair 1996, 2004, Sorace 2001, Crooks et al. 2004, Marzluff 2005, Tratalos et al. 2007, Catterall 2009). The humped-shaped response appears the more ubiquitous, although some work indicates otherwise (see the studies reviewed in Clergeau et al. [2001]), and a recent analysis finds support for both patterns (Lepczyk et al. 2008). In general, however, highly urbanized areas have far fewer bird species than natural areas. In highly urbanized areas, native specialist species are replaced by native generalist and introduced species that reach very high abundances, which may result in an increase in total bird abundance or density with urbanization (Germaine et al. 1998, Crooks et al. 2004, Donnelly and Marzluff 2004, Lim and Sodhi 2004, Donnelly and Marzluff 2006, Shochat et al. 2006, Tratalos et al. 2007, Pennington et al. 2008, Catterall 2009). Thus, extreme urbanization results in the simplification of the bird community, which is transformed from a diverse assemblage in natural areas to one dominated by a few abundant species. This is supported by recent work that has found that bird communities in different urban areas are more similar to one another than are bird communities in different natural areas (Blair 2004, McKinney 2006, Sorace and Gustin 2008). The uniform structure of the built-up environment and the wide distribution of the avian species adapted to this environment have resulted in an increase in the similarity between bird communities in cities worldwide (McKinney 2006).

Few studies have looked at the effects of urbanization on ground beetle (Coleoptera: Carabidae) communities, focusing on community structure in forest fragments surrounded by varying intensities of urbanization. Urban forest fragments have fewer individuals than suburban or rural forest fragments, but it is unclear whether the number of species remains unchanged or declines with urbanization (Niemelä et al. 2000, 2002, Ishitani et al. 2003, Magura et al. 2004, Weller and Ganzhorn 2004, Gaublotte et al. 2008). Ground beetle communities in rural forest fragments are composed mostly of forest specialist species, whereas beetle community composition in urban forest fragments is dominated by open-habitat and generalist species (Niemelä et al. 2000, Sadler et al. 2006, Elek and Lövei 2007, Magura et al. 2008). Finally, it appears that β -diversity of ground beetles in forest fragments increases with increasing surrounding urbanization so that beetle communities in urban forest fragments are more dissimilar to one another than are those in rural fragments (Magura et al. 2008).

Here we compare the responses of breeding birds and carabid beetles to urbanization to determine whether the emerging generalizations of the effects of urbanization

on birds also apply to ground beetles. First, we determine if carabid beetle species richness, particularly the richness of specialist species, declines with urbanization. Second, we test for an increase in carabid beetle total abundance with urbanization, driven by increases in the abundances of native generalist and introduced species. Third, we determine if changes in species richness and abundance simplify the carabid beetle community, such that communities become dominated by a few species and become more similar in their compositions with increasing urbanization. We also directly test for congruence between birds and ground beetles using correlations between variables describing bird and beetle community structure and correlations between bird and beetle distance matrices. We hypothesize that urbanization is a strong environmental determinant of community structure, and as such, birds and beetles should show similar responses to it and be positively correlated.

METHODS

We collected relative abundance and species richness data for both birds and ground beetles in two groups of sites: (1) developed sites representing a gradient in housing density (hereafter referred to as “housing density” sites), and (2) forested sites adjacent to developments of varying housing densities (hereafter referred to as “neighboring housing density” sites). All analyses were carried out separately for these two groups of sites. We also carried out analyses at two spatial scales: the site scale and the station scale, the latter being the sampling scale within sites. The descriptions of the study area and the site selection and sampling methodologies that follow were modified from Gagné and Fahrig (2010a, b).

Study area

We sampled breeding birds and carabid beetles at 25 0.25-km² sites in and around Ottawa, Ontario and Gatineau, Quebec, Canada (Fig. 1). The study area encompassed ~4040 km² on both sides of the Ottawa River. The northern half of the study area forms part of the Southern Laurentians ecoregion of Quebec, where elevation is commonly 300–600 m above sea level. The St. Lawrence Lowlands ecoregion is south of the Ottawa River with elevations rarely >150 m above sea level. All site categories were approximately equally represented in both ecoregions to account for possible differences in forest composition (Fig. 1). In addition, we tested a posteriori for differences in tree community composition between ecoregions using a redundancy analysis. The single canonical axis was not significant (100 permutations, $F_{1,2} = 2.37$, $P = 0.29$).

Site selection

We selected four sites in each of four categories representing a gradient in housing density: Forested (0 dwellings/km²), Exurban (<56 dwellings/km², 31 ± 9

dwellings/km²; mean \pm SE), Suburban (140–712 dwellings/km², 555 \pm 101 dwellings/km²) and Urban (>1244 dwellings/km², 3754 \pm 492 dwellings/km²) (Fig. 2a). Sites in these four categories made up the housing density group of sites described above. Housing density values for each category were consistent with those of several other authors (Kluza et al. 2000, Odell and Knight 2001, Gillham 2002). Each site comprised the area within a 500 \times 500 m square (0.25 km²). In addition to these 16 sites, we selected nine forested sites, equal in size to those described above, adjacent to developments of Exurban, Suburban, and Urban housing densities (three sites each) (Fig. 2b). These Exurban Neighbor, Suburban Neighbor, and Urban Neighbor sites, in addition to the Forested sites previously described, which were adjacent to other forest (no development), made up the neighboring housing density group of sites described previously.

We searched for sites using a combination of historical topographic maps (~1:50 000, currently produced by the Centre for Topographic Information, Natural Resources Canada, Ottawa, Ontario, Canada) and the most recent aerial photographs available (2002, 1:15 000, produced by the City of Ottawa, Ontario, Canada). We selected sites that had not been subjected to agricultural use for at least as many years as topographic maps have been produced (~80 years). We minimized edge effects (with the exception of the forest/development edge in our neighboring housing density sites [Fig. 2b]) by choosing only sites that were surrounded by >100 m of development of a similar housing density or forest cover, depending on the category. Site selection was conditional upon landowner consent. Finally, we ground-truthed all sites to ensure they met our criteria.

Breeding bird surveys

We counted breeding birds at four stations in each site using the Canadian Wildlife Service's Ontario Forest Bird Monitoring Program (OFBMP) protocol (Cadman et al. 1998). The OFBMP protocol follows the standards of Ralph et al. (1995) for the use of point counts to monitor population changes over time or assess population responses to habitat alteration (Welsh 1995). Stations were 250 m apart (Fig. 2). We conducted two point count surveys at each station in 2006, the first between 24 May and 6 June and the second between 13 and 28 June. Two surveys was the maximum number we could perform at each station during the allowable time periods of the OFBMP (24 May–17 June and 13 June–10 July) considering the number of stations (100) and the other criteria of our survey design. We chose to sample more locations fewer times, rather than fewer locations more times for the same amount of survey effort, to emphasize the spatial variation among locations (Thompson et al. 2002) because of the large within-site spatial variability in habitat quality inherent in sites representing an urban gradient. In addition, our goal

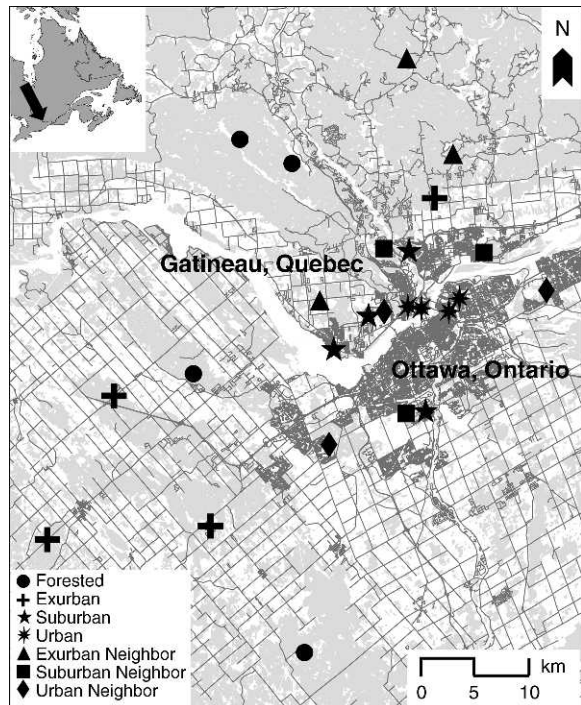


FIG. 1. The study area surrounding the cities of Ottawa, Ontario and Gatineau, Quebec, Canada. The inset depicts the location of the study area in eastern Canada. Sites are 0.25-km² areas indicated by symbols representing four housing density categories: Forested (0 dwellings/km²); Exurban (<56 dwellings/km²); Suburban (140–712 dwellings/km²); Urban (>1244 dwellings/km²). In addition, there are three categories of forested sites adjacent to developments of Exurban, Suburban, and Urban densities, respectively: Exurban Neighbor; Suburban Neighbor; Urban Neighbor. Dark gray lines indicate the road network. Forest cover is depicted in light gray.

was to estimate the population sizes of all species present at a site, necessitating as many sampling locations as possible per site (four was the maximum number allowable according to the OFBMP protocol) to do so. Despite likely interannual variation in breeding bird abundance and species richness, we chose to survey breeding birds during a single year because it appears that the effects of urbanization on bird community structure are strong enough to be detected with one year of sampling (e.g., Germaine et al. 1998). Notably, the average species richness of birds in our Forested sites sampled in one year (29 \pm 3 species per site; mean \pm SE [Table 1]) exceeds the average recorded over a 10-year period by the OFBMP in 298 forested sites approximately the same size as those used in this study (20 \pm 4 species per site) (Cadman et al. 1998). During each time period, we surveyed two sites per day with the exception of one day when we surveyed three sites. Each day, we chose sites from different categories and points on the urbanization gradient and as far as possible from one another. The order of sites surveyed per day was reversed between the two surveys to minimize any

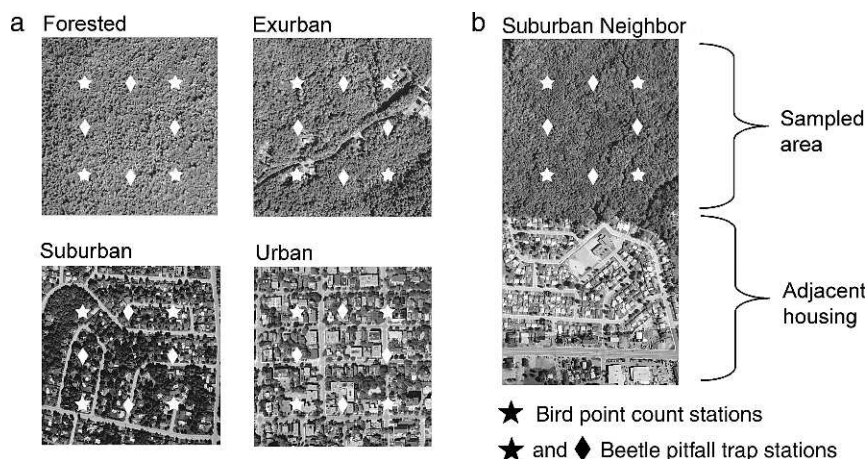


FIG. 2. Typical sites in which breeding birds and carabid beetles were surveyed. Sites were 500×500 m. (a) Example sites representing a range of housing densities. We surveyed four replicate sites of each type. (b) Example Suburban Neighbor site. The 500×500 m forested site, in which birds and beetles were surveyed, was adjacent to at least 500×500 m of Suburban-density development. We surveyed three replicate Neighbor sites adjacent to each of the Exurban, Suburban, and Urban housing density levels.

time-of-day bias in the data. We visited stations within sites in the same order during both surveys.

During each survey, we conducted a 10-minute point count at each station between a half-hour before sunrise and five hours after sunrise. We only performed point counts when the wind was <3 on the Beaufort scale and it was not raining. If these conditions were not met, we cancelled the count(s) and resumed the next possible day. We counted all adult birds seen or heard during the 10-minute period at an unlimited distance from the station. We chose an unlimited distance within which to count birds to maximize the number of individuals and species detected (Gates 1995). Also, the use of point counts with an unlimited radius has been shown to result in greater power (greater mean detections per point and lower coefficient of variation) to detect population changes in a bird community in Hoosier National Forest, Indiana compared to counts with a 50 m radius (Thompson et al. 2002). During counts, we did not include birds flying at a high altitude and obviously passing over the site. The primary author performed all point counts.

We chose to use unlimited distance point counts rather than estimating detection probabilities using

distance sampling (Buckland et al. 2001) for three primary reasons (Johnson 2008). First, most species in a multispecies study such as this are not detected frequently enough to reliably estimate their detectability function. Second, observer distance estimation has been found to be highly inaccurate, which further confounds the estimation of detectability functions. Finally, distance sampling only estimates one of the four components of detection, the probability that an individual is detected by an observer (p_d) given that its home range or territory coincides at least in part with the sampling area (p_s), that the individual is present during the survey period (p_p), and that it is available to be detected, i.e., vocalizing (p_a) (Nichols et al. 2009). The probability p_d varies in relation to factors such as weather and survey date that affect p_s , p_p , and p_a . Thus, to account for variation in p_d , separate detectability functions would have to be estimated for each combination of p_s , p_p , and p_a , which was not feasible.

We calculated the relative abundance of each species at each station as the maximum number of birds counted during either point count survey. For each species, we summed station relative abundances within each site during each survey and chose the maximum of

TABLE 1. The effects of housing density on measures of breeding bird and carabid beetle diversity.

Taxon	Response variable	$F_{3,12}$	Adjusted R^2	Housing density site category			
				Forested ($n = 4$)	Exurban ($n = 4$)	Suburban ($n = 4$)	Urban ($n = 4$)
Birds	species richness	23.64***	0.82	29.00 ^a \pm 2.74	29.50 ^a \pm 1.76	20.00 ^b \pm 1.92	12.00 ^c \pm 1.08
	Simpson's index	54.39***	0.91	0.93 ^a \pm 0.01	0.94 ^a \pm 0.01	0.91 ^a \pm 0.01	0.75 ^b \pm 0.02
	Fisher's α	36.30***	0.88	15.46 ^a \pm 2.27	15.28 ^a \pm 1.22	7.54 ^b \pm 0.79	3.47 ^c \pm 0.44
Beetles	open-habitat species richness	4.90*	0.44	2.25 ^a \pm 0.95	6.75 ^{ab} \pm 2.59	11.75 ^b \pm 1.70	11.00 ^b \pm 2.27

Notes: The mean value of each response variable \pm SE is presented for each site category. Different lowercase letters indicate significant ($P < 0.05$) pairwise differences between site categories for each response variable.

* $P < 0.05$; *** $P < 0.001$.

these two values as the relative abundance of the species at the site. Thus, for both stations and sites, relative abundance values reflected the highest abundance a species achieved in the two surveys. The use of the maximum count of individuals over all surveys as an index of abundance was suggested by Bibby et al. (2000) as a means of minimizing the error associated with the imperfect detectability of birds during point counts. In a comparison of point count summary statistics, the maximum count was found to exhibit the highest overall success in predicting the reproductive activity of forest and grassland birds (Betts et al. 2005).

Carabid beetle trapping

We installed pitfall traps for carabid beetles at each bird point count station and at four additional stations in each site in late April and early May 2007, immediately following the spring thaw (Fig. 2). Traps were 125 m apart. Initially, a ninth trap was also installed in the center of each site, but these traps were only operated for the first week of the season before being removed. Traps consisted of two plastic cups, ~8 cm wide at the mouth and 10 cm tall. We buried traps in the ground with the rim of the inner cup flush with the ground surface. The base of the outer cup was punctured to allow for water drainage. We placed a 10 × 10 cm plastic roof, supported by 2.54-cm nails at each corner, above each trap to prevent rain and debris from falling in the trap. We filled traps with 100 mL of propylene glycol and a drop of dish soap. We opened the traps on 14 May and replaced trap contents weekly until 3 August. Thus, we collected beetles continuously over a 12-week period that encompassed the peak in carabid breeding activity in the region (Levesque and Levesque 1986). Carabid beetles were identified to species using Lindroth (1961–1969). Nomenclature followed Bousquet and Laroche (1993).

Catches from pitfall traps represent not only carabid beetle abundance, but also the activity level of individuals, trap efficiency, and the sampling design. We maximized the detectability of carabid beetles, i.e., the probability that pitfall trap catches represent the largest possible proportion of the true number of carabid beetles in the environment, by (1) trapping beetles during the peak activity period of species in our region, thus maximizing the likelihood that individuals would encounter a trap, (2) using a fluid in traps that has been recommended for use in pitfall trapping of carabid beetles due to its low evaporation rate and high preservation of specimens (Lemieux and Lindgren 1999, Isono 2005), (3) using dish soap in traps to prevent escape (H. Goulet, *personal communication*), (4) using traps with a diameter large enough to capture large-bodied beetle individuals but small enough to minimize the catch of vertebrates (amphibians and small mammals) (Work et al. 2002), (5) installing traps with drainage holes and roofs to ensure their proper functioning throughout the season, (6) collecting trap

contents weekly to minimize predation by necrophagous beetles (H. Goulet, *personal communication*), and (7) installing the maximum number of traps per site that we could feasibly operate considering our weekly collection schedule, site size (0.25 km²) and the driving distances between sites. In addition, we used the summed catch of individuals over the entire season as our estimate of the relative abundance of species at stations and sites because this measure has previously been shown to be significantly positively correlated with true density ($r \geq 0.91$) for two carabid beetle species (Baars 1979).

We summed the number of individuals of each species collected at each station and at each site over the 12 weeks of sampling to calculate species relative abundances. Unfortunately, a few traps were removed or damaged during sampling, which created missing or incomplete values in our data set. Of the 79 trap-weeks for which data was missing or incomplete, 30% were in Forested sites, 23% were in Exurban Neighbor sites, 14% were in Urban Neighbor sites, 13% were in Suburban Neighbor sites, 11% were in Urban sites, 5% were in Suburban sites, and 4% were in Exurban sites. Thus, no single site category represented a large proportion of missing or incomplete values. In addition, the proportion of missing or incomplete values did not appear to covary with housing density (the Forested, Exurban, Suburban, and Urban site categories) or neighboring housing density (the Forested, Exurban Neighbor, Suburban Neighbor, and Urban Neighbor site categories). For these reasons and because they represented only 3.25% of the data collected, we chose to ignore missing and incomplete values.

Analyses

We tested for the effects of urbanization on breeding bird and carabid beetle communities to determine if two aspects of community change along the urbanization gradient occurred in both taxa: (1) compositional changes (i.e., changes in species richness and abundance as described in our first two research objectives), and (2) community simplification (i.e., increases in dominance and similarity as described in our third research objective). To further determine the congruence between birds and beetles in their responses to urbanization, we tested correlations between bird and beetle descriptors used in the above analyses. We performed all analyses separately for two categorical predictor variables: housing density, represented by the Forested, Exurban, Suburban, and Urban site categories, and neighboring housing density, represented by the Forested (the same category as that used for housing density), Exurban Neighbor, Suburban Neighbor, and Urban Neighbor site categories. In addition, we performed all analyses at both the site scale and the station scale, with the following exception: analyses that tested the significance of predictor variables were subject to pseudoreplication at the station scale (stations within a site were not independent observations) and so we carried out these

analyses at the site scale only. We carried out all analyses using R version 2.6.2 (R Development Core Team 2008).

Compositional changes.—We used general linear models (GLMs) to test for the effects of housing density and neighboring housing density on total species richness, total abundance, the Simpson's index, Fisher's α , the abundance and species richness of habitat affinity groups (see the following paragraph), and the abundance of introduced species of birds and beetles. When the assumptions of normality and/or homoscedasticity were not met, we transformed response variables such that assumptions were no longer violated (Grafen and Hails 2002). Simpson's index is a proportion, so values were transformed by taking the arcsine of the square root (Zar 1999). When the predictor variable had a significant effect, we used Tukey's Honestly Significant Difference (hsd) test with P values adjusted for multiple comparisons to determine the significant differences between pairs of housing density or neighboring housing density categories.

We classified the habitat affinity of native bird species as "forest interior," "forest edge," or "open habitat" according to Poole (2005) (Appendix A). We defined forest interior species as those that occur only in forest habitat, being most abundant in the forest interior and avoiding the forest edge. Species classified as forest edge were those that are most common in forest habitat but also occur in a wide range of other habitat types. We defined open-habitat species as those that occur in a broad range of open habitat types with at most scattered trees and including human-modified environments. We classified the native beetle species we collected as "forest" or "open-habitat" species according to Lindroth (1961–1969) (Appendix A). If the habitat affinity of a species was not recorded in Lindroth (1961–1969), we classified the species based on information provided by H. Goulet (*personal communication*) with two exceptions. The habitat affinity of *Cicindela sexguttata* was determined according to Schultz (1998), and the habitat affinity of *Trichotichnus vulpeculus* was determined according to Stanton et al. (2003) and Webster and Bousquet (2008). We defined forest and open-habitat beetle species as having similar habitat affinities as forest interior and forest edge birds and open-habitat birds, respectively. Introduced bird and beetle species were identified according to the sources previously mentioned (Appendix A).

We used redundancy analyses (RDAs) to determine the effects of housing density and neighboring housing density on bird and beetle communities. Community data were Hellinger transformed prior to analyses (Legendre and Gallagher 2001). We tested the significance of canonical axes and predictor variables using permutation tests (Legendre and Legendre 1998).

Community simplification.—We used GLMs to test for the effects of housing density and neighboring housing density on the Berger-Parker dominance index of each

taxon. The Berger-Parker index is the proportional abundance of the most abundant species in a community and reflects the degree to which a community is dominated by a single species (Berger and Parker 1970). To meet the assumptions of the tests, we arcsine transformed the square root of the response variables and, in the case of the test of the effect of housing density on the Berger-Parker index of birds, we applied a negative inverse transformation. For predictor variables with significant effects, we tested the significance of pairwise comparisons of site categories with Tukey's hsd test.

We constructed k -dominance curves (Lambhead et al. 1983) of the bird and beetle communities collected at each site and station to determine whether communities become dominated by a few species with increasing urbanization. The k -dominance curves of individual communities of varying richnesses can be compared in a single plot, with species ranked according to abundance on the abscissa (k). The ordinate is the cumulative proportional abundances of all species to the left of and including each species (k -dominance). A community is considered to be dominated by a few species to a greater degree than another community if its k -dominance curve lies above and never intersects that of the other community.

We partitioned the bird and beetle diversity of each site category (Forested, Exurban, Suburban, Urban, Exurban Neighbor, Suburban Neighbor, and Urban Neighbor) into α and β components according to Crist et al. (2003). The total species richness of each site category (γ) was the sum of the average station species richness (α_1), the average species richness among stations (β_1), and the average species richness among sites (β_2) in that category. Species richness values for each station or site were weighted by the proportion of the total number of individuals found at each station or site.

We used nonmetric multidimensional scaling (NMDS) to determine the similarity in bird community composition among sites and among stations and beetle community similarity among sites and among stations (Legendre and Legendre 1998). Data were standardized by dividing the abundance of each species at each site or station first by the species' maximum abundance at any site or station and then by the total abundance of all species at the site or station (Wisconsin double standardization). We used the Kulczynski distance measure to calculate dissimilarities between pairs of sites or stations (Faith et al. 1987). The Kulczynski distance is a measure of the dissimilarity between the communities of two different sites or stations and is calculated by summing species abundance minima and dividing this value by each site's or station's total abundance. One minus the average of these two values is the distance between the two sites or stations.

We used GLMs to test for the effects of housing density and neighboring housing density on the

Kulczynski distance between pairs of sites, for birds and beetles. We applied transformations as described above to satisfy the assumptions of normality and homoscedasticity. Transformations were ineffective in the case of the effect of housing density on the distance between beetle communities so we used the nonparametric Kruskal-Wallis rank sum test instead. Tukey's hsd test and the Wilcoxon rank sum test with P values adjusted for multiple comparisons were used to test for significant differences between pairs of housing density or neighboring housing density categories when predictor variables were significant.

Correlations.—We used Kendall's rank correlation coefficient (τ) to test for correlations between the total species richnesses, the total abundances, the Simpson's indices, Fisher's α values, the abundances and species richnesses of habitat affinity groups, the abundances of introduced species, and the Berger-Parker indices of birds and beetles at the site and station scales. We assessed significance at the station scale using the same number of degrees of freedom as the site scale because stations were not independent observations. For all correlations, we limited the beetle data to only the four stations at each site where birds were also surveyed. (Recall that beetles were surveyed at four additional stations to the bird survey stations at each site.) Species richness correlations may be subject to biases in sampling effort (Gaston 2000). For this reason, we also tested the correlations between bird and beetle standardized richnesses, calculated by dividing species richnesses by abundances.

Finally, we performed Mantel tests on bird and beetle distance matrices at the site and station scales (Legendre and Legendre 1998). We used the Kulczynski distance measure to calculate dissimilarities between pairs of sites or stations. We calculated correlations between bird and beetle distance matrices with Kendall's rank correlation coefficient and tested for significance with permutation tests. We did not assess the significance of correlations between bird and beetle distance matrices at the station scale because stations were not independent observations.

RESULTS

We counted 2435 birds of 76 species and collected 5145 beetles of 95 species during our surveys (see Supplement). We counted 203 individuals of the most abundant bird species, the Black-capped Chickadee *Poecile atricapilla*, and 13 bird species were counted only once during surveys. We trapped 703 individuals of the most abundant beetle species, *Pterostichus mutus*, and collected only one individual of 17 beetle species.

Effects of housing density

Compositional changes.—Housing density had significant effects on bird species richness, the Simpson's index of birds, and Fisher's α for birds, all of which decreased with increasing housing density (Table 1).

Forest interior and forest edge bird abundance and species richness were significantly different among housing density categories (forest interior bird abundance, $F_{3,12} = 28.80$, $P < 0.001$, adjusted $R^2 = 0.85$; forest interior bird species richness, $F_{3,12} = 32.64$, $P < 0.001$, adjusted $R^2 = 0.86$; forest edge bird abundance, $F_{3,12} = 34.62$, $P < 0.001$, adjusted $R^2 = 0.87$; forest edge bird species richness, $F_{3,12} = 18.93$, $P < 0.001$, adjusted $R^2 = 0.78$), with Forested and Exurban sites generally having significantly greater abundances and species richnesses than Suburban and Urban sites (Fig. 3a, b). Housing density also had a significant effect on the abundance of introduced bird species ($F_{3,12} = 62.41$, $P < 0.001$, adjusted $R^2 = 0.92$). Forested and Exurban sites had significantly fewer introduced birds than Suburban sites, which had significantly fewer introduced birds than Urban sites (Fig. 3c).

The abundance and species richness of forest beetles were also significantly different among housing density categories (abundance, $F_{3,12} = 35.20$, $P < 0.001$, adjusted $R^2 = 0.87$; species richness, $F_{3,12} = 37.24$, $P < 0.001$, adjusted $R^2 = 0.88$). Forest beetle abundance and species richness were significantly greater in Forested and Exurban sites than in Suburban and Urban sites (Fig. 3a, b). Housing density had a significant effect on open-habitat beetle species richness (Table 1) and the abundance of introduced beetle species ($F_{3,12} = 11.74$, $P < 0.001$, adjusted $R^2 = 0.68$). Suburban and Urban sites had significantly more open-habitat beetle species and introduced beetle individuals than Forested sites (Table 1, Fig. 3c).

Based on the RDA, we found that housing density explained 63% of the variance in bird community composition ($F_{3,12} = 6.81$, $P < 0.01$). The first canonical axis explained 48% of the variance in bird community composition, and the second canonical axis accounted for an additional 12%. The RDA consisted of a principal component analysis (PCA) on the fitted values from analyses of variance of individual species abundances on housing density, which resulted in three canonical axes, and a PCA on the residuals from these analyses, which resulted in 12 noncanonical axes; thus, the canonical axes of the RDA represent the contribution of housing density to variability in bird community composition. The first and second canonical axes were significant (RDA1, $F_{1,12} = 15.45$, $P < 0.01$; RDA2, $F_{1,12} = 3.84$, $P = 0.01$). In the distance biplot of species points and site category centroids (where distances among objects (points or centroids) approximate their ecological distances [Legendre and Legendre 1998]), forest interior and forest edge bird species were located near the Forested and Exurban centroids, respectively, whereas open-habitat species were located near the Suburban centroid (Fig. 4a). The three introduced bird species were located near the Urban centroid, separate from the rest of the bird community.

Similarly, RDA indicated that 55% of the variance in beetle community composition was explained by hous-

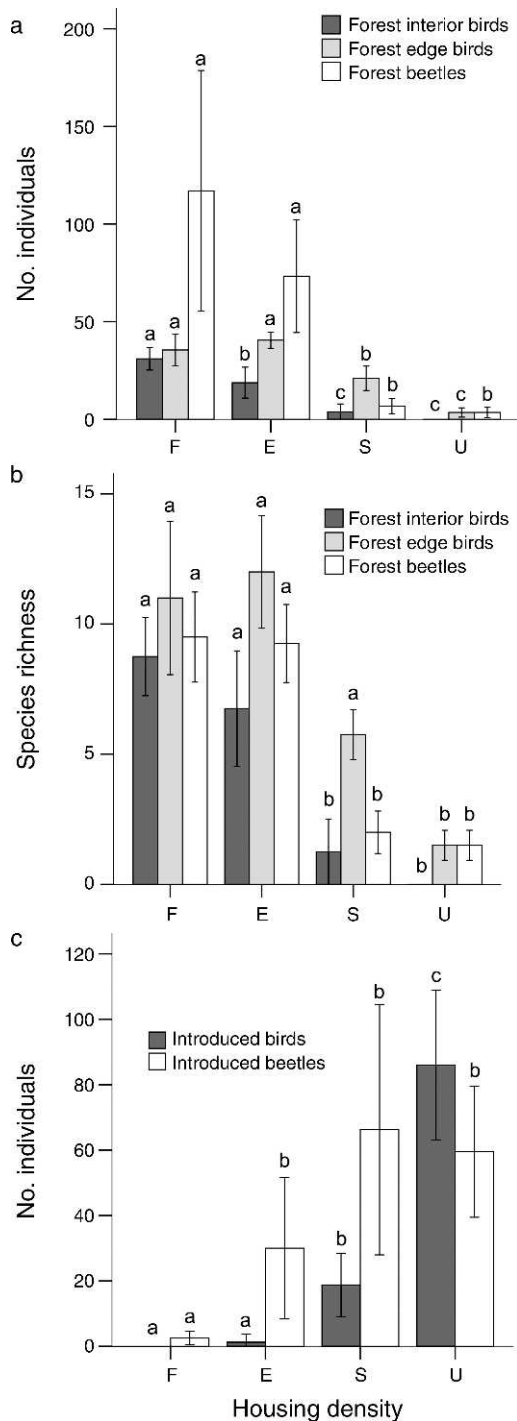


FIG. 3. The (a) abundance and (b) species richness of forest birds and carabid beetles and (c) the abundance of introduced birds and carabid beetles (all mean \pm 2 SE) in Forested (F), Exurban (E), Suburban (S), and Urban (U) sites. Dark gray bars represent forest interior birds in panels (a) and (b) and introduced birds in panel (c). Light gray bars represent forest edge birds. Open bars represent carabid beetles. Habitat affinities are described in *Methods*. Different lowercase letters above bars indicate significant ($P < 0.05$) pairwise differences between site categories for each taxon and habitat affinity group.

ing density ($F_{3,12} = 4.81$, $P < 0.01$). The first canonical axis explained 40% of the variance in beetle community composition and the second explained an additional 9%. Only the first canonical axis was significant ($F_{1,12} = 10.44$, $P < 0.01$). In the distance biplot of species points and site category centroids, forest beetle species were located near the Exurban and Forested centroids, whereas open-habitat and introduced beetle species were located near the Suburban and Urban centroids (Fig. 4b).

Community simplification.—Housing density had a significant effect on the Berger-Parker index of birds ($F_{3,12} = 44.23$, $P < 0.001$, adjusted $R^2 = 0.90$). Urban sites had significantly higher index values (0.37 ± 0.01 ; mean \pm SE) than sites in the other categories (Suburban, 0.16 ± 0.02 ; Exurban, 0.12 ± 0.02 ; Forested, 0.14 ± 0.01). There was no effect of housing density on the Berger-Parker index of beetles.

At both the site and station scales, the k -dominance curves of Urban bird communities were above those of bird communities in the other housing density categories

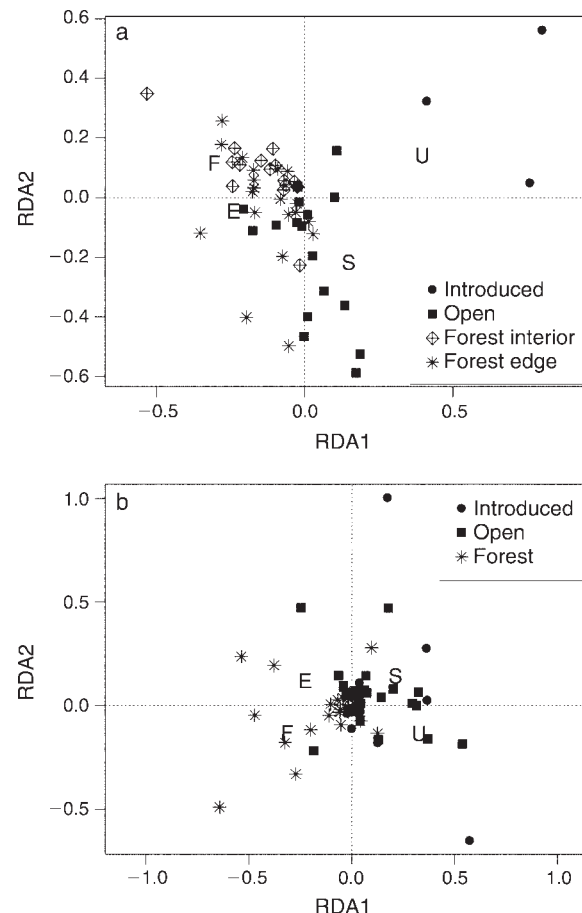


FIG. 4. Distance biplots showing the locations of (a) bird and (b) carabid beetle species scores from redundancy analyses (RDAs) with housing density as a predictor. The centroids of the Forested (F), Exurban (E), Suburban (S), and Urban (U) housing density categories are also shown.

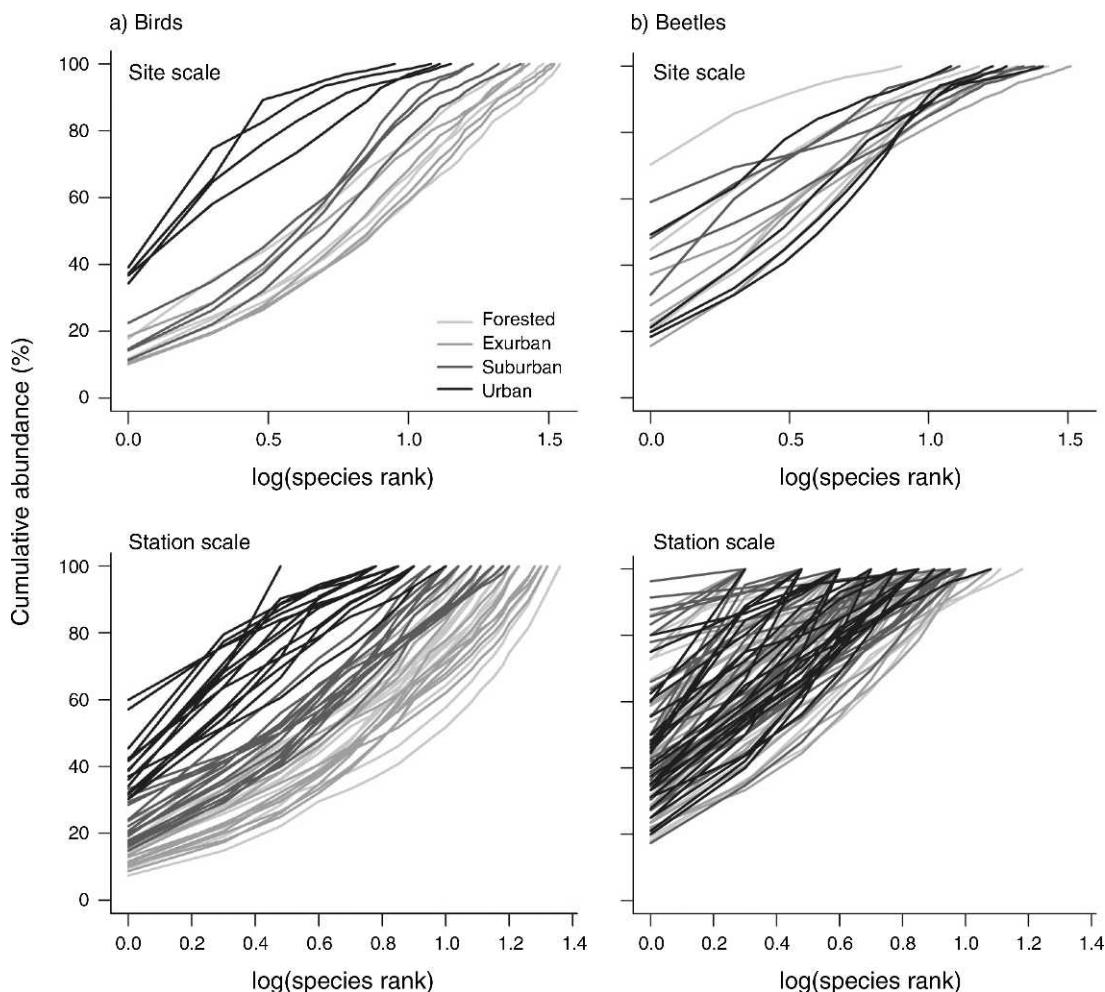


FIG. 5. The k -dominance curves of (a) birds and (b) carabid beetles at two spatial scales. Each curve represents the data collected at a single site or station. Forested sites and stations are shown in light gray, Exurban sites and stations are shown in medium gray, Suburban sites and stations are shown in dark gray, and Urban sites and stations are shown in very dark gray. A community is considered to be dominated by a few species to a greater degree than another community if its k -dominance curve lies above and never intersects that of the other community.

(Fig. 5a), indicating that bird communities in Urban sites and stations exhibited a greater degree of dominance by a few species than did bird communities in Forested, Exurban, and Suburban sites and stations. In contrast, the k -dominance curves of beetle communities were not segregated by housing density category (Fig. 5b).

Additive partitioning of diversity revealed that the average bird species richness among sites (β_2) was lower in the Urban category than in the other housing density categories (Fig. 6a). No differences in beetle diversity components with increasing housing density were apparent (Fig. 6a). The NMDS of bird communities in housing density categories at the site scale showed that Urban and Suburban bird communities were more similar to one another than were those in Exurban sites, which were more similar to one another than were those

in Forested sites (Fig. 7a). The similarity among beetle communities in the housing density categories at the site scale showed a congruent but weaker pattern. Beetle communities in Urban and Suburban sites were more similar to one another than were those in Exurban and Forested sites (Fig. 7a). Suburban sites had the most similar beetle communities. NMDS analyses did not converge to a solution at the station scale for either taxon. Finally, housing density had a significant effect on the Kulczynski distance between pairs of sites for birds ($F_{3,20} = 15.66$, $P < 0.001$, adjusted $R^2 = 0.66$) and for beetles ($\chi^2 = 9.37$, $P = 0.02$). Birds displayed a decline in the Kulczynski distance between sites as housing density increased, whereas beetles showed no clear trend (Fig. 8).

Correlations.—With the exception of forest bird and forest beetle species richnesses in housing density sites,

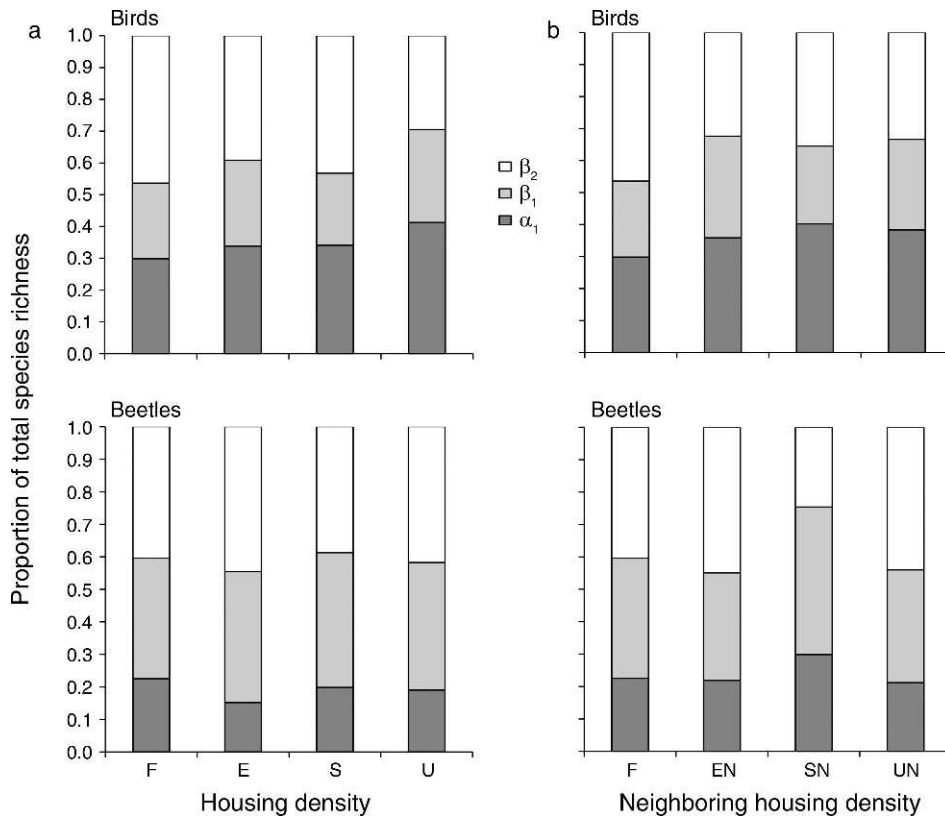


FIG. 6. Additive partitioning of bird and carabid beetle diversity in (a) housing density and (b) neighboring housing density categories. Dark gray bars are the average station species richness (α_1), light gray bars are the average species richness among stations (β_1), and open bars are the average species richness among sites (β_2). Key to abbreviations: F, Forested; E, Exurban; S, Suburban; U, Urban; EN, Exurban Neighbor; SN, Suburban Neighbor; UN, Urban Neighbor.

none of the correlations between bird and beetle descriptors in housing density sites or stations was significantly different from zero (Table 2). Total bird and total beetle abundances in housing density sites were weakly positively correlated (Table 2, Appendix B). Introduced bird and introduced beetle abundances, forest bird and forest beetle abundances, and forest bird and forest beetle species richnesses exhibited relatively strong positive correlations at both spatial scales. Open-habitat bird and open-habitat beetle abundances and open-habitat bird and open-habitat beetle species richnesses exhibited weaker positive correlations in housing density sites and stations (Table 2, Appendix B). When forest bird and beetle and open-habitat bird and beetle species richness values were corrected for sampling effort, the strength of correlations diminished markedly (Table 2, Appendix B). However, we did not observe a change in correlation strength when total bird and total beetle species richnesses were standardized by total abundances (Table 2). Bird and beetle distance matrices of housing density sites were significantly positively correlated with each other ($\tau = 0.53$, $P < 0.001$). Bird and beetle distance

matrices of stations were more weakly positively correlated ($\tau = 0.36$).

Effects of neighboring housing density

Few analyses yielded significant effects of neighboring housing density on bird or beetle community structure. The abundance of introduced beetles was one of the few response variables to vary significantly with neighboring housing density ($F_{3,9} = 11.09$, $P < 0.01$, adjusted $R^2 = 0.72$). Urban Neighbor (107.33 ± 64.54 individuals; mean \pm SE) and Suburban Neighbor sites (123.33 ± 67.40 individuals) had significantly more introduced beetles than Forested sites (2.50 ± 1.04 individuals) but not Exurban Neighbor sites (13.00 ± 4.51 individuals). No introduced bird species were observed in neighboring housing density sites.

The average bird species richness among sites (β_2) was lower in the Exurban Neighbor, Suburban Neighbor, and Urban Neighbor categories than in the Forested category (Fig. 6b). Beetle β_2 was lower in the Suburban Neighbor category than in the other neighboring housing density categories (Fig. 6b). For both birds and beetles, NMDS analyses revealed that sites within the Exurban Neighbor, Suburban Neighbor, and Urban

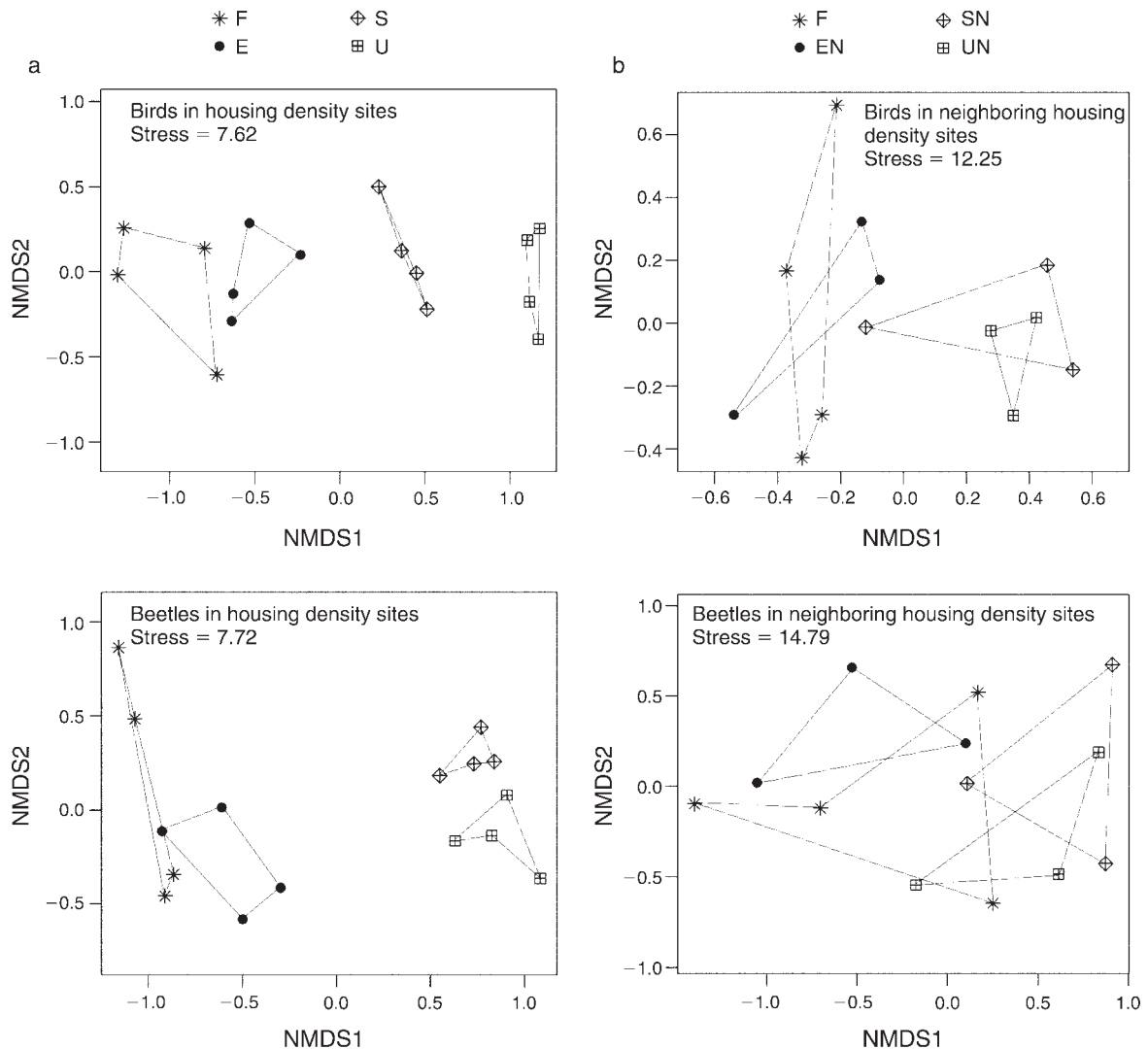


FIG. 7. Nonmetric multidimensional scalings (NMDS) of bird and carabid beetle community data collected in Forested (F), Exurban (E), Suburban (S), Urban (U), Exurban Neighbor (EN), Suburban Neighbor (SN), and Urban Neighbor (UN) sites: (a) ordination of housing density sites; (b) ordination of neighboring housing density sites.

Neighbor categories were more similar to one another than were sites within the Forested category, this trend being slightly stronger for birds (Fig. 7b). However, there was much overlap of category polygons indicating that bird and beetle community similarity was not well described by neighboring housing density. As above, NMDS analyses did not converge to a solution at the station scale for either taxon. Finally, neighboring housing density had a significant effect on the Kulczynski distance between pairs of sites for birds ($F_{3,11} = 4.07$, $P < 0.04$, adjusted $R^2 = 0.40$). Pairs of Urban Neighbor sites had significantly lower Kulczynski distances (0.33 ± 0.01 ; mean \pm SE) than pairs of Forested sites (0.50 ± 0.04), with Suburban Neighbor (0.42 ± 0.03) and Exurban Neighbor site pairs ($0.50 \pm$

0.01) having intermediate distances that were not significantly different from those of other categories.

None of the correlations between bird and beetle descriptors in neighboring housing density sites and stations was significantly different from zero (Table 2). Open-habitat bird and open-habitat beetle abundances, as well as open-habitat bird and open-habitat beetle species richnesses, were relatively weakly positively correlated in neighboring housing density sites and stations (Table 2, Appendix B). Standardizing species richness values by abundances yielded changes in correlation strength only for open-habitat species at the site and station scales (Table 2, Appendix B). Bird and beetle distance matrices of neighboring housing density sites were significantly but weakly positively correlated ($\tau = 0.17$, $P = 0.03$). Similarly, bird and beetle

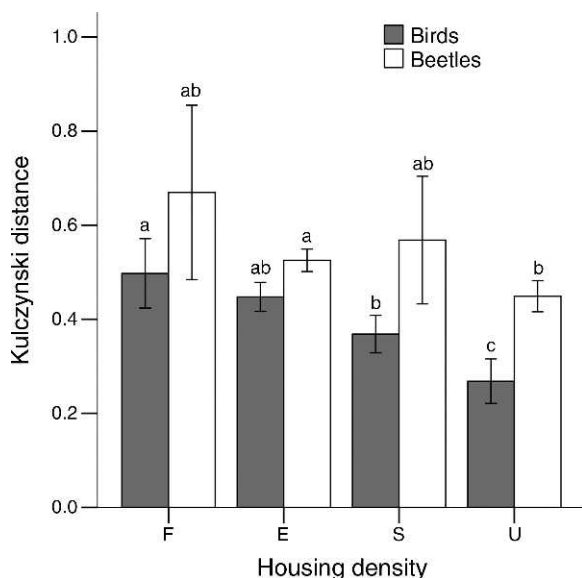


FIG. 8. The Kulczynski distance (mean \pm 2 SE; see *Methods*) between pairs of Forested (F), Exurban (E), Suburban (S), and Urban (U) sites. The Kulczynski distance between two sites was calculated by summing species abundance minima and dividing this value by each site's total abundance. One minus the average of these two values was the distance between the two sites. Gray bars represent the distances between bird communities, and open bars represent those between carabid beetle communities. Different lowercase letters above bars indicate significant ($P < 0.05$) pairwise differences between site categories for each taxon.

distance matrices of neighboring housing density stations were weakly positively correlated ($\tau = 0.14$).

DISCUSSION

Breeding birds and carabid beetles do not respond similarly to increasing housing density, but they do exhibit some similar responses to increasing neighboring housing density. Birds displayed strong declines in

diversity (Table 1), compositional changes (Figs. 3 and 4a), and community simplification (Figs. 5a, 6a, 7a, and 8) in response to increasing housing density. Although beetles did exhibit some similar compositional changes to birds (Figs. 3 and 4b), they showed no response of overall diversity and no (Figs. 5b and 6a) or weak (Figs. 7a and 8) patterns of community simplification with increasing housing density. In contrast, both birds and beetles showed no compositional changes (with the exception of an increase in introduced beetle abundance with increasing neighboring housing density) and similar patterns of community simplification with respect to neighboring housing density (Figs. 6b and 7b).

A comparison of the responses of two or more taxa to a common predictor variable, such as in this paper, requires that each taxon be sampled to the same degree. Otherwise, any differences in response between the taxa, namely, one taxon exhibiting a response whereas the other does not, may reflect differential sampling rather than reality. To address this, we assessed bird and beetle sampling intensity in all housing density sites, all neighboring housing density sites, and in sites of each housing category (see Appendix C for a description of the methods and results of this analysis). We assessed sampling intensity in sites in each housing category to ensure that responses exhibited by one taxon and not the other, such as a decline in bird diversity with increasing housing density or an increase in open-habitat beetle species richness with increasing housing density, were not the result of under-sampling one end of the urban gradient. The results of our assessment indicated that, with very few exceptions, sampling intensity for birds and beetles was the same (Appendix C). The exceptions in our assessment indicated that beetles were not sampled as well as birds in Urban sites (where we estimated that we sampled 100% of the bird species predicted to be present) and that bird species were not sampled as well as beetles in Neighbor sites, particularly Suburban Neighbor sites (where we estimated that we

TABLE 2. Correlations (Kendall's τ) between bird and carabid beetle variables describing community structure at two spatial scales in categories representing two predictor variables: housing density and neighboring housing density.

Variable	Housing density		Neighboring housing density	
	Site ($n = 16$)	Station ($n = 64$)	Site ($n = 13$)	Station ($n = 52$)
Total species richness	0.03	0.08	-0.04	-0.02
Total abundance	0.28	0.09	0.10	0.01
Standardized total richness	-0.10	0.00	0.00	-0.03
Simpson's index	0.12	0.00	-0.06	-0.13
Fisher's α	-0.07	-0.08	-0.18	0.07
Berger-Parker index	0.04	-0.05	-0.10	-0.16
Introduced species abundance	0.58	0.45	NA	NA
Forest species abundance	0.59	0.50	-0.13	0.00
Forest species richness	0.64***	0.52	0.03	-0.04
Standardized forest richness	0.01	0.07	0.00	0.05
Open-habitat species abundance	0.36	0.38	0.39	0.31
Open-habitat species richness	0.43	0.35	0.43	0.33
Standardized open-habitat richness	-0.02	-0.12	0.10	-0.04

Note: No introduced bird species were observed in neighboring housing density categories.
*** Significant at $\alpha = 0.05/50 = 0.001$ (Bonferroni correction for 50 comparisons).

sampled close to 100% of the beetle species predicted to be present). The former is not a likely cause of the differences we observed in bird and beetle responses to increasing housing density. The latter suggests that if sampling intensity for birds in neighboring housing density sites were increased, we might observe responses by the bird community to increasing neighboring housing density that we presently may not have had the power to detect.

In contrast to birds, for which increasing housing density resulted in a species-poor community, for beetles, increasing housing density resulted in the original forest beetle community being replaced by one adapted to open habitats. Both forest birds and forest beetles declined in abundance and richness with increasing housing density (Fig. 3a, b), but only beetles exhibited an increase in the number of open-habitat species with increasing housing density (Table 1). This trend would explain the weak patterns of community simplification in response to increasing housing density exhibited by beetles. If a large number of open-habitat beetle species are found in urban areas, then one would not expect the overall community to be dominated by few species or to be similar to other urban communities. Such a pattern has been reported for plants: nonnative species from distant sources, which increase in number with urbanization, promote the differentiation of urban plant communities (La Sorte and McKinney 2006).

Our results are similar to those of other authors who found higher open-habitat beetle species richness in forest fragments situated in more highly urbanized areas (Elek and Lövei 2007, Magura et al. 2008), although ours are the first to our knowledge (with the exception of Gagné and Fahrig [2010a]) to describe this trend for open-habitat carabid beetles in the urban matrix, i.e., in developed areas outside of forest fragments. Despite the higher disturbance in urban environments (e.g., from pesticide use [Bednarska et al. 2009] or increased predation [Shochat et al. 2006]), open-habitat beetle species seem to profit from the availability of suitable microhabitats in these areas. Microhabitat variation was found to be an important predictor of carabid distribution in forest habitat (Niemelä et al. 1992) and in an urban botanical garden (Clark and Samways 1997). Urbanization may actually create a variety of open microhabitats for beetles, such as lawns, bare soil, moss and gravel ground covers, and plant litter-covered ground, resulting in the increase in open-habitat beetle species richness in this study. Another possibility is that urbanization results in increased slug abundance (Holland et al. 2007), a common prey of some carabid beetle species (e.g., slugs are a major part of the diet of *P. melanarius* (Symondson et al. 2002), an open-habitat beetle species collected in this study). More slugs in urban areas could result in the greater abundance of some open-habitat beetle species, possibly contributing to the increased species richness of this group.

Community simplification, here defined as the loss of specialist species and their replacement by a few abundant native generalist and introduced species, is a possible mechanism underlying biotic homogenization (Olden and Poff 2003). Studies investigating biotic homogenization along urban gradients are commonly carried out between different cities (e.g., for birds, see Blair [2004], Clergeau et al. [2006], McKinney [2006], and Sorace and Gustin [2008]). In this paper, we report patterns of increasing compositional similarity for birds between sites along an urban gradient within a single metropolitan region (Figs. 6, 7, and 8), which are consistent with the intercity patterns reported by the authors just cited. Thus, biotic homogenization of bird communities in urban areas appears to be occurring both within and between cities (although similarity decays with intercity distance [McKinney 2006]). Biotic homogenization at these different scales could be the result of different mechanisms or variation in their relative contributions (Olden and Poff 2003), making investigations of homogenization patterns both within and between cities essential to our understanding of the mechanisms underlying those patterns. This is particularly true for carabid beetles for which, to date, patterns of homogenization or compositional similarity between communities in urban areas have only been investigated within a single metropolitan region (Knapp et al. [2008], Magura et al. [2008], and the present study).

Breeding birds and carabid beetles interact with their environment at very different spatial scales. Our results of diversity declines and community simplification with increasing urbanization for birds but not for beetles indicate that, at the spatial scale of this study, our sites likely contained a greater variability of habitat types for beetles than for birds. If this was the case, one would expect greater among-station variability in beetle species richness compared to birds. This pattern was exhibited when we partitioned the species richness of each taxon in each housing density category (Fig. 6a). The average proportion of diversity contributed by among-station species richness (β_1) for all site categories combined was higher for beetles (40%) than for birds (26%). A similar pattern was exhibited across all neighboring housing density categories as well (Fig. 6b). At larger spatial extents than that used in this study (i.e., 0.25 km²), a greater diversity of habitats for both birds and beetles would be encompassed by each site, possibly resulting in both taxa exhibiting similar patterns of community change in response to urbanization. For instance, bird and carabid beetle community similarity responded in the same manner to land use intensification in 16-km² agricultural landscapes across Europe (Dormann et al. 2007). A timely avenue of future work would be the investigation of the scale dependence of patterns of community change in response to urbanization for a variety of taxa. In this way, one could identify the taxon-specific spatial scales at which management and mitigation may be most effective. For instance, bird

diversity may be most effectively maintained in urban regions through large-scale conservation of habitat remnants, whereas the creation of diverse backyard microhabitats might most effectively promote beetle diversity in urban areas.

Evidence to support the congruence of biodiversity in human-dominated systems is slim (Allen et al. 1999, Oertli et al. 2005, Dormann et al. 2007, Billeter et al. 2008, but see Blair 1999, Sauberer et al. 2004). Most studies conclude that correlations between taxa are too weak to be of any predictive use. Our results support this conclusion. In particular, birds and carabid beetles in the urban matrix exhibited different changes in diversity and community simplification in response to increasing housing density. To better understand and mitigate the effects of urbanization on biodiversity, we suggest that, in addition to the responses of birds, future research should evaluate the responses of other taxa in the urban matrix, particularly in light of the scarcity of such work at present (McDonnell and Hahs 2008, McIntyre and Rango 2009).

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APPENDIX A

Native bird and carabid beetle species classified as “forest interior,” “forest edge,” “forest,” or “open-habitat” species (*Ecological Archives* A021-104-A1).

APPENDIX B

Scatterplots of bird and carabid beetle variables describing community structure (*Ecological Archives* A021-104-A2).

APPENDIX C

Comparison of sampling intensity for birds and beetles (*Ecological Archives* A021-104-A3).

SUPPLEMENT

Bird and beetle community data collected in housing density and neighboring housing density sites and stations (*Ecological Archives* A021-104-S1).