

Similar effects of residential and non-residential vegetation on bird diversity in suburban neighbourhoods

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Abstract Estimating the relative importance of vegetation on residential land (gardens, yards, and street-trees) and vegetation on non-residential land (parks and other large green spaces) is important so that competing options for urban conservation planning can be prioritized. We used data from an urban breeding-bird monitoring program to compare the relative effects vegetation on residential land and vegetation on non-residential land (both the amount and type of vegetation at local and landscape scales) on bird species richness and an index of conservation value for the bird community. We then estimated the realised relative benefit of managing the amount of vegetation on these two types of land (i.e., as alternative management options for promoting biodiversity), which might be achieved within the practical limits imposed by human population density. The local effects of increasing residential and non-residential vegetation amount were similar and positive on all measures of bird species richness and conservation value. Non-residential vegetation had an additional landscape-scale influence on bird diversity that residential vegetation did not. Options for managing the amount of non-residential vegetation appear to be more limited by high human population density than for managing the amount of residential vegetation. This suggests that there may be greater realised benefits to bird diversity from managing the amount of vegetation on residential land than from the more common focus of urban planning of managing vegetation on non-residential land.

Keywords Avian · Conservation value · Garden · Green space · Park · Species richness

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Introduction

Urban areas are much more important for biodiversity conservation than their relatively small physical footprint would suggest. They provide habitat for many species, including species at risk (Evans et al. 2009); and the habitat they provide may be particularly important because urban areas tend to coincide with regions of high biodiversity (Balmford et al. 2001; Deguise and Kerr 2006). Urban areas also have a vital role in promoting the importance of biodiversity conservation within society, because an increasing majority of the human population lives in urban areas and more frequent positive interactions with native flora and fauna help build an appreciation for local biodiversity and social acceptance of environmental attitudes (Turner et al. 2004; Miller 2005).

The amount and type of vegetation has a strong influence on bird diversity in urban areas (reviewed in Chase and Walsh 2006; McKinney 2008). Urban areas with more vegetation have higher species richness (Lancaster and Rees 1979) and fewer non-native species (Blair 1996). In addition, vegetation type has a strong effect on urban birds; increased vertical vegetation structure (e.g., more trees and shrubs and less mowed grass) increases bird species richness and functional diversity (Melles et al. 2003; Clergeau et al. 1998).

Studies of urban biodiversity have identified effects of both vegetation in residential land (hereafter, residential vegetation) and vegetation in non-residential land (hereafter, non-residential vegetation) but their relative effects are unknown. Most studies have focused on the effects of non-residential vegetation (e.g., large areas of natural vegetation such as parks and vacant land) and found positive effects of increasing amount and structural complexity of non-residential vegetation (Lancaster and Rees 1979; Clergeau et al. 1998; Chase and Walsh 2006). Some more recent studies have found similar effects of residential vegetation (e.g., privately-owned gardens and street-trees, Fernandez-Juricic 2000; Daniels and Kirkpatrick 2006; Lerman and Warren 2011). A few studies have examined both types of vegetation. However, these studies either combined the effects of residential and non-residential vegetation (e.g., Melles et al. 2003; Evans et al. 2009), or estimated their separate effects on different response variables (e.g., species richness measured either in residential or non-residential areas, Donnelly and Marzluff 2006); no studies have yet estimated and compared the relative effects of residential and non-residential vegetation on birds.

It is important to know the relative effects of vegetation in residential and non-residential land because, although they are often correlated (Smith et al. 2005; Melles et al. 2003; VanHeezik et al. 2008), they can be managed independently (Wilson et al. 2007). For example in the city of Ottawa, Canada, the regulations controlling the area of non-residential parks and natural vegetation retained in a new development (City of Ottawa bylaw #2009-95) are independent of the sizes of yards or the building density in the residential portions of the development, which are largely driven by market forces. Similarly, there are separate regulations related to trees (planting and cutting) in residential (bylaw #2009-200) and non-residential land (bylaw #2006-279) of the city.

The relative effects of residential and non-residential vegetation may also be scale-dependent, if the relevant mechanisms that link vegetation with biodiversity vary with scale (Addicott et al. 1987; Smith et al. 2011). At a local scale (i.e., within the area surveyed for bird-diversity), because both residential and non-residential vegetation act as habitat for native species (Jokimaki and Suhonen 1998), the species area relationship should lead to increasing native species richness with increasing amounts of both (Rosenzweig 1995; McKinney 2008). Alternatively, residential vegetation is often less suitable for some native species and more suitable for non-native species (i.e., biotic homogenization, McKinney 2006). If biotic homogenization processes are locally important, the positive relationship

between vegetation amount and native species richness may be weaker for residential vegetation than for non-residential vegetation. In addition, increasing the amount of residential vegetation may have weaker positive effects because it is more highly fragmented (roads and buildings throughout) than non-residential vegetation; negative edge effects such as reduced nest success and increased disturbance (Marzluff and Ewing 2001), may reduce the overall quality of residential vegetation for many species.

At the landscape-scale (i.e., the area surrounding the surveyed area), different mechanisms may be relevant. Increasing residential and non-residential vegetation in the surrounding landscape may have similar positive effects because both should decrease isolation (Schmiegelow and Monkkonen 2002). However, residential vegetation is generally more structurally connected than non-residential vegetation so it may decrease isolation more effectively for a given increase in amount than non-residential (Gaston et al. 2005).

The realised benefit to biodiversity from managing residential or non-residential vegetation may be different from their per-area relative effects, if there are different practical or theoretical limits to their management (Grace and Bollen 2005). Human population density is one of the strongest limiting factors in urban development (Nilsson and Flørgård 2009) and the feasible manipulations to vegetation amount imposed by the social and economic forces linked to population density, may impose limits on the amount of vegetation, which likely differ between residential and non-residential lands (Farber 2005). For example, there are more direct economic incentives for designers of new suburban developments to increase the amount of residential vegetation (i.e., more private yard space that factors directly into house prices) than to retain non-residential vegetation (i.e., areas of communal or public space that only indirectly factor into house prices). Although conservation science (e.g., Chapman and Reich 2007) and conservation recommendations (e.g., Marzluff and Ewing 2001; Environment Canada 2007) have largely focused on non-residential land, without quantitative estimates of the realised benefit to conservation from managing residential and non-residential vegetation, many opportunities may be missed for urban biodiversity conservation.

A planning or land management decision would ideally include a full assessment of the relative costs and benefits of managing vegetation area in residential versus non-residential land—e.g., the benefits to biodiversity for a given social or economic cost. Estimating these costs in any absolute sense would depend on many socio-economic factors that are far beyond the scope of this single ecological study. However, we can derive an approximate estimate of the relative costs at high and low human population densities by assuming that the costs are indirectly proportional to the observed range of variation in residential or non-residential vegetation. That is, the existing relationships between human population density and vegetation area in each land-type approximately reflect the range of feasible options for management. For example, for a given human population density, the maximum amount of non-residential vegetation that is currently observed in the city's landscapes, is an approximate estimate of the maximum feasible limit to non-residential vegetation area at that human population density. If we also assume that the relative costs are indirectly proportional to the range of these limits (i.e., a larger range of variation, implies a lower cost for management), then we can estimate the relative benefits considering the relative costs by rescaling the per-area effects (i.e., the coefficients) of residential and non-residential vegetation to a percent of the range of these limits. In effect, we re-scale the coefficients so that instead of representing the average change in the response for a one-unit change in the predictor (i.e., per hectare of residential vegetation), they represent the average change in the response for a change in the predictor equal to 1 % of the feasible range. In practice, estimates scaled to 10 % of the feasible range are likely easier to interpret. We are not aware

of any other study that has done exactly this, but Grace and Bollen (2005) suggested this approach in concept. In addition, this sort of coefficient re-scaling is directly analogous to using standardized regression coefficients that are re-scaled to units of standard deviation; yet it is a more explicit and thoughtful alternative.

Our objectives were to answer three questions. 1) What are the relative per-area effects of vegetation in residential land versus vegetation in non-residential land on the diversity and conservation value of an urban bird community? 2) Are the relative effects on bird diversity different at local and landscape scales? 3) What is the likely realised benefit of managing vegetation amount and type on residential versus non-residential land, within the practical limits to management that are imposed by human population density?

Methods

Study area

Ottawa, Ontario, Canada is an urban centre of approximately 800,000 residents, surrounded by a landscape composed of agricultural fields and coniferous-deciduous, mixed-wood forests. The city is within the Mixedwood Plains ecozone (Ecological Stratification Working Group 1996) and the Lower Great Lakes/St. Lawrence Plain, North American Bird Conservation Region number 13 (hereafter BCR 13, Rich et al. 2004). Residential vegetation in Ottawa is primarily mowed lawns, ornamental gardens, and a mix of deciduous and coniferous trees and shrubs. Non-residential vegetation is a mix of: city parks, which include areas managed for natural vegetation, mowed lawns, planted trees, and sports fields; a large greenbelt surrounding the urban core, which includes large areas of forest, pastures (both active and abandoned), wetlands, and agricultural fields; and other large areas of primarily tall-grass and shrub vegetation, which includes verges along highways, vacant lots, and power-line rights-of-way.

Field methods

Bird observations were made by volunteers with the Ottawa Breeding Bird Count (OBBC) – a breeding season monitoring program for birds within the urban and suburban areas of the city of Ottawa, Ontario, Canada (www.ottawabirds.ca). OBBC surveys are conducted at randomly selected locations within an approximately 900 km² study area that includes the city's urban core, the greenbelt, and the surrounding suburban developments. Observers conducted 10-minute, 75 m fixed-radius point counts, between 30 min before sunrise and 8:00am. Point counts were done during the peak of the breeding season and in appropriate weather conditions (the same conditions and season used by the North American Breeding Bird Survey, Peterjohn 1994). Surveys were completed earlier in the day than many standard bird-monitoring protocols, to limit the influence of traffic and other human activity on bird detectability. Observation protocols allowed us to estimate detectability using removal models (Farnsworth 2002) by dividing each ten-minute count into five two-minute segments, during which only new bird observations were recorded. If the count was located beside a road, observers also recorded the number of vehicles passing them during the ten-minute count. Each point count was conducted at a randomly selected, publicly-accessible location, separated from other count locations by at least 250 m, and distributed so that there was one count location within each cell of a 1 km × 1 km

grid covering the entire study area. These publicly-accessible locations were primarily on sidewalks, roadsides, or city walking paths. Because this study was focused specifically on birds in residential areas, we selected 246 of these locations that were within the areas designated as residential by the city's official plan (Fig. 1). This selection included points that were sampled during the breeding seasons of 2007, 2008, or 2009. In cases where observations were available from more than 1 year, the most recent year's data were used. We did not combine data from multiple years at the same site because there were relatively few locations with multiple years of observations.

We tested for variation in bird detectability among observers and levels of traffic noise, to ensure this variation did not bias our results. We used a “Huggins, full closed captures with heterogeneity” version of the removal model, which allows for variation in detectability among species (Huggins 1989). We estimated the cumulative (across the full 10 min point count period) proportion of the true number of species that were actually observed, averaged for each observer and for two levels of traffic (low and high traffic corresponding to points with fewer or more than 15 vehicles per 10 min count, respectively). Although our analyses in this paper used only 246 counts of the >1000 available in the OBBC database, we also estimated detectability using the entire database, to increase precision. Detectability was analysed using the program Mark (White and Burnham 1999), though the R-package, RMark (Laake 2010).

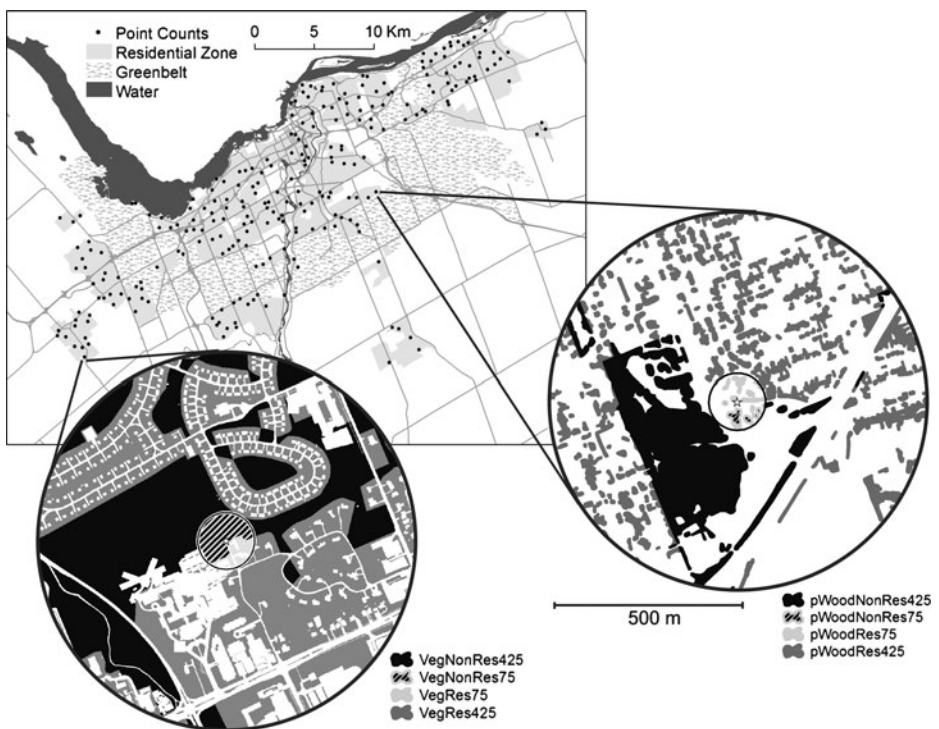


Fig. 1 Map of study area in Ottawa, Canada, showing the distribution of point counts (*black dots*) across the city. Insets demonstrate the four variables for vegetation amount (left inset, *shaded areas* indicate residential and non-residential vegetation within local and *landscape areas*), and vegetation type (right inset, residential and non-residential wooded vegetation within local and *landscape areas*). See Table 1 for an explanation of the variable names

Measures of bird diversity and conservation value

At each point count location, we calculated three measures of bird species richness and one index of bird conservation value. We calculated species richness for the following three groups: 1) native species (hereafter, S.Native), including all species native to North America but excluding three native species that are considered pests of urban environments in our region because of over-abundance – Ring-billed Gulls (*Larus delawarensis*), Herring Gulls (*Larus argentatus*), and Canada Geese (*Branta canadensis*); 2) native, forest-dependent species (hereafter, S.Forest) including species within S.Native that primarily depend on forest habitat; and 3) native, shrub-dependent species (hereafter, S.Shrub) including species within S.Native that primarily depend on shrub or early-successional forest habitat. We also calculated total native species richness including the two gulls and one goose species that were excluded from S.Native; however, we have not presented those results here, because they were very similar to those for S.Native, and we feel that S.Native is a more intuitive measure of the biodiversity that most urban planners and managers are likely to manage for. Other habitat guilds (e.g. wetland, or grassland-dependent species) were too rarely observed in our surveys to be modeled effectively. In addition to the three species richness measures, we included an index of conservation value (Nuttall et al. 2003), which weighted species abundances by a species-specific conservation priority value. Conservation priority values for each species were taken from the Partners in Flight (PIF) species threat scores specific to our study region (i.e., scores for BCR 13, Panjabi et al. 2005). We combined these scores with the bird observations at each point count to create the following conservation index measure:

$$CI.Rank = \sum_{j=1}^S PIF.Rank_j \times ((\log_{10}n_j) + 1) \quad (1)$$

Where n represents the number of individuals for species j and $PIFRank$ is the PIF priority ranking suggested by Nuttall et al. (2003), which combines the five PIF threat scores (scores related to population size, population trend, threats to breeding, breeding distribution, and BCR area importance) into a single 0 – 5 ranked scale. These threat scores weight the species' abundances, which are then summed over all species observed at each point count (S). Weighting the index by species abundance on a log scale (as suggested by Herrando et al. 2010) accounts for relative abundance at a site without over-prioritizing common species (e.g., because of its higher threat score, 1 Sedge Wren contributes twice as much to the index as 10 Red-winged Blackbirds). Non-native species do not contribute to this index (i.e., $PIFRank = 0$, Nuttall et al. 2003).

Vegetation

Measures of vegetation amount and type were calculated separately at two scales: local – within the 75 m radius point count plot; and landscape – within a 425 m buffer around the edge of the point count plot (i.e., a circle, 500 m in radius that excludes the plot area itself, Fig. 1).

The local measures were made using high resolution (20 cm pixel) aerial photographs (taken in 2008, Ontario Ministry of Natural Resources- Digital Raster Acquisition Project for the East), in combination with data produced by the city of Ottawa's planning department that identifies all impervious surfaces (i.e., paved surfaces such as roads, parking-lots, and

sidewalks, as well as the footprints of all buildings in the city). With these two data sources we estimated the area of water, tree canopy, shrubs, tall grass, and mowed grass. The other local covariate included in the analyses was the presence or absence of high-traffic roads within the count area. This covariate represented an index of human activity that may influence bird diversity and could confound our analyses, Fernandez-Juricic and Telleria 2000. High-traffic roads included any highways or major commuting routes but excluded the residential streets of quiet neighbourhoods.

Landscape measures were made by combining four base-layers created by the city's planning department. Layers for surface water, natural vegetation in non-residential areas, and tree canopy coverage in residential areas were based on aerial photography and ground-truthed with field observations. The natural vegetation layer was a 20-class ecological categorization that we reclassified into tree, shrub, and tall grass categories to match the local-scale data. The fourth base-layer was the city's impervious surfaces coverage (see above). We considered any area not classified by these four layers as surface water, one of the types of natural vegetation, tree canopy, or impervious surface as an estimate of the mowed grass coverage within the surrounding landscape. The result was a continuous layer with the same five categories as were measured in the local plots. The four base layers from the city's planning department were considered current up to 2007, but because urban areas develop at a high rate, we visually compared the base-layers with the 2008 aerial photography and manually updated the data in areas under active development.

Separately for local and landscape measures, vegetation amount was calculated as the sum of the tree, shrub, tall grass, and mowed grass areas. Throughout the remainder of the text, measures of vegetation amount (i.e., total area of vegetation in either residential or non-residential portions of the landscape) are referred to as "Veg" followed by modifiers indicating residential or non-residential, and the scale within which it was measured (e.g., VegRes75 = amount of residential vegetation within the local scale). For vegetation type (i.e., the kinds of vegetation included in the total amounts above), the percent of wooded vegetation was the percent of the vegetation amount made up of tree and shrub classes, and the percent of shrub vegetation was calculated using the amount of shrub and tall grass (areas of tall grass were included here because there were often scattered small shrubs within them). These measures are referred to as "pWood" or "pShrub" respectively, followed by the same modifiers as were used for vegetation amount (e.g., pWoodNonRes425 = percent of non-residential vegetation that is wooded).

Although we have chosen relatively simple measures of vegetation, our simple measures match the broad nature of both the study's objectives and the community-level response variables. These simple measures of vegetation (residential versus non-residential and wooded or shrub) can provide only very coarse metrics of the functional effects of vegetation on the suburban bird community. Indeed, some aspects of the community composition, physical structure and landscape configuration of vegetation likely vary more within our two coarse categories and other aspects likely vary more between the two categories. However, more complex measures would be more likely to have conflicting effects among the individual species within the suburban bird community; and, the relationships between our coarse measures and bird diversity have clear and simple implications at the broad scale where city-wide planning and management decisions are made.

Statistical modelling

We used generalized linear models with a log link and Poisson error distribution (after checking for overdispersion) for all species richness responses (i.e., S.Native, S.Forest, and

S.Shrub) and an identity link and Gaussian error distribution for CI.Rank. To account for spatial autocorrelation, we used spatial Eigenvectors as covariates in all models (Griffith and Peres-Neto 2006; Bivand et al. 2010). Eigenvectors were included that removed any significant ($p < 0.10$) autocorrelation (measured by Moran's I) in the residuals of a regression of each response on the amount of local vegetation. All analyses were conducted in R, version 2.10.1 (R Development Core Team 2009).

Relative effects of residential and non-residential vegetation

We modeled the separate effects of residential and non-residential vegetation at local and landscape scales for both vegetation amount and vegetation type. The final models were as follows:

$$\begin{aligned} \text{Richness or CI.Rank} = & \text{VegNonRes75} + \text{VegRes75} + p\text{WoodRes75} + \\ & p\text{WoodNonRes75} + \text{VegNonRes425} + \text{VegRes425} + \\ & p\text{WoodRes425} + p\text{WoodNonRes425} + \text{HighTraffic} + \text{SpEigen} + \text{Error} \end{aligned} \quad (2)$$

$$\begin{aligned} \text{S.Shrub} = & \text{VegNonRes75} + \text{VegRes75} + p\text{ShrubRes75} + \\ & p\text{ShrubNonRes75} + \text{VegNonRes425} + \text{VegRes425} + \\ & p\text{ShrubRes425} + p\text{ShrubNonRes425} + \text{HighTraffic} + \text{SpEigen} + \text{Error}, \end{aligned} \quad (3)$$

where the first eight terms represent the effects of vegetation amount and type in residential and non-residential areas at the two scales, *HighTraffic* represents a categorical covariate indicating the presence or absence of a high traffic road, and *SpEigen* represents one or more spatial Eigenvectors to account for spatial autocorrelation in the residuals. Equation 2 was used to model all response variables, except the richness of shrub-successional species (S.Shrub), in which case, Eq. 3, with the Shrub-based vegetation type variables, was used. We did not include quadratic terms because neither the bivariate plots of the raw data nor the residuals of the models indicated there were non-linear effects. We plotted and compared the coefficients and their 95 % confidence intervals, scaled for a 10-unit change in the percent of the landscape that is residential or non-residential vegetation or a 10 unit change in the percent of the vegetation that is wooded. Plotted coefficients therefore represent the expected change in the response for a 10 % change in the predictor, while keeping all other predictor variables in Eqs. 2 and 3 constant.

There were correlations among the predictors in our final models (Table 1), but we are confident that our results are not overly influenced by these correlations for three reasons. First, it is reasonable to assume that each of the vegetation predictors has some true influence on the response (i.e., none are spurious, Anderson et al. 2001), because the area and type of vegetation, whether it occurs on residential or non-residential property, has been previously shown to influence bird diversity (e.g., Lerman and Warren 2011). Therefore, removing (or failing to include) one of the variables in the final model would generate biased estimates of their effects (Smith et al. 2009). Although the variance of our estimates is influenced by the correlations, the inflation of that variance is, at worst approximately 3-fold (all VIF < 3.5, Table 1), and the inflated variance primarily makes our conclusions more conservative.

Second, to further increase our confidence that our results were not overly influenced by the correlations among predictors, we replicated all of our analyses for a subset of the data, in which there were reduced correlations among predictors

Table 1 Correlations among the key predictors of urban bird richness. Values above the diagonal are for the full dataset ($n = 246$), those below the diagonal are for a subsample of points chosen to reduce the correlation between VegNonRes75 and VegRes75

	VegNonRes75 (3.27)	VegRes75 (2.69)	pWoodNonRes75 (1.76)	pWoodRes75 (2.05)	VegNonRes425 (3.46)	VegRes425 (3.14)	pWoodNonRes425 (1.42)	pWoodRes425 (2.15)
VegNonRes75 (2.25)								
VegRes75 (2.16)	-0.51		0.53	0.17	0.47	-0.38	0.11	0.09
pWoodNonRes75 (1.56)	0.26	0.06	-0.34	-0.08	-0.24	0.43	-0.02	0.00
pWoodRes75 (1.76)	0.11	-0.09	0.37	0.40	0.31	-0.29	0.32	0.31
VegNonRes425 (2.66)	0.30	0.03	0.09	-0.06	-0.05	0.00	0.22	0.66
VegRes425 (2.37)	-0.09	0.27	-0.02	-0.03	-0.62	-0.75	0.23	-0.01
pWoodNonRes425 (1.51)	0.06	0.00	0.38	0.17	0.20	-0.07	-0.11	0.04
pWoodRes425 (1.97)	0.11	-0.06	0.36	0.60	-0.02	0.05	0.44	0.44

Values in parentheses are the variance inflation factors for each predictor in the full model (i.e., $1/(1-R^2)$) of a linear regression of each predictor on all other predictors). Variable names indicate either vegetation amount (“Veg”) or vegetation type (percent of vegetation that is trees and shrubs “pWood”), followed by modifiers indicating residential or non-residential vegetation and the scale (75 = local, 425 = landscape). The pattern of pairwise correlations and VIF for pShrub variables, used to model shrub-successional species richness, are similar to those for pWood variables

(Table 1). To create this less-correlated sub-sample, we removed all points where local residential or non-residential vegetation was greater than 1.0 ha (i.e., > 56 % of the total plot area). These points were removed because the very high amount of vegetation in one type of land (i.e., residential or non-residential) within a finite plot area, imposes a strict limit on the amount of vegetation of the other type. The specific cut-off was a compromise between reducing the correlation and retaining a sufficient sample size for analysis. We then removed an additional random sample of points where residential vegetation was high (> 0.7 ha) and non-residential vegetation was low (< 0.3 ha) because this combination was highly over-represented. The resulting, less correlated dataset included 130 locations of the original 246 and reduced the correlation between residential and non-residential vegetation amount from -0.70 in the full dataset to -0.51 in the reduced dataset (Table 1).

Third, we compared the coefficients and confidence intervals from our full models with model-averaged coefficients and unconditional confidence intervals from all possible sub-models of our full models (i.e., coefficients averaged across all models, weighted by each model's Akaike weight— $\bar{\beta}$, pg. 152, Burnham and Anderson 2002). If our results were strongly dependent on the correlations among predictors, models missing some of the predictors would have relatively strong support (i.e., large Akaike weights), which would shrink their weighted average coefficients towards zero and increase the unconditional confidence intervals. We have not presented these model-averaged coefficients because their point estimates were almost identical to the estimated coefficients from the full model, and the unconditional confidence intervals were only slightly wider.

Likely realised benefits of managing vegetation amount

We converted our estimates of the relative effects of vegetation amount into estimates of the likely realised benefits of managing residential and non-residential areas, given the practical limits imposed by human population density. To do this, we re-scaled the coefficients for vegetation amount to units of 10 % of the range within the limits imposed by high human population density. Therefore these re-scaled coefficients estimate the expected change in the response for a change in the amount of vegetation equal to 10 % of the range that could feasibly be achieved through management.

To estimate the feasible ranges of residential and non-residential vegetation amounts at high human population density, we assumed a lower limit of 0 for both residential and non-residential vegetation and then used a 95 % quantile regression (Koenker 2005) to identify the upper limits. The quantile regression analyses regressed the amount of vegetation (separately for residential and non-residential) on human population density (from the 2006 Canadian national census) within the 500 m radius landscapes surrounding our point counts. We used the predictions from the 95 % quantile regression lines at a human population density of 300 people/hectare to identify the upper limit of residential and non-residential vegetation amount at high human population density.

Results

Detectability

The percent of species present that were observed ranged from 91 – 96 % across the 7 volunteers whose observations were included in our sample of 246 point counts. More

than 95 % of the counts were conducted by 5 volunteers whose average detection probabilities were ≥ 95 %. We ran all analyses both with all the data and with a reduced dataset that excluded data from volunteers with < 95 % detection probability; the plotted coefficients and confidence limits were indistinguishable. Although there was a weak effect of traffic on detection probability, we did not correct for traffic in the final analysis for three reasons. First, the cumulative detection probabilities for high and low noise sites were 94.5 % and 96.3 % respectively (i.e., traffic noise had a very small effect on detectability). Second, there were count locations where volunteers had not recorded traffic, and therefore, including a correction for traffic would have reduced the overall sample size. Finally, using only the point counts for which we had traffic data, we ran the relative effects analyses with a term for traffic level. This term was not statistically significant for any of the response variables, and including it always increased the model AIC and had little effect on the coefficient estimates for the remaining predictors.

Relative effects of residential and non-residential vegetation

When measured only within the local point count site (75 m radius), the effects of residential vegetation amount were as strong as, or slightly stronger than, the effects of non-residential vegetation amount (upper plots in Fig. 2). By contrast, in the surrounding landscape, the effects of non-residential vegetation amount were generally stronger than the effects of residential vegetation (lower plots in Fig. 2). In general, the effects of non-residential vegetation were about half as strong in the surrounding landscape as they were at the local scale (i.e., per 10 % change in the amount of the landscape made up of non-residential vegetation, the percent change in richness or CI.Rank was approximately half of what was expected for the same change at the local scale, Fig. 2). By comparison, the effects of residential vegetation amount in the surrounding landscape were effectively absent (i.e., the coefficient estimates were near zero with large confidence limits). Overall the summed effects of residential vegetation amount at local and landscape scales were very similar to the summed effects for non-residential vegetation amount (i.e., adding the effects in upper and lower plots of Fig. 2). The slightly stronger local effects of residential vegetation amount with their weak landscape effects give a combined effect that is very similar to that from the slightly lower local but much stronger landscape effects of non-residential vegetation. The results for the less correlated sub-sample of data were essentially the same as for the full dataset—so are not shown here—except that due to the smaller sample size, the confidence intervals were larger and included zero for more coefficients.

The effects of vegetation type (“pWood” and “pShrub” variables) were generally weaker and less certain than those of vegetation amount; they depended more on the choice of response variable (Fig. 3). In general, the relative effects of residential and non-residential vegetation type were uncertain because they were either both very weak (e.g., S.Native, Fig. 3) or highly variable (S.Shrub and CI.Rank, Fig. 3). However, at the local scale, the percent of wooded area in residential vegetation had a slightly stronger positive effect on S.Forest than did non-residential vegetation. At the landscape scale, this positive effect of pWood on S.Forest was not evident. In contrast, the positive effect (although weak and uncertain) of wooded amount in non-residential lands on S.Forest was consistent at both the local and the landscape scales (Fig. 3). Finally, the strongest estimated effect of vegetation type was for the percent of residential vegetation in the landscape that was shrub or long grass on S.Shrub

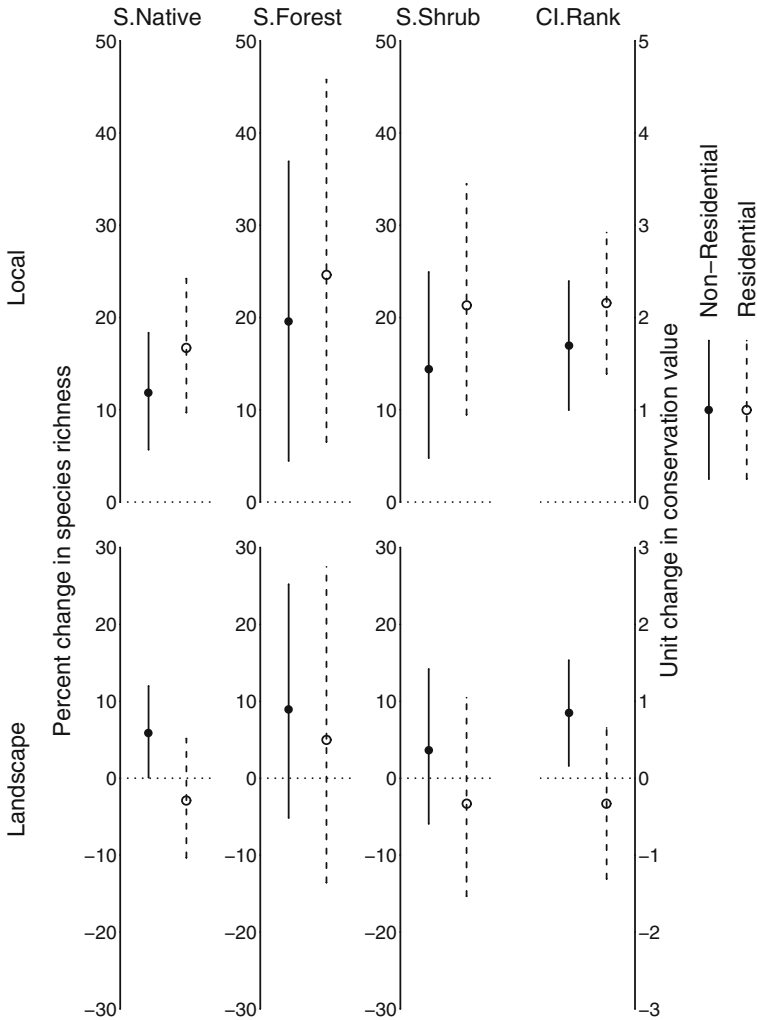


Fig. 2 Relative effects of residential and non-residential vegetation amount on four measures of bird diversity, at local (*upper plots*) and landscape (*lower plots*) scales. *Points* represent the expected % change in species richness or unit change in conservation index for a 10 % increase in the amount of either residential or non-residential vegetation at each scale, after controlling for the remaining effects in Eq. 2 or, for S.Shrub, Eq. 3. *Error bars* represent 95 % confidence intervals

(~17 % increase in S.Shrub for a 10 % increase in pShrubRes425, Fig. 3). However, this effect had wide confidence limits (-5 % to +35 %).

Likely realised benefits of managing vegetation amount

The amount of non-residential vegetation declines more quickly with increasing human population than does the amount of residential vegetation (Fig. 4). Within our 500 m landscapes, the 95 % quantile of residential vegetation amount declines by approximately 4 % for an increase of 100 people/ha (dotted line in Fig. 4). In contrast, the 95 % quantile for non-

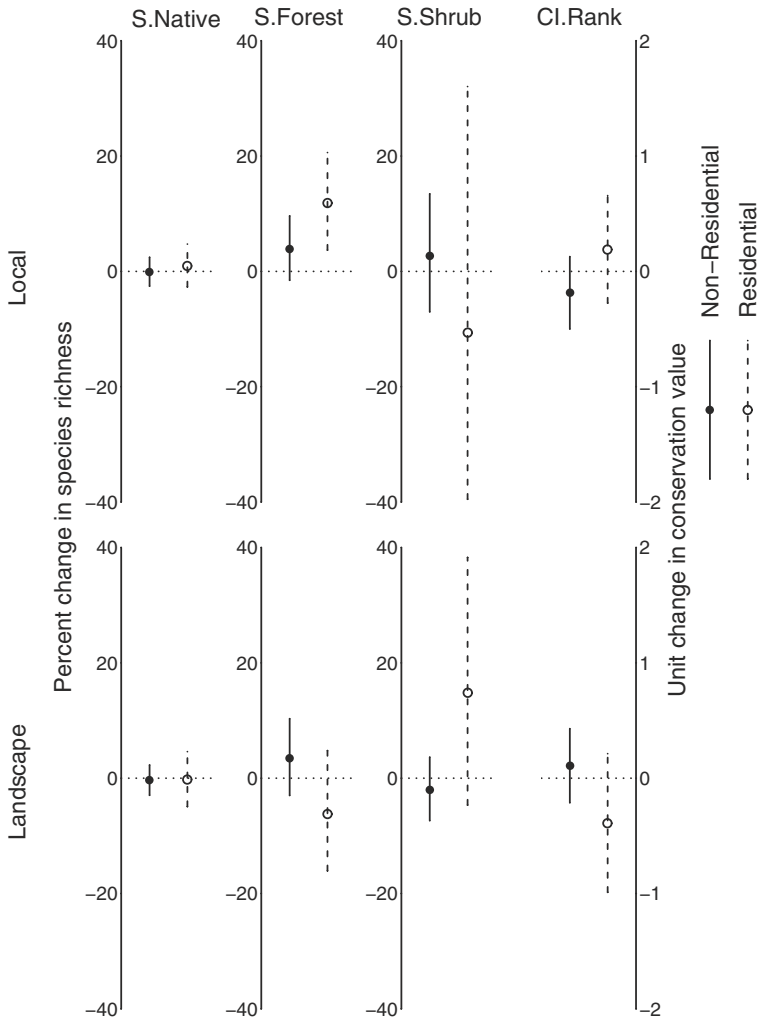


Fig. 3 Relative effects of residential and non-residential vegetation type on four measures of bird diversity, at local (*upper plots*) and landscape (*lower plots*) scales. *Points* represent the expected % change in species richness or unit change in conservation index for a 10 % increase in the percent of either residential or non-residential vegetation that is wooded (or shrub for S.Shrub) at each scale, after controlling for the remaining effects in Eq. 2 or, for S.Shrub, Eq. 3. *Error bars* represent 95 % confidence intervals. Numbers in parentheses are the proportion of deviance explained by the model in Eqs. 2 or 3

residential vegetation amount declines by 18 % over the same increase in population density (solid line in Fig. 4). This suggests that management options for non-residential vegetation are more constrained by population density than are management options for residential vegetation. We used these quantiles as upper limits to management and re-scaled partial coefficients for residential and non-residential vegetation amount. The re-scaled coefficients indicate that at high human population densities (300/ha), the realised potential benefit to bird diversity from managing vegetation amount is likely much greater for residential vegetation than for non-residential vegetation (i.e., the summed effects of local and landscape vegetation amounts are much greater for residential than for non-residential vegetation Fig. 5).

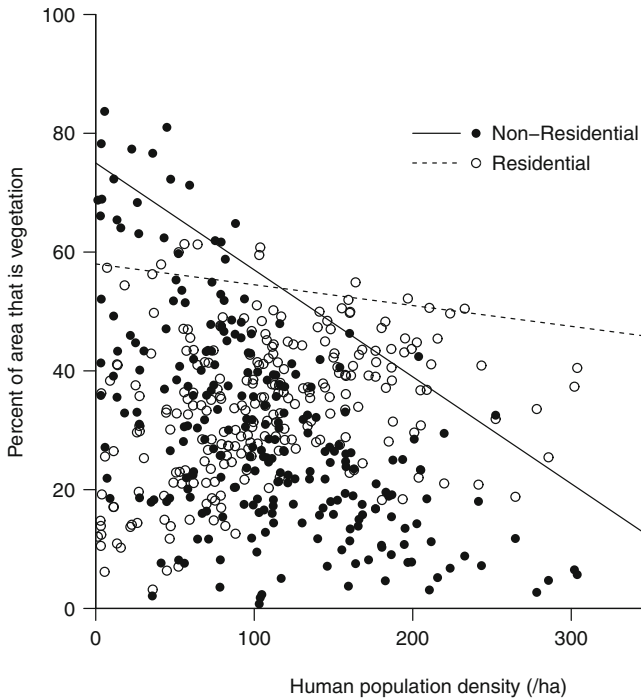


Fig. 4 Estimated upper limits to residential and non-residential vegetation area with increasing human population density. Lines represent 95 % quantile regression models, fit separately to non-residential vegetation (solid line) and residential vegetation (dotted line)

Discussion

Residential vegetation amount (i.e., the area of private yards around houses and apartments) and non-residential vegetation amount (i.e., parks and other large green spaces) had very similar effects on the richness and conservation value of an urban bird community, when the effects were combined across both the local and landscape scales. Therefore, developers and city planners can have the greatest influence the bird community of an urban area by managing both the amount of vegetation within residential developments in addition to the amount that is set aside for parks and green spaces.

The similar local-scale relative effects of residential and non-residential vegetation suggests that residential vegetation is not necessarily of lower overall quality for most bird species, nor even for species of greater conservation value (Chase and Walsh 2006). In fact, residential vegetation amount had a similar or even slightly stronger positive effect on our conservation value index than non-residential vegetation. At the local scale (i.e., within the area surveyed), the effects of residential vegetation were just as strong as, or slightly stronger than, those of non-residential vegetation for the same change in amount. Therefore, the potentially negative effects on the urban bird community of homogenization or the negative edge effects associated with fragmented residential vegetation are not as relevant at this scale as are the positive species-area effects of increasing vegetation amount.

Increasing the tree and shrub cover of residential vegetation had a positive effect on forest bird richness at both the local and landscape scales. Otherwise, the effects of vegetation type

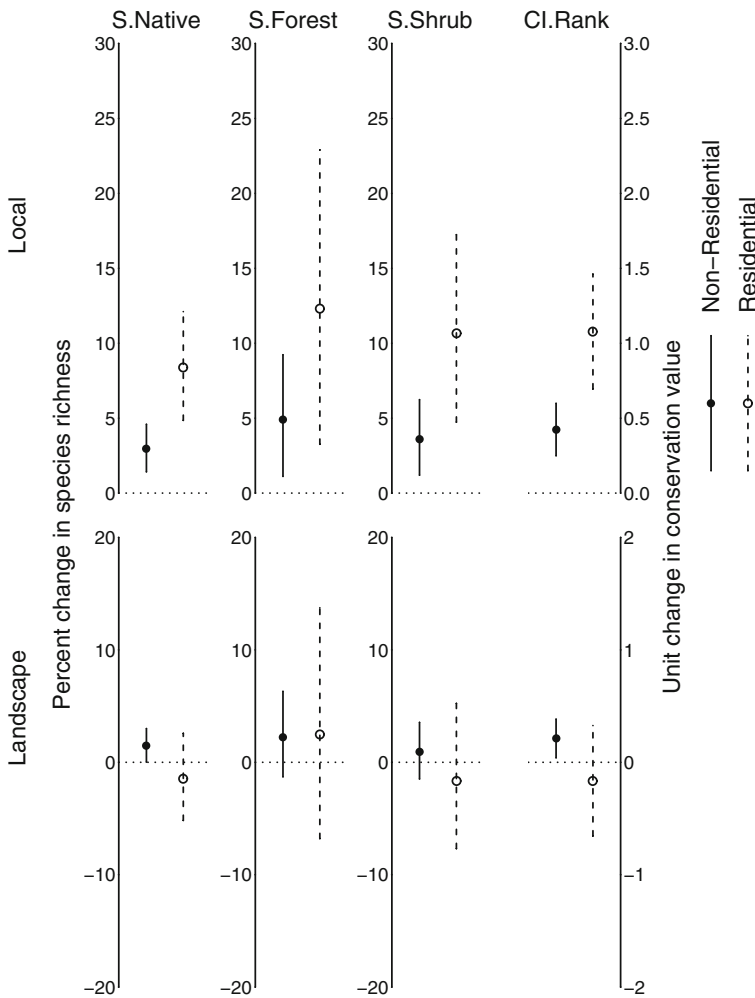


Fig. 5 Relative effects of the amount of residential or non-residential vegetation at high human population density (300 residents/ha). Points represent the partial coefficients from Fig. 2, scaled to represent the expected % change in species richness or unit change in conservation index for a change in vegetation amount that is 10 % of the range within practical limits to management. The upper practical limits to management were estimated from 95 % quantile regression lines in Fig. 4 (i.e., the point where the lines in Fig. 4 at a density of 300). Error bars represent 95 % confidence intervals

were weak, uncertain, and depended more on the choice of response variable, in comparison to the effects of changing vegetation amount. Although percent tree and shrub cover is a simple variable that can be easily measured and is reflected well by existing planning laws, it is also a very coarse measure which may not represent the complex structural features of urban vegetation that affect birds. For example, because we have measured vegetation from aerial photos, we have no information on the variation in vertical structure, which is an important factor for many bird species (Murgui 2007; White et al. 2005).

The additional landscape effect of non-residential vegetation amount on bird richness may capture the influence of large patches of vegetation. Large areas of relatively natural vegetation provide habitat structure and resources (e.g., understory vegetation in forests,

Donnelly and Marzluff 2004) that are less common in small areas of non-residential vegetation and absent from residential vegetation. These resources provide opportunities for some species to use urban areas that would be absent otherwise (Fernandez-Juricic and Jokimaki 2001; Melles et al. 2003; Donnelly and Marzluff 2004).

Increasing residential vegetation amount within suburban and urban developments benefits more than just common, urban-tolerant species; it also benefits bird species of high conservation value. Residential vegetation had a strong positive effect on an index of community conservation value, which down-weights common species with stable populations and fewer threats to their breeding habitat (Nuttall et al. 2003). Across a broad range in urbanization intensity (i.e., from large reserves through to the urban core), some species of high conservation value may be lost from the local bird community and replaced with tolerant species that are generally of lower conservation value (Blair 1996; McKinney 2006). However, within an intermediate portion of that range (i.e., within residential neighbourhoods), residential and non-residential vegetation both play an important role in creating a bird community with value to conservation.

As human population density in a neighbourhood increases, managing the amount of residential vegetation may have a greater potential benefit to bird diversity than managing the amount of parks or other large green spaces. In our study area, increasing human population density appears to impose stricter limits on the amount of non-residential vegetation than it does on the amount of residential vegetation. Therefore at relatively high population densities, a given per-area change is likely more feasible for residential vegetation than for non-residential vegetation. And given their similar per-area effects, planners or managers may realise greater benefits to suburban bird biodiversity from managing the amount of residential vegetation than from managing the amount of non-residential vegetation.

The particular limits to managing vegetation amount that we have identified here reflect the current development patterns in the city. However, thoughtful planning and design of urban areas could conceivably create residential areas with high human population density and much higher levels of non-residential vegetation than currently exist in Ottawa. For example, conservation subdivisions (Arendt 2004) or clumped housing developments (Gagne 2010) would change the limits to managing non-residential vegetation and thereby our estimates of the likely realised benefit to bird diversity.

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